Neanderthal diet at Vindija and Neanderthal predation: The evidence from stable isotopes

Michael P. Richards*†, Paul B. Pettitt*‡, Erik Trinkaus§¶‖, Fred H. Smith, Maja Paunović††, and Ivor Karavanić‡‡**

*Research Laboratory for Archaeology and the History of Art, University of Oxford, 6 Keble Road, Oxford OX1 3QJ, United Kingdom; †Department of Archaeology, Simon Fraser University, Burnaby, BC V5A 1S6, Canada; ‡Keble College, Oxford OX1 3PG, United Kingdom; §Department of Anthropology, Campus Box 1114, Washington University, St. Louis MO 63130; ¶Unité Mixte de Recherche 5809 du Centre National de la Recherche Scientifique, Laboratoire d'Anthropologie, Université de Bordeaux I, 33405 Talence, France; **Department of Anthropology, Northern Illinois University, DeKalb, IL 60115; ††Zavod za paleontologiju i geologiju kvartara, Hrvatske akademije znanosti i umjetnosti, Ulica A. Kovačića 5/II, HR-10000 Zagreb, Croatia; and ‡‡Arheološki zavod Filozofskog fakulteta Sveučilišta u Zagrebu, I. Lučića 3, HR-10000 Zagreb, Croatia

Contributed by Erik Trinkaus, April 19, 2000

Archeological analysis of faunal remains and of lithic and bone tools has suggested that hunting of medium to large mammals was a major element of Neanderthal subsistence. Plant foods are almost invisible in the archeological record, and it is impossible to estimate accurately their dietary importance. However, stable isotope (δ^{13}C and δ^{15}N) analysis of mammal bone collagen provides a direct measure of diet and has been applied to two Neanderthals and various faunal species from Vindija Cave, Croatia. The isotope evidence overwhelmingly points to the Neanderthals behaving as top-level carnivores, obtaining almost all of their dietary protein from animal sources. Earlier Neanderthals in France and Belgium have yielded similar results, and a pattern of European Neanderthal adaptation as carnivores is emerging. These data reinforce current taphonomic assessments of associated faunal elements and make it unlikely that the Neanderthals were acquiring animal protein principally through scavenging. Instead, these findings portray them as effective predators.

paleodiet | Croatia | Europe | δ^{13}C | δ^{15}N

Reconstructions of European Neanderthal subsistence strategies have overwhelmingly focused on the specialized hunting and scavenging of herbivores as the predominant method of obtaining food (1–6). These reconstructions are based principally on the analysis of the abundantly preserved faunal remains, supplemented by artifactual evidence of lithic and wood hunting apparatuses, as well as on the relative importance of the faunal biomass in the environments that European Neanderthals occupied during later oxygen isotope stage 5 and especially oxygen isotope stages 4 and 3 of the Late Pleistocene. Understanding Neanderthal diet has implications for understanding Neanderthal land use, social organization, and behavioral complexity. Yet despite the abundant evidence for successful hunting techniques across Neanderthal Eurasia, faunal remains can indicate only hunting or scavenging *episodes*; they cannot tell us about the predominant foods in the diet over the long term.

By contrast, the measurement of the ratios of the stable isotopes of carbon and nitrogen in mammal bone collagen provides an indication of aspects of diet over the last few years of life (7–9). This stable isotope evidence can therefore provide us with *direct* information on Neanderthal diet. This method has been applied to Neanderthal remains from the sites of Marillac, France (10), and Scladina Cave, Belgium (11). These studies, focusing particularly on their high δ^{15}N values, indicated that the Neanderthals measured occupied the top trophic level, obtaining nearly all of their dietary protein from animal sources. In the context of this finding, we undertook stable isotope analyses of the two late Neanderthal specimens from Vindija Cave, in the Hrvatsko Zagorje of northern Croatia [Vi-207 and Vi-208 (12)], and of the fauna with which they were stratigraphically associated.

