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ScienceDirect
Journal of Human Evolution 55 (2008) 179–185

Isotopic dietary analysis of a Neanderthal and associated fauna from the site of Jonzac (Charente-Maritime), France

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Received 13 February 2007; accepted 11 February 2008

Abstract

We report here on the isotopic analysis (carbon and nitrogen) of collagen extracted from a Neanderthal tooth and animal bone from the late Mousterian site of Jonzac (Charente-Maritime, France). This study was undertaken to test whether the isotopic evidence indicates that animal protein was the main source of dietary protein for this relatively late Neanderthal, as suggested by previous studies. This was of particular interest here because this is the first isotopic study of a relatively late Neanderthal associated with Mousterian of Acheulian Tradition (MTA, dating to approximately 55,000 to 40,000 BP) technology. We found that the Jonzac Neanderthal had isotopic values consistent with a diet in which the main protein sources were large herbivores, particularly bovids and horses. We also found evidence of different dietary niches between the Neanderthal and a hyena at the site, with the hyena consuming mainly reindeer.
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Keywords: Diet; France; Isotopes, Mousterian; Neanderthals

Introduction

The measurement of the stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) in bone collagen is an established method for reconstructing the diets of past humans and nonhuman animals [see Sealy (2001) and Katzenberg (2000) for reviews]. One of the most successful applications of the method has been to European Neanderthals, in which it has been consistently inferred that dietary protein was most likely obtained from the consumption of large herbivores. To date, this method has been applied to thirteen adult Neanderthals from three sites in France, two sites in Belgium, and one site in Croatia (Fizet et al., 1995; Bocherens et al., 1999, 2001, 2005; Richards et al., 2000; Bocherens and Drucker, 2003; Beauval et al., 2006). In all cases, the Neanderthal isotopic results were compared to isotopic values of fauna from the site or from nearby sites when fauna from the site itself was not available. In each case, Neanderthals had $\delta^{15}N$ values that were similar to or higher than top-level carnivores at these sites, leading the researchers to conclude that Neanderthals were also top-level carnivores in these ecosystems.

In this paper we present the results of the isotopic analysis of a relatively recent Neanderthal from a Mousterian of Acheulian Tradition (MTA) level at the site of Jonzac (Charente-Maritime, France). This is the first isotopic analysis on a Neanderthal associated with MTA technology, and we undertook it to determine whether this relatively late Neanderthal had a dietary adaptation that was similar to that of the other Neanderthals studied so far. Additionally, we were able to better define

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doi:10.1016/j.jhevol.2008.02.007

Neanderthal diet at this site because we were able to measure the isotopic values of a wide range of fauna from different levels at the site, including from the levels contemporary with the Neanderthal, which is not always possible in studies of this type.

Isotopic analysis for dietary reconstruction

Isotopic analysis of bone collagen is a useful tool for reconstructing past human and nonhuman animal diets and has been increasingly applied since its first use in archaeology in the late 1970s and early 1980s (Vogel and van der Merwe, 1977; van der Merwe and Vogel, 1978; Tauber, 1981). The method is based on the principle that the carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) ratios in bone collagen are related to the carbon and nitrogen isotopic ratios in foods that have been consumed over the lifetime of the human or nonhuman animal of interest (Schwarcz and Schoeninger, 1991; Ambrose, 1993). Numerous controlled feeding experiments and field studies have established that, for mammals with diets with adequate amounts of protein, the $\delta^{13}C$ value is most related to dietary protein, $\delta^{13}C$ values (Ambrose and Norr, 1993). Nitrogen is only present in dietary protein, so the $\delta^{15}N$ value must reflect dietary protein $\delta^{15}N$ values. There is an approximately 5% offset between the $\delta^{13}C$ values for mammalian collagen and dietary protein, and similarly, there is an increase of approximately 2–4% in $\delta^{15}N$ values of consumer collagen compared to dietary protein $\delta^{15}N$ values [see references in Sealy (2001) and Katzenberg (2000)]. As mammalian bone collagen constantly turns over, the measured $\delta^{13}C$ and $\delta^{15}N$ values reflect a long-term average of dietary protein, likely over many years, although the exact length of time for collagen turnover remains unknown. Tooth dentine has relatively little turnover, and therefore the isotope values will reflect the diet at the time of dentine formation, usually during later childhood.

