Chapter 10

Neanderthal to Neanderthal Evolution: Preliminary Observations on Faunal Exploitation from Mousterian to Châtelperronian at Arcy-sur-Cure

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Introduction

The karst system at Arcy-sur-Cure provides substantial information pertinent to the transition from the Middle to Upper Paleolithic (Leroi-Gourhan 1988; Farizy 1990; Baffier and Girard 1997). One of the most important stratigraphic sequences is found in the Grotte du Renne (Fig. 10.1), with a sequence from Mousterian through Châtelperronian to Aurignacian. The Châtelperronian includes a fairly large sample of Neanderthal fossil material, including teeth (Bailey and Hublin 2006) and a distinctive temporal fragment (Hublin et al. 1996). The neighboring Grotte du Bison includes a stratigraphic sequence spanning from the Mousterian through the Châtelperronian (Leroi-Gourhan and Leroi-Gourhan 1964) and provides the data discussed in this paper.

While much attention has been paid to the transition from Neanderthals to anatomically modern humans (e.g., Discamp et al. 2011), relatively little has been paid to the ecological or economic contexts of the transition from flake to blade industries *within* the context of a pre-modern hominid species, the Neanderthals. This study attempts a preliminary exploration of indications of continuity or change in environment or subsistence practices *prior to* the transition from the Châtelperronian to the Aurignacian, focusing on potential differences or similarities between the Mousterian and the Châtelperronian at the Grotte du Bison at Arcy-sur-Cure. There are clearly important technological innovations or changes in the transitional industries such as the Châtelperronian and the Uluzzian (Neruda and Nerudová 2011; Perisani 2012). Some have argued that because the species lists of prey are very similar for both the Mousterian and early Upper Paleolithic, the ecological niches occupied by their producers were identical; this does not address whether changes in technology might have had a more profound effect not only on the weaponry that was used to acquire prey but also on the organization of other aspects of the exploitation of prey species (Enloe 2001, 2003a, b). While environment and subsistence are clearly linked in terms of the availability of prey and the techniques necessary to procure and process game, a discussion of the interactions between technology and prey choice, acquisition and processing is beyond the scope of this paper.

Grotte du Bison

At Arcy-sur-Cure, the Cure River cuts through a coral massif amidst softer limestone sedimentary marine deposits. This harder reef formed a barrier to the flow of the river, resulting in large east-west bends in the northward flowing Cure (Fig. 10.1). This resulted in rather spectacular south facing cliffs perforated by karstic galleries leading through the massif north to the next bend in the river. These galleries offer openings at several different levels above the river which were sequentially exposed and dry as the river entrenched itself into the valley according to variations in the climatic regime. Among the upper caves are the Grotte du Renne and the Grotte du Bison. Today, a mere 5 m separates these two collapsed cave mouths, and they were certainly interconnected at the time of their occupation. The Grotte du Bison includes a stratigraphic sequence from the Mousterian through the Châtelperronian. Two levels in the lengthy geological sequence were considered for this analysis (Fig. 10.2). Of primary interest is Level D, which corresponds to Level VIII in the adjacent Grotte du Renne. It includes material from the Châtelperronian and is dated to 34,050 ± 750 ^{14}C BP and 33,670 ± 450 ^{14}C BP (David et al. 2006: 11). In recent excavation of the earlier Mousterian Level I, the discovery of new Neanderthal fossil

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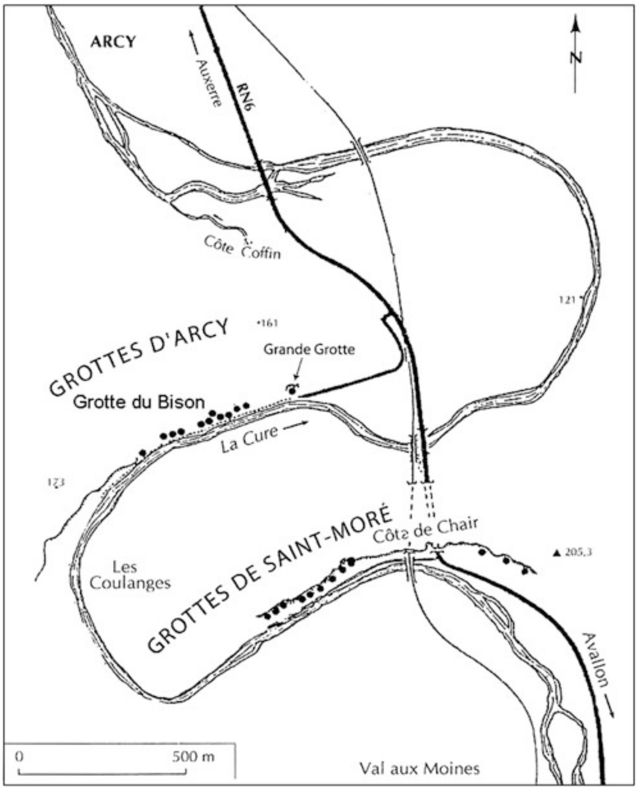

Fig. 10.1 Location of Arcy-sur-Cure caves

specimens adds to knowledge about the authorship of final Middle Paleolithic industries (David et al. 2009a, b).

Faunal materials from the Grotte du Bison have been recovered and recorded using a variety of methods, reflecting the long period of time over which excavations were performed. The site was discovered in 1958 as a lateral gallery during the excavation of the Grotte du Renne by the team lead by Andre Leroi-Gourhan. From 1961 through 1963 excavation of test pits and trenches established a stratigraphic sequence of seven geological levels (D through J) which contained archaeological evidence of human occupation (Leroi-Gourhan 1961; Leroi-Gourhan and Leroi-Gourhan 1964). In 1995, a team led by Francine David began a series of more comprehensive excavations. Primary goals included: (1) correlation of the stratigraphy of the Grotte du Bison with that of the Grotte du Renne and to acquire modern chronometric dates for the levels, (2) investigation of the evolution of the cave and of the climatic conditions, and (3) expansion of the excavated surface to allow observation of spatial patterning. This last goal dictated the excavation method of décapage procedures pioneered by Leroi-Gourhan, privileging the examination of horizontal surfaces rather than vertical stratigraphic cuts. It included vertical photo cartography of each square meter for recording provenience, and retrieval of each archaeological specimen and fine-mesh water screening of all sediment. Beginning in 2006, a total station theodolite was used to record three-dimensional data on potentially identifiable material. The following year, that three-dimensional recording was expanded to include the small, unidentifiable splinters, primarily bone fragments (David et al. 2010). Results of those measurements are indicated in Table 10.1, but are not divided by occupation levels. Thus, the material was recorded and analyzed at differing degrees of intensity, precluding across-the-board comparisons for such things as anatomical part representation and taphonomic observations.