Vindija Neanderthal and Faunal Specimens. Recently, the Vi-207 and Vi-208 Neanderthal specimens, as well as various other archeological materials from level G_1 of Vindija Cave, Croatia, were submitted for accelerator mass spectrometer radiocarbon dating at the Oxford Radiocarbon Accelerator Unit, University of Oxford (13). The two Neanderthal specimens were dated to 29,080 ± 400 years before present (B.P.) (OxA-8296, Vi-207) and 28,020 ± 360 years B.P. (OxA-8295, Vi-208), making them the youngest directly dated Neanderthal specimens in Europe (13). Because the radiocarbon sample preparation process includes assessments of stable isotopes, in part to control for potential contamination, this analysis also yielded stable isotope profiles for these late archaic humans. Combined with similar data obtained from faunal remains from level G_1 and the older level G_3 of Vindija Cave, this provides a means of assessing the dietary profiles of these Neanderthals.

Stable Isotope Analyses. Mammal bone collagen δ^{13}C and δ^{15}N values reflect the δ^{13}C and δ^{15}N values of dietary protein (14). They furnish a long-term record of diet, giving the average δ^{13}C and δ^{15}N values of all of the protein consumed over the last years of the measured individual's life. δ^{13}C values can be used to discriminate between terrestrial and marine dietary protein in humans and other mammals (15, 16). In addition, because of the canopy effect, species that live in forest environments can have δ^{13}C values that are more negative than species that live in open environments (17). δ^{15}N values are, on average, 2–4‰ higher than the average δ^{15}N value of the protein consumed (18). Therefore, δ^{15}N values can be used to determine the trophic level of the protein consumed. By measuring the δ^{13}C and δ^{15}N values of various fauna in a paleo-ecosystem, it is possible to reconstruct the trophic level relationships within that ecosystem. Therefore, by comparing the δ^{13}C and δ^{15}N values of omnivores such as hominids with the values of herbivores and carnivores from the same ecosystem, it is possible to determine whether those omnivores were obtaining dietary protein from plant or animal sources.

Vindija Neanderthal and Faunal Isotope Values. Collagen was extracted from the two Neanderthal specimens from level G_1 of Vindija Cave and from various faunal remains from level G_1 and the older level G_3 according to standard collagen extraction procedures; the Neanderthal specimens were extracted according to the methods outlined in Law and Hedges (19), and the faunal specimens were extracted according to the procedure outlined in Richards and Hedges (16). The collagen extracts varied in quality, and only those samples that had acceptable collagen attributes were used. These attributes are based on

‖To whom reprint requests should be addressed. E-mail: trinkaus@artsci.wustl.edu.

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

Article published online before print: *Proc. Natl. Acad. Sci. USA*, 10.1073/pnas.120178997. Article and publication date are at www.pnas.org/cgi/doi/10.1073/pnas.120178997

ANTHROPOLOGY

Table 1. Bone collagen $\delta^{13}C$ and $\delta^{15}N$ values of Neanderthals and associated fauna from Vindija Cave, Croatia

Sample	Species	Level	$\delta^{13}C$	$\delta^{15}N$	C:N	% Coll.	% C	% N
Vi-207	Neanderthal	G_1	−19.5	10.1	3.2	6.5	37.1	13.5
Vi-208	Neanderthal	G_1	−20.5	10.8	3.6	4.2	36.1	11.7
V1	*Bos/Bison* spp.	G_3	−20.4	5.3	3.2	11.4	18.8	6.8
V3	Cervid	G_1	−20.3	5.2	3.2	16.1	20.4	7.4
V4	*Ursus spelaeus*	G_3	−21.1	1.3	3.3	29.1	14.4	5.1
V5	*Ursus spelaeus*	G_1	−20.7	1.5	3.3	12.6	18.8	6.7

$\delta^{13}C$ values are measured relative to the Vienna Pee Dee Belemnite standard, and $\delta^{15}N$ values are measured relative to the ambient inhalable reservoir standard. "% Coll." is the mass of freeze-dried "collagen" produced as a percentage of the starting total bone mass. % C and % N are the percent amounts of carbon and nitrogen measured in the mass spectrometer compared with the starting mass of extracted collagen. Measurement errors on the $\delta^{13}C$ values are ±0.3‰; errors on the $\delta^{15}N$ values are ±0.4‰.

values determined by DeNiro (20) and Ambrose (21) and used by the majority of stable isotope researchers and radiocarbon dating labs. The acceptable values are a C:N ratio between 2.9 and 3.6, "percent collagen" >1%, and %C and %N in the extracted collagen of >13% for carbon and >5% for nitrogen. These collagen attributes allow us to identify and exclude collagen that is heavily degraded or contaminated. This is in contrast to stable isotope measurements of bioapatite in bone mineral and enamel, where no such criteria exist. The stable isotope values and various collagen attributes are given in Table 1; based on these, we are confident that the collagen $\delta^{13}C$ and $\delta^{15}N$ values reported here are robust and reflect the organisms' original collagen $\delta^{13}C$ and $\delta^{15}N$ values. The Neanderthal samples were measured at the Oxford Radiocarbon Accelerator Unit, and the faunal samples were measured at the Stable Isotope Laboratory, Research Laboratory for Archaeology and the History of Art, University of Oxford.