The application of mammal collagen carbon and nitrogen stable isotope measurements in archaeology has focused mainly on three areas. The first is the use of carbon isotopes to discriminate between the consumption of marine and terrestrial resources, as there is a difference in $\delta^{13}C$ values between these two ecosystems. The second application is the use of $\delta^{13}C$ values to discriminate between the consumption of C_3 and C_4 plants, as there is a difference in the $\delta^{13}C$ values between plants using these photosynthetic pathways. However, this application is not of relevance in Paleolithic Europe, where most edible plants were C_3. Finally, the third application of this method is the measurement of $\delta^{15}N$ values to determine the trophic level of organisms within a food web, especially to discriminate between herbivores, carnivores, and omnivores. This latter application is of relevance to determining the diets of omnivores like Neanderthals and modern humans in Europe.

The Jonzac site

Jonzac (also known as Chez Pinaud) is a collapsed rock shelter located in a small river valley in southwest France, the Seugne, a tributary of the Charente River. The site was rediscovered in the 1990s and excavated by Airvaux (2004). In 2004, two of us (Hublin and Jaubert) began a new program of multidisciplinary research on the site. The material reported on here comes from the new program of excavations in the upper portions of the Middle Paleolithic sequence (Fig. 1), in which Level 8, consisting of a Denticulate Mousterian with predominance of Levallois technology, is overlain by two levels (7 and 6) of Mousterian of Acheulian Tradition (MTA). Level 5 contains Aurignacian industries; however, artifact and bone densities are very low, and it contains no identifiable archaeological horizons. Our excavations used independent level designations and, depending on which portion of the site is being discussed, do not necessarily correspond with those of Airvaux (2004; Airvaux and Soressi, 2005). In this case, our Level 8 corresponds to Airvaux's 8, but what

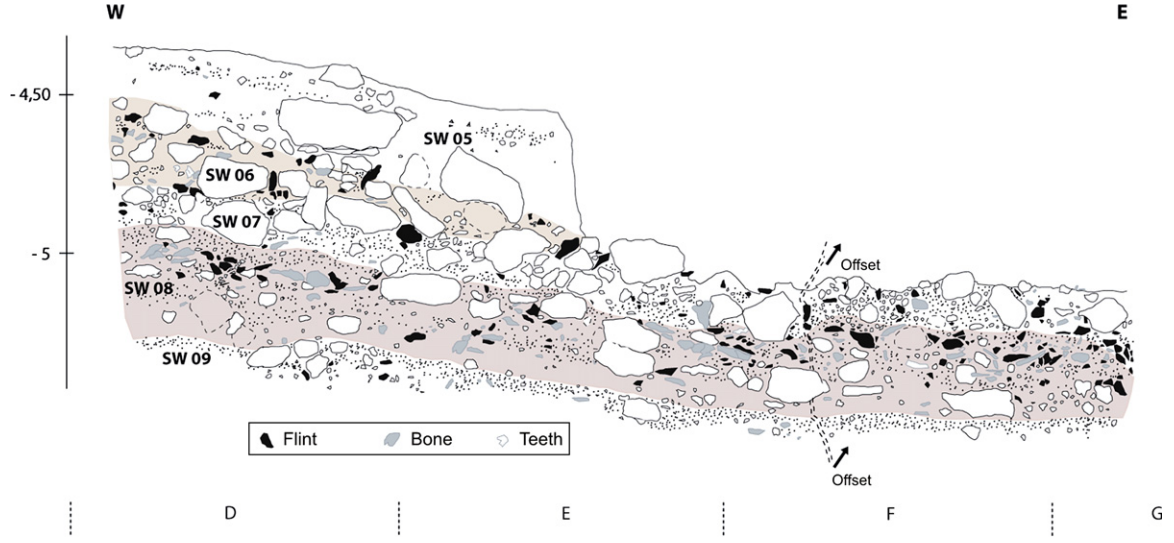

Fig. 1. North profile (Units D18–G18) from the southwest sector of Jonzac excavations. Level 05 contains Aurignacian artifacts. Levels 06 and 07 contain Mousterian of Acheulian Tradition industries. Level 08 is a Denticulate Levallois industry. The hominin tooth comes from near the top of Level 07, a little more than 1 m into (north of) this section.

Airvaux labeled 7 and 7s, we call Level 6 and 7, respectively. The hominin tooth comes from Level 7 (SW-US07). The sediments in these levels are sandy-clay with frequent small limestone clasts. Levels 6 and 7 are associated with a period of shelter collapse and characterized by numerous larger limestone blocks. Taphonomic studies (sedimentological, artifact orientations and edge damage) suggest some downslope movement of materials in this portion of the site; however, there is no evidence of mixing between levels. There is, for instance, a distinct break between the MTA of Levels 7 and 6 and the overlying Upper Paleolithic of Level 5. Likewise, there is a distinct techno-typological break between the underlying Level 8 and Levels 6 and 7. Additionally, the hominin tooth was found near the top of Level 7, making it approximately 10–15 cm above the underlying Level 8 and approximately 20 cm below the overlying Upper Paleolithic levels.

