Neither hot nor cold but dry: a NW European view of Neanderthal environments in late MIS 7 and beyond.

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1. Introduction

The ecological tolerances of Neanderthals have been frequently rehearsed in the literature, with particular reference to their apparent thermoregulatory adaptations for tolerating the extreme cold and dry conditions of Late Pleistocene Europe (Trinkaus, 1983; Steegmann et al., 2002; Churchill, 2014). The well-established suite of morphological features includes a "barrel-shaped" thorax (Howell, 1952; Coon, 1962; Franciscus and Churchill, 2002) and wide bi-iliac breadth (Ruff, 1991). These are consistent with predictions for endothermic species in higher latitudes and corroborated by the inferred greater body mass for northern European Neanderthals when compared to modern humans (Franciscus and Churchill, 2002), although the cross-comparison between hominin species is questionable with reference to Bergmann's Rule. Neanderthals also displayed relatively short distal limb proportions (Trinkaus, 1981, Holliday, 1997) consistent with surface area:volume ratio predictions for vertebrates in cold environments (Allen's Rule), whereas aspects of the cranium have further been identified as cold-climate adapted (Beals et al., 1983), in particular the supposed enlarged paranasal sinuses for warming cold air (Coon, 1962; Churchill, 1998), which give rise to the distinctive Neanderthal facial form.

However, the widespread assumptions regarding autapomorphic arctic or even hyper-arctic adaptations in Neanderthals have been challenged in recent years, for example by Aiello and Wheeler (2003), who demonstrated that the Neanderthal body form conferred no significant advantages over modern humans in terms of lower critical and minimum sustainable temperatures. These authors further concluded that Neanderthals would have been unable to survive winter periods, even during the interstadials of the last glaciations, without some form of cultural insulation or maintaining extremely high levels of dietary energy intake. Stewart (2005) has further explained the stocky postcranial proportions of Neanderthals as an adaptation for moving through dense forest environments and a number of authors have associated Neanderthals preferentially with warm-adapted, closed habitat mammalian communities, in contrast to modern humans, which they correlate with cold-adapted, open ground taxa (e.g. Finlayson et al., 2000; d'Errico and Sanchez-Goñi, 2003; Stewart, 2004). In a revision of the nasal morphology of Neanderthals, Rae et al. (2011) have further established that paranasal pneumatisation in Neanderthals was neither expanded (as previously assumed), nor reduced, as might in fact be expected from their accompanying analyses of low-temperature species. These observations have therefore now undermined, in large part, the historical 'pillar of wisdom' that Neanderthals were explicitly adapted to cold and open environments. Indeed, as indicated by Roebroeks et al. (2011), the NW European loess record reveals significant gaps in the presence of Neanderthals during the pleniglacial climatic conditions of MIS 6 and MIS 4, which cannot be readily explicable by depositional processes, these being the times of highest rate of loess formation.

The extraction of Neanderthals from a cold and open environment is a revision that might sit more comfortably with the discovery of Middle Palaeolithic open sites of Last Interglacial (Eemian, Marine Oxygen Isotope sub-Stage [MIS] 5e) age in northern Europe. These include Caours (Antoine *et al.*, 2006) and a small cluster of poorly-dated sites in the Cotentin peninsula of northern France (Lautridou, 1988), together with Lehringen (Thieme and Veil, 1985), Gröbern (Heussner and Weber, 1990), Grabschutz (Eissmann *et al.*, 1988), Rabutz (Toepfer, 1958), Wallertheim A (Adler and Conard, 2005), Neumark Nord 2 (Gaudzinski-Windheuser and Roebroeks, 2014), Stuttgart-Untertürkheim (Wenzel, 1988) and Taubach (Kahlke, 1977), all in Germany, where multiproxy biological and geochemical evidence have suggested that Neanderthals were present in association with fully temperate climatic conditions and thermophilous woodland. Nevertheless, the vast majority of these sites are in the more continental areas of central Europe and after more than 150 years of investigation, such open sites remain extremely rare and are apparently entirely absent from mainland Britain (Ashton, 2002). There is no escaping the fact that the roll-call of cave sites in Belgium and Germany with apparent Eemian occupation (e.g. Otte *et al.*, 1983; Niven, 2006) adds scarcely more to this very short list.