Faunal Assemblages, Levels I and D

Data from Level I (Table 10.2) were chosen for examination of the earlier Neanderthal occupation of the Grotte du Bison. This is the most recently excavated part of the cave, which has been made even more interesting by the discovery of new Neanderthal fossil specimens (David et al. 2009a, b). The lithic assemblage is a denticulate Mousterian (Lhomme et al. 2004). We are still awaiting results from several dating techniques, but overlying levels E and F have been dated to 38 and 40 ka (David et al. 2006: 12). Level I probably dates to around 50 ka or more. This level has had the most comprehensive collection and recording over the history of investigations in the Grotte du Bison. The faunal assemblage included 2,616 identified faunal specimens (NISP) reported from the 1961–1963 excavations. In addition to these, a total of 9,949 faunal remains (NR) were plotted and recovered from Level I during the 2006–2009 field seasons. Of these, 3,225 were numbered; the remainder (6,724) was largely unidentified diaphysis fragments smaller than 2.5 cm in length.

Microfauna were recorded separately in 2007 through 2009, totaling 1,234 specimens that were not included in the macrofaunal count. Due to the frequently porous nature of the *éboulis* fill, it was deemed impossible to distinguish between more recent intrusive burrowers and those specimens that might have been deposited during the Pleistocene. Microfaunal remains were dominated by incisors and molars of rodents, primarily recovered in 2 mm water screening, but also included cranial and postcranial elements from shrews and bats. A substantial portion probably derive from ancient or recent rejection pellets from hawks and owls. None of these remains were taken into account for this study.

The faunal assemblage of Level I (Table 10.2; Fig. 10.3) is dominated by horse and reindeer, together representing over 65 % of the NISP, with MNI counts of twelve each. Reports of the earlier faunal analysis from the 1961–1963 excavations preclude comparisons of skeletal element representation, as those data were not published in the

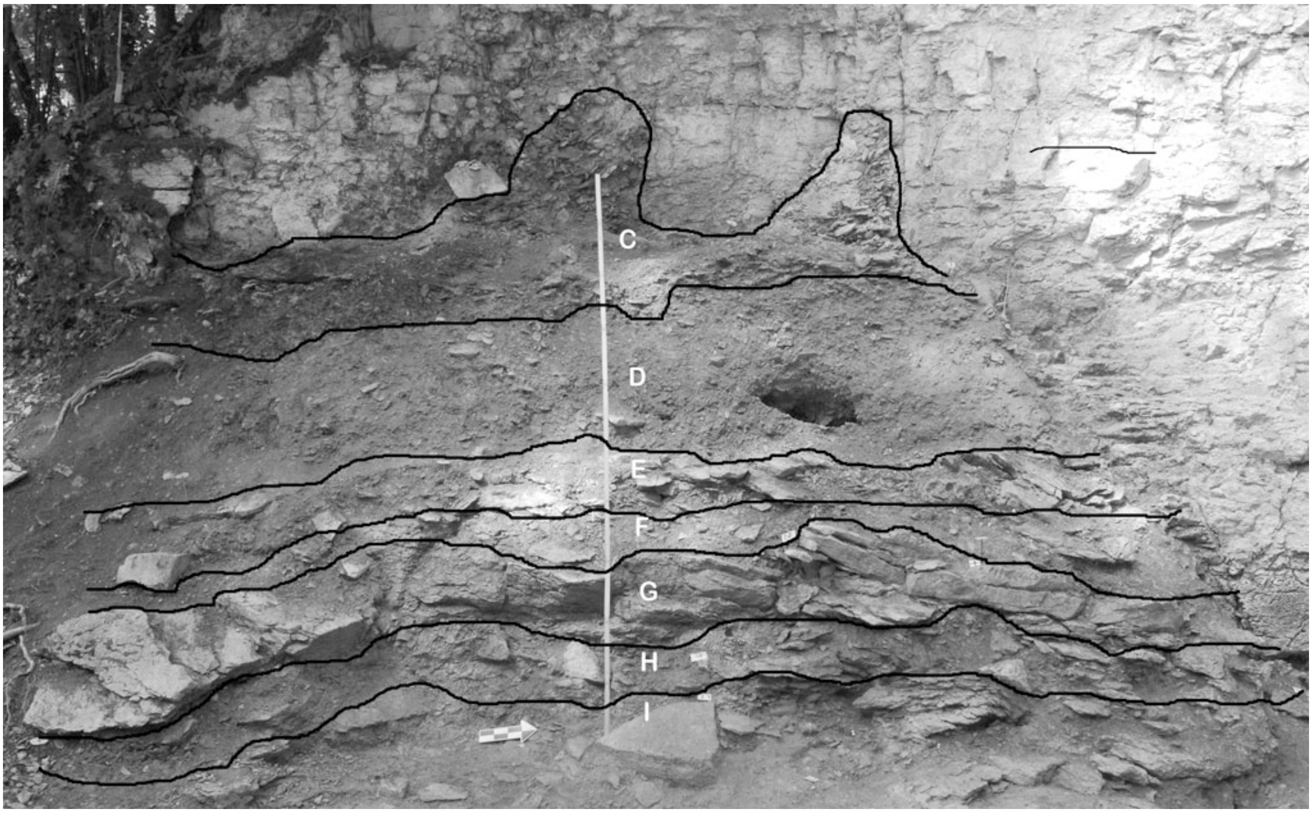

Fig. 10.2 Stratigraphic sequence, as preserved in the witness block against the west wall of the cave prior to excavation of those units (photo J. G. Enloe)

