

CHAPTER 8

DIETARY COMPETITION BETWEEN NEANDERTHALS AND MODERN HUMANS: INSIGHTS FROM STABLE ISOTOPES

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***Abstract.** Carbon and nitrogen isotopic abundances in mammalian bone collagen directly reflect those of the dietary protein averaged over a period of several years. The isotopic signatures of collagen preserved in fossil bone provide direct information on the type of plants consumed by herbivores, as well as on the potential prey consumed by predators. Numerous Upper Pleistocene humans have been investigated using this approach, including Middle Palaeolithic Neanderthals, Neanderthals from the transition between the Middle and Upper Palaeolithic, as well as early Upper Palaeolithic modern humans. All studied Neanderthals present a diet rich in proteins from open environment herbivores. Neanderthals from the Middle to Upper Palaeolithic transition do not exhibit any significant deviation from this pattern. The currently available isotopic data point to a similar diet for Neanderthals and early Upper Palaeolithic modern humans. This diet was based primarily on proteins from open environment herbivores. In areas where they coexisted, both hominids would have been in direct dietary competition. Cave bear and brown bear present another case of two related large mammal species with large dietary breadth coexisting in Upper Pleistocene Europe. In contrast with the situation for humans, the available data for cave and brown bears indicate distinctive dietary niches as well as a temporal and spatial coexistence throughout much of the Upper Pleistocene.*

INTRODUCTION

The possibility of dietary competition between Neanderthals and anatomically modern humans in western Europe between 40,000 and 25,000 years BP is a key factor in the debate about the cause of Neanderthal extinction (e.g., d'Errico and Sanchez Goñi 2004; Finlayson et al. 2004; Stewart 2004). Indeed, environmental change is considered an unlikely cause for Neanderthal extinction since this hominid group had witnessed several major environmental shifts during its history as the only human species in Europe. Moreover, the chronological coincidence between the first appearance of anatomically modern humans and the last occurrence of Neanderthals in Europe is intriguing. It is thus generally argued that a superior ability of anatomically modern humans in acquiring food resources, owing to their more efficient cognitive, technological, and linguistic competence relatively to Neanderthals eventually led to the competitive exclusion of the latter from Europe, and from the surface of the Earth (e.g., Stewart 2004).

Many field observations of mammals illustrate the fact that two closely related species do not usually manage to coexist on the long term if they compete for the same dietary resources. One common situation is the invasion of one species' territory by a closely related species with similar dietary habits. Such a situation is experienced by coyotes *Canis latrans* in northwestern Montana (USA), which are now competing with recolonizing wolves *Canis lupus* (Arjo et al. 2002). In this case, both canid species should be able to coexist owing to the ability of coyotes to exploit prey species different than those exploited by wolves, such as small mammals (Arjo et al. 2002). In contrast, the invasion of the American grey squirrel *Sciurus carolinensis* in the territory of the European red squirrel *Sciurus vulgaris* leads to the displacement and local extinction of the European species due mainly to food competition between both squirrel species (e.g., Gurnell and Pepper 1993; Bertolino and Genovesi 2003).

During the last two decades, stable isotopic ecology has been used as a powerful tool to decipher trophic relationships, especially between mammal species in case of dietary competition (e.g., Jacoby et al. 1999; Hobson et al. 2000; Lavin et al. 2003). A significant application of this approach is the case of the two bear species dwelling nowadays in northwestern North America, i.e., brown bear *Ursus arctos* and black bear *Ursus americanus* (Jacoby et al. 1999; Hobson et al. 2000). These investigations showed that when both species coexist in a given area, their stable isotopic signatures are different due to varying proportions of different dietary resources, such as vegetation versus animal food resources, or salmon versus terrestrial food items. In Alaska, black bear isotopic signatures indicate consumption of salmon when brown bears are absent, ; but differences in the isotopic signatures of coexisting black bears and brown bears indicate a resource partitioning, with black bears consuming no salmon in contrast to brown bears (Jacoby et al. 1999).

Since organic matter such as bone collagen can survive in Upper Pleistocene fossil remnants, this approach could be used for ancient mammals, such as brown bears and short-faced bears *Arctodus simus* in Alaska and the Yukon (Barnes et al. 2002). The collagen isotopic signatures of these bears showed that brown bears were avoiding direct dietary competition with the carnivorous short-faced bears by sticking mostly to plant food, and that they shifted to a more carnivorous diet after the extinction of the carnivorous bear species. Thus, isotopic data showed that the coexistence of both bear species in Alaska and the Yukon was possible owing to a dietary partitioning of these species.

