

The ecology and adaptation of Neanderthals during the non-analogue environment of Oxygen Isotope Stage 3

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Abstract

The ecology of Neanderthals is discussed using an analysis of the fauna present in Europe during OIS 3, the period during which they became extinct. The environment of the Neanderthals is demonstrated to be without modern analogue. The non-analogue nature is characterised by the combination of mammals living together in OIS 3 Europe that are not found in sympatry today as well as the extinct elements of the fauna. The singularity of OIS 3, in terms of the arrival of modern humans and climatic variability, has been formerly implicated in the extinction of the Neanderthals. These perspectives are discussed in the light of related work on evolution and extinction. Finally, the cold-temperature adaptations of Neanderthals, such as their robusticity and limb proportions, are considered in the light of the interpretations of similar traits in other animals in the Late Pleistocene.

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1. Introduction

The extinction of an organism is often related to the demise of the environment to which it has become adapted. This may be true of Neanderthals as much as it is for any other organism (Finlayson et al., 2000a,b; Stewart, 2000; Stewart, 2004b; Stewart et al., 2003a). The dominant theory for Neanderthal extinction is however, that they were driven to extinction by competition with modern humans (e.g., Pettitt, 1999). Others have proposed a multiple cause theory whereby a combination of environmental stress and human competition are to blame (d'Errico and Sanchez Goñi, 2003; Stringer et al., 2003). If an environmental cause for Neanderthal extinction is to be supported, it is crucial that a correct understanding of their preferred environment is achieved. Stewart (2004a) concluded that Neanderthals were more likely to be associated with warmer adapted, closed habitat mammals than were modern humans, who were more likely to be associated with colder adapted, open-vegetation mammals. This is consistent with other studies, such as those of Finlayson

et al. (2000b), d'Errico and Sanchez Goñi (2003) and Grayson and Delpech (2003) that had similar findings.

In relation to climate, Neanderthals are generally described as cold or even hyper-arctic adapted (e.g., Trinkaus, 1981; Holliday, 1997). This conclusion has been drawn from ecomorphological characters of the Neanderthal skeleton such as their relatively short distal limb proportions and their general robusticity. These cold adaptations have been questioned by Stewart (2000). More recently confirmation for this was provided by Aiello and Wheeler (2003), who used Neanderthal site distributions from the Stage Three Project archaeological database (Davies, 2001a) to derive the climatic values from the Stage Three Project climate models (Barron and Pollard, 2002; Pollard and Barron, 2003) with which these sites are associated.

It would seem therefore that there is a continuing debate over the preferred habitat of the Neanderthals and that this should be given further attention if the cause for their extinction is to be seen in realistic light. Therefore the results of the analyses of the Stage Three Project mammalian database (Stewart et al., 2001; Stewart, 2003) are discussed with particular reference to the likely implications for Neanderthal adaptations.

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2. The environment of OIS 3 as seen from the mammalian faunas

Recently, Stewart et al. (2003b) concluded the analysis of the Stage Three Project mammalian database. The main conclusions were as follows:

1. Europe could be divided into latitudinal faunal provinces with a northern band, a southern band and an overlap zone (Davies et al., in press; Stewart et al., 2003b) (see Fig. 1). This marked North-South faunal provinciality includes mammals associated today with Boreal conditions and the classic cold adapted extinct megafauna in the northern and overlap provinces. Southern endemic taxa and three of the interglacial survivors (megafauna that went extinct in OIS 3) were found in the southern province and reached as far as the overlap zone. Many other taxa were found in all three provinces.
2. Temperate mammals that might be expected to be restricted to the south at this time, such as wood mice (*Apodemus* sp.) and moles (*Talpa* sp.), were not restricted, and reached as far north as 50° latitude (e.g. the Belgian Ardennes). The initial expectation was derived from a common assumption in many quarters that such a pattern, where temperate taxa were restricted to the southern refugia of peninsular Europe, must have existed (Hewitt, 2000; Willis and Whittaker, 2000).
3. There is also a degree of East-West provinciality, although much less marked. This is exemplified by the presence of more continental taxa, such as mole rats (*Spalax*), in the East that were not present in the West Europe during OIS 3 (Stewart et al., 2003b).
4. Other taxa that are restricted to more eastern areas today, such as souslik (*Spermophilus* sp.) and the

saiga (*Saiga tartarica*), were found as far West as France and Belgium.