Where it is present in stratigraphic association with other recent Middle Paleolithic assemblages, the MTA is relatively late and often last in the Middle Paleolithic sequence (Mellars, 1996), as is the case at Jonzac. There are relatively few absolute dates for the MTA, but they support a late date of roughly 55 ka to 40 ka (Valladas et al., 1987; Mellars, 1996; Soressi, 2002; Soressi et al., 2007). A series of radiocarbon and thermoluminescence dates for this portion of the sequence at Jonzac are currently being produced. Preliminary radiocarbon dates of ca. 36 ka on two pieces of cut-marked bone from Level 7 support a temporal attribution to the very end of the Middle Paleolithic in this region (Richards et al., unpubl. data).

To date, almost 2,000 faunal remains from Jonzac have been identified to taxon (species) or ungulate size-class from Level 6 (number of identified specimens, NISP = 299), Level 7 (NISP = 488), and Level 8 (NISP = 1193). The species present reflect an open, temperate environment. Large bovids (*Bison priscus* and/or *Bos primigenius*) dominate the large-mammal remains (Level 6 = 73%, 7 = 61%, 8 = 61%). In comparison to Level 6, the abundance of bovids in Level 7 is lower relative to reindeer (*Rangifer tarandus*: Level 6 = 7%, 7 = 15%, 8 = 18%) and horses (*Equus cabullus*: Level 6 = 10%, 7 = 18%, 8 = 15%). Similar relative abundances are observed in Level 8. A few examples of an extinct equid (*Equus hydruntinus*), rhinoceros, red deer (*Cervus elaphus*), and giant deer (*Megaloceros giganteus*) are also present. Unfortunately, in these levels, weathering, root etching, and acidic soils have damaged bone surfaces. Despite the limited ability to detect human and carnivore impacts on the bones, cut, percussion, and utilization marks and burning can be seen throughout these assemblages (bovid/horse: Level 6 = 7%, 7 = 7%, 8 = 12%; reindeer: Level 6 = 4%, 7 = 12%, 8 = 18%); carnivore marks (chewed or digested bones) are virtually absent (Level 6 = 0%, 7 = 0%, 8 = <1%). There are very few carnivore remains at the site; only three specimens were found from the three levels: a bear (*Ursus* sp.) scapula was found in three pieces in Level 7, a cave hyena (*Crocuta spelaea*) occipital condyle was found in Level 8, and a cave lion (*Panthera spelaea*) canine was recovered from Level 7. The presence of these three carnivore species is typical of this time period and geographical location (e.g., Tournepiche, 1996; Beauval et al., 2005; Costamagno et al., 2005). Our analysis of the fauna from the levels considered here indicates that Neanderthals were the primary consumers of the herbivore remains from Levels 6–8. Moreover, large bovids dominate the faunal assemblage, and we conclude that they also dominated the large-game part of the Jonzac occupants' diet.

A hominin tooth was found in the southwest area of the excavation (Square E14, Level 7). The tooth's surface was badly degraded and the crown was strongly abraded during the lifetime of the individual. The buccal and lingual cusps are almost equal in size, although the buccal cusp is slightly more projecting. The root is forked. In spite of the poor condition of the crown, it is possible to identify the tooth as an upper right premolar, most likely a P^3, but it may be a P^4. In terms of morphology, Neanderthal and modern human upper premolars do not display clear diagnostic differences. Regarding metrics, the mesiodistal diameter of the Jonzac crown is 6.5 mm and the buccolingual diameter is 10.7 mm. Both values should be considered minima. When these values are compared to the 95% equiprobable ellipses for extant human, Upper Paleolithic modern European, and Neanderthal bivariate distributions compiled by Verna (2006) (which, for the P^3, included 22 Neanderthals, 27 Upper Paleolithic modern Europeans, and 322 recent humans of various origins, and, for the P^4, 22 Neanderthals, 28 Upper Paleolithic modern Europeans, and 317 recent humans of various origins), the Jonzac individual falls within the Neanderthal range, well outside the range for recent human populations, and just outside of the Upper Paleolithic modern European range for both P^3 and P^4 distributions. Finally, it should be noted that all identifiable human remains found in Mousterian contexts in western Europe, including in MTA sites, are Neanderthal.