This chapter assesses dietary flexibility of Neanderthals and dietary competition between the last Neanderthals and the first anatomically modern humans in Europe around 40–30 kyr BP by directly comparing the trophic ecology of these two hominids using stable isotope signatures in fossil collagen. In parallel, the same approach will be used to compare the dietary ecology of two species of bears occurring in Europe at the same period, brown bear and cave bear *Ursus spelaeus*. Indeed, this pair of bear species exhibits several similarities with the pair of human species: (1) a large dietary breadth including the same type of plant material, such as fruits and tubers, animal food items, such as small and large terrestrial mammals, and marine food resources; (2) two very closely related species in each pair with a phylogenetic split between the respective species of each pair that occurred at the same period, around 800,000 years ago; and (3) both pairs witness the extinction of one of the species between 30,000 and 10,000 years ago (i.e., Neanderthal and cave bear), whereas the other species survives until the modern era (i.e., modern human and brown bear). However, one major difference between the carnivore and the primate pair of species is the coexistence of both bear species in Europe for dozens of thousands of years whereas the human species

did not coexist for long after the arrival of modern humans. It is thus worth comparing both situations, coexistence or exclusion of closely related species, in view of trophic ecology as deduced from bone stable isotope geochemistry.

PRINCIPLES AND CONDITIONS OF USE OF CARBON AND NITROGEN STABLE ISOTOPIC ABUNDANCES IN COLLAGEN FOR PALAEO-TROPHIC RECONSTRUCTIONS

The isotopic signatures ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$)¹ of a predator reflect those of its average prey in a predictable way (e.g., Bocherens and Drucker 2003a). The $\delta^{13}\text{C}$ values of a plant-eater bone collagen closely monitor those of the consumed plants, whereas those of a predator bone collagen are 0.8 to 1.3 ‰ more positive than those of its average prey collagen. Different types of plants exhibit variable $\delta^{13}\text{C}$ values due to the use of different inorganic carbon pools and variations in the fractionation of carbon stable isotopes during photosynthesis under different environmental conditions (e.g., Tieszen 1991; Heaton 1999). In terms of categorizing plants according to their $\delta^{13}\text{C}$ values in western European modern and Pleistocene environments, it is possible to distinguish between plants growing under a dense canopy forest and plants growing in open conditions (i.e., top of the canopy, steppe, grassland, and tundra), the former ones having more negative $\delta^{13}\text{C}$ values than the latter ones, while freshwater plants exhibit highly variable $\delta^{13}\text{C}$ values. The $\delta^{15}\text{N}$ values of a mammal bone collagen are systematically enriched relative to those of its diet, by 3 to 5 ‰ (see review in Bocherens and Mariotti 2002). Therefore, the $\delta^{15}\text{N}$ values of a mammal bone collagen depend on its trophic level and on the $\delta^{15}\text{N}$ values at the basis of the trophic web it belongs to. Moreover, some environmental parameters such as aridity, temperature, and soil microbiological activity have an influence on plant $\delta^{15}\text{N}$ values (e.g., Bocherens and Mariotti 2002; Drucker et al. 2003; Richards and Hedges 2003; Stevens and Hedges 2004). Using both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of bone collagen thus allows deciphering the trophic relationships of Upper Pleistocene mammals, using $\delta^{13}\text{C}$ values as tracers of the type of plants at the beginning of the food web, and using $\delta^{15}\text{N}$ values to test the predator-prey relationships of predators and their potential prey.

Before interpreting carbon and nitrogen isotopic values measured on collagen extracted from fossil bones, one must make sure that the conditions of use are respected. Three conditions must be fulfilled: 1) high degree of chemical integrity of the extracted collagen, 2) firm knowledge of the ontogenic stage of the studied specimens, and 3) knowledge of the trophic context of the humans relatively to contemporaneous mammals. These conditions are summarized in table 1.

Table 1. Summary of the conditions of use of collagen stable isotopic signatures for palaeotrophic reconstructions.