5. The comparison of the regional climate model results with the distribution of certain small mammalian taxa, using modern distribution-climate correlations as controls, yields various discrepancies that were dependant on the taxa used (Stewart et al., 2003b). Table 1 shows the major results of this analysis, with a particular contradiction existing between the cold taxon *Alopex lagopus* (the arctic fox) and the continental taxon *Spermophilus* (the sousliks). The temperatures simulated were too warm for the cold taxa (*Alopex* and *Lemmus*) and too cold for the continental taxon (*Spermophilus*). There are a number of possible reasons for these discrepancies, although it seems clear that the phenomenon is allied to that of the “non-analogue community”, which has been recognized previously in Europe and elsewhere (e.g., most recently FAUNMAP Working Group, 1994, 1996; Huntley, 1996; Stafford et al., 1999).
6. The mapped OIS 3 mammalian faunas of Europe were compared with the vegetation as indicated by output from the BIOME models coupled to the regional Stage Three Project climate models as well as the pollen data for the period (Stewart et al., 2003b). The results of these comparisons indicate that there were clear discrepancies between the BIOME model outputs and the mammalian distributions (Stewart et al., 2003b). The models indicate the presence of taiga-type forest over much of the mid-latitudes of Europe for OIS 3 (Huntley et al., 2003), a fact which was difficult to reconcile with the dominance amongst the mammalian fossils of open grassland (or “mammoth steppe”) species (Stewart et al., 2003b). The pollen data also disagree with this BIOME model output, although the dominant reconstruction based on

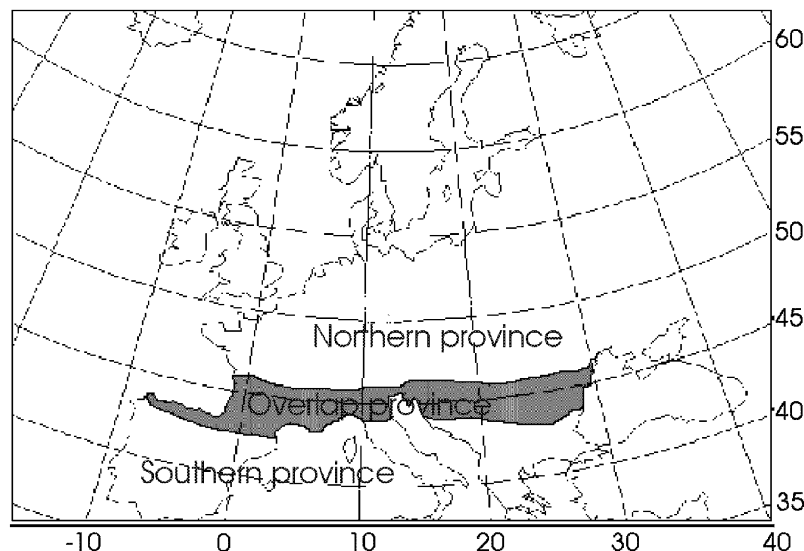


Fig. 1. Map of Europe showing the two main faunal provinces during OIS 3, together with the area where they overlap.

Table 1

Comparison between observed modern climate small mammal associations with simulated OIS 3 climate small mammal fossil associations

	Warm		21 K	
	Air temperature	Precipitation	Air temperature	Precipitation
<i>Lemmus</i> sp.	≈ Winter 1 site too hot in summer	≈ Winter 1 site too wet in summer	≈ Winter 1 site too cold in summer	≈ Winter ≈ Summer
<i>Alopex</i> sp.	A few sites too hot in winter A few sites too hot in summer	≈ Winter Skewed too wet in summer	1 site too hot in winter A few sites too hot in summer	≈ Winter A few sites too wet in summer
<i>Spermophilus</i> sp.	1 site too cold in winter ≈ Summer	≈ Winter 1 site too wet in summer	A few sites too cold in winter A few sites too cold in summer	1 site too dry in winter 1 site too wet in summer
<i>Apodemus</i> sp.	≈ Winter ≈ Summer	≈ winter ≈ Summer	≈ Winter ≈ Summer	≈ Winter ≈ Summer
<i>Talpa</i> sp.	≈ Winter ≈ Summer	≈ Winter 1 site too dry in summer	≈ Winter ≈ Summer	≈ Winter 1 site too dry in summer

pollen was of tundra. This heralded the well-trodden argument between mammalian palaeontologists and palynologists, who prescribe mammoth steppe (steppe-tundra) and tundra, respectively (Ritchie and Cwynar, 1982 versus Guthrie, 1990b; Ritchie, 1984; Colinvaux, 1986). Stewart et al., 2003b does point out that there are consistencies between the pollen data and the mammalian faunal data and particularly in the common occurrence of reindeer, arctic fox and lemming species, which today can be found on tundra (amongst other vegetation types). Not pointed out in detail, is the fact that if the original pollen data sources are consulted—such as the publication on Sokli in Finnish Lapland (Helmens et al., 2000)—there are relatively high amounts (up to 20%) of grass (gramineae) and sedge (Cyperaceae) pollen, as well as herbs such as Chenopodiaceae and *Artemisia* that are today characteristic of steppe. Although these occurrences are not used to justify the description of steppe-tundra by palynologists it is clear that such vegetational types and particularly the grasses may well have satisfied the dietary requirements of the large numbers of different grazers of the mid to northern latitudes of Europe during OIS 3. It may be that this long-standing argument is overstated.