Table 10.1 Three-dimensionally recorded artifacts, Level I

Remains/year	2006	2007	2008	2009	2010	Total
Total	1,045	4,032	4,964	2,866	3,608	16,515
Bone	1,000	3,336	4,064	2,006	3,120	13,526
Numbered bone	1,000	458	1,147	777	1,583	4,920
Bone splinters	0	2,878	2,917	1,229	1,538	8,562
Burned bone	0	194	35	29	128	386
Microfauna	0	417	488	345	156	1406
Coprolite	0	223	190	392	117	1,922
Lithic industry	24	27	30	42	87	210
Lithic splinters	0	12	26	10	29	77
Cobbles	6	7	103	49	73	838
Carbon	0	7	16	4	6	33
Ochre	0	1	10	12	14	37
Miscellaneous	15	9	2	6	1	33

excavation report (Leroi-Gourhan 1961) and the assemblages were not available for examination. Notable among the remains in the recent excavations are reindeer antler and largely intact horse metapodials, neither of which offers significant nutritional utility. Other species, in decreasing importance by respective NISP counts are hyena, bear, fox, aurochs or bison, and wolf, with MNI counts ranging from 5 to 10. Mammoth, red deer, chamois, marmot, hare, rhinoceros and a large felid are represented by small NISP counts and minimum numbers of individuals of one.

Table 10.2 Taxonomic diversity, Level I

Level I	NISP	NISP (%)
Horse	453	31.37
Reindeer	494	34.21
Hyena	123	8.52
Fox	80	5.54
Bear	125	8.66
Bovid	67	4.64
Wolf	47	3.25
Red deer	8	0.55
Mammoth	21	1.45
Chamois	8	0.55
Marmot	5	0.35
Hare	10	0.69
Large feline	1	0.07
Rhinoceros	2	0.14
NISP	1,444	99.99

In Level I, a great proportion of all specimens identified to species were teeth. This was true for both carnivores and herbivores. Among the herbivores, teeth represent 50 % of the identified specimens for horse and red deer, and 25 % for reindeer. The proportions are even greater among the carnivores, with 68 and 67 % for wolf and hyena, 50 % for fox, and 25 % for bear (David et al. 2006: 39–40). These figures suggest significant taphonomic effects on the preservation and identifiability of the faunal assemblage. Of 13,526 bone specimens, only 1,444 (10.7 %) were identifiable, with small (<2.5 cm) diaphysis fragments representing the overwhelming majority of the assemblage. One factor that may account for this pattern is mechanical crushing by the extremely large roof block falls in Level I, but carnivore attrition is likely an even larger factor.

Carnivore to herbivore ratios may suggest who had predominance or exclusivity of occupation of the cave, hominins or other carnivores, and who might be responsible for the accumulation of the faunal assemblage. Of the specimens identified to species (NISP) for level I, the ratio is 1:2.56, suggesting a considerable proportion of carnivores. This is emphasized by the large number of coprolites—505—largely constituted of very fine bone fragments and attributed to hyenas. In summary, a varied faunal spectrum is probably the product of numerous agents of accumulation and modification. The relative paucity of human artifactual remains suggests that other large carnivores were largely responsible for the faunal assemblage. Even the human fossils show evidence of carnivore gnawing (David et al. 2009a: 808). And yet, there is arguably a significant portion of the faunal assemblage in Level I that was contributed by Mousterian Neanderthals, as suggested in a spatial study by Enloe (2011), in which no single species focus could be discerned. These mixed results make it very difficult to assign authorship for the faunal assemblage and render it ambiguous for discovering patterns of human hunting.

Level D (Fig. 10.2) is the last human occupation of the Grotte du Bison, which corresponds to Level VIII in the adjacent Grotte du Renne. It includes material from the Châtelperronian and is dated to 34,050 ± 750 BP and 33,670 ± 450 BP (David et al. 2006: 12). Most of this level was excavated during 1997 and 1998 (David et al. 2006). An additional 7 m^2 had been left along the west wall of the cave as a witness block for stratigraphic control and long-term dosimeter placement for dating; level D of this block