Criteria	Objectives	Recommendations
Chemical integrity of collagen	to guarantee that measured carbon and nitrogen isotopic signatures are not significantly modified by post-mortem alteration	exclude “collagen” with atomic C:N ratio outside a 2.9–3.6 range or with %N < 5 (DeNiro 1985; Ambrose 1990)
Ontogenic stage	to take into account possible nursing effects on nitrogen isotopic signature (e.g., Fogel et al. 1989; Katzenberg and Pfeiffer 1995)	avoid unweaned specimens (e.g., children < 5 years old) and teeth that erupted during youth (e.g., Bocherens and Mariotti 1997)
Trophic context	to take into account possible isotopic shifts at each trophic level through time or space (e.g., Drucker et al. 2003; Richards and Hedges 2003; Stevens and Hedges 2004)	compare isotopic signatures of ancient humans with those of herbivores and carnivores from the same region and chronological context (Drucker and Bocherens 2004)

ISOTOPIC DATA ON NEANDERTHAL AND EARLY MODERN HUMANS IN EUROPE

Review of the Available Isotopic Data

Since 1991, when the first investigation of the isotopic signature of collagen in a Neanderthal was performed (Bocherens et al. 1991), numerous data of this kind have been gathered on European Upper Pleistocene hominids (e.g., Bocherens et al. 1999, 2001; Richards et al. 2000, 2001; Bocherens and Drucker 2003*b*; Pettitt et al. 2003; Drucker and Henry-Gambier 2005). We will consider here all the European Neanderthal specimens for which isotopic data are available, and the oldest modern humans in Europe, chronologically as close as possible to the Middle to Upper Palaeolithic transition (fig. 1; table 2). Since the youngest Neanderthals directly dated so far are around 28,000 year BP old (Smith et al. 1999), and the oldest anatomically modern humans dated in Europe are around 36,000 years BP old (Trinkaus et al. 2003; Conard et al. 2004), this time span is the one under scrutiny here for the supposed overlap between Neanderthals and modern humans in Europe. A careful examination of the available data did not allow us to include some of the published isotopic data which did not meet at least one of the requirements presented previously (table 1).

Neanderthals

Following the criteria of chemical integrity of collagen, the first Neanderthal specimen from Les Pradelles will be excluded from the discussion. Indeed, the chemical integrity of its collagen was considered sufficient at the time of publication, based on an amino acid pattern similar to that of fresh collagen (Bocherens et al. 1991). However, the deviation observed

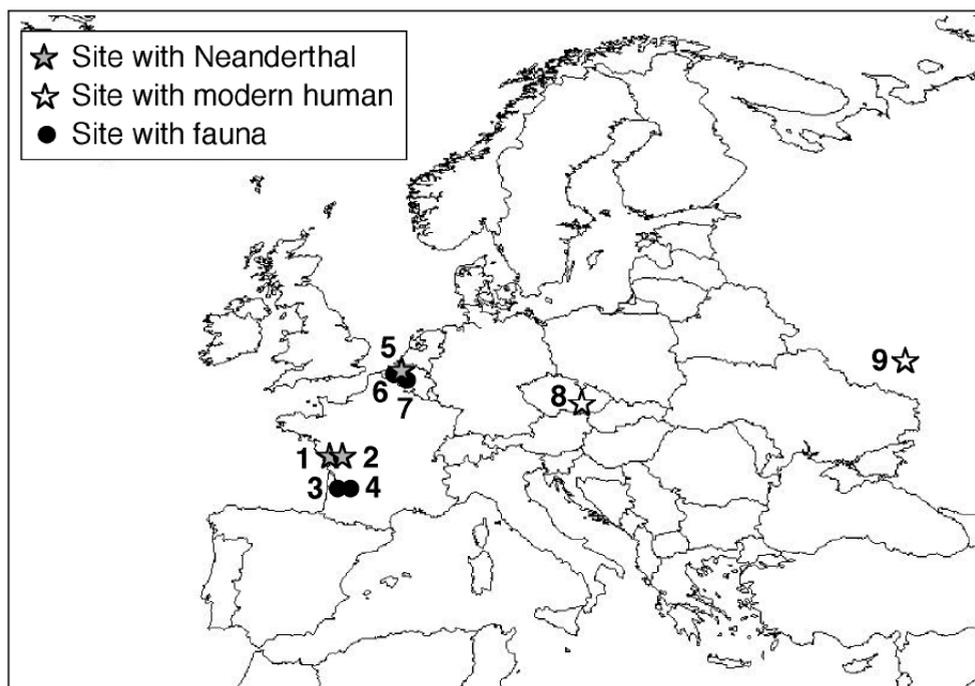


Fig. 1. Location map of the sites from which the studied material originates. Keys for numbers are the following: 1) Saint-Césaire; 2) Les Pradelles; 3) Camiac; 4) La Berbie; 5) Spy; 6) Sladina; 7) Goyet; 8) Brno, Dolní Věstonice; 9) Kostenki.

between the patterns suggests that some isotopic shift may have occurred post-mortem. It is thus safer not to consider these data for further discussion.