3. Non-analogue communities and Neanderthal environments

The comparison between the regional climate model output and small mammal distributions of OIS 3, using modern distribution climate correlations as a control, yield differences that depended upon the taxon used (Stewart et al., 2003b). The possible ways to explain the discrepancy between taxonomic “tolerances” inferred

from modern geographic ranges and simulated climates for the fossil localities are as follows:

1. The modern geographical ranges of the taxa, and hence the climatic ranges within which they live today, do not extend to the maximum area possible. Human and other factors may be restricting their present geographical and climatic ranges, giving a falsely restricted view of their “tolerances”.
2. The fossils were misidentified and hence give a false negative indication of the climates simulated.
3. The dates of the fossils may be misleading. Time averaging may be falsely creating regional assemblages that are in fact mixtures of animals living at different times under different climatic regimes during OIS 3 and beyond.
4. The taxa in the past may not have pertained to the same genotypic populations as those we see today. Either they may have evolved into the populations we see today, or the populations of the past may have become extinct and hence have not contributed to the gene pools and associated climatic tolerances of the species today.
5. The regional climate model does not encompass a consideration of fine-scale topography. Topography may produce a wider range of climates in any one area of Europe than is simulated by the climate model, because smaller scale microclimatic differences are invisible to the model. This phenomenon was discussed recently by Stewart and Lister (2001) and Stewart (2003) who showed that northern refugia existed that may explain the colder than expected temperatures accompanying taxa such as *Talpa* and *Apodemus*. These would be particularly important with regard to the smaller mammals being used in the comparative study used here.
6. The climatic parameters, such as temperature and precipitation, are not so important to mammals as are snow cover, type of vegetation, and the

co-occurrences with other mammal species (Markova, 1992; Musil, 2003).

7. Finally, the regional climate model simulations may simply be wrong at all scales. This possibility was raised by Huntley et al. (2003), when comparing BIOME model simulated vegetation with inferred palaeovegetational data from pollen studies.

The seven possible explanations for the discrepancies caused by the different mammal–climate comparisons should be considered in turn. The first factor—that the modern distributions have been restricted by human landscape alterations—is difficult to address adequately, as detailed knowledge of pre-agricultural distributions are not available for small mammal taxa. However, the use of smaller mammals was designed to minimize this problem, as smaller areas of suitable habitat can support these taxa. The possibility of misidentification was negated by knowledge of the practical problems of identification of each taxon. Hence, most were not dealt with beyond the genus level. The possibility that time-averaging is causing apparent mixtures of taxa which in fact belong to distinct episodes (interstadials and stadials, or even interglacials and glacials), is difficult to negate, but the very consistency of the phenomena may be proof that they are genuine. In North America and Russia, the coeval nature of non-analogue taxonomic elements of faunas has been demonstrated using direct dates on bones (Stafford et al., 1999).

The fourth possible problem is likely to be a genuine factor, as it would seem unlikely, for instance, that the populations of arctic foxes and Norway lemming in the Dordogne (southwest France) during OIS 3 contributed to the modern gene pools of those taxa in Scandinavia today. The topographic averaging effect is also likely to be a partial explanation, as the model does not address topographic variation at a fine, local scale. The fact that other factors may be guiding the presence/absence of mammalian taxa (such as snow cover or the presence/absence of other mammal taxa) cannot be ignored and such criteria have already been given as influencing the distribution of certain taxa (Markova, 1992).

The model may itself, however, be the most important problem, as its output was meant to be tested by the various proxy-data collected during the Stage Three Project. The comparative exercise above would therefore cause one to question the validity of the climate model output comparisons to mammalian taxa, without any reference to modern climate associations e.g. Aiello and Wheeler (2003). Such exercises are seductive for extinct species, as their climatic tolerances are not known, although, based on the comparisons achieved above, it would seem premature to do so.

The findings from the analysis of the mammalian distribution data compared with the simulated climates of OIS 3, shows that different taxa gave different results.

The use of modern distributions, and corresponding climates as a control, demonstrated that a non-analogue fauna did exist. It also shows that the climate model outputs were likely to be incorrect in terms of their absolute values. This is not to say that the patterns of the relative values, and in particular the temperature cline in winter, grading from northeast to southwest, are incorrect. It is the winter temperature pattern that is most likely to be the determining natural selective factor. This pattern holds true today, as it probably did during OIS 3. Therefore, correlating Neanderthal distribution with this pattern shows that it is likely to be the cold encroaching from the northeast that caused Neanderthals to retreat in a southwesterly direction. The absolute values associated with this retreat, however, cannot be reliably derived from the OIS 3 climate simulations, as these outputs are likely to be inaccurate.

