

Neanderthal–Modern Human Competition? A Comparison between the Mammals Associated with Middle and Upper Palaeolithic Industries in Europe during OIS 3

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ABSTRACT The extinction of the Neanderthals is generally believed to be due to interspecific competition with modern humans. This hypothesis is tested using the faunas accompanying Upper and Middle Palaeolithic archaeology in Europe dating to OIS 3 and the start of OIS 2 (60–20 ka BP). The issue is also considered in the light of ecological theory, controlled experiments and field studies of competition between congeneric species. This paper concludes that competition between modern humans and Neanderthals is not easily demonstrated and that if it did exist it need not have caused Neanderthal extinction. Copyright © 2004 John Wiley & Sons, Ltd.

Key words: Neanderthals; modern humans; competition; mammals; resources; climate; Oxygen Isotope Stage 3

Introduction

The notion that Neanderthals were driven to extinction by climatic and environmental factors alone, as recently advocated by Finlayson *et al.* (2000), Stewart *et al.* (2003a) and Stewart (2000, 2004), is not a popular one. The dominant palaeoanthropological hypothesis generally involves various forms of competition with modern humans who arrived in Europe 'shortly' before the expiry of the last Neanderthals. The types of competition invoked include cognitive (e.g. Mellars, 1989; Mithen, 1996; Klein, 2000), technological (e.g. Pettitt, 1999), linguistic (e.g. Lieberman, 1989), demographic (e.g. Bocquet-

Appel & Demars, 2000) and dietary resource based competition (e.g. Cachel, 1997; Pike-Tay *et al.*, 1999). Although these forms of competition have been described as distinct, ultimately they all involve competition for the means by which the different human species survived. The cognitive, cultural or demographic potential of a population will not cause competition unless it is being used to compete for food, lithic resources or habitat space (including caves). This is certainly true of the cultural aspects or abilities of a population (which themselves could well be related to cognition). Demographic aspects of a population are again not relevant unless they reflect the greater ability of that population to acquire resources and even then, only if they are using the same resources or habitat space as another 'competing' population. The inherent abilities of one population compared to another

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is not in itself competition as is often stated. These abilities may be proxies for behavioural modernity but that does not therefore suggest that competition took place.

A number of authors using various types of analysis have studied the difference in resource exploitation between modern humans and Neanderthals. Differences in diet are also linked inseparably to their ability to procure various dietary elements (e.g. Shea, 1998). The proposed differences between Neanderthal versus modern human diets include the relative proportions of plant to animal foods (Richards *et al.*, 2000, 2001), the mode of procurement of the animals (for a review see Burke, 2000), whether through scavenging or hunting, and the range of animals included as prey (Marean & Assefa, 1999). This last distinction shall be dealt with in the present analysis, although only by implication as the larger mammalian remains found associated with humans may not all represent the diet of those people but may have reached the location by some other means. For instance large mammalian remains may have reached the site because they were taken there by other predators such as hyaenas, lions, wolves, foxes, etc., the animals themselves may have lived and died at the site or were accumulated by physical processes such as flowing water. For those taxa that are accumulated by humans the mode of procurement may have varied according to the particular species sought and therefore different hunting strategies (e.g. encounter or intercept) are implied (Shea, 1998).

The purpose of this research is to test the hypothesis that there was competition between Neanderthals and modern humans during the time that they coexisted, i.e. during Oxygen Isotope Stage Three (OIS 3) (*ca.* 60–20 ka BP) and that this competition led to the extinction of the Neanderthals. To this end, this paper will analyse European mammalian fossil data associated with both Neanderthals and modern humans during OIS 3 (Stewart *et al.*, 2001) in order establish whether or not they were exploiting the same faunal resources. If the two human taxa are not associated with the same large mammals, it is more difficult to invoke competition between them and the hypothesis is falsified. However, if there is a level of similarity of faunal

association this could mean one of two things: 1) there is competition as the two human groups are competing for the same resource; or 2) they are able to exploit the same prey species because competition was low or non-existent. This will give some indication as to the likely levels of competition, if any, between the two hominins.

The final part of this paper will discuss the likelihood that competition, if it did exist between Neanderthals and modern humans, would lead to extinction.