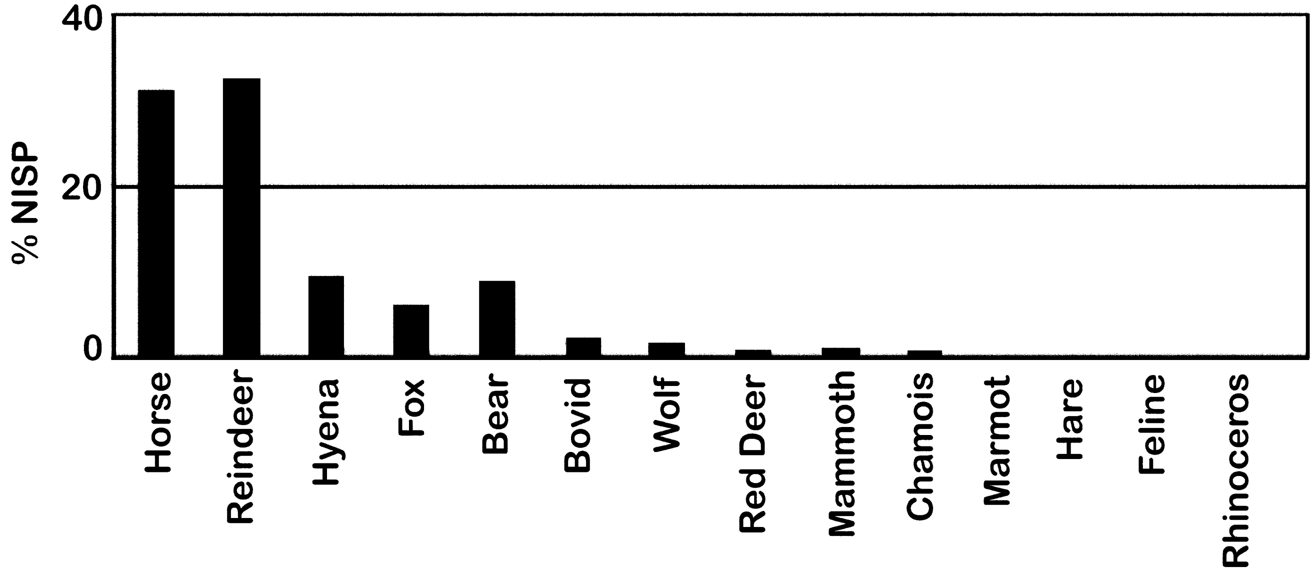

Fig. 10.3 Proportional representation of taxonomic diversity of Level I

Table 10.3 Taxonomic diversity, Level D, with and without bear counts

Level D	NISP	No bear	NISP (%)
Bear	1,169	0	0
Horse	126	126	30.66
Reindeer	199	199	48.42
Hyena	18	18	4.38
Fox	12	12	2.92
Bovid	32	32	7.79
Wolf	4	4	0.97
Red deer	10	10	2.43
Mammoth	0	0	0
Chamois	7	7	1.7
Marmot	2	2	0.49
Hare	1	1	0.24
Feline	0	0	0
Rhinoceros	0	0	0
NISP	1,580	411	100

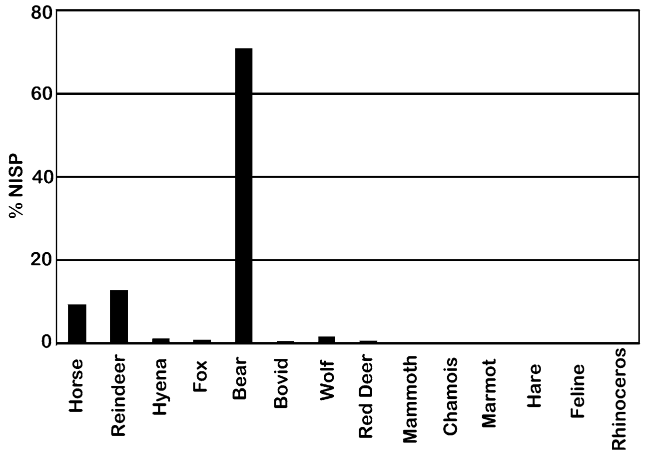

Fig. 10.4 Proportional representation of taxonomic diversity of Level D

was excavated in 2009 by the author (Enloe and David 2010). The faunal spectrum (Table 10.3; Fig. 10.4) is almost as varied as that of Level I, lacking only rhinoceros, mammoth and the large felid. Again, reindeer and horse are the most frequent herbivores, followed by bovid, red deer and chamois. Carnivores include bear, hyena, fox and wolf.

Level D had a carnivore to herbivore ration of 1:0.31, but this may be misleading, as the entire faunal assemblage is dominated by bear remains, particularly fetal bones and deciduous teeth, which are very characteristic of an occupation exclusively for winter hibernation (Baryshnikov and David 2000; David 2002). Level D is the thickest geological stratum in the Grotte du Bison, generally over 50 cm thick, as can be seen in Fig. 10.2. David et al. (2006) anecdotally reported that most of the bear remains from the 1997 and 1998 excavations were found in the upper portion of the level, while reindeer and horse were found at the bottom, suggesting potential differences in the agents of accumulation according to depth in Level D. Figure 10.5 portrays a back plots of the elevations of artifactual material recovered during the 2009 excavation of the western witness block in square N and O, 6 through 10, for which detailed three-dimensional coordinates were recorded with the total station. Three-dimensional data were not systematically recorded for level D during the earlier Leroi-Gourhan or David excavations. A total of 195 object locations were measured, including 2 ochre fragments, 11 cobble fragments, 24 lithic artifacts, 11 burned bones and 148 other faunal remains. The NISP of this faunal sample was 47, of which 35 were identified as bear, including 33 teeth.

Figure 10.5 presents the west-facing coordinates of 6 through 10. A small hearth was discovered in square O8, consisting of a roughly 30 cm diameter circular concentration of ash, burned bone and specks of charcoal, at the base of Level D, on the edge of a projecting limestone bench along the west wall. In Fig. 10.5, non-bear and unidentified faunal specimens are represented by small points; bear remains are represented by "b" symbols; cultural remains, including flint, chert, fire-cracked cobbles, burned bone and charcoal, are represented by "c" symbols. As is evident in Fig. 10.5, almost all of the bear remains came from the upper portions of that stratigraphic unit, the vast majority (33 of 35) above +0.05 m elevation. About 45 % of the unidentified faunal specimens, principally small splinter of diaphyses, were dispersed through the upper 0.55 m of level D above +0.05 m elevation; the remaining 55 % were concentrated in the lower portion, between +0.05 m and −0.10 m elevation. Most of the other identified species' remains and the Châtelperronian cultural materials came from that same thin elevation range at the very bottom of Level D, at the same elevation as the O8 hearth. This suggests that it was after the last Châtelperronian occupation at the base of Level D that the use of the cave passed from intermittent human occupation in the lower Mousterian levels and more exclusive human occupation in Level D, to bear hibernation for the duration of the accumulation of the upper portion of that thick geological layer, until the final roof collapse occurred in level C (David et al. 2006).