As far as the ontogenic stage is concerned, the collagen of two Neanderthal children has been isotopically analysed. The Neanderthal child from Engis (Belgium) is only 5–6 years old based on the dental eruption pattern (Tillier 1983), and the nitrogen isotopic signature of a child this age may still be affected by its consumption of mother's milk if weaning occurred later than for most modern human populations, or if the growth rate of Neanderthal children was faster than those of modern humans (Bocherens et al. 2001). Thus, this specimen will not be discussed in palaeodietary terms due to the uncertainty regarding his nursing status. Another Neanderthal child is the specimen from layer 4A in Sladina Cave. This specimen is aged around 11 years (Toussaint et al. 1998), thus old enough to have erased the nursing isotopic signal and therefore acceptable for palaeodietary reconstruction.

Some interesting specimens could not be interpreted due to the lack of a reliable trophic context. This is the case for the Neanderthals from Vindija. Indeed, only one deer from the same layer (G1) than the human specimens had its isotopic signatures measured (Richards et al. 2000). The few other members of the fauna from the same site are from an older stratigraphical layer, layer G3 (Richards et al. 2000). Since this layer is more than 12,000 years

Table 2. Summary of the Neanderthal and early modern human specimens analysed for their isotopic signatures in Europe. Only specimens with a reliability of "OK" are discussed in terms of palaeodiets.

No analysis (No excavation)	Site	Age	Species	Piece	Chemical integrity	Ontogeny	Trophic context	Reliability	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	reference
27801	Les Pradelles (Marillac-le-Franc, Charente, France)	OIS3	Neanderthal	skull	?	+	+	no	-20.2	9.3	Bocherens et al. (1991)
64801	Les Pradelles (Marillac-le-Franc, Charente, France)	OIS3	Neanderthal	skull	+	+	+	OK	-19.1	11.6	Fizet et al. (1995)
RPB7000	La Roche-a-Pierrot (Saint-Césaire, Charentes-Maritimes, France)	OIS3	Neanderthal	fibula	+	+	+	OK	-19.8	11.4	Bocherens and Drucker (2003)
MT500 (SCLA-1B 4)	Scladina Cave (Sclayn, Belgium)	OIS5b?	Neanderthal	phalanx	+	+	-	no	-21.2	11.8	Bocherens et al. (2001)
SCI8800 (SCLA-4A 2)	Scladina Cave (Sclayn, Belgium)	OIS5c	Neanderthal	skull	+	+	+	OK	-19.9	10.9	Bocherens et al. (1999)
MT100 (Engis 2)	Awirs Cave (Belgium)	OIS3	Neanderthal	skull	+	-	+	no	-19.6	12.6	Bocherens et al. (2001)
MT200 (SPY OMO 1)	Spv (Bêche-al-Roche) Cave (Belgium)	OIS3	Neanderthal	scapula	+	+	+	OK	-19.8	11.0	Bocherens et al. (2001)
VI-207	Vindija Cave (Croatia)	OIS3 (29,080 ± 400 BP)	Neanderthal	mandible	+	+	-	no	-19.5	10.1	Smith et al. (1999)
VI-208	Vindija Cave (Croatia)	OIS3 (28,020 ± 400 BP)	Neanderthal	parietal	+	+	-	no	-20.5	10.8	Smith et al. (1999)
ETH-19660 (NN 1)	Neander Valley (Germany)	OIS3 (39,240 ± 670 BP)	Neanderthal	humerus	+?	+	-	no	-20.0 (±1.2)*	n.d.	Schmitz et al. (2002)
ETH-19661 (NN 4)	Neander Valley (Germany)	OIS3 (40,360 ± 760 BP)	Neanderthal	tibia	+?	+	-	no	-18.8 (±1.2)*	n.d.	Schmitz et al. (2002)
ETH-20981 (Nean 1)	Neander Valley (Germany)	OIS3 (39,900 ± 620 BP)	Neanderthal	humerus	+?	+	-	no	-19.6 (±1.1)*	n.d.	Schmitz et al. (2002)
OxA-11711 (Oase 1)	Peștera cu Oase (Romania)	OIS3 (>35,200 BP)	Modern Human	mandible	+	+	-	no	-18.7	n.d.	Trinkaus et al. (2003)
GrA-22810 (Oase 1)	Peștera cu Oase (Romania)	OIS3 (34,290 BP +970 -870)	Modern Human	mandible	+	+	-	no	-19.0	n.d.	Trinkaus et al. (2003)
OxA-7073 (1)	Kostenki (Russia)	OIS3 (32,600 ± 1100 BP)	Modern Human	?	+	+	(+)	OK	-18.2	15.3	Richards et al. (2001)
OxA-8292 (35)	Dolní Vestonice (Czech Republic)	OIS3 (22,840 ± 200 BP)	Modern Human	?	+	+	+	OK	-18.8	12.3	Richards et al. (2001)
OxA-8293 (2)	Erno-Francouzka (Czech Republic)	OIS3 (23,680 ± 200 BP)	Modern Human	?	+	+	+	OK	-19.0	12.3	Richards et al. (2001)