The Stage Three Project mammalian database and methods

As part of the Stage Three Project, an investigation into the role of climate change and associated ecological developments in the disappearance of the Neanderthals, databases of absolutely dated hominin fossils, archaeological assemblages, and mammalian faunas were constructed (Stewart *et al.*, 2001, 2003b; Davies, 2001; van Andel, 2002). The databases comprise all the available published absolutely dated European archaeological and mammalian fossil sites for OIS 3. During the analysis of the mammalian database (Stewart, 2004; Stewart *et al.*, 2003a) it became apparent that certain taxa are better represented on archaeological sites believed to have been formerly occupied by modern humans (Upper Palaeolithic sites) than on ones formerly occupied by Neanderthals (Middle Palaeolithic sites) and vice versa. Specifically, mammoth remains were seen to occur on 4.5 times as many Upper Palaeolithic sites as Middle Palaeolithic ones, while there were only approximately three times as many Upper Palaeolithic sites. This may indicate that Upper Palaeolithic humans were exploiting the mammoth in a more systematic manner than were those of the Middle Palaeolithic. This result seemed to be related to the broad-spectrum revolution, a hypothesis which proposes that humans exploit a wider range of taxa if their populations are larger (Stiner, 2001). The larger population of modern humans compared with Neanderthals is supported by the work of Bocquet-Appel & Demars (2000). This observation prompted the current investigation into whether the disproportionate occurrences of

certain taxa on Upper Palaeolithic versus Middle Palaeolithic sites was caused by differences in prey preferences, or by some other factor.

The Stage Three Project mammalian database contains 447 dated faunas from 291 archaeological and non-archaeological sites. These contain 119 distinct mammalian taxa. The archaeological industry associated with the faunas is recorded in the database. The database includes material dated to between 60 and 20 Kyr, that is, beyond the end of OIS 3. OIS 3 is normally agreed to have finished *ca.* 25 kyr ¹⁴C BP (radiocarbon kiloyears) or *ca.* 26.5 kyr cal BP (calendrical kiloyears), but ending after the beginning of the Late Glacial Maximum (*ca.* 20 kyr ¹⁴C BP or *ca.* 21.4 kyr cal BP), seemed a more reasonable punctuation and guaranteed the inclusion of dates up to the end of OIS 3. Most sites are dated by radiocarbon, whether by conventional or the accelerator mass spectrometry technique. The dates were calibrated (more properly calendric-age converted) by the method developed by Jöris & Weninger (1996). Also included are thermoluminescence dates (TL), optically-stimulated luminescence dates (OSL), electron spin resonance dates (ESR) and uranium-series dates.

The Stage Three Project mammalian database is structured so that each line represents an absolute date and attached to each date are all the attributes of the associated layer at each site. Attributes include whether the site is open air or a cave, the archaeological industry (if any) found in the layer as well as the taxa making up its fauna. The Upper Palaeolithic (Aurignacian, Gravettian, Solutrean, Magdalanian and unspecified Upper Palaeolithic industries) is here taken to represent modern humans *Homo sapiens* while the Middle Palaeolithic (Mousterian and unspecified Middle Palaeolithic industries) is thought to represent Neanderthals *H. neanderthalensis*. Industries such as the Chatelperronian, Bohunician, Uluzzian, Szeletian, Bachokirian and Micoquian have been left out of the analysis because they are mostly local in geographical extent and do not constitute a great proportion of the sites in the database. Longitudes and latitudes were recorded for each site as digital degrees to allow geographical analysis. Mammals present in any one dated horizon are divided into large and small mammals and recorded as present. No

quantitative presence of taxa (minimum number of individuals—MNI or number of individual specimens—NISP) was recorded as this was inconsistently reported in the literature. Small mammals include all rodents, insectivores and lagomorphs; while large mammals comprise carnivores, ungulates and proboscideans. Human fossils were included as part of the large mammalian faunal field. In certain instances decisions needed to be made in order to standardize the taxonomy of the mammals in the database. Therefore, *Bos* and *Bison* were not distinguished but were lumped together as *Bos/Bison* in the manner that they are often reported in the literature due to difficulties in the morphological distinction of these two taxa. The species in the genera *Capra* and *Martes*, and fossils simply recorded to these genera were not distinguished in the database. Furthermore, only the records that specifically mentioned *Dama dama* rather than *D. dama/Cervus elaphus* were included.

Next, the ratio of the number of absolutely dated faunas associated with individual taxa on Middle Palaeolithic (Neanderthal) to Upper Palaeolithic sites was calculated. These ratios are shown in Table 1 and plotted against the total number of sites containing each taxon in Figure 1. Before any analysis could be performed the database was reduced to one record for each faunal assemblage. This step was necessary in order to prevent site/levels with multiple radiocarbon dates from skewing the database. No attempt was made to quantify the faunas further as MNI and NISP were not consistently reported in the literature.