The faunal province most likely to be occupied by Neanderthals is the overlap zone (Fig. 1). It is this area that has the greatest number of sites in Europe, as it encompasses the site clusters of the Dordogne, the Rhone Valley and Cantabria (Davies et al., *in press*). It may be significant that it is this area that has the greatest number of non-analogue associations. Others have noted that Neanderthals often occupy areas of ecological transition, such as the edges of limestone massifs adjacent to lowland plains (Davies et al., 2003). This may be a similar phenomenon whereby Neanderthals favoured areas of greater ecological diversity, as expressed by a greater diversity of mammalian species including non-analogues. Indeed ecological diversity has been identified as a general characteristic of late Pleistocene faunas as a whole (Graham, 1986).

The Northern Province also has a high level of non-analogue elements, while the Southern Province is devoid thereof. This raises the question as to why the Neanderthals retreated into the Southern Province as OIS 3 progressed (Stewart et al., 2003b). However, this would ignore the fact that the whole of Europe was becoming impoverished in carrying capacity towards the Last Glacial Maximum. The Southern Province and overlap zone may have contained the richest faunas towards the end of OIS 3. This said, the northernmost distribution of Neanderthals in the later part of OIS 3 is in the Belgian Ardennes in the Northern Province. However, this region is likely to be affected by microclimates, caused by topographic variation, which in turn supported a “cryptic” northern refugium, non-analogue community (Stewart et al., 2003b; Stewart and Lister, 2001). When climate was optimal, Neanderthals lived in the most non-analogue regions. However, when the climates deteriorated, they retreated to more equable areas in the south or to small refugial areas in the more northern areas.

4. Neanderthals survived previous cold stages and OIS 3 climatic variability

A common objection to climate/environment-based causes for extinction of Neanderthals (and indeed other megafaunal components of the Late Pleistocene) is that they had survived previous major climatic transitions (e.g., Van Andel, 2003). This apparently quite reasonable response to such explanations is usually rapidly followed by a statement to the effect that the only new factor in the Late Pleistocene of Europe was the arrival of modern humans and that this is either compelling evidence that they out-competed the Neanderthals or hunted all the megafauna to extinction. This reasoning is one, however, that makes use of circumstantial evidence, namely that the modern humans arrived “immediately” before the “event” of extinction. It is important in such situations to eliminate the possibility that the arrival of the modern human “culprits” was not caused by the same phenomenon as the extinction of the Neanderthals. Indeed there are reasons to suspect that the arrival of modern humans is connected with the same phenomenon that eventually may have caused Neanderthal extinction. There is evidence that modern humans were attracted to the increased presence of open

habitats, as Europe became colder at the approach of the Last Glacial Maximum (Finlayson et al., 2000a, b; d’Errico and Sanchez Goñi, 2003). Stewart (2004) found that modern humans were more likely to be associated with animals indicative of open habitats and cold climates than were Neanderthals (Table 2). A similar point was made by Guthrie (1990a), who pointed out that the Late Pleistocene megafaunal extinctions were accompanied by other ecological changes and could therefore be described as a faunal revolution. This is similar to my finding, because Guthrie uses a single global phenomenon to explain all the changes at the end of the Pleistocene. Among these are included the fact that changes in the distributions of animals took place as a result of perturbations in climate and the environment. The arrival of modern humans is a distribution change and could in turn be explained by climate oscillations during OIS 3.

In recent work on the faunas from Grotte XVI in the Dordogne, Grayson and Delpech (2003) found little difference among the ungulates associated with Neanderthals and modern humans. However, the differences they did find across the Middle/Upper Palaeolithic transition (such as the decrease in red deer and increase in reindeer) was explained as due to

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 kirchbirgensis</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>Crocuta 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

climatic deterioration, rather than prey preference. Also coinciding with this transition was a decrease in the number of cave bear remains. This, Grayson and Delpech attribute to an increase in human population pressure and competition for cave space with the cave bear populations. They termed this the “Kurtén Response,” after Bjorn Kurtén, who had noted this phenomenon across Europe 45 years ago (Kurtén, 1958). They mentioned that Kurtén had abandoned the hypothesis of a human cause when he discovered that the phenomenon also existed in areas uninhabited by the Aurignacians (Kurtén, 1968a). Grayson and Delpech (2003) stated that the original cause should be revived because, at the Grotte XVI, the Mousterian/Aurignacian transition is marked by a decrease in the cave bear-to-ungulate ratio. They proposed a combination of increased human group size and residence times as a cause for the Kurtén Response. They do not, however, explain the decrease in cave bear noted by Kurtén in areas without the Aurignacians. Therefore, it may be simpler to explain all these phenomena as caused by climatic deterioration. This would signify that the reindeer increase, the red deer and cave bear decrease, the disappearance of the Neanderthals, and the appearance of the modern humans were all caused by the increase in cold as the Last Glacial Maximum (LGM) was approached.