Methods

To understand $\delta^{13}C$ and $\delta^{15}N$ values of collagen from fossil human and nonhuman animals, it is necessary to establish an isotopic food web, where the $\delta^{13}C$ and $\delta^{15}N$ values of various contemporary fauna from the site of interest are measured to provide baseline comparisons for the species of interest, such as Neanderthals or modern humans. This is not always possible, as many sites do not have faunal remains clearly associated with the species of interest. However, it may be of key importance in understanding the isotopic values of Pleistocene humans, as there has been a recently observed shift in baseline $\delta^{15}N$ values of various herbivores in Europe, likely related to climatic shifts (Richards and Hedges, 2003; Drucker et al., 2003; Stevens and Hedges, 2004). At the site of Jonzac, there is an abundant faunal record, and thus we were able to measure a range of species in order to establish an appropriate isotopic food web for comparison with the Neanderthal isotopic results.

We extracted bone collagen from a range of species from five different stratigraphic levels at the site, with most of the samples coming from Level 7 (which is where the Neanderthal tooth was discovered) and Level 8. Collagen-extraction

methods followed those outlined in Richards and Hedges (1999) and involved demineralization of whole bone in 0.5 M HCl at 5 °C for 3–5 days, gelatinization, ultrafiltration using 30 kDa filters (Brown et al., 1988), and lyophilization. The Neanderthal tooth was sectioned for complementary studies on histology, and while the tooth was in section, we drilled powder from the pulp chamber and the roots. The extracted dentine powder was then demineralized following the same procedures outlined above, with the addition of an extra ultrafiltration step to isolate the 10–30 kDa and <10 kDa fractions. The resulting "collagen" fractions were measured for the $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios at the Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology (Leipzig, Germany). Isotopic measurements ($\delta^{13}C$ and $\delta^{15}N$) were made on a ThermoFinnigan Flash EA coupled to a Delta Plus XP isotope ratio monitoring mass spectrometer. The $\delta^{13}C$ values are reported relative to the V-PDB standard, and the $\delta^{15}N$ values are reported relative to the AIR standard. The analytical precision based on repeated measurements was better than 0.2% in both cases. The international standards NBS-22, IAEA-CH6, IAEA-CH7, IAEA-N1, and IAEA-N2 were used to calibrate the reference gas and to check within- and between-batch accuracy and precision.

Isotope results

The isotopic results from the Neanderthal tooth and the nonhuman animal bone collagen are given in Tables 1 and 2. Also presented are the C:N ratios, %C, %N, and collagen yields for all of the samples. Only the animal samples that had acceptable C:N ratios (following DeNiro, 1985) are presented in Table 2. The collagen yields are relatively low, including yields below 1%. However, the use of ultrafiltration helped in the extraction and isolation of intact collagen, even at these low levels, as evidenced by the C:N ratios of the >30 kDa fraction.

The $\delta^{13}C$ and $\delta^{15}N$ data and averages for *Bison/Bos*, *Equus*, and *Rangifer* from Levels 6, 7, and 8 are plotted in Figs. 2 and 3. The $\delta^{13}C$ values show little difference within species between the levels. This is as expected, as there generally is little variation in herbivore bone collagen $\delta^{13}C$ during the European late Pleistocene (Richards and Hedges, 2003). There is, however, variation in $\delta^{15}N$ values in this period, with the most marked changes occurring at the Pleistocene/Holocene transition (Richards and Hedges, 2003; Drucker et al., 2003; Stevens and Hedges, 2004). As shown in Fig. 2, the $\delta^{15}N$ values for horse and reindeer from Level 6 are lower than those from Levels 7 and 8, but there is no clear difference between Levels 7 and 8. Differences in the $\delta^{15}N$ values for the same species of herbivores have been linked to aridity (e.g., Heaton et al., 1986), so it is possible that Level 6 represents a warmer and moister period than those represented by Levels 7 and 8 at the site. The large mammalian faunal assemblage tentatively supports this conclusion because of the low abundance of large bovids in Levels 7 and 8 compared to Level 6. The micromammals from these levels, which are currently under study, may reflect even more subtle differences.

Table 1
Isotopic results, %C, %N, C:N ratios, and collagen yields for the Neanderthal tooth from Level 7

Sample number	$\delta^{13}C$	$\delta^{15}N$	%C	%N	C:N	%Yield
S-EVA-2152	−20.7	10.6	30.2	9.7	3.6	0.1
S-EVA-2152.1	−19.7	11.2	33.5	12.1	3.2	0.2
S-EVA-2152.2	−21.3	10.3	26.7	8.4	3.7	0.3

The >30 kDa (S-EVA-2152) and 10–30 kDa (S-EVA-2152.1) fractions had acceptable C:N and %C and %N values, while the <10 kDa fraction (S-EVA-2152.2) did not.