Results

The ratio of occurrence of taxa on Middle to Upper Palaeolithic sites in Table 1 should be seen in the context of the ratio of all Middle to Upper Palaeolithic sites with mammalian remains. This is because there are approximately three times as many Upper Palaeolithic dates as Middle Palaeolithic ones. Figure 1 is a plot of the total number of sites for a species against the ratio of Upper to Middle Palaeolithic sites with that species. The taxa with ratios exceeding 4 are considered to be better represented than expected on Upper

Table 1. Ratio of the larger mammalian associations on Upper (UP) and Middle Palaeolithic (MP) sites during OIS 3

ID No.	Taxa Latin	English	UP	MP	Total MP + UP	Ratio of UP : MP
1	All taxa		239	83	322	2.88
2	<i>Alces alces</i>	Elk	13	2	15	6.50
3	<i>Cervus elaphus</i>	Red deer	130	56	186	2.32
4	<i>Rangifer tarandus</i>	Reindeer	164	40	204	4.10
5	<i>Dama dama</i>	Fallow deer	4	6	10	0.67
6	<i>Capreolus capreolus</i>	Roe deer	58	13	71	4.46
7	<i>Megaloceros giganteus</i>	Giant deer	21	11	32	1.91
8	<i>Bos/bison</i>	Auroch/bison	162	57	219	2.84
9	<i>Rupicapra rupicapra</i>	Chamoix	93	32	125	2.91
10	<i>Capra</i>	Ibex	116	33	149	3.52
11	<i>Ovibos moschatus</i>	Musk ox	4	3	7	1.33
12	<i>Saiga tartarica</i>	Saiga antelope	14	1	15	14.00
13	<i>Sus scrofa</i>	Wild boar	57	24	81	2.38
14	<i>Equus ferus</i>	Horse	147	54	201	2.72
15	<i>Equus hydruntinus</i>	European wild ass	42	10	52	4.20
16	<i>Stephanorhinus kirchbergensis</i>	Merck's rhino	1	4	5	0.25
17	<i>Stephanorhinus hemitoechus</i>	Narrow-nosed rhino	3	6	9	0.50
18	<i>Coelodonta antiquitatis</i>	Woolly rhino	51	16	67	3.19
19	<i>Mammuthus primigenius</i>	Mammoth	91	20	111	4.55
20	<i>Elephas antiquus</i>	Straight-tusked elephant	3	2	5	1.50
21	<i>Panthera leo</i>	Lion	41	13	54	3.15
22	<i>Panthera pardus</i>	Leopard	4	10	14	0.40
23	<i>Lynx lynx</i>	Lynx	17	3	20	5.67
24	<i>Lynx pardina</i>	Iberian lynx	6	7	13	0.86
25	<i>Felis sylvestrus</i>	Wild cat	17	15	32	1.13
26	<i>Crocuta crocuta</i>	Spotted hyaena	59	35	94	1.69
27	<i>Canis lupus</i>	Wolf	113	35	148	3.23
28	<i>Cuon</i>	Dhole	5	5	10	1.00
29	<i>Vulpes vulpes</i>	Red fox	123	33	156	3.73
30	<i>Alopex lagopus</i>	Arctic fox	74	13	87	5.69
31	<i>Ursus arctos</i>	Brown bear	25	17	42	1.47
32	<i>Ursus spelaea</i>	Cave bear	67	29	96	2.31
33	<i>Meles meles</i>	Badger	21	6	27	3.50
34	<i>Mustela</i>	Weasle/stoat	25	3	28	8.33
35	<i>Putorius putorius</i>	Polecat	9	2	11	4.50
36	<i>Martes</i>	Marten	10	4	14	2.50
37	<i>Gulo gulo</i>	Wolverine	34	2	36	17.00
38	<i>Lutra lutra</i>	Otter	2	1	3	2.00
39	Leporidae	Rabbits and hares	61	14	75	4.36

Palaeolithic sites, while taxa with ratios lower than 2 are better represented on Middle Palaeolithic sites. These threshold ratios were chosen on the basis of the fact that the ratio of all the Upper and Middle Palaeolithic sites with mammals combined is 2.88 (i.e. a value of 3 is taken to be the cut-off point). The taxa that clearly show a disproportionate occurrence over the whole of OIS 3 on either Upper Palaeolithic or Middle Palaeolithic sites are listed in Table 2 together with various ecological and behavioural characteristics that describe them today.