Returning to the original point more fully, namely that Neanderthals survived the cold climates of OIS 6 and earlier, so why would they have succumbed to the cold of the last pleniglaciation? In a paper comparing the warming of the climate at the end of OIS 12 with that of OIS 2, Barnosky et al. (1996) found that no two such transitions are completely the same and therefore they claimed that such an objection is invalid. The same would presumably be true of a cooling transitional episode, so that comparing the cooling towards OIS 6 with that towards OIS 2 and the LGM may not be correct either. The latter is attested to by the survival of the straight-tusked elephant and the Merck’s rhino during the earlier transition. The same is true of the cold-adapted megafauna of Europe, which survived the transition into OIS 5 from OIS 6, but did not survive the OIS 2–OIS 1 transition. Conversely, previous transitions caused extinctions as attested to by the turn over in mammalian species seen across OIS 12 (Parfitt, 1999a). Species such as *Sorex savini*, *Pliomys episcopalpis*, *Ursus deningeri*, *Megaloceros dawkinsi*, *M. verticornis*, *M. savini*, *Stephanorhinus hundsheimensis* all became extinct across this glaciation in Britain at least.

Another important point addressed in Stewart et al. (2003a) and Stewart (2004) is that there were other ecological results of the downturn in climate as the LGM approached that could not readily be explained by the recent appearance of modern humans. Also, the modern humans eventually found conditions of the

LGM too harsh themselves and were pushed into southern refugia, such as that of Iberia (Straus et al., 2000; Gamble et al., 2004). The ecological changes include the extinction of interglacial survivors (the straight-tusked elephant and Merck’s rhino) as well as an apparent decline in numbers of certain smaller carnivores of the period (Stewart et al., 2003a). There was also the disappearance from Europe of the mammoth (Stuart et al., 2002), the best-known cold element of the Late Pleistocene and the megafaunal taxon with the northernmost distribution in Europe during OIS 3 (Ukkonen et al., 1999; Stewart et al., 2003b). Also occurring was the decline in the cave bear. To this one can add the decline in genetic diversity seen in both the brown bear (Barnes et al., 2001) and the bison (Shapiro et al., 2004) in Beringia. Although these did not take place in Europe, the phenomena are probably also due to global climate change, so extinctions of genotypic diversity seen in other areas at this time are relevant. The downturn in carrying capacity in Europe during the period approaching the LGM may be best exemplified by the disappearance in this region of the dung beetle, *A. holdereri* (Coope, 1973). This taxon would presumably have relied on the presence of readily available supplies of dung from megaherbivores and since it became extirpated in Europe at this time, this may suggest that the whole biome was suffering dramatically from the effects of cold climate. It is interesting that this beetle died out at precisely this time and not during the transition to warmer temperatures at the Holocene/Pleistocene boundary when the Mammoth Steppe finally completely disappeared in Europe, although other dung beetles went extinct at that time (S. Elias, personal communication, 2004).

A new climatic theory has recently been considered by Stringer et al. (2003). In this scenario, the onset of greater climatic variability during OIS 3 is considered as a possible cause of extinction of the Neanderthals. This interesting perspective has merit, as it may be that the climatic variability of the time of global cooling towards the LGM may have been unprecedented. However, there are reasons for questioning this hypothesis, as it is difficult to see why an organism would react to variability in climate that has amplitudes that exceed an individual’s lifetime as natural selection cannot act on a species beyond the lifespan of individuals of that species. Extinction is the extreme and ultimate result of natural selection and would surely result from the downward (or upward) turn experienced in a climate record, rather than the succeeding changes that occur after the individual has died. A similar criticism has been made of variability selection, a novel evolutionary mechanism proposed by Potts (1996, 1998). Variability selection is a process whereby adaptive change is supposedly linked to environmental variability. Lister (2004) suggested another mechanism to

explain phenotypic plasticity in mammals such as the red deer *Cervus elaphus*. Red deer can develop their rumen to cope with either browse or graze, depending on the dominant vegetation available to them during their growth. Although this is an evolutionary mechanism rather than a mechanism of extinction, evolution through natural selection in itself involves the extinction of all the lineages that do not produce offspring. An extinction of all such lineages of a species would lead to the global extinction of a species, as the organism could not change in response to the variability that its individuals encountered. Lister and Sher (1995) proposed a similar extinction mechanism for the mammoths and other megafauna of the terminal part of the Pleistocene. Here the opposite, a downturn in climatic variability, as seen in the Greenland ice records at the Holocene transition (Dansgaard et al., 1993), was proposed as the reason for the demise of the “mammoth steppe” or steppe-tundra. This mammoth steppe was described by Guthrie (1990b) as rich in carrying capacity and mosaic in structure, with great spatial variability in composition. It was apparently this biome that was crucial to the existence of the megafauna of the Late Pleistocene. Once it was replaced by the latitudinally banded vegetation of the Holocene, the animals that had relied on the high carrying capacity of the steppe-tundra died out. Therefore, for an extinction mechanism involving climatic variability to successfully explain the fate of the Neanderthals an intermediate effect would need to be involved. If an increase in climate variability caused a change in the ecological biomes this could then mediate in an effect on the Neanderthals population but it would not be a direct effect of climate variability.