When the bear remains are excluded from the Châtelperronian occupation (Table 10.3; Fig. 10.6), a radical change in proportional representation by NISP is produced. Reindeer make up almost half of the remains, horse a third, and all of the other species are insignificant. The carnivore to herbivore ratio drops to 1:11.09, which is substantially different from that of Level I. I have argued elsewhere (Enloe and David 2010) that spatial analyses suggest greater

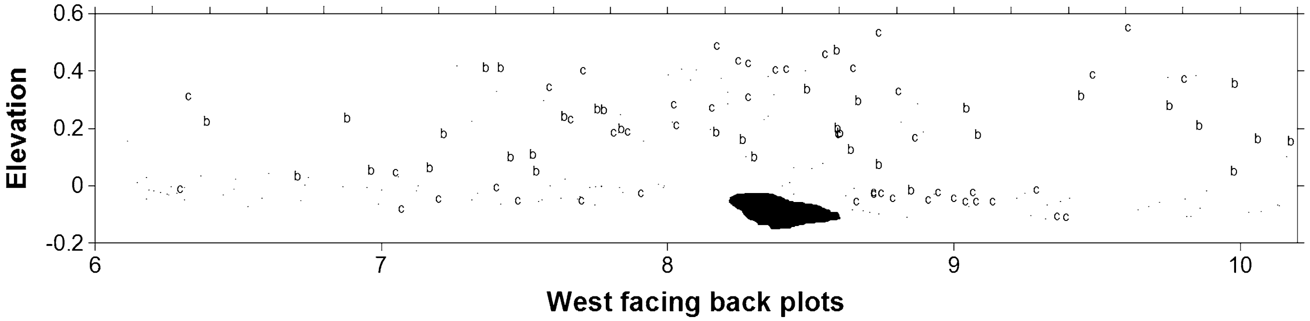

Fig. 10.5 West facing back plots of the elevation of bear (*b*), cultural (*c*) and other fauna (.) from the total station controlled provenience data of level D from 2009 excavations. Hearth O8 indicated by dark mass in lower part of the stratum

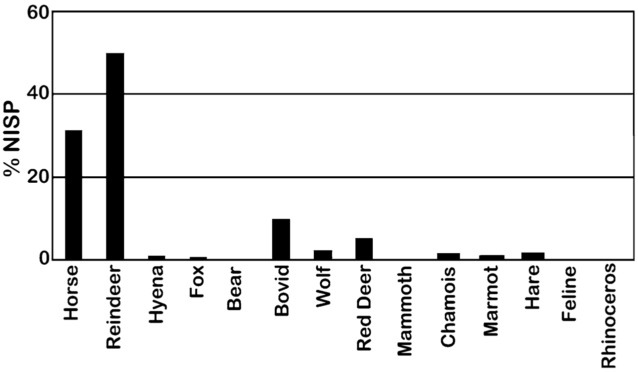

Fig. 10.6 Proportional representation of taxonomic diversity of Level D without bear

exclusivity of occupation by the Châtelperronian inhabitants of the Grotte du Bison, with a more restricted prey spectrum, almost exclusively reindeer and horse. This may well have been the case for the earlier Mousterian occupation of Level I, but the palimpsest deposition obscures clear patterning in taxonomic representation.

Taphonomy

Any consideration of taxonomic representation must commence with a taphonomic assessment. The relatively low 10.7 % of identifiable remains already mentioned for level I is similarly reflected in a 10.3 % NISP for Level D. Clearly, large and robust species are generally better preserved and more identifiable in the paleontological and archaeological record (Grayson 1984; Lyman 1994), but a more precise assessment might be found in the element representation of two of the dominant species for which sample sizes allow the strongest statistical evaluation, reindeer and horse, in Level D (Tables 10.4, 10.5). Anatomical landmarks and portion and segment overlaps were used to derive minimum numbers of element (MNE) frequencies, which were converted into % survivorship proportions, based on minimum numbers of individuals (MNI) for those two well-represented species. For reindeer, the MNI = 3 was derived from MNE counts of metacarpi and tibiae. For horse, the MNI = 2 was derived from counts of crania, mandibles and radii-ulnae. Those proportions were compared with mineral density derived from Lam et al. (1999) calculated for the respective elements of the two species. While % survivorship and mineral density may both qualify as interval-scale variables, we cannot assume a bivariate normal distribution. Therefore, a nonparametric statistic would be most appropriate to evaluate that relationship, so in this case Spearman's Rank Order Correlation Coefficient was employed to assess the significance of the relationship between mineral density and element survival in these samples. For horse (n = 26), Spearman's rho = 0.420*, p = 0.033. For reindeer, Spearman's rho = 0.546**, p = 0.004. In both cases, skeletal element representation is significantly correlated with bone mineral density. Density mediated attrition may be a result of numerous agencies; it is very difficult to distinguish among multiple causes of equifinality such as carnivore ravaging, differential transport or human processing (Enloe et al. 2000; Enloe 2004).

These are small sample sizes and there are a considerable number of zero cells for each data set, which could potentially affect the correlation. As an exploratory data analysis approach, the correlations were run without the zero cells for those elements entirely missing in the assemblage, in an attempt to discern patterning that may be indicative of what might be affecting differential element representation. When the zero cells for horse are removed from the calculation, Spearman's rho = 0.629**, p = 0.009, an even stronger correlation. Clearly, with or without zero cells, skeletal element representation for horse indicates density mediated attrition.

Mid-density elements are well represented in reindeer. The zero cells are primarily the low-density elements, although the highest density of all non-tooth elements, the cranium, is also missing. When the zero cells are removed

Table 10.4 Density mediated attrition of reindeer in Level D (MNI = 3)

Element	MNE	Mineral density	Survivorship (%)
Cranium	0	1.29	0
Mandible	2	1.07	33.33
Atlas	0	0.49	0
Axis	0	0.62	0
Cervical	0	0.45	0
Thoracic	0	0.38	0
Lumbar	2	0.45	4.76
Sacrum	0	0.37	0
Caudal	0	0.43	0
Rib	0	0.47	0
Scapula	1	1.01	16.67
Humerus	3	0.62	50
Radius-ulna	4	1.08	66.66
Carpals	3	0.69	10
Metacarpal	5	0.68	83.33
Coxal	1	0.64	16.67
Femur	4	0.74	66.6
Patella	0	0.57	0
Tibia	5	0.73	83.33
Astragalus	0	0.7	0
Calcaneum	2	0.94	33.33
Navicular	0	0.62	0
Cuneiform	0	0.71	0
Metatarsal	3	0.71	50
Phalanx 1	3	0.61	12.5
Phalanx 2	3	0.48	12.5

Table 10.5 Density mediated attrition of horse in Level D (MNI = 2)