Roebroeks *et al.* (1992), Speleers (2000) and Locht (2002) sought to explain the paucity of Last Interglacial sites as a taphonomic artefact, stemming from the erosion of Eemian deposits by the subsequent Wicheselian glacial or periglacial activity in all but a few locations. However, as Adler and Conard (2005, 135) have subsequently stated, "*it is unlikely that such forces were capable of erasing or obscuring the entire slate of Eemian occupations across the continent*", especially when the preceding Saalian glaciation created sufficient accommodation space for the deposition of MIS 5e sediments in infilling glacial basins (Turner, 2000) and so many more remains of older interglacial deposits persist. The issue is not, therefore, a lack of MIS 5e palaeoenvironmental sites, of which there are many; indeed, a recent review of Last Interglacial sites in Britain counted 39 localities that may be confidently attributed to this age on the basis of stratigraphy, biostratigraphy, amino acid racemisation or other geochronology (Lewis *et al.*, 2011), to which may be added deposits at Gloucester (Schreve, 2009) and Channel IV at Clacton-on-Sea (Schreve, unpublished data). Lewis *et al.* (2011) suggested that the lack of MIS 5e sites in Britain may be explained by a lack of visibility of any archaeology, for example caused through small-scale investigations or temporary exposures. Nevertheless, this applies only to a minority of the sites listed, the remainder having long histories of investigation, intensive systematic excavation or collecting and more extensive areas to explore, thus providing ample opportunity to recover appropriate evidence.

Where rare hominin occupation *is* noted during the Last Interglacial in continental Europe, Adler *et al.* (2003) concluded that it is associated with a concentration of key resources and facilitated by the presence of locally more open terrain. Certainly in Britain, megafauna such as *Hippopotamus amphibius* (hippopotamus) were responsible for maintaining open ground adjacent to water bodies, as evidenced by the predominance of herb pollen and inwashing of soils suggesting local deforestation (Gibbard and Stuart, 1975). Nevertheless, despite the presence of such locally open areas, the prevailing picture of large tracts of Last Interglacial Britain remains one of relatively dense forest, stocked by rich supplies of game and

plants, but resoundingly empty of hominin presence. It is perhaps no coincidence that the absence of Neanderthals from Britain coincides with that of horse (Sutcliffe, 1995; Currant and Jacobi, 2011), a predominantly open-ground specialist, and that Bocherens et al. (1999, 2001) have established that the Neanderthal diet was characterised by high proportions of animal protein from open environment herbivores, even during forested episodes. Rapid sea level rise at the start of the Last Interglacial (Gupta et al., 2007; Toucanne et al., 2009) evidently may have played a critical role in barring Neanderthals specifically from Britain but this cannot explain the extreme scarcity of Last Interglacial archaeological evidence to the west of central Germany. One must inevitably return to the possibility suggested by Gamble (1986, 1999) that the presence of dense, deciduous forests during interglacials precluded Neanderthal presence, largely because of limitations to accessible and edible animal resources. These environments may have placed demands on technical and planning skills, and networks of alliance and information exchange that Neanderthal groups were seemingly unable to meet. These ideas therefore remain as current today as when they were first mooted thirty years ago.

2. Wet or Dry?

If not well suited to cold climates or densely forested habitats, what can be said about Neanderthal environmental preferences? This question has been somewhat skewed by the recent focus of many studies on last cold stage palaeoenvironments of southern Europe, in particular from the Iberian peninsula. While this is entirely understandable in the context of interest in the final extinction of the Neanderthals, this Ibero-centric view of the closing phases of Neanderthal existence does not accurately portray the totality of their adaptations and indeed, potential preferences for the range of habitats they encountered. In particular, many Iberian studies consistently associate Neanderthals with forested environments (e.g. López-Garcia et al., 2008, 2011a and b, 2012a and b; Burjachs et al., 2012), leading to a deep-rooted view in the literature that this is the *only* type of habitat in which Neanderthals were truly at home. However, since the Iberian peninsula acted as a major refugium for various tree taxa during Pleistocene glaciations further north (Carrión 2002; Carrión et al., 2010; López de Heredia et al., 2007; Linares, 2011), the association of Neanderthals with woodland may not have a particularly strong foundation.

Equally perplexing is the prevailing view that Neanderthals were intolerant of dry environments. Even in southern Spain, where progressive aridification of the landscape has been a feature since the Middle Miocene (Carrión et al., 2010) and where herpetofauna-based mean precipitation reconstructions for Late Pleistocene Neanderthal sites indicate *drier* conditions than at present (e.g. Blain et al., 2013), authors have stated that Neanderthals "*avoided areas of low rainfall*" (Jennings et al., 2011, 1182). Finlayson (2014), in particular, has made great play of the effects of freshwater shortages on Neanderthals, although it is not explained why modern humans should be any less affected by lack of water in the same area.