*The comparatively large standard-deviation for the $\delta^{13}\text{C}$ values of Neander Valley specimens is due to a different analytical technique for these specimens.

older than the one that yielded the Neanderthal specimens (Ahren et al. 2004), the fauna from this layer cannot be directly compared to the Neanderthal specimens. A palaeodietary reconstruction of the diet of Vindija Neanderthals' diet is thus pending isotopic data on contemporary herbivorous and carnivorous fauna. Another specimen that is lacking proper faunal context is Neanderthal specimen SC-1B from Scladina (Bocherens et al. 2001). This specimen was formerly believed to be from layer 1B from this cave, and therefore compared to fauna from this layer (Bocherens et al. 2001). However, a recent stratigraphical reevaluation indicated that it comes from layer 3 (D. Bonjean, personal communication, 2003). An isotopic study of the fauna from this layer is currently in progress, and it will allow a palaeodietary interpretation of the isotopic data obtained on this specimen.

Some Neanderthal specimens from Neander Valley had their $\delta^{13}\text{C}$ values measured as well in the process of their radiocarbon dating (Schmitz et al. 2002). However, these data cannot be used since the $\delta^{13}\text{C}$ values were not measured with an accurate enough technique, and the $\delta^{15}\text{N}$ values are missing as is the trophic context.

The isotopic data obtained for other Neanderthals could be compared with of those of contemporary fauna from the same site (layer 4A in Scladina Cave, Les Pradelles) or from contemporary fauna from neighbouring sites (Saint-Césaire Neanderthal compared to fauna from Saint-Césaire, La Berbie, and Camiac; Spy Neanderthal compared to fauna from layer 1A in Scladina Cave).

Modern Humans

The specimen Kostenki 1 is the only modern human directly dated from the transition time span and with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values available (Richards et al. 2001). This case is, however, delicate, since no isotopic data on fauna from the same area and the same age is available yet. Nevertheless, isotopic data from contemporaneous fauna could be found in other regions of Europe, i.e., Great Britain and southwestern France (Drucker and Bocherens 2004).

Other modern human specimens from the early Upper Palaeolithic in Europe are not suitable for isotopic palaeodietary determination so far. The recently discovered specimen from Peștera cu Oase (Romania) is lacking $\delta^{15}\text{N}$ values, as well as a reliable trophic context (Trinkaus et al. 2003). Mladeč modern human specimens have not been directly dated seemingly due to lack of collagen (Svoboda et al. 2002), a situation that also precludes stable isotopic investigations. Moreover, several key modern human specimens that were traditionally considered of Aurignacian age, such as the Cro-Magnon, Vogelherd, Velika Pećina, Zlatý kůn, and Svitavka specimens, have been recently dated and the results were younger than previously thought (Smith et al. 1999; Henry-Gambier 2002; Svoboda et al. 2002; Conard et al. 2004). Although collagen could be extracted from most of these specimens, their young age renders them irrelevant for the present study.

A few specimens younger than the Middle/Upper Palaeolithic transition from the Czech Republic have been considered as a comparison for anatomically modern humans posterior to the extinction of Neanderthals in Europe (Richards et al. 2001). The isotopic data obtained for these modern human specimens could be compared with of those of contemporary fauna from neighbouring sites (Brno and Dolní Věstonice modern human isotopic data from Richards et al. 2001, compared to fauna from Milovice from Ambrose 1998).

TROPHIC RECONSTRUCTION OF NEANDERTHALS AND ANATOMICALLY MODERN HUMANS

Trophic “Rigidity” of Neanderthals?

The isotopic data available for Neanderthals suggests that no significant dietary change occurred between individuals dwelling under more forested and more open environments: a subsistence pattern based on open environment herbivores continues even under forested conditions, such as during OIS 5c in Scladina Cave (Bocherens et al. 1999; Bocherens and Drucker 2003b). This is not to say that Neanderthals were not affected by environmental changes. The changes in environment that occurred in Europe from 150 to 30 kyr BP coincide with changes in Middle Palaeolithic lithic industries and possibly with population bottlenecks (e.g., Jöris 2002). It is possible that the dietary flexibility of Neanderthals varied through time, and this is a hypothesis that can now be tested using bone stable isotope composition.