Table 2
Isotope data for animal bone collagen from different levels at Jonzac

Sample number	Species	Level	$\delta^{13}C$	$\delta^{15}N$	%C	%N	C:N	% Collagen
S-EVA-887	*Bison/Bos*	6	−19.5	5.7	31.1	11.3	3.2	0.6
S-EVA-888	*Bison/Bos*	6	−20.4	4.2	22.9	8.1	3.3	0.3
S-EVA-889	*Bison/Bos*	6	−20.7	5.1	22.4	8.0	3.3	0.3
S-EVA-890	*Bison/Bos*	6	−20.4	4.1	36.3	13.0	3.2	0.9
S-EVA-2035	*Bison/Bos*	6	−20.4	6.3	31.7	11.6	3.2	0.6
S-EVA-892	*Equus*	6	−20.1	3.7	27.4	10.1	3.2	1.0
S-EVA-893	*Equus*	6	−20.7	4.5	37.3	13.3	3.3	0.4
S-EVA-894	*Megaceros*	6	−20.0	4.5	35.1	12.7	3.2	0.8
S-EVA-895	*Rangifer*	6	−18.8	5.6	21.1	7.3	3.4	0.3
S-EVA-896	*Rangifer*	6	−20.2	5.3	36.5	13.0	3.3	0.5
S-EVA-2025	*Ursus*	7	−21.1	9.2	31.2	11.3	3.2	0.2
S-EVA-897	*Bison/Bos*	7	−20.2	5.8	35.4	12.7	3.2	0.7
S-EVA-898	*Bison/Bos*	7	−20.5	5.2	14.6	5.2	3.3	0.2
S-EVA-899	*Bison/Bos*	7	−19.8	7.9	27.6	9.9	3.2	0.9
S-EVA-900	*Bison/Bos*	7	−20.2	4.9	32.7	11.8	3.2	0.6
S-EVA-901	*Bison/Bos*	7	−20.1	5.3	35.6	12.8	3.2	0.9
S-EVA-2027	*Bison/Bos*	7	−20.6	4.8	43.1	15.5	3.3	0.7
S-EVA-2029	*Bison/Bos*	7	−20.3	6.9	27.1	9.6	3.3	0.4
S-EVA-2031	*Bison/Bos*	7	−19.7	9.5	34.4	12.5	3.2	0.6
S-EVA-2033	*Bison/Bos*	7	−20.2	5.0	42.6	15.4	3.2	0.7
S-EVA-2034	*Bison/Bos*	7	−20.4	6.4	31.7	10.8	3.4	0.4
S-EVA-902	*Equus*	7	−21.1	5.2	33.3	11.7	3.3	0.9
S-EVA-903	*Equus*	7	−20.5	7.1	27.7	10.0	3.2	0.5
S-EVA-2026	*Equus*	7	−20.2	4.6	40.0	14.4	3.3	0.5
S-EVA-2023	*Rangifer*	7	−19.5	7.9	32.8	11.4	3.4	0.2
S-EVA-2030	*Rangifer*	7	−19.0	6.7	37.6	13.5	3.2	0.5
S-EVA-905	*Rangifer*	7	−19.5	9.4	33.1	12.0	3.2	0.6
S-EVA-907	*Rangifer*	7	−19.5	7.3	29.5	10.6	3.2	0.5
S-EVA-909	*Rangifer*	7	−19.8	7.4	36.6	13.1	3.3	1.0
S-EVA-910	*Rangifer*	7	−19.2	7.2	23.2	8.5	3.2	0.3
S-EVA-2024	*Crocuta*	8	−19.1	8.6	37.3	13.2	3.3	0.3
S-EVA-911	*Bison/Bos*	8	−20.7	6.5	28.5	10.3	3.2	0.5
S-EVA-912	*Bison/Bos*	8	−20.2	4.3	29.5	10.8	3.2	0.5
S-EVA-913	*Bison/Bos*	8	−20.2	4.6	28.3	10.4	3.2	0.4
S-EVA-914	*Bison/Bos*	8	−19.8	6.5	31.7	11.7	3.2	0.7
S-EVA-915	*Bison/Bos*	8	−20.2	4.2	29.3	10.7	3.2	0.6
S-EVA-917	*Equus*	8	−20.7	6.0	39.7	14.3	3.2	0.5
S-EVA-918	*Equus*	8	−20.1	6.2	41.9	15.0	3.3	0.4
S-EVA-919	*Equus*	8	−20.4	5.2	41.5	15.0	3.2	0.5
S-EVA-920	*Equus*	8	−20.5	5.6	25.4	9.3	3.2	0.3
S-EVA-921	*Equus*	8	−20.6	4.6	26.4	9.7	3.2	0.9
S-EVA-922	*Megaceros*	8	−20.1	5.0	24.5	9.1	3.2	0.8
S-EVA-923	*Rangifer*	8	−18.7	7.7	29.3	10.7	3.2	0.6
S-EVA-924	*Rangifer*	8	−18.4	7.2	27.8	10.2	3.2	0.4
S-EVA-925	*Rangifer*	8	−19.3	7.0	29.3	10.6	3.2	0.3
S-EVA-926	*Rangifer*	8	−19.2	8.3	35.9	13.0	3.2	0.5