Element	MNE	Mineral density	Survivorship (%)
Cranium	3	1.25	75
Mandible	3	0.98	75
Atlas	0	0.64	0
Axis	1	0.53	50
Cervical	0	0.5	0
Thoracic	2	0.32	7.14
Lumbar	0	0.42	0
Sacrum	0	0.36	0
Rib	2	0.36	3.57
Scapula	1	1.03	25
Humerus	2	1.05	50
Radius-ulna	3	1.04	75
Metacarpal	1	0.6	25
Coxal	1	0.65	25
Femur	2	0.99	50
Patella	0	0.4	0
Tibia	2	0.45	50
Astragalus	0	0.64	0
Calcaneum	0	0.69	0
Navicular	0	0.71	0
Cuneiform	0	0.6	0
Metatarsal	2	0.6	50
Phalanx 1	0	0.67	0
Phalanx 2	0	0.62	0
Phalanx 3	1	0.57	25
Styloid	1	0.69	12.5

from the calculation, the picture is not quite the same for reindeer as it was for horse. Spearman's rho = 0.499, p = 0.069, which is not significant, in strong contrast to the very high significance of the same statistic for horse. Without the zeros, the low and high density elements are represented by low to moderate proportions. Axial elements are poorly represented irrespective of their density. What appears to render the relationship insignificant is the comparatively high representation of mid-density elements. These were plotted on a log/log basis which would emphasize the linearity of the relationship and more clearly show what fell outside of that forced linearity. Figure 10.7 plots the 95 % confidence intervals for reindeer skeletal elements. The only elements over-represented are appendicular elements, both forelimbs and hindlimbs. While these may represent substantial meat packages, such as carcass quarters that were differentially transported to the cave, it is important to note that not only the major meat-bearing elements of the humerus, femur and tibia (Binford 1978) are highly represented, but also that the low meat utility elements of the lower limbs, the metacarpals and metatarsals, are highly represented, while carpals, tarsals and phalanges are poorly represented or absent. This suggests that the metapodials are not merely carried along as riders to the major limb bones (since the carpals, tarsals and phalanges were not attached), but were actively selected and transported. These metapodials have very low meat utility; their primary value was as a marrow source (Morin 2007). In fact, most of the major meat-bearing elements in question have higher marrow utility values than meat utility values (Binford 1978: 21, 27). The conclusion appears to be that carcass portions which are present beyond the proportions expected based on to bone mineral density were selected for transport to the Grotte du Bison primarily for the caloric value of their marrow (Speth and Spielmann 1983). This is quite consistent with the discovery of six "pockets" of bones on the main occupation surface at the base of level D reported by David et al. (2006: 42). These were exclusively reindeer diaphysis fragments on which all of the cut marks from the entire level were concentrated.

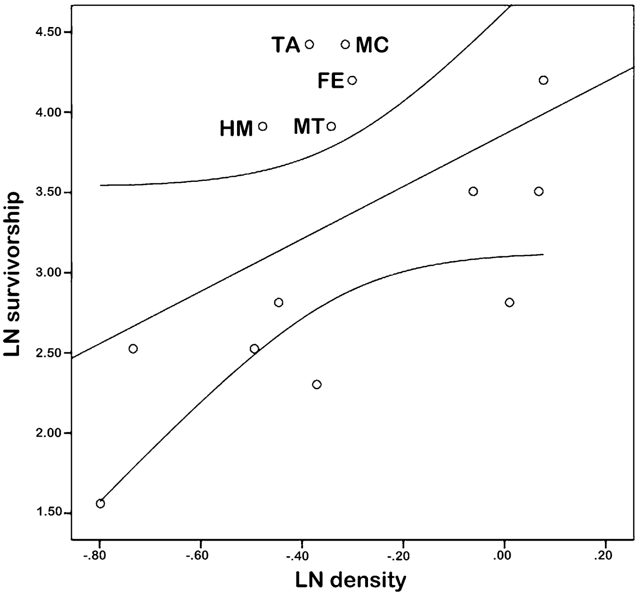

Fig. 10.7 95 % confidence interval of regression of log bone mineral density with log survivorship of reindeer in level D, Grotte du Bison, Arcy-sur-Cure. Over-represented outlier elements include tibia, metacarpal, femur, metatarsal and humerus

They correspond to putative marrow processing areas on that level identified by Enloe and David (2010). Blumenschine and Madrigal (1993) have demonstrated that, despite substantial differences in body size, cervid metapodials can yield more than ten times the volume of marrow than can equid metapodials, due to differences in wall thickness affecting medullar cavity volume and proportion of cancellous trabecular tissue (see Fig. 10.8). It is substantially easier to extract the marrow mechanically from reindeer (see Binford 1978: 152–157), in contrast to horse, which requires boiling to extract the maximum of fatty tissues from the metapodial (Enloe 2007). A greater and more systematic focus on nutritionally rich marrow, particularly in the increased exploitation of reindeer, may have been particularly significant for Châtelperronian adaptation compared to that of earlier Mousterian Neanderthals at Arcy-sur-Cure.

Conclusions: Ecology and Taphonomy

Fig. 10.8 Relative marrow cavity volume of horse (*left*) and reindeer (*right*) metapodials (photo J. G. Enloe)

Many attempts have been made to compare or contrast the Middle and Upper Paleolithic, whether to demonstrate continuity in patterns of faunal exploitation, and thus basic continuity in ecological niche of Neanderthals and anatomically modern humans, or to demonstrate radical differences to explain differential evolutionary success. Zooarchaeologists typically report species representation, numbers of individuals, element representation, and utility indices to try to enlighten ourselves about the nature of food acquisition, preparation and consumption. While these may be appropriate ways of examining subsistence among modern populations, I am not sure if our traditional ways of looking at faunal assemblages are the best for exploring the potential evolutionary significance of the Middle to Upper Paleolithic transition.