The taxa that are preferentially found on Middle Palaeolithic sites include herbivores,

carnivores and an omnivore (Table 2). Many of them are today associated with closed deciduous woodland vegetation, although not exclusively, as the extinct rhinoceros (*Stephanorhinus hemitoechus*) appears to have been a grazer and therefore associated with some degree of grassland (Loose, 1975). *S. kirchbergensis* meanwhile is thought to have been a browser as its teeth are more hypsodont (Loose, 1975). The straight-tusked elephant (*Elephas antiquus*) is also believed to have been a browser. The giant deer (*Megaloceros giganteus*) is one of the classic late Pleistocene megafauna which became extinct at the end of the Pleistocene and presumably was adapted to the steppe-tundra of the late Pleistocene, although it is also

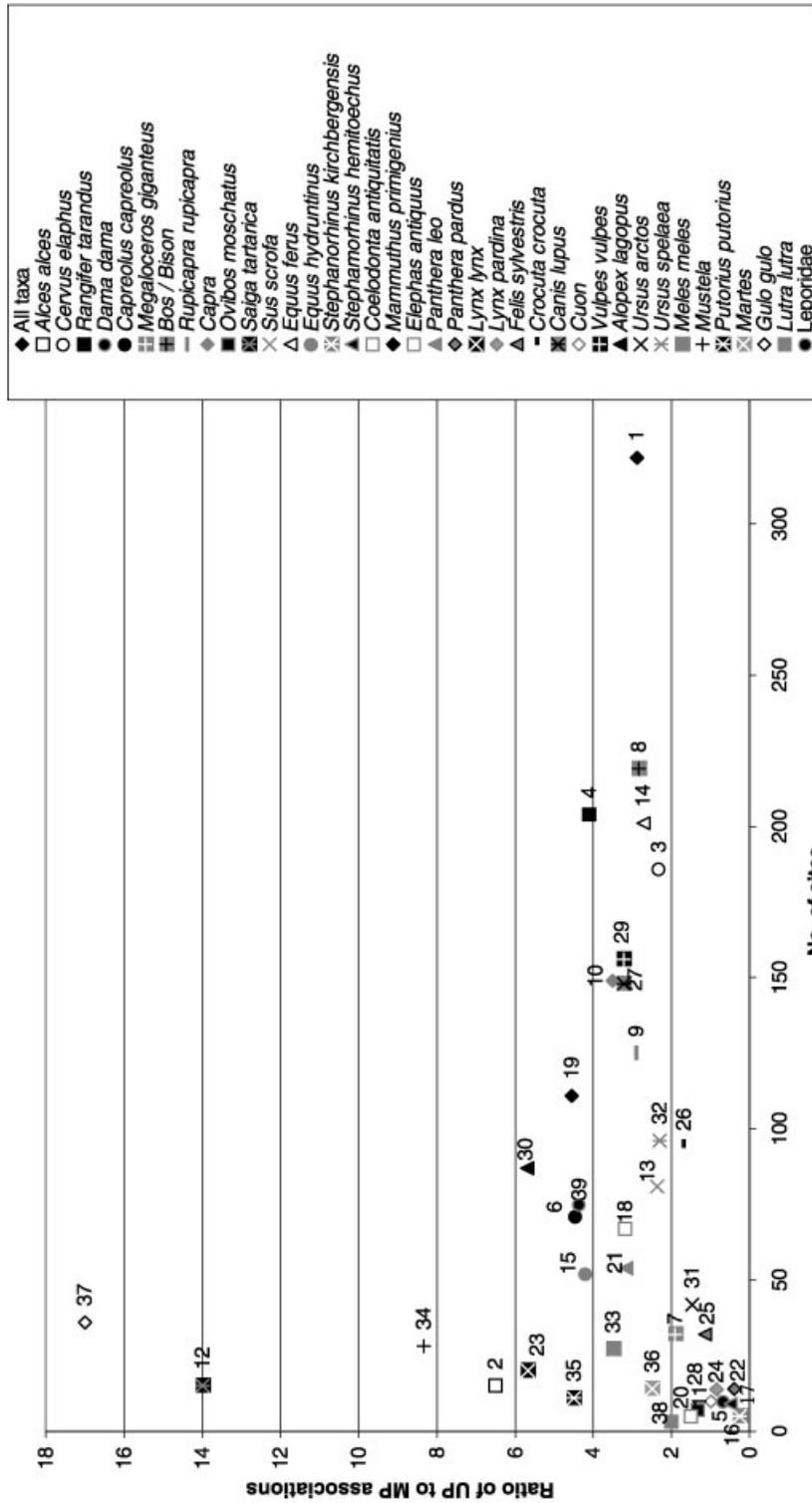


Figure 1. Scattergram of ratios of large mammals on Upper (UP) to Middle Palaeolithic (MP) sites plotted against the number of sites they occur on during OIS 3.