Isotope measurement, C:N ratio, %C, %N, and collagen yield is for the >30 kDa fraction only. $\delta^{13}C$ values are measured relative to the V-PDB standard, and $\delta^{15}N$ values are measured relative to the AIR standard.

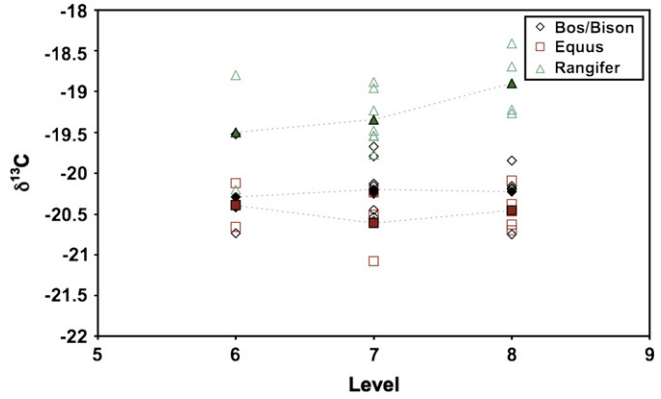

Fig. 2. Plot of the $\delta^{13}C$ values from bone collagen extracted from fauna from three levels at Jonzac.

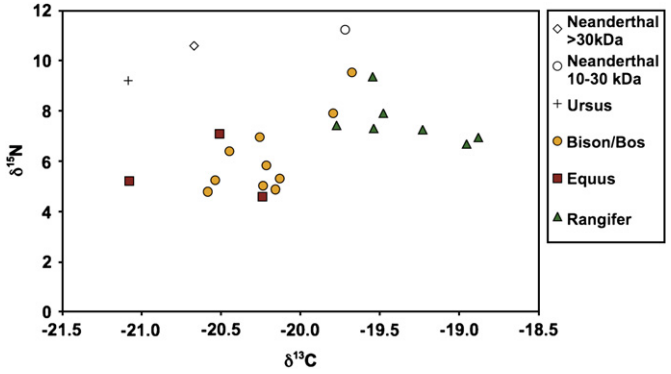

Fig. 4. Plot of the Neanderthal tooth collagen and animal bone collagen $\delta^{13}C$ and $\delta^{15}N$ values from Layer 7 at Jonzac.

The herbivores from the site plot generally as expected, with a clear C_3 terrestrial signal for most of the bovids and horses. The reindeer samples have a shifted $\delta^{13}C$ value, which is commonly observed; it is most likely due to the consumption of lichens, which have unusual (i.e., less negative) $\delta^{13}C$ values compared to most C_3 plants (Beazley et al., 2002; Batts et al., 2004). There are two unusual results—a reindeer and a bovid with quite elevated $\delta^{15}N$ values. These individuals may be from another, more arid, region, where the baseline $\delta^{15}N$ values were higher than they were in the region of late Pleistocene Jonzac. Herbivores with elevated $\delta^{15}N$ values have been observed in arid regions (i.e., Heaton et al., 1986; Ambrose, 1993; Schwarcz et al., 1999; Thompson et al., 2005), and perhaps the specimens analyzed here are from a colder and much drier region.

The *Ursus* sample has a strongly carnivorous $\delta^{15}N$ signal with a more negative $\delta^{13}C$ value than most of the other fauna. The $\delta^{15}N$ value for the *Ursus* sample indicates the consumption of animal protein from species with $\delta^{15}N$ values similar to those for the bovids and horses from the site. However, the $\delta^{13}C$ value is too negative to be explained by the consumption of these species, and instead points to the consumption of a single species with a $\delta^{13}C$ values of approximately −22%. We did not measure any species that has this value, so we cannot suggest a possible candidate. Alternatively, this value may indicate a mix of protein sources, with some consumed species, such as freshwater fish, with more negative $\delta^{13}C$ values of less than −23% and the herbivores that we measured here (Dufour et al., 1999; Müldner and Richards, 2005).