The complicating issue is always taphonomic. Most Middle Paleolithic cave occupations contain a considerable contribution by other carnivores (e.g., Stiner 1994; Stiner et al. 1996). This makes it difficult to assign agency for the accumulation and modification of any faunal materials recovered from such deposits. It is exceedingly problematic to recognize signature patterning of overall assemblages attributed to the various agents. There is a substantial literature debating the morphology, frequency, location and superposition of cut marks and tool marks, but such evidence is infrequently sufficiently represented in the totality of an assemblage to resolve the recognition problem.

We need additional information about pure Neanderthal subsistence ecology because at least some portion of our database consists of assemblages that may be substantially mixed with the residues of other carnivore inhabitants of the sites. While the goal of this research was to compare the Mousterian and Châtelperronian at Arcy-sur-Cure, the results are not entirely clear. The Level I faunal assemblage is not entirely anthropogenic, but at least a portion of it can be attributed to Mousterian Neanderthals (Enloe 2011), although it is not internally spatially structured as argued for the Châtelperronian Level D at the Grotte du Bison (Enloe and David 2010).

While Neanderthal sites are generally lacking in structures or much else in the way of spatial organization, some earlier Middle Paleolithic sites appear to have some elements of differential space use and organization of space, such as in the Mousterian levels at the Abric Romaní (Vaquero and Pastó 2001; Vaquero et al. 2001) or at the Grotta di Fumane (Perisani et al. 2011). The picture for the Châtelperronian seems perhaps a bit clearer. Spatially structured site organization is more evident through differential space use and maintenance of cleaned space at Arcy-sur-Cure, in both the Grotte du Renne's "huts" (Leroi-Gourhan 1961) and in the processing and discard areas in the Grotte du Bison (Enloe and David 2010). These appear to occur in more of an exclusive occupation of the site, where evidence of other carnivores is absent or minimal, or where they become part of the species exploited by humans rather than independent contributors to the faunal assemblage, as demonstrated by David (2004) for the Grotte du Renne. In this case, there also appears to be a substantial focus on the acquisition and processing of marrow-rich skeletal elements from reindeer, seen in taxonomic and element representation, as well as in cut mark and spatial distribution. With those late Neanderthal cases, we can perhaps begin to build a clearer picture of human hunting behavior, and to identify subsistence practices that had greater significance for modern human origins and evolutionary success. These practices may not be evident in the proportions of different species as much as in how we can see differences in the ways species were exploited. They might be functions of seasonal or nutritional characteristics of the prey species that formed the bases for new behavioral patterns among the human exploiters of those species, visible in carcass processing or social mechanisms for cooperative acquisition and consumption, as have been demonstrated for carcass processing and food sharing in the Late Upper Paleolithic (e.g. Enloe 1999, 2003a, b, 2007).

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References

Baffier, D., & Girard, M. (1997). Le karst d'Arcy-sur-Cure (Yonne) et ses occupations humaines paléolithiques. *Quaternaire, 8*, 245–255.

Bailey, S. E., & Hublin, J. J. (2006). Dental remains from the Grotte du Renne at Arcy-sur-Cure (Yonne). *Journal of Human Evolution, 50*, 485–508.

Baryshnikov, G., & David, F. (2000). Les ours des cavernes à Arcy-sur-Cure (Yonne, France)—*Ursus* (*Spelearctos*) *spelaeus* Rosenmüller et Heinroth, 1794. *Quaternaire, 11*, 65–79.

Binford, L. R. (1978). *Nunamiut ethnoarchaeology*. New York: Academic Press.

Blumenschine, R. J., & Madrigal, T. C. (1993). Variability in long bone marrow yields of East African ungulates and its zooarchaeological implications. *Journal of Archaeological Science, 20*, 555–587.

David, F. (2002). Les ours du Châtelperronien de la Grotte du Renne à Arcy-sur-Cure (Yonne). In T. Tillet & L. R. Binford (Eds.), *L'Ours et l'Homme* (pp. 185–192). Etudes et Recherches Archéologiques de l'Université de Liège (ERAUL) 100. Liège: Université de Liège.

David, F. (2004). Note sur l'hyène des cavernes (*Crocuta crocuta spelaela* G.) dans trois secteurs de la grotte du Renne à Arcy-sur-Cure (Yonne): Moustérien de la Galerie Schoepflin et de la Rotonde, Châtelperronien du Xc. *Revue de Paléobiologie, 23*(2), 761–769.

David, F., Connet, N., Girard, M., Miscovsky, J.-C., Mourer-Chauviré, C., & Roblin-Jouve, A. (2006). Les niveaux du Paléolithique supérieur à la Grotte du Bison (Arcy-sur-Cure, Yonne): Couches A à D. *Revue Archéologique de l'Est, 54*, 5–50.

David, F., D'Iatchenko, V., Enloe, J. G., Girard, M., Hardy, M., Lhomme, V., et al. (2009a). New Neandertal remains from the Grotte du Bison at Arcy-sur-Cure, France. *Journal of Human Evolution, 57*, 805–809.

David, F., D'Iatchenko, V., Enloe, J. G., Girard, M., Hardy, M., Roblin-Jouve, A., et al. (2009b). Nouvelles découverts de dents néandertaliennes dans la grotte du Bison à Arcy-sur-Cure (Yonne). *Bulletin de la Société Préhistorique Française, 106*, 375–390.

David, F., Connet, N., D'Iatchenko, V., Enloe, J. G., Girard, M., Hardy, M., et al. (2010). *Arcy-sur-Cure (Yonne), Grotte du Bison, Rapport 2006–2010*. Dijon: Quadrennial Report to the Service Régionale d'Archéologie de Bourgogne.

Discamp, E., Jaubert, J., & Bachellerie, F. (2011). Human choices and environmental constraints: Deciphering the variability of large game procurement from Mousterian to Aurignacian times (MIS 5–3) in Southwestern France. *Quaternary Science Reviews, 30*, 2755–2775.

Enloe, J. G. (1999). Hunting specialization: Single-species focus and human adaptation. In J. P. Brugal, F. David, J. G. Enloe, & J. Jaubert (Eds.), *Le Bison: Gibier et Moyen de Subsistance des Hommes du Paléolithique aux Paléoindiens des Grandes Plaines* (pp. 501–509). Antibes: Éditions APDCA.