D’Errico and Sanchez Goñi (2003) also consider the millennial scale climatic variability of OIS 3 in relation to Neanderthal extinction, but with an emphasis on the Iberian Peninsula. In this spatially and temporally fine-scale analysis, they considered the climatic record from the ocean cores drilled adjacent to Iberia. They note an apparent contraction of Neanderthal populations in southern Iberia coinciding with the Heinrich 4 (H4) cooling event (as attested in the IMAGES pollen-rich deep-sea cores). At this time, modern humans (Aurignacians) first colonized France and northern Iberia. D’Errico and Sanchez Goñi (2003) reject a solely climatic cause for Neanderthal extinction, as they state that the Aurignacians only colonized southern Iberia after the cooling of H4 had subsided. Hence, the climatic amelioration following H4 supposedly provided conditions more suitable to modern humans and thus finally precipitated a tardy competition with the Neanderthals in southern Iberia. This detailed analysis sheds light on the fine-scale response of human populations (Neanderthal and modern human) to climate change during OIS 3 on a regional basis. However, there appears to be an a priori assumption that competition was the

ultimate cause of Neanderthal extinction. It has recently been suggested by O’Regan et al. (2002) that, for large carnivores, the southern European refugia may have been too small to allow a sustainable population to survive, and thus inbreeding may have resulted, leading to extinction during the height of glaciations in these areas. This could be a large contributory reason for the extinction of Neanderthals once they had diminished in population at the H4 event. D’Errico and Sanchez Goñi (2003) suggest that the H4 event halted the moderns at the edge of the Neanderthal distribution in northern Spain, thereby delaying their demise. The analysis is commendable, but there is no clear indication as to the mechanism of extinction. The evidence is circumstantial and, if other models of the change in Neanderthal distribution through OIS 3 are accepted, the timing of the eventual encounter between Neanderthals and moderns may be wrong. Therefore, the most compelling aspects of the analysis of d’Errico and Sanchez Goñi (2003) are their observations that, during the H4 cooling event, the Neanderthals retreated and, conversely, the modern humans colonised southwest France and northern Iberia. It is also interesting that northern Iberia is the southern limit of the cold-adapted mammalian faunas of OIS 3. It may also be significant that it was only later that modern humans spread further south, a fact which may have had more to do with increases in population pressure that coincided with the residential phase of the Aurignacian, as described by Davies (2001b). Certainly, the southern areas of Iberia may not have been ideal for the moderns and only later were they able to expand into these regions. This may not have been because of the better conditions in southern Iberia after H4, but because of the demographic expansion of modern humans. The modern humans also expanded to the north as time progressed during OIS 3 (Davies, 2001a), although they eventually retreated into southern refugia at the LGM (Gamble et al., 2004). Whether this expansion led to the extinction of the Neanderthals is a paradigmatic position to take. I have shown elsewhere that competition, if it could be shown to exist between the moderns and Neanderthals, need not have led to extinction (Stewart, 2004). Inter-specific competition between sympatric congeners (or the competitive exclusion hypothesis) is no longer believed to be valid within the science of ecology (Tattersall, 1995).

A more fundamental problem with any analysis such as that by d’Errico and Sanchez Goñi (2003) is that correlation between archaeological radiocarbon dates, with standard errors of up to and over ± 1000 years, and climatic oscillations such as H4 lasting as little as 1000 years would at best seem tentative. This was why in Stewart et al. (2003a) OIS 3 was divided up into three sections and correlations were achieved at a coarser scale.

Another recent paper on the transition between the Upper and Middle Palaeolithic (Jöris et al., 2003) suggests that there was no temporal overlap between the two industries and therefore between the Neanderthals and modern humans. This conclusion was drawn after a data-mining exercise whereby C14 dates on bones were found in general to be older than those on charcoal by as much as several thousand years. They concluded from an analysis of vetted dates that “regional in situ development of the SW European Aurignacian out of the latest Middle Palaeolithic was made by Neanderthals” (p. 15) had taken place. This certainly should be considered as a possibility, lest we take for granted and acceptance of the “Out of Africa” explanation for the emergence of the Early Upper Palaeolithic in Europe. However, they do not consider that this punctuation event may have involved extinction of one Middle Palaeolithic-producing population and the replacement of it by the Aurignacian-producing population. Such an explanation for punctuation events in evolutionary biology using an allopatric population as the explanation for a lack of gradual evolution of one population into another is often accepted as an explanation of such events. Otherwise there is no explanation as to where in particular within Iberia the gradual evolution of Middle Palaeolithic into Aurignacian took place. It would seem unlikely that the change took place without an admixture of both industries at any location. It is acknowledged, however, in other publications that this transitional phase may be described in the interpretation of, for instance, the “Aurignacian” of El Castillo in the north of Spain as a Neanderthal industry (e.g., Zilhão and d’Errico, 2003), although this is speculative, as the now-lost associated human remains were apparently non-diagnostic (Straus, personal communication).