The isotopic values of two of the fractions (>30 kDa and 10–30 kDa) of the collagen extracted from the Neanderthal tooth from Level 7 and faunal bone collagen isotopic values from the same level are plotted in Fig. 4. There is a slight difference in $\delta^{15}N$ values between the two collagen fractions for the Neanderthal and a larger difference in the $\delta^{13}C$ values. Our interpretation of the difference in $\delta^{13}C$ values between the two fractions is that the >30 kDa fraction contains some slight carbon contamination, most likely from soil humics, which resulted in the higher C:N ratio of 3.6 (although this is still considered an acceptable value for collagen). The $\delta^{13}C$ value of the >30 kDa fraction is shifted towards the humics/soil $\delta^{13}C$ values of ca. −30%, as compared to the 10–30 kDa fraction, supporting the idea of some humic contamination in this fraction. The 10–30 kDa fraction has a C:N ratio and %C and %N closer to modern collagen, and it is therefore likely to be the more accurate result. However, we have plotted both values to highlight the differences between the different fractions and to point out that the values are close enough,

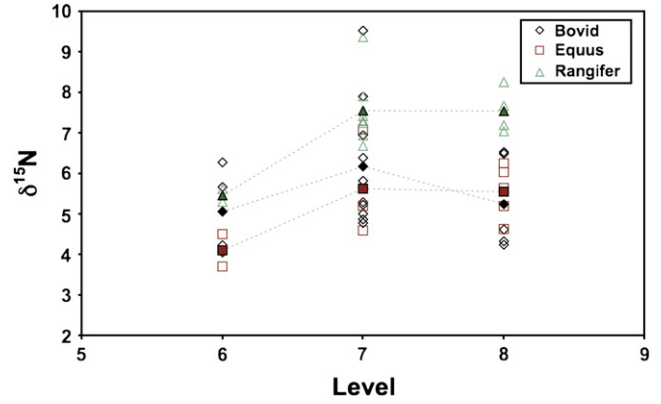

Fig. 3. Plot of the $\delta^{15}N$ values from bone collagen extracted from fauna from three levels at Jonzac.

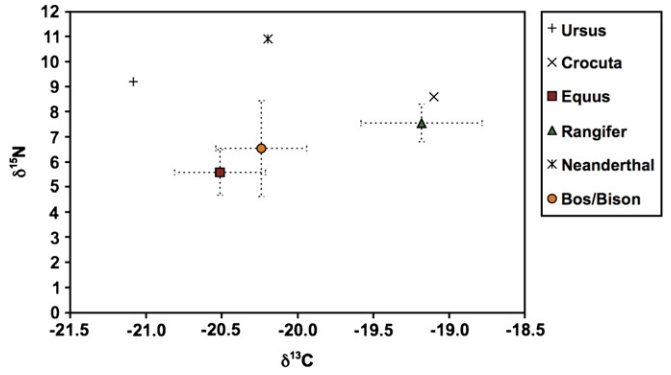

Fig. 5. Plot of average Neanderthal (combined >30 kDa and 10–30 kDa fractions) and animal bone collagen $\delta^{13}C$ and $\delta^{15}N$ values from Levels 7 and 8 at Jonzac.

Table 3
Isotopic results of adult European Neanderthals

Specimen	Country	$\delta^{13}C$	$\delta^{15}N$	Age	Source
Scladina 4A-2	Belgium	−19.9	10.9	ca. 80–130 ka	Bocherens et al., 1999
Scladina 1B-4	Belgium	−21.2	11.8	ca. 40 ka	Bocherens et al., 2001
Spy	Belgium	−19.8	11.0	ca. 35–40 ka	Bocherens et al., 2001
Les Pradelles 9	France	*−20.2*	*9.3*	ca. 40–45 ka	Bocherens et al., 2001
Les Pradelles 10	France	−19.1	11.6	ca. 40–45 ka	Fizet et al., 1995
Les Pradelles M300	France	−19.1	11.5	ca. 40–45 ka	Bocherens et al., 2005
Les Pradelles M400	France	−19.5	11.4	ca. 40–45 ka	Bocherens et al., 2005
Les Pradelles M100	France	*−21.8*	*8.4*	ca. 40–45 ka	Bocherens et al., 2005
St. Césaire	France	−19.8	11.4	OIS 3	Bocherens and Drucker, 2003
Les Rochers-de-Villeneuve	France	−19.0	11.6	ca. 45 ka	Beauval et al., 2006
Jonzac	France	−19.7	11.2	ca. 40 ka	This study
Vindija 207	Croatia	−19.5	10.1	ca. 28–29 ka	Richards et al., 2000
Vindija 208	Croatia	−20.5	10.8	ca. 28–29 ka	Richards et al., 2000