Enloe, J. G. (2001). Investigating human adaptations in the early upper Paleolithic. In M. A. Hayes & P. Thacker (Eds.), *Questioning the answers: Re-solving fundamental problems of the early upper Paleolithic* (pp. 21–26). BAR International Series S1005. Oxford: Archaeopress.

Enloe, J. G. (2003a). Food sharing past and present: Archaeological evidence for economic and social interaction. *Before Farming, 2003/1*(1), 1–23.

Enloe, J. G (2003b). Acquisition and processing of reindeer in the Paris Basin. In S. Costamagno & V. Laroulandie (Eds.), *Zooarchaeological insights into Magdalenian lifeways* (pp. 23–31). BAR International Series S1144. Oxford: British Archaeological Reports.

Enloe, J. G. (2004). Equifinality, assemblage integrity and behavioral inferences at Verberie. *Journal of Taphonomy, 2*(3), 147–165.

Enloe, J. G. (2007). L'écologie du renne et les adaptations des chasseurs: un aperçu du Paléolithique. In S. Beyries & V. Vaté (Éds.)*, Les Civilisations du Renne d'Hier et d'Aujourd'hui: Approches Ethnohistoriques, Archéologiques et Anthropologiques*. XXVIIe Rencontres Internationales d'Archéologie et d'Histoire d'Antibes (pp. 209–221). Antibes: Éditions APDCA.

Enloe, J. G. (2011). Middle Paleolithic spatial analysis in caves: Discerning humans from hyenas at Arcy-sur-Cure, France. *International Journal of Osteoarchaelogy*. doi:10.1002/oa.1276.

Enloe, J. G., & David, F. (2010) *Châtelperronian at the Grotte du Bison, Arcy-sur-Cure: Stratigraphic correlations and spatial organization*. Paper Presented at the 19th Annual Meeting of the Paleoanthropology Society, St. Louis, MO, April 12–13, 2010.

Enloe, J. G., David, F., & Baryshnikov, G. (2000). Hyenas and hunters: Zooarchaeological investigations at Prolom II Cave, Crimea. *International Journal of Osteoarchaelogy, 10*, 310–324.

Farizy, C. (1990). Du Moustérien au Châtelperronien à Arcy-sur-Cure: un état de la question. In C. Farizy (Ed.), *Paléolithique Moyen et Paléolithique Supérieur Ancien en Europe* (pp. 281–189). Mémoires 3. Nemours: Musée de Préhistoire d'Île-de-France.

Grayson, D. K. (1984). Quantitative Zooarchaeology: Topics in the Analysis of Archaeological Faunas. Orlando: Academic Press.

Hublin, J.-J., Spoor, F., Braun, M., Zonneveld, F., & Condemi, S. (1996). A late Neandertal associated with upper Palaeolithic artefacts. *Nature, 381*, 224–226.

Lam, Y. M., Chen, X., & Pearson, O. M. (1999). Intertaxonomic variability in patterns of bone density and the differential representation of bovid, cervid, and equid elements in the archaeological record. *American Antiquity, 64*, 343–362.

Leroi-Gourhan, A. (1961). Les fouilles d'Arcy-sur-Cure (Yonne). *Gallia Préhistoire, 4*, 3–16.

Leroi-Gourhan, A. (1988). Le passage Moustérien-Châtelperronien à Arcy-sur-Cure. *Bulletin de la Société Préhistoire Française, 85*, 102–104.

Leroi-Gourhan, A., & Leroi-Gourhan, A. (1964). Chronologie des Grottes d'Arcy-sur-Cure (Yonne). *Gallia Préhistoire, 7*, 1–64.

Lhomme, V., David, F., & Thiebaut, C. (2004). Les industries de la fin du Paléolithique Moyen de la Grotte du Bison à Arcy-sur-Cure (Yonne). In N. Molines, M.-H. Moncel, & J.-L. Monnier (Eds.), *Les Premiers Peuplements en Europe* (pp. 379–499). BAR International Series S1364, Oxford: Hadrian Books.

Lyman, R. L. (1994). Vertebrate Taphonomy. Cambridge: Cambridge University Press.

Morin, E. (2007). Fat composition, skeletal part selection, and Nunamiut decision making. *Journal of Archaeological Science, 34*, 69–82.

Neruda, P., & Nerudová, Z. (2011). The middle-upper palaeolithic transition in Moravia in the context of the middle Danube region. *Quaternary International*. doi:10.1016/j.quaint.2011.08.035.

Perisani, M. (2012). Fifty thousand years of flint knapping and tool shaping across the Mousterian and Uluzzian sequence of Fumane cave. *Quaternary International, 247*, 125–150.

Perisani, M., Chrzavzez, J., Danti, A., DeMarch, M., Duches, R., Gurioli, F., et al. (2011). Fire-places, frequentations and the environmental setting of the final Mousterian at Grotta di Fumane: a report from the 2006–2008 research. *Quatär, 58*, 131–151.

Speth, J. D., & Spielmann, K. A. (1983). Energy source, protein metabolism, and hunter-gatherer subsistence strategies. *Journal of Anthropological Archaeology, 2*, 1–31.

Stiner, M. C. (1994). *Honor among thieves: A zooarchaeological study of Neandertal ecology*. Princeton: Princeton University Press.

Stiner, M. C., Arsebük, G., & Howell, F. C. (1996). Cave bears and Paleolithic artifacts in Yarimburgaz Cave, Turkey: Dissecting a palimpsest. *Geoarchaeology, 11*, 279–327.

Vaquero, M., & Pastó, I. (2001). The definition of spatial units in middle Paleolithic sites: The hearth-related assemblages. *Journal of Archaeological Science, 28*, 1209–1220.

Vaquero, M., Vallverdú, J., Rosell, J., Pastó, I., & Allué, E. (2001). Neandertal behavior at the middle Paleolithic site of Abric Romaní, Capellades, Spain. *Journal of Field Archaeology, 28*, 93–114.