We used the ecosystem approach and compared the omnivores of interest, in this case the Neanderthals, with the isotope values of temporally and geographically associated fauna. Unfortunately, it was possible to extract collagen from only a few of the faunal samples taken from Vindija. A particular problem was our inability to extract collagen from our carnivore samples. For this reason, we have supplemented the Vindija faunal sample with data from the slightly later (≈23,000–26,000 B.P.) sites of Dolní Věstonice II and Milovice in the Czech Republic (22). In addition, we have contributed a single herbivore sample from the site of Brno-Francouzská, which dates within this time range (23).

There are fluctuations in faunal $\delta^{15}N$ values through time that are correlated with climate changes (24, 25). For example, Richards *et al.* (26) observed faunal $\delta^{15}N$ values dated to ≈12,000 years B.P. from Gough's Cave, U.K. that were ≈2‰ lower than the $\delta^{15}N$ values of similar species from the Holocene. Therefore, comparing isotope values between sites, especially sites of different ages, could be problematic. However, by employing fauna that are as geographically and temporally as close to our samples as possible, we should be providing an appropriate comparative framework for the Vindija Neanderthal samples. Moreover, the relative distribution, especially of $\delta^{15}N$ values, for the species included in this pooled sample is similar to the distributions derived for various faunal species from single sites (10, 11).

Fauna. The *Bos/Bison* and cervid samples from Vindija (Table 1) have herbivore $\delta^{13}C$ and $\delta^{15}N$ values that are within the ranges observed for European Holocene specimens (25, 27). The $\delta^{13}C$ values are more indicative of open-ranging species (≈20‰), rather than forest-dwelling species (≈22‰), but ranges of variation in Late Pleistocene *Bos/Bison* $\delta^{13}C$ values (24) as well as the hilly terrain in the vicinity of Vindija Cave make it difficult to assess which of these bovine genera is most likely represented. The cave bear samples are interesting from a paleobiological, rather than an anthropological, perspective as they have very low $\delta^{15}N$ values. Similarly low *Ursus spelaeus* $\delta^{15}N$ values have been observed for samples from Slovenia (28), France (29), and Belgium (30). The low *U. spelaeus* values probably reflect a high degree of herbivory (31); they may also be a result of their unusual metabolism related to hibernation (32), although the hibernation model has been disputed (30).

Neanderthals. The Neanderthal samples from Vindija have high $\delta^{15}N$ values, which indicate that the overwhelming majority of their dietary protein was from animal, rather than plant, sources (Table 1, Fig. 1). The associated $\delta^{13}C$ values indicate the exploitation of more open-ranging herbivores, despite the hilly terrain of the Hrvatsko Zagorje. The Neanderthal values are close to the later carnivore isotope values from Dolní Věstonice II and Milovice (22), as well as those of earlier carnivores from Marillac and Scladina (10, 11), indicating that these Neanderthals had diets similar to nonhuman carnivores.

The insufficient associated faunal samples make it impossible to identify which herbivore species were preferentially being consumed by the Neanderthals. The mammoth $\delta^{15}N$ values from Milovice are intriguing, as they are higher than the other herbivores. This pattern of higher mammoth values has been observed previously (30, 33, 34) and may relate to mammoths targeting specific plant species, whereas other herbivores consume a wider range of species. The higher mammoth $\delta^{15}N$ values may be of relevance here, as the Neanderthal $\delta^{15}N$ values could make sense if their main dietary protein source was mammoths rather than the other faunal species. However, archeological evidence for Neanderthal exploitation of proboscideans is ex-