Jennings et al. (2011) further identified what they termed a "major refugium" of warm and wet conditions in the last cold stage, centred on the Cádiz-Málaga sierras. By reducing modern rainfall and temperature values by up to 2°C and -400mm per annum respectively, in order to simulate last cold stage conditions, Jennings et al. (2011) describe a core refugial area of south-western Spain with annual precipitation

values of 600->1000mm. Interestingly, this corresponds with the modern day values for southern England, from the South Downs and Dorset (the wettest, at around 950mm per annum) to the Thames valley and North Kent (around 600mm per annum, data from www.metoffice.gov.uk). However, despite the authors' averred strong correlation between Neanderthal presence and the wettest areas of south-western Spain, they themselves observe that just under 80% of Middle Palaeolithic sites in their study area are associated with <u>areas of lower rainfall</u>, 400-600mm per annum. A further 9% of sites are associated with arid and semi-arid conditions (100-300mm of rainfall per annum). In contrast, only 11% of sites are associated with sub-humid and humid/hyper-humid conditions (700-1000mm and above). While nobody is suggesting that Neanderthals did not need access to fresh water provided by rivers or lakes, their supposed aversion to dry environments is far from demonstrated.

Is it possible to test Neanderthal adaptations to dry environments outside the western Mediterranean? Leaving aside the rich record of Neanderthals from the Near East and the extreme influences of arid or semi-arid climates on those populations, it seems fruitful to examine the climatic and environmental tolerances of Neanderthals during the penultimate interglacial, MIS 7, in NW Europe. Following the widespread appearance of Levallois assemblages during MIS 8, this is the first full interglacial in that region in which the Middle Palaeolithic can be reliably identified (Bridgland, 1994, 1996) and should therefore provide an important baseline for understanding the habitat preferences of early Neanderthals in the north-west of their range.

3. Climatic and environmental structure of MIS 7

MIS 7 (243-191ka BP, Lisiecki and Raymo, 2005) is an unusual (and indeed unique) interglacial in that its pattern of climate forcing is driven by coincidence with the most extreme peak in orbital eccentricity seen over the last 800ka (Figure 1). Eccentricity modulates the effect of precession (Hays *et al*., 1976; Droxler *et al*., 2003; Berger and Loutre, 2003) so MIS 7 is characterised by higher magnitude insolation variability than any other warm stage of the Middle and Late Pleistocene, contrasting with the long and relatively stable warm conditions of MIS 1, 11 and 19 (Berger and Loutre, 2002). A defining characteristic of MIS 7 is therefore that it is a relatively "cool" temperate episode relative to MIS 5, 9 and 11 (Ruddiman *et al*., 1989; EPICA, 2004; Jouzel *et al*., 2007; Lawrence *et al*., 2009; Candy *et al*., 2010). In contrast to other late Middle and Late Pleistocene interglacials (MIS 5e, 9, 11), where the warmest part of the interglacial is clearly represented by the first temperate peak, followed by more muted interstadials, multiple marine records of both benthic $\delta^{18}O$ and sea surface temperatures record three warm peaks in MIS 7 (MIS 7e, 7c and 7a) of broadly comparable magnitude, with no obvious main peak (e.g. McManus *et al*., 1999, Figure 2). In other records, and depending on geographical location, the warmest peak varies from MIS 7e, 7c or even 7a (Imbrie *et al*., 1984; Martinson *et al*., 1987; EPICA, 2004; Lisiecki and Raymo, 2005; Jouzel *et al*., 2007). Most recently, revision of the definition of Pleistocene interglacials by Berger *et al*. (2015), based on the presence/absence of significant northern hemisphere ice outside Greenland and past sea level highstands, has proposed two full interglacials of equal magnitude within MIS 7, MIS 7e and MIS 7a-c combined.

The recognition of the penultimate interglacial is now well established in NW Europe. In Britain, a combination of river terrace stratigraphy and mammalian (and to a certain extent molluscan) biostratigraphy has proved to be the most effective means of identifying deposits of this age (Sutcliffe, 1976, 1995; Bridgland, 1994; Keen, 2001; Schreve, 2001a; Schreve et al., 2007), underpinned (wherever possible) by absolute dating (Candy and Schreve, 2007) and by aminostratigraphy (Bowen et al., 1989; Penkman et al., 2011). Although correlating the fragmentary terrestrial records with those provided by marine cores remains challenging, it has nevertheless been possible to identify additional structure *within* this interglacial, thought to correspond with climatic oscillations at sub-Milankovitch level (Schreve, 2001a, b; Candy and Schreve, 2006; Langford et al., 2014; Murton et al., 2015). Palynological studies by