Neanderthals and Modern Humans during the Middle to Upper Palaeolithic Transition

The Middle to Upper Palaeolithic transition seems to correspond to a shift in the $\delta^{15}\text{N}$ values in human bones, with higher $\delta^{15}\text{N}$ values in the first anatomically modern humans relatively to older Neanderthals (fig. 2). This pattern had been initially interpreted as reflecting the consumption of freshwater resources by early modern humans in Europe in comparison with the $\delta^{15}\text{N}$ values of Mesolithic humans from the Danube Valley (Richards et al. 2001). However, this interpretation did not take into account the shifts in $\delta^{15}\text{N}$ values that seem to occur in the terrestrial food webs at that time (Drucker and Bocherens 2004). When compared to the isotopic signatures of contemporaneous herbivorous and carnivorous species, the $\delta^{15}\text{N}$ values of the late Neanderthals and the early anatomically modern humans are very similar (fig. 2). In a situation with different prey species exhibiting different isotopic signatures, as it was the case around 40–30 kyr ago in Europe (Bocherens 2003), predators consuming different prey exhibit different isotopic signatures (Drucker and Bocherens 2004). In such a context, two predators with similar isotopic signatures are most likely to have also consumed similar prey. Thus, the last Neanderthals and the early modern humans from Europe exhibiting similar $\delta^{15}\text{N}$ values relative to contemporary ungulates and carnivores, such as hyaena and wolf, were most probably consuming a similar combination of prey species. In the case of Neanderthals, a reliance on large ungulate species, such as mammoth and woolly rhinoceros, is suggested by a quantitative reconstruction of prey proportions based on a mathematical model (Drucker and Bocherens 2004). Although the skeletal remains of these species are usually not very numerous in Middle Palaeolithic sites, the contribution of these species as meat weight can be high since one individual of these megaherbivores can yield much more meat than several individuals of a smaller prey, such as deer (e.g., Patou-Mathis 1993). No such reconstruction could be performed for early modern humans yet, but their $\delta^{15}\text{N}$ value more positive than that of wolf seems to reflect a similar diet including a significant proportion of large herbivores such as woolly mammoth (Drucker and Bocherens 2004).