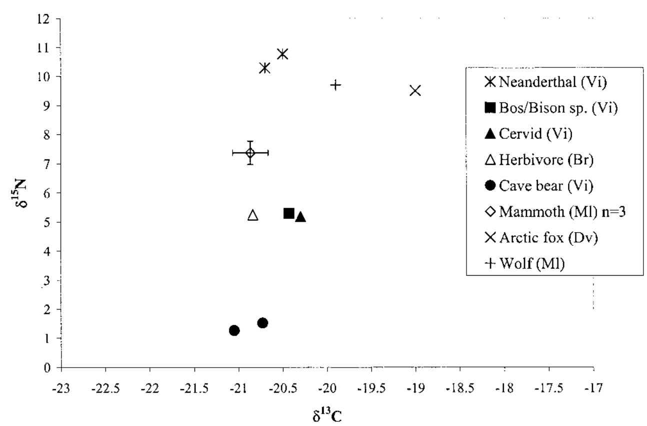

Fig. 1. Bone collagen $\delta^{13}C$ and $\delta^{15}N$ values of Neanderthals and associated fauna from Vindija Cave, Croatia (Vi), dated to ≈28,500 years B.P. Included is a single faunal value from the site of Brno-Francouzská (Br), Czech Republic (≈24,000 years B.P.). Also plotted are faunal values from Ambrose (22) from ≈22,000–26,000 years B.P. sites in the Czech Republic: Dolní Věstonice II (Dv) and Milovice (Ml).

Table 2. Isotope values of Neanderthals from Marillac, France (10), and Scladina, Belgium (11)

Site	Sample	Site age	$\delta^{13}C$	$\delta^{15}N$
Marillac	Layer 9	40,000–45,000 BP	−20.2	9.3
Marillac	Layer 10	40,000–45,000 BP	−19.1	11.6
Scladina Cave	SC18800	80,000–130,000 BP	−19.9	10.9

tremely rare, and a broader series of fauna needs to be analyzed before the spectrum of predated herbivores can be evaluated through stable isotope analysis.

Our findings concerning the diet of the Vindija Neanderthals are remarkably similar to those observed by Bocherens and colleagues for other European Neanderthals (10, 11). They obtained similar $\delta^{13}C$ and $\delta^{15}N$ values for two Neanderthals from the site of Marillac dated to ≈40,000–45,000 years B.P. and for a Neanderthal specimen from Scladina Cave, Belgium, which is earlier, dated to between 80,000 and 130,000 years B.P. (Table 2). Moreover, the high $\delta^{15}N$ for the Marillac Neanderthal remains are most closely approached by the values for *Canis lupus* and *Crocuta crocuta* from that site (10), whereas the earlier Neanderthal $\delta^{15}N$ value from Scladina is most closely approached in that site's faunal assemblage by *Panthera spelaea* and secondarily by slightly lower values for *Crocuta crocuta* and *Canis lupus* (11). For these five Neanderthal specimens, therefore, we have stable isotope data indicating that geographically and chronologically dispersed Neanderthals consistently behaved as top-level carnivores.

Neanderthals as Predators. Neanderthal subsistence strategies were varied in space and time, with carcass utilization patterns varying on intersite and interspecies levels (4, 35). The role of hunting versus scavenging in meat acquisition by Middle Paleolithic humans has been debated particularly over the last two decades (3, 36, 37), and from this discussion it has become clear that the Neanderthals were capable of, and frequently engaged in, predation on mammals.

In particular, taphonomic analyses of a number of Middle Paleolithic, Neanderthal-associated mammalian faunal assemblages in recent years have concluded that focused and selective hunting strategies resulting in high meat utility acquisition were carried out by these late archaic humans in areas of Europe and the Near East as dispersed as France (Bau de l'Aubesier, La Borde, Canalettes, Coudoulous, Mauran, Le Portel), Germany (Salzgitter Lebenstedt, Wallertheim), Italy (Grotta Breuil), Croatia (Krapina), Iran (Kobeh), Israel (Kebara), and Russia (Il'skaja) (1–3, 6, 35, 38–44). These interpretations are based principally on mortality profiles and/or distributions of skeletal part frequencies of the prey species being processed, combined with direct evidence of human carcass processing with lithic tools. In the former, prime age-dominated assemblages are usually taken to indicate selective and active predation by these hominids. In the latter, a proximal limb element-dominated assemblage or a preserved skeletal distribution representative of anatomical frequencies, as opposed to a head and foot-dominated assemblage, are generally taken to indicate primary carcass access and hence active predation.