Table 2. Ecological correlates of the taxa preferentially associated with modern humans or Neanderthals through the whole of OIS 3

Taxon	Ratio UP : MP (N)	Ecological correlates		
		Warm vs. cold	Open vs. closed vegetation	Herbivore vs. carnivore vs. omnivore
Preferentially on Upper Palaeolithic sites				
<i>Alces alces</i>	6.5 (15)	Catholic	Closed	Herbivore
<i>Rangifer tarandus</i>	4.1 (204)	Cold	Open	Herbivore
<i>Capreolus capreolus</i>	4.46 (71)	Catholic	Closed	Herbivore
<i>Saiga tartarica</i>	14 (15)	Cold	Open	Herbivore
<i>Equus hydruntinus</i>	4.2 (52)	Cold/Catholic?	Open	Herbivore
<i>Mammuthus primigenius</i>	4.55 (111)	Cold	Open	Herbivore
<i>Lynx lynx</i>	5.67 (20)	Catholic	Closed	Carnivore
<i>Alopex lagopus</i>	5.69 (87)	Cold	Open	Carnivore
<i>Mustela</i>	8.33 (28)	Catholic	Both	Carnivore
<i>Putorius putorius</i>	4.5 (11)	Warm/Catholic	Closed	Carnivore
<i>Gulo gulo</i>	17 (36)	Cold	Closed	Carnivore
Leporidae	4.36 (75)	Catholic	Open	Herbivore
Preferentially on Middle Palaeolithic sites				
<i>Dama dama</i>	0.67 (10)	Warm	Closed	Herbivore
<i>Megaloceros giganteus</i>	1.91 (32)	Catholic?	Open?	Herbivore
<i>Ovibos moschatus</i>	1.33 (7)	Cold	Open	Herbivore
<i>Stephanorhinus hemitoechus</i>	0.5 (9)	Warm	Open	Herbivore
<i>Stephanorhinus kirchbergensis</i>	0.25 (5)	Warm	Closed	Herbivore
<i>Elephas antiquus</i>	1.5 (5)	Warm	Closed	Herbivore
<i>Panthera pardus</i>	0.4 (14)	Catholic?	Ubiquitous	Carnivore
<i>Lynx pardina</i>	0.86 (13)	Warm	Closed	Carnivore
<i>Felis sylvestris</i>	1.13 (33)	Catholic	Closed	Carnivore
<i>Crocota crocuta</i>	1.68 (94)	Catholic?	Open?	Carnivore
<i>Cuon</i>	1 (10)	Catholic?	Closed	Carnivore
<i>Ursus arctos</i>	1.47 (42)	Catholic	Both	Omnivore
<i>Lutra lutra</i>	2 (3)	Catholic	Aquatic	Carnivore

UP = Upper Palaeolithic; MP = Middle Palaeolithic.

known from interglacials such as the Eemian (Sutcliffe, 1995). The leopard (*Panthera pardus*) is found in a variety of habitats today from dry grassland to dense forest, while the spotted hyaena (*Crocota crocuta*) exists now only in Africa, mostly in savanna contexts, avoiding dense forest (Dorst & Dandelot, 1970). The spotted hyaena is a very common element during the vegetation climax of the penultimate Eemian interglacial fauna in Britain, however, which is often characterized as being a time of closed deciduous forest (Sutcliffe, 1995; Turner, 2002). The fallow deer (*D. dama*) prefers Mediterranean open woods but is adaptable (Mitchell-Jones *et al.*, 1999). The wild cat (*Felis sylvestris*) is mostly a woodland species in Europe today, preferring deciduous woodlands with populations scattered throughout Europe. The Iberian lynx (*Lynx pardina*) is mostly found in Mediterranean woodlands and maquis thickets and seems to be dependent today on an abundance of rabbits (*Oryctolagus cuniculus*)