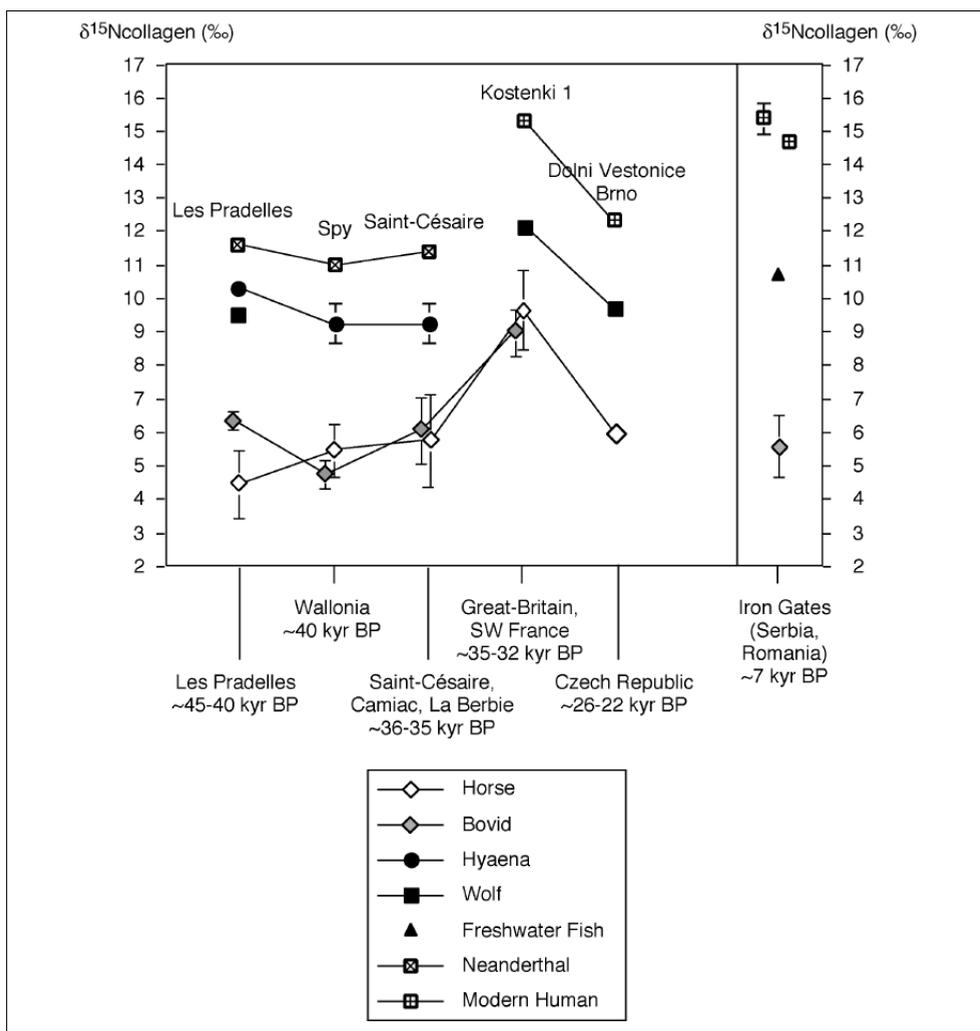


Fig. 2. Nitrogen isotopic signatures of Neanderthals and anatomically modern humans around the Middle to Upper Palaeolithic transition in Europe, relative to those of herbivores (horses, bovids), carnivores (hyaenas, wolves). These isotopic signatures are compared to those of Mesolithic modern humans from the Danube Valley (modified from Drucker and Bocherens 2004).

COMPETITION BETWEEN CLOSELY RELATED PREDATORS: THE CASE OF BEARS IN EUROPE

Around 100 kyr BP, brown bears and cave bears from layer 4A of Scladina Cave (Belgium) exhibit different carbon and nitrogen isotopic signatures, which suggest a more forested habitat and more vegetarian diet for cave bear than for brown bears (Bocherens et al. 1999).

Around 40–36 kyr BP, brown bears and cave bears exhibit different $\delta^{15}\text{N}$ values in two Belgian caves, Goyet (level B4) and Scladina (layer 1A) (fig. 3). The low $\delta^{15}\text{N}$ values of cave bear indicate a purely vegetarian diet for this species. Such a pattern has been recognized for all cave bear populations studied so far, from Spain, Slovenia, Croatia, France, Belgium, and the Alps (Bocherens et al. 1994, 1997, 2001; Fernandez-Mosquera 1998; Nelson et al. 1998; Richards et al. 2000; Fernandez-Mosquera et al. 2001). The variable $\delta^{15}\text{N}$ values of brown bears indicate a more varied diet including high proportions of animal proteins, a pattern that has been recognized in Upper Pleistocene Great Britain as well (Bocherens et al. 1995; Richards 2000). Moreover, the $\delta^{13}\text{C}$ values of brown bear collagen are systematically more positive than those measured on cave bear collagen, which also indicates dietary differences between both species (Bocherens et al. 1997, 1999; Richards 2000).

Thus, in contrast to humans, two bear species, brown bear and cave bear, managed to coexist in Europe during the Upper Pleistocene owing to their trophic differences, as demonstrated by the $\delta^{15}\text{N}$ values of their bone collagen. Although closely related, these two species avoided dietary competition while in direct contact and managed to subsist side by side in Europe.

CONCLUSION AND PERSPECTIVES

Were Neanderthals sufficiently flexible in their dietary habits to shift food resources and avoid direct competition with anatomically modern humans? So far, stable isotopes studies suggest that Neanderthals stuck to protein resources based on open-environment large herbivores, even during forested temperate episodes (Bocherens et al. 1999; Bocherens and Drucker 2003*b*). Moreover, the isotopic signatures of the last Neanderthals that are likely to have co-occurred in Europe with anatomically modern humans suggest that they did not change their subsistence habits relatively to their ancestors prior to the arrival of modern humans in Europe. Additional isotopic studies of Neanderthals should allow us to draw a more detailed picture of the evolution of their dietary habits during the the Upper Pleistocene. Unfortunately, such investigations will always be limited by the available material that fulfill the conditions of use of isotopic biogeochemistry. A complementary approach is to study the isotopic signature of the prey consumed by Neanderthals. This should provide direct information on the habitat of these prey on a large chronological and geographical scale with much less limited access to material than direct study of Neanderthal skeletal remains (Bocherens n.d.). More isotopic studies should focus on predators, which can be used as tracers of the terrestrial trophic webs through their isotopic signatures. For instance, the prey of animal predators from layer 4A in Scladina Cave are from forested environments, whereas the Neanderthal specimen exhibits the consumption of open-environment prey (Bocherens et al. 1999). Thus, forest preys were available for the subsistence of the predators, but the Neanderthals do not seem to have made use of them. Dietary competition with other predators may have limited the range of prey available to Neanderthals at this time, and led to dietary partitioning, as was the case for cave bears and brown bears in Europe.