However, not only do a significant number of these assemblages not meet both criteria for active predation on the part of the Neanderthals, it is increasingly apparent that a variety of factors can contribute to the mortality and skeletal element distributions documented in archeological faunal assemblages. These factors include prey population demographic dynamics, nonhuman predator prey selection patterns, carcass consumption patterns by both humans and other carnivores, human carcass element transport variation, and postdepositional processes acting differentially on skeletal elements. Moreover, it remains unclear how representative of overall Neanderthal diet such episodes are. Consequently, current taphonomic analyses of these and other archeological faunal assemblages do not always permit assessment of the degrees to which the assemblages were accumulated through active predation versus scavenging.

Neanderthal predation has also been supported by the evidence for spears (stone-tipped and wooden) among both the Neanderthals and their Middle Pleistocene European predecessors (45–49), combined with rare examples of such weapons in the remains of apparent prey animals [e.g., the wooden spear in the ribs of an *Elephas* skeleton at Lehringen, Germany, and the Levallois point embedded an *Equus* cervical vertebra from Umm el Tlel in Syria (45, 50)]. In addition, indirect measures of Neanderthal subsistence such as the Levallois point to core frequencies have been used to suggest that the Neanderthals were highly predatory in the Near East (ref. 51; but see refs. 52 and 53), despite the absence of evidence for the kind of projectile weaponry seen in the Upper Paleolithic that would increase the mechanical efficiency and safety of hunting or for the patterned variance in extractive technologies widely seen in Upper Paleolithic and more recent hunter–gatherer toolkits (54).

This inference of active predation on the part of the Neanderthals is further supported by their anatomical distribution of trauma, which suggests proximate encounters with large animals (55) of the kind necessitated by their predominantly heavy available weaponry (45, 47, 48, 56). Yet, their pattern of trauma does not permit distinctions between injuries sustained during hunting versus those suffered in competition with other carnivores for carcasses or space.

Consequently, although several lines of evidence support active mammalian predation by the Neanderthals and contradict the previous models of the Neanderthals acquiring their animal protein principally through scavenging, the archeological data nonetheless remain frequently ambiguous as to the extent to which these late archaic humans were the primary predators of the mammals whose remains they processed. The consistent stable isotope data indicating their position as top-level carnivores provides insight into this issue.

There are no true mammalian scavengers, as all are omnivores (ursids and canids) and/or actively hunt (hyenas) (57). This is because the search time for scavenging relative to the return is too expensive for terrestrial homeothermic vertebrates, and most predators actively defend their kills, thereby increasing risk to any potential terrestrial scavenger (57). If the Neanderthals were obtaining their animal protein principally through scavenging, they would have had to obtain most of their food from plants, as a reliable food source, and only supplemented this with scavenged animal products. Even though the isotope data cannot distinguish the species or even the sizes of the animals consumed, they clearly show that animal products were the overwhelming source of protein in European Neanderthal diets and that protein from plants was insignificant. It is therefore likely that scavenging, although undoubtedly practiced on an opportunistic basis by these European Neanderthals, must have been distinctly secondary to predation.

Summary and Conclusions

Isotope analyses of two Neanderthals and associated fauna from Vindija Cave, Croatia, have indicated that the bulk of their dietary protein came from animal sources. Comparison with faunal remains from this and other sites of similar age indicates that the Vindija Neanderthal isotope values were similar to those of other carnivores. These results are very close to the results for earlier Late Pleistocene Neanderthals from France and Belgium.

Therefore, the emerging picture of the European Neanderthal diet indicates that although physiologically they were presumably omnivores, they behaved as carnivores, with animal protein being the main source of dietary protein. This finding is in agreement with the indirect archeological evidence and strongly points to the Neanderthals having been active predators.

We thank H. Bocherens, F. B. Marshall, and M. C. Stiner for helpful comments. The collection and analysis of the Vindija hominid samples was supported by the L. S. B. Leakey Foundation, by the Wenner–Gren Foundation, and by the Prehistoric Society of the United Kingdom. The analysis of the Vindija faunal samples was supported the Natural Environment Research Council (U.K.) and the Social Sciences and Humanities Research Council of Canada.