(Mitchell-Jones *et al.*, 1999). The brown bear (*Ursus arctos*) is found in a variety of habitats including forests, tundra, steppes and the edges of deserts (Mitchell-Jones *et al.*, 1999). The otter (*Lutra lutra*) is an aquatic species requiring rivers, lakes or coastal waters to subsist and is found over much of Europe today (Mitchell-Jones *et al.*, 1999). The dhole (*Cuon*) is today found in forested areas of Central Asia, Eastern Siberia, through India, China, Malaya to Sumatra and Borneo (Corbet, 1978). Finally, the musk ox (*Ovibos moschatus*) is an enigma in this group as it is a boreal species living in the tundra of North America and Greenland today, but formerly widely distributed in the Palaeoartic. What is most compelling is the fact that most of these taxa are relatively thermophilous in their climatic associations today. Therefore, as regards the taxa over-represented on Neanderthal sites it would appear that the dominant pattern is one of preferential association with taxa that are indicative

of warmer and to some extent closed habitats, which were more prevalent in the south of Europe during OIS 3 (e.g. Tzedakis *et al.*, 2002). The pattern of over-representation is more probably indicative of the geographic/climatic preference of Neanderthals rather than the prey species that they preferentially hunt. This analysis therefore is in agreement with the findings about the Neanderthal's preferred environment suggested in Stewart (2004) and Stewart *et al.* (2003a). In these papers it is suggested that Neanderthals were not primarily cold adapted as often proposed (Trinkaus, 1981). This is because they could be seen to be retreating in a southwesterly direction before becoming extinct while the cold of the Late Glacial Maximum encroached on them from the northeast.

The taxa over-represented on modern human sites have a similar mix of carnivores and herbivores with an omnivorous element. The proportion of taxa associated with open versus closed vegetation is more ambiguous. There are taxa that are clearly grazers of open grassland habitats like the saiga (*Saiga tartarica*) and the mammoth (*Mammuthus primigenius*), as well as ones that are more ambiguous such as the roe deer (*Capreolus capreolus*), the elk (*Alces alces*) and the reindeer (*Rangifer tarandus*). The reindeer today has two main habitats consisting of tundra and taiga (Mitchell-Jones *et al.*, 1999). The elk lives in a variety of forest habitats today and particularly likes some proximity to wetlands (Mitchell-Jones *et al.*, 1999). The species' range in Europe is restricted to the northeast of Europe today, but it was formerly more widely distributed and its range has been seriously reduced due to habitat destruction and persecution. The roe deer is known from a wide variety of habitats today including woodlands and agricultural lands, and is found over most of Europe (Mitchell-Jones *et al.*, 1999). According to Markova *et al.* (1995) the steppe ass (*Equus hydruntinus*) inhabited dry steppe and semi-deserts in the more southerly regions of northern Eurasia, which is similar to the steppe to forest-steppe described as their habitat by Musil (1985). The wolverine (*Gulo gulo*) today is dominantly found in taiga and the polecat (*Putorius putorius*) is a carnivore often found in woodlands (Mitchell-Jones *et al.*, 1999). Northern lynx (*L. lynx*) are well adapted for snow cover and

are associated in Europe today with woodlands. They are also found in greater population densities when preying on roe deer than when hares are the main prey (Mitchell-Jones *et al.*, 1999). The latter may explain the association of both roe deer and lynx with modern humans. The arctic fox (*Alopex lagopus*) is particularly associated with tundra although they do venture into taiga in times of food shortage (Mitchell-Jones *et al.*, 1999). The genus *Mustela*, which includes the weasel and stoat, is found in a wide range of habitats and cannot be used to inform us about modern human associations without reliable species identifications. The leporids (rabbits and hares) are found throughout Europe today from the Mediterranean to the arctic and live in a wide variety of habitats (Mitchell-Jones *et al.*, 1999).

The taxa that are equally well-represented on Upper and Middle Palaeolithic sites should also be discussed. They also include both carnivores and herbivores, many of which are ubiquitous taxa that are generalist herbivores or widely distributed carnivores. These taxa include three of the four most common taxa on OIS 3 archaeological sites, all of which are herbivores (red deer *Cervus elaphus*, bovids *Bos/Bison*, and horse *E. ferus*—in addition to less common taxa such as the wild boar *Sus scrofa*, ibex *C. ibex/pyrenaica*, chamoix *Rupicapra rupicapra* and woolly rhino *Coelodonta antiquitatis*). The carnivores equally represented are the lion (*P. leo*), wolf (*Canis lupus*), red fox (*Vulpes vulpes*), badger (*Meles meles*) and the martens (*Martes*).