Did Neanderthals and anatomically modern humans actually compete for food resources? Without isotopic measurements of individuals from both species who really lived at the same place and at the same time, this question cannot yet be solved. Isotopic signatures of fossil collagen indicate that the individuals analysed so far from both species across the

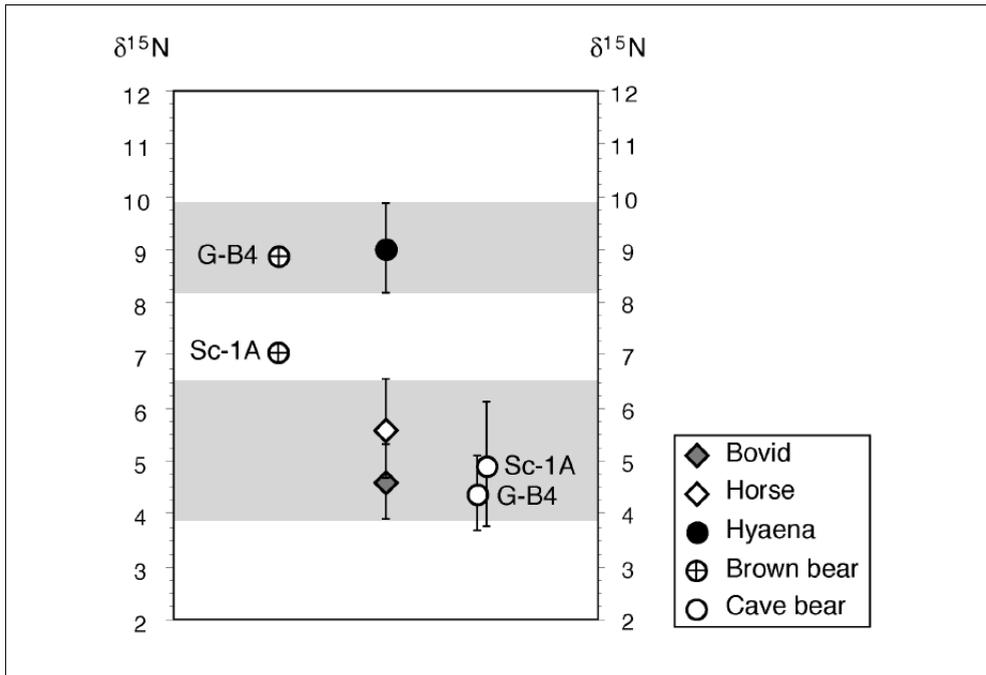


Fig. 3. Nitrogen isotopic signatures of brown bears, cave bears, carnivores (hyaenas), and herbivores (large bovids, horses), from Scladina, layer 1A (Sc-1A) and Goyet, layer B4 (G-B4), dated around 36–40 kyr ¹⁴C BP (Bocherens et al. 1997; Germonpré 2004). Data for Scladina-1A are from Bocherens et al. (1997), data for Goyet-B4 are from Bocherens and Germonpré (unpublished). All data are from bone, except for the brown bear specimen from Scladina, layer 1A (Bocherens et al. 1997). For this specimen, the $\delta^{15}\text{N}$ value of bone is probably around 1 ‰ lower than the $\delta^{15}\text{N}$ value measured on tooth (Bocherens and Mariotti 1997).

Middle-Upper Palaeolithic transition did exploit the same prey species. Although it does not prove dietary competition, these data provide direct evidence for a situation that would lead to dietary competition in case of contact between both hominids.

ENDNOTE

¹ Isotopic abundances are reported as “ δ ” (delta) values, as follows: $\delta\text{EX} = (\text{R}_{\text{sample}}/\text{R}_{\text{standard}} - 1) \cdot 1000$ (‰), where X stands for C or N, E stands for 13 or 15, respectively, and R stands for the isotopic ratios ¹³C/¹²C and ¹⁵N/¹⁴N, respectively. The internationally defined standard is V-PDB for carbon and atmospheric nitrogen (AIR) for nitrogen. Analytical error is typically 0.1 ‰ and 0.2 ‰ for $\delta^{13}\text{C}$ values and $\delta^{15}\text{N}$ values, respectively.

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