1. Jaubert, J., Lorblanchet, M., Laville, H., Slott-Moller, R., Turq, A. & Brugal, J.-P. (1990) *Les Chasseurs d'Aurochs de La Borde: Un Site du Paléolithique Moyen (Livernon, Lot)* (Maison des Sciences de l'Homme, Paris).
2. Farizy, C., David, F. & Jaubert, J. (1994) *Hommes et Bisons du Paléolithique Moyen à Mauran (Haute-Garonne)* (Centre National de la Recherche Scientifique, Paris).
3. Stiner, M. C. (1994) *Honor Among Thieves: A Zooarchaeological Study of Neandertal Ecology* (Princeton Univ. Press, Princeton).
4. Mellars, P. (1996) *The Neanderthal Legacy* (Princeton Univ. Press, Princeton).
5. Gamble, C. (1999) *The Palaeolithic Societies of Europe* (Cambridge Univ. Press, Cambridge).
6. Gardeisen, A. (1999) *J. Archaeol. Sci.* **26,** 1145–1158.
7. Ambrose, S. H. (1993) in *Investigations of Ancient Human Tissue: Chemical Analyses in Anthropology*, ed. Sandford, M. K. (Gordon & Breach, Langhorne, PA), pp. 59–130.
8. Schwarcz, H. & Schoeninger, M. (1991) *Yearb. Phys. Anthropol.* **34,** 283–321.
9. Bocherens, H. (1999) *Bull. Mém. Soc. Anthropol. Paris* **ns 11,** 261–287.
10. Fizet, M., Mariotti, A., Bocherens, H., Lange-Badré, B., Vandermeersch, B., Borel, J. & Bellon, G. (1995) *J. Archaeol. Sci.* **22,** 67–79.
11. Bocherens, H., Billiou, D., Mariotti, A., Patou-Mathias, M., Otte, M., Bonjean, D. & Toussaint, M. (1999) *J. Archaeol. Sci.* **26,** 599–607.
12. Wolpoff, M. H., Smith, F. H., Malez, M., Radovčić, J. & Rukavina, D. (1981) *Am. J. Phys. Anthropol.* **54,** 499–545.
13. Smith, F. H., Trinkaus, E., Pettitt, P. B., Karavanić, I. & Paunović, M. (1999) *Proc. Natl. Acad. Sci. USA* **96,** 12281–12286.
14. Ambrose S. H. & Norr, L. (1993) in *Prehistoric Human Bone: Archaeology at the Molecular Level*, eds. Lambert, J. & Grupe, G. (Springer, New York), pp. 1–37.
15. Schoeninger, M. DeNiro, M. & Tauber, H. (1983) *Science* **220,** 1381–1383.
16. Richards, M. P. & Hedges, R. E. M. (1999) *J. Archaeol. Sci.* **26,** 717–722.
17. van der Merwe, N. J. & Medina, E. (1991) *J. Archaeol. Sci.* **18,** 249–259.
18. Schoeninger, M. & DeNiro, M. (1984) *Geochim. Cosmochim. Acta* **48,** 625–639.
19. Law, I. A. & Hedges, R. E. M. (1989) *Radiocarbon* **31,** 247–254.
20. DeNiro, M. J. (1985) *Nature (London)* **317,** 806–809.
21. Ambrose, S. H. (1990) *J. Archaeol. Sci.* **17,** 431–451.
22. Ambrose, S. H. (1998) in *Neandertals and Modern Humans in Western Asia*, eds. Akazawa, T., Aoki, K. & Bar-Yosef, O. (Plenum, New York), pp. 277–289.
23. Pettitt, P. B. & Trinkaus, E. (2000) *Anthropologie (Brno)*, in press.
24. Iacumin, P., Bocherens, H., Delgado Huertas, A., Mariotti, A. & Longinelli, A. (1997) *Earth Planet. Sci. Lett.* **148,** 349–357.
25. Richards, M. P. (1998) D. Phil. thesis (Univ. of Oxford, Oxford).
26. Richards, M. P., Jacobi, R., Currant, A., Stringer, C. & Hedges, R. E. M. (2000) *J. Archaeol. Sci.* **27,** 1–3.
27. Bocherens, H., Fizet, M., Mariotti, A., Lange-Badré, B., Vandermeersch, B., Borel, J. P. & Bellon, G. (1991) *J. Hum. Evol.* **20,** 481–492.
28. Lidén, K. & Angerbjörn, A. (1999) *Proc. R. Soc. London Ser. B* **266,** 1779–1783.
29. Bocherens, H., Fizet, M., Mariotti, A., Gangloff, R. A. & Burns, J. A. (1994) *Hist. Biol.* **7,** 187–202.