Discussion and conclusion

The results of the analysis above should be treated with caution. There is a great temptation to interpret the presence of fur-bearing carnivorous mammals on Upper Palaeolithic sites as the result of clothing manufacture. This temptation is particularly strong as it is only after the appearance of the Upper Palaeolithic technologies that 'awls', 'punches' and even needles appear significantly in the archaeological record (Klein, 1999). To this fact, one should add that the wolverine is well known today as a mammal with a particularly warm pelt (Macdonald and Barrett, 1993). Indeed it has been proposed that wolverine finds at

Pavlov probably represent animals hunted for pelts (Musil, 1997). This may be less easily justified as an interpretation of the larger numbers of *Mustela* finds on Upper Palaeolithic than Middle Palaeolithic sites as these animals are very small and do not individually yield much pelt. It could, however, be argued that the white colour of the stoat (*M. erminea*) may have been sought after as it has been in more recent times (i.e. ermine).

The disproportionate number of finds of arctic fox and mammoth on Upper Palaeolithic sites seem to be related to the hunting of these species by modern humans because there is physical evidence on their remains of having been modified. The arctic fox is often represented by pierced canine teeth used as decorative pieces and the mammoth likewise, is often known from ivory carved into various objects both utilitarian and decorative (Gamble, 1999). A caveat should be mentioned for the mammoth as there is a possibility that ancient ivory was picked up by people of the past and utilized. This could signify that the mammoths were not contemporary with the people utilising their ivory. The reindeer may have been hunted for meat as they are known to have formed a significant part of the diet of modern humans although their antlers were also made use of in the production of artefacts (Gamble, 1999). The preponderance of rabbits and hares on Upper Palaeolithic sites compared with Middle Palaeolithic ones would seem to be similar to the observed increase in the exploitation of such prey by modern humans (Stiner, 2001). Stiner (2001) explained the observation as due to population growth during the Upper palaeolithic but it may be that it was more a result of technological innovation and that the increased use of such prey happened earlier than the episode she describes. The over-representation on Upper Palaeolithic sites of these lagomorphs is unlikely to be due to climate as the hares and the rabbit were ubiquitously distributed in Europe during OIS 3. The modern human associations appear, therefore to indicate a mixture of climatic/environmental causes and choice of prey.

Animals over-represented on Neanderthal sites, on the other hand, have a pattern that can not easily be related to exploitation as a greater

proportion are carnivorous mammals without evidence for predation such as cut marks. The pattern would therefore seem to be related to the Neanderthal warmer climate correlation rather than to do with their prey preferences confirming the observations of Stewart (2004) and Stewart *et al.* (2003a). The musk ox is anomalous in this regard, being an obligate species of cold climates. Therefore when the mammals that are more common on Upper and Middle Palaeolithic sites are scrutinized, it appears that over-representation is due in part to climatic/ecological correlates of the industries (Table 2).

The animals roughly equally represented on Upper and Lower Palaeolithic sites are geographically wide-ranging and highly adaptable today. It seems that this combined with the fact that many of the herbivores, and particularly the three best represented taxa i.e. the horse, red deer and bison/uroch, are described as prey species of both the modern humans and Neanderthal in the literature (e.g. Pike-Tay *et al.*, 1999). This suggests that both differences and similarities exist between Neanderthals and modern humans in the taxa they exploited. The biggest difference may have been the greater use by modern humans of both the largest (mammoth) and smallest (leporids) mammals of the period. Competition between species of humans is difficult to confirm using the present data and it seems that if there was competition the modern humans, with their greater dietary breadth and resource base, may have avoided its pressure by diversifying.

Another perspective little considered in relation to modern human/Neanderthal competition is the literature, both theoretical and observation derived, on the ecology of competing closely related species (for reviews see: Schoener, 1974; Smith & Smith, 1998). Mathematical modelling by both Lotka (1925) and Volterra (1926) has suggested that extinction is only one of four possible outcomes to competition between two different species occupying the same niche. The first two outcomes involve one or other species increasing population size at the expense of the other leading to its extinction. The third outcome is where each species if abundant impedes the growth of the other and so both survive for a while but eventually only one succeeds (short-term equilibrium). Finally, there is the outcome

where neither species can increase enough to affect the growth of the other and both survive (long-term equilibrium). The latter outcome occurs when both species individually control their own population levels more than the other species does. Therefore, under the Lotka-Volterra model, extinction due to interspecific competition is by no means certain.