5. Neanderthal ecomorphological characters

Ecomorphological characters are those phenotypic attributes of an organism that can be explained by ecological factors. The two main ecomorphological traits of Neanderthals discussed in this context are their robusticity and size, and their limb proportions. However, it is incorrect to compare the Neanderthal body plan to that of modern humans, as is usually practiced, because the ecomorphological traits explained by the ecogeographic rules Bergman’s Rule and Allen’s Rule are intra-specific rules, not inter-specific rules (Mayr, 1970). Therefore, if Neanderthals and modern humans are separate species, they cannot be compared reliably. If they are the same species, then the comparison would be appropriate, but then the underlying subject of this paper, the extinction of Neanderthals, would be inappropriate, as they would not be extinct.

Attempts to apply Bergmann’s Rule inter-specifically to mammals demonstrate that it is not necessarily valid. For example, the smallest representatives of the shrew genus are the ones with the northernmost distributions. Hence, the least shrew, *Sorex minutissimus*, is found exclusively in the northernmost parts of Europe today (Mitchell-Jones et al., 1999). The same might be said of the arctic fox, *A. lagopus*, when compared to the red fox, although they are in separate genera. The least weasel, *Mustela nivalis*, has populations of the smallest individuals in such northern areas in Europe (Macdonald and Barrett, 1993). This is an intra-specific comparison, as recommended by Mayr (1970), but demonstrates that Bergmann’s Rule does not follow at all times. This last example is interesting, as some have considered the least weasel to be a separate species, which would make its case similar to that of the least shrew. It should also be pointed out that such rules are not infallible, as intra-specific studies have shown that natural selective variables, other than simply temperature, may influence physical characters of a warm-blooded animal (see below).

5.1. Size and robusticity

Size and robusticity (which is often related to size), are regularly used to indicate temperature adaptations by invoking Bergmann’s Rule. However, the rule has been applied too liberally at times. The interpretation of the relative robusticity of the incomplete tibia found at Boxgrove in Britain was used to infer that *Homo heidelbergensis*—the presumed specific identity of the tibia—was arctic-adapted (Trinkaus et al., 1999). This is, however, contradicted by the evidence of temperate climate often cited for the level at Boxgrove that produced the hominid remains (Parfitt, 1999b). The paper by Trinkaus et al. (1999) is slightly contradictory, as it does acknowledge that Late Pliocene to Late Pleistocene archaic *Homo*—including those from Africa—are generally robust. It may therefore be that this character—robusticity—is in fact present in all archaic *Homo*, because it is a primitive trait that says more about the phylogenetic history of the taxon than its ecomorphological adaptations.

Other interpretations of relatively large body size in intra-specific populations in the Late Pleistocene have been proposed, although they usually do not involve Bergmann’s Rule (but see Davis, 1981). Animals as diverse as red deer (*C. elaphus*), ptarmigan (*Lagopus mutus*), grouse (*L. lagopus*), and brown bear (*Ursus arctos*) have all been shown to have larger bodied populations in the Later Pleistocene (Lister, 1987; Kurtén, 1968b; Stewart, 1999). However, the more common explanation of such body size variation is not thermoregulation. Indeed, Bergmann’s Rule has lost favor in other areas of vertebrate paleontology (Geist,

1986). Instead, explanations involving higher carrying capacity are invoked (e.g., Guthrie, 1990b).

5.2. Limb proportions

The limb proportions of Neanderthals, expressed as crural (hind-limb) and brachial (fore-limb) indices, are usually interpreted as conforming to Allen's Rule (e.g., Trinkaus, 1981). The relatively short distal limb bones, when compared to the proximal ones, are thought to reflect thermoregulatory selection for a lower surface area to volume ratio. However, because limbs are primarily used in locomotion and not in thermoregulation, other possible explanations should be explored. In Neogene African bovids and suids, for example, the limb proportions are used to indicate relative degrees of habitat openness (e.g., Plummer and Bishop, 1994). In this instance, climate is not thought to be important, although the locomotory demands of closed versus open vegetational habitats are believed to be relevant. This could be an alternative perspective to explain the limb proportions of Neanderthals. Their short distal limb proportions might in fact reflect their greater use of closed habitats, as attested by their greater likelihood to being associated with closed-habitat mammals than modern humans, who are disproportionately associated with open-habitat taxa (Table 2). The Neanderthals retreated southwards as the cold climate encroached from the northeast. If southern Europe is the area where the greatest amount of tree cover is likely to have been, then this argument still holds.