The Jonzac result is from the 10–30 kDa collagen fraction extracted from the Jonzac tooth. Results in italics are from collagen samples with low %C and %N, which indicate poorly preserved collagen (Les Pradelles M100), or from samples where those criteria were not measured (Les Pradelles 9). The data from these two samples are not considered in this paper, following similar practice of the researchers who produced these original data (Bocherens et al., 2005).

especially in $\delta^{15}N$, so as to not alter the interpretation of the values in relation to the other fauna from the site.

Discussion

Based on the faunal isotopic data from Level 7, we interpret the Neanderthal isotopic result as indicating a diet in which protein came mainly from large herbivores, such as bovids and horses. Based on the $\delta^{13}C$ value, reindeer do not appear to have been a major source of dietary protein (although they may have been occasionally consumed). Currently, we cannot further refine the identification of the most likely source of dietary protein, but it is clear that plant foods were not a significant component of dietary protein.

As there is little difference between the isotopic values of fauna from Level 7 and 8, we combined the results in Fig. 5 to compare with the Neanderthal value. For this plot we combined the isotopic results for the >30 kDa and 10–30 kDa fraction from the Neanderthal tooth. We have also included a *Crocuta* specimen from Level 8 for comparison to the Neanderthal. As can be seen, the conclusions about the diet of the Neanderthal using only the fauna from Level 7 still hold, and the Neanderthal remains a top-level carnivore, with the most likely source of dietary protein being from bovids and horses. Interestingly, the hyena plots close to the reindeer, perhaps indicating that there were different dietary niches in this ecosystem, with hyenas focusing more on reindeer during this time period. However, it should be noted that this is a preliminary interpretation based on a single individual and the existing isotope data. The hyena isotopic values from Jonzac ($\delta^{13}C = -19.1\%$, $\delta^{15}N = 8.6\%$) are very similar to those reported by Bocherens et al. (2005) for the site of Les Pradelles ($\delta^{13}C = -19.3 \pm 0.3\%$, $\delta^{15}N = 9.3 \pm 0.5\%$, $n = 5$). Indeed, in their study, Bocherens et al. (2005) also concluded that, based on the isotopic evidence, reindeer were likely a key food resource for hyena.

It should be noted that most of the previous isotopic studies of Neanderthals have used bone instead of teeth for isotopic analysis. Unlike bone, tooth dentine likely does not alter over a lifetime, and therefore it reflects a specific period of time of formation. Therefore, the isotopic data from this Neanderthal premolar do not reflect the lifetime average, but instead the diet at the ages of later childhood/early adolescence.

Our isotopic results for the Jonzac Neanderthal are compared to the those reported for other European Neanderthals in Table 3. The isotopic values are remarkably similar for all of the Neanderthals, and in all cases, the authors of the various studies concluded, as we have for Jonzac, that the main source of dietary protein was animal protein, likely from large herbivores. In no case do we see isotopic evidence for the significant consumption of aquatic (marine or freshwater) protein, as has been observed from Gravettian humans in Europe (Richards et al., 2001; Pettitt et al., 2003). The results of our isotopic study of the Jonzac Neanderthal therefore support the emerging picture from isotopic studies that Neanderthals have a similar dietary adaptation over a wide range of environments and over a relatively long period of time.

Summary and conclusions

We reported here the carbon and nitrogen isotope results from collagen extracted from a Neanderthal tooth and bone from various species of fauna from the site of Jonzac. By comparing the isotopic results from the Neanderthal with contemporary fauna from the site, we conclude that the Neanderthal obtained its dietary protein mainly from large herbivores, namely bovids and horses. The Neanderthal isotopic result matches well with previously published results for Neanderthals from France, Belgium, and Croatia and adds to the emerging picture of a conservative and clearly successful dietary adaptation in Neanderthals of hunting large herbivores. Clearly, as this research progresses, we need to have more Neanderthal results from different environments, especially coastal regions, to determine if Neanderthal diets, as determined by stable isotope analysis, are really this similar throughout Europe in the middle Pleistocene.

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