The advent of the Lotka-Volterra mathematical modelling led to laboratory experimentation to test its reliability. Perhaps the most famous of such experiments conducted were achieved by Gause (1935). He used various *Paramecium* taxa fed on bacteria in tubes to show that some combinations of paired species led to one species surviving at the expense of the other while with other pairs both survived. The circumstances where both survived involved one species feeding on bacteria in suspension while the other fed on bacteria at the bottom of the tube. The Lotka-Volterra equations thus gave rise to the competitive exclusion principle which states that complete competitors cannot exist together.

While laboratory experiments have tended to support competitive exclusion, field observations have been more ambiguous. Some organisms show a dominance of interspecific competition which leads to exclusion of one species, while in other cases intraspecific competition is strong enough to prevent populations reaching levels where competitive exclusion can take place. David Lack worked on the birds in the genus *Parus* (the tits) and found that in broad-leaved woodlands in Britain five species can coexist even when sharing similar diets and nesting behaviour (Lack, 1971). This was deemed possible because subtle differences between the five species existed, such as their feeding station location, the size of their prey and the hardness of the seeds they eat. The latter was possible because of corresponding differences in overall size and the size and shape of the bills of the individual taxa meant that each species could differentiate its niche sufficiently to avoid competition. Since the work of Gause and Lack much work has been conducted in this area and continues today on a whole range of organisms including plants and animals, vertebrates and invertebrates (Schoener, 1974; Shea & Chesson, 2002). However, Vandermeer *et al.* (2002) have suggested

that the orthodoxy regarding competitive exclusion is oversimplified. Non-linearity appears to characterise high-level competition and under such conditions species are more likely to avoid competitive exclusion.

Despite these developments it seems that there is and has been a common belief among palaeoanthropologists and archaeologists that two species of hominin cannot exist in sympatry due to the competitive exclusion principle. This belief originally manifested itself as the single species hypothesis which maintained that two hominin species could not occupy the same niche (Tattersall, 1995). The making of stone tools was held to be part of the human niche and this behaviour was only believed possible in one species at a time (Brace, 1964; Wolpoff, 1968). This was subsequently shown to be untrue when *H. habilis* was found together with *Paranthropus boisei* at Lake Turkana in Kenya (Leakey, 1970) and then when *H. erectus* was found with *Australopithecus* at Koobi Fora in East Turkana (Leakey & Walker, 1976).

The single species hypothesis was ill conceived with a strict ecological species concept at its heart. The ecological species concept was described by Van Valen (1976) as: 'A species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from any other lineage in its range and which evolves separately from all lineages outside its range'. It appears to have latterly given rise to the belief that all members of the genus *Homo* that have been named from the fossil record should be synonymized with *H. sapiens* (Wolpoff, 1989). This view has been used to support a belief in the multiregional origins of modern human populations around the world and which maintains that all modern humans evolved from the archaic populations that lived in those areas. The fact that the single species concept as adhered to by Wolpoff influenced his eventual belief in multiregionalism is even acknowledged in his recent co-authored book (Wolpoff & Caspari, 1997). The opposite belief regarding the origins of modern human populations is the 'out of Africa' theory (e.g. Stringer, 1989). The interesting perspective that these polarized views seem to share is that if two members of the genus *Homo* come into contact they will necessarily compete (Stringer & Davies, 2001). This seems to hark

back to the days of 'single species concept' as originally invoked by Brace (1964) and confirms that Tattersall's (1995) caution against this paradigm continues to be very pertinent long after the case was apparently resolved.

It would seem, from the above, that before any assertion that competition with modern humans necessarily caused the extinction of Neanderthals a number of factors should be demonstrated. First of all, the overlap in resources exploited by the two species should be sufficiently broad to cause competitive exclusion. The results presented above tend to minimize dietary overlap, making this proposition at best uncertain and at worst false. The large mammalian taxa found equally on Neanderthal and modern human sites may cause one to question this, as many were important dietary elements. However, because the two human taxa were able to hunt these common and important species, this may suggest that competition was not so great as to prevent both species from doing so. Second, intraspecific competition within modern human and Neanderthal populations would have to be shown to have been low, so as to allow the pressures of interspecific competition. Finally, there is little point in considering the likely Lotka-Volterra competitive scenario between modern humans and Neanderthals because the four theoretical outcomes assume that all other aspects of the physical environment remain the same and this is clearly not the case. This is notwithstanding the more recent theoretical considerations of Vandermeer *et al.* (2002) which question the role of interspecific competition in extinction.

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