A possible criticism of this argument is that the brachial index of the Neanderthals appears to be the same as the crural index. This may be invoked as evidence for a thermoregulatory explanation, since natural selection would be acting on both limbs. Therefore, thermoregulation could better explain both indices, while a locomotory explanation would only explain that of the hind limbs. However, it seems likely that selection for hind limb proportions in bipeds will affect the forelimbs, as has been shown by other pleiotropic effects in fowl (Cock, 1969).

A recent paper on the running adaptations of hominins has suggested that the elongated stature of *Homo*, as well as other anatomical features, are related to running long distances (Bramble and Lieberman, 2004). The suggestion is that *Homo* is adapted to endurance running in their quest for meat whether as carcasses or live prey. The fact that the humans they studied (*Homo erectus* and *H. sapiens*) were likely to be hunting in open areas is likely to be significant. A hypothesis that may have merit is that 'pursuit hunting' was facilitated by the ability to endurance run and that 'encounter hunting', as sometimes proposed for Neanderthals, did not require such an adaptation. It may even be that humans of closed habitats, such as

suggested for Neanderthals, are likely to be more adapted to sprinting as encounter hunting would require rapid explosive reactions and speed to respond when coming across prey. Neanderthals are clearly powerfully built humans therefore it would be of interest to investigate their potential *relative* sprinting abilities.

6. Conclusion

The discussion above regarding the recent papers on Neanderthal extinction, and the transition from the Middle Palaeolithic to the Upper Palaeolithic in general, shows that a large part of any conclusion is based on the paradigm followed by any group of scientists. This holds true of the present conclusions as much as it does about any other. The two main paradigms are respectively whether (1) competition with modern humans is believed to have had a role in Neanderthal extinction or (2) climate and environmental change are believed to be the sole reason. The argument made here and elsewhere (Stewart et al., 2003a; Stewart, 2004, in press), is that, given the number of phenomena that took place towards the end of OIS 3 which are unlikely to have been caused by the arrival of modern humans, there may be no need to consider that modern humans had a role in the demise of the Neanderthals. Therefore, the paradigm followed here is influenced by a belief in parsimony. This would suggest that Neanderthal extinction, modern human colonisation, the eventual disappearance of animals as varied as mammoths and the dung beetle (*Aphodius holdereri*) from Europe, the decrease in numbers of certain smaller carnivores, the decrease in numbers of cave bear, the extinction of the straight-tusked elephant and the Merck's rhino were all caused by the general, overall decrease in temperature and carrying capacity during the downturn culminating in the LGM. The decrease in genetic diversity of brown bear and bison in Beringia during OIS 3 may be further evidence of this global climatically induced ecological revolution.

The ecology of Neanderthals is discussed in this paper using an analysis of the fauna present in Europe during OIS 3, the period during which they became extinct. There is a marked North-South faunal provinciality in Europe at this time, with Boreal mammalian taxa reaching as far south as Cantabria and temperate mammals reaching as far north as the Belgian Ardennes. Meanwhile, there were interglacial survivors extending as far north as the Dordogne. The Neanderthals near the beginning of OIS 3 were almost ubiquitous, but they ended mostly in the southern faunal province, with some sites distributed in areas that have been postulated as northern refugia. The unfamiliar nature of the OIS 3 faunas, with mixtures of temperate, boreal and steppic taxa, was probably caused by the climate of the time

which has no modern analogue. A far greater degree of continentality must have existed compared to today, with greater seasonality affecting the Atlantic seaboard. Cold winter temperatures maintained open steppe-tundra plains and warm summers allowed the topographically sheltered, temperate taxa to exist near those plains in the mid-latitudes. Neanderthals seem to have belonged in part to the group of interglacial survivors, in so much that they went extinct together with them as the Last Glacial Maximum approached (Stewart, et al., 2003b; Stewart, 2004) and partly to the group of temperate mammals that survived in the north in cryptic temperate refugia (Stewart, et al., 2003a). This highlights the fact that Neanderthals lived at a time of great mosaic characteristics in habitat, with non-analogue mixtures of mammalian elements living in the same communities. This signifies that the climate and environment of the Neanderthals have no modern equivalents and this further indicates that any reconstruction of Neanderthals using the principle of uniformitarianism will be likely to produce flawed results. The existence of extinct organisms, including the Neanderthals themselves, provides perhaps the most graphic means of demonstrating that a past environment has no modern equivalent and was thus non-analogue.

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