30. Bocherens, H., Billiou, D., Patou-Mathis, M., Bonjean, D., Otte, M. & Mariotti, A. (1997) *Quat. Res.* **48,** 370–380.
31. Kurtén, B. (1958) *Acta Zool. Fennica* **95,** 1–59.
32. Nelson, D. E., Angerbjörn, A., Lidén, K. & Turk, I. (1998) *Oecologia* **116,** 177–181.
33. Bocherens, H., Fizet, M. & Mariotti, A. (1994) *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **107,** 213–225.
34. Bocherens, H., Pacaud, G., Lazarev, P. & Mariotti, A. (1996) *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **126,** 31–44.
35. Gaudzinski, S. (1999) in *The Middle Palaeolithic Occupation of Europe*, eds. Roebroeks, W. & Gamble, C. (Univ. of Leiden Publishers & European Science Foundation, Leiden, The Netherlands), pp. 215–233.
36. Binford, L. R. (1985) *J. Anthropol. Archaeol.* **4,** 292–327.
37. Chase, P. G. (1989) in *The Human Revolution*, eds. Mellars, P. A. & Stringer, C. B. (Princeton Univ. Press, Princeton), pp. 321–327.
38. Gaudzinski, S. (1996) *Proc. Prehist. Soc.* **62,** 19–40.
39. Patou-Mathis, M. (1993) in *L'abri des Canalettes: Un habitat moustérien sur les grands Causses (Nant, Aveyron)*, ed. Meignen, L. (Centre National de la Recherche Scientifique, Paris), pp. 199–237.
40. Fernandez, P., Faure, M., Guérin, C. & Lebel, S. (1998) in *Économie Préhistorique: Les Comportements de Subsistence au Paléolithique* (Éditions de l'Association pour la Promotion et la Diffusion des Connaissances Archéologiques, Sophia Antipolis, France), pp. 309–323.
41. Speth, J. & Tchernov, E. (1998) in *Neandertals and Modern Humans in Western Asia*, eds. Akazawa, T., Aoki, K. & Bar-Yosef, O. (Plenum, New York), pp. 223–239.
42. Marean, C. W. & Kim, S. Y. (1998) *Curr. Anthropol.* **39,** S79–S113.
43. Miracle, P. (2000) *The Krapina Fauna: Catalog and Zooarchaeology of the Faunal Remains* (Hrvatski Priodoslovni Muzej, Zagreb, Croatia).
44. Gaudzinski, S. & Roebroeks, W. (2000) *J. Hum. Evol.* **38,** 497–521.
45. Jacob-Friesen, K. H. (1956) *Jahrb. Röm.-German. Zentralmuseums Mainz.* **3,** 1–22.
46. Oakley, K. P., Andrews, P., Keeley, L. H. & Clark, J. D. (1977) *Proc. Prehist. Soc.* **43,** 13–30.
47. Beyries, S. (1987) in *La Main et l'Outil: Manches et Emmanchements Préhistoriques*, ed. Stordeur, D. (Travaux de la Maison de l'Orient, Lyon, France), pp. 55–64.
48. Shea, J. J. (1988) *J. Field Archaeol.* **15,** 441–450.
49. Thieme, H. (1997) *Nature (London)* **385,** 807–810.
50. Boëda, E., Geneste, J. M., Griggo, C., Mercier, N., Muhesen, S., Reyss, J. L., Taha, A. & Valladas, H. (1999) *Antiquity* **73,** 394–402.
51. Shea, J. J. (1998) *Curr. Anthropol.* **39,** S45–S78.
52. Churchill, S. E. (1998) *Curr. Anthropol.* **39,** S61–S62.
53. Kuhn, S. L. (1998) *Curr. Anthropol.* **39,** S66–S67.
54. Kuhn, S. L. (1995) *Mousterian Lithic Technology: An Ecological Perspective* (Princeton Univ. Press, Princeton).
55. Berger, T. D. & Trinkaus, E. (1995) *J. Archaeol. Sci.* **22,** 841–852.
56. Churchill, S. E. (1993) *Archeol. Pap. Am. Anthropol. Assoc.* **4,** 11–24.
57. Houston, D. C. (1979) in *Serengeti: Dynamics of an Ecosystem*, eds. Sinclair, A. R. E. & Norton-Griffiths, M. (Univ. of Chicago Press, Chicago), pp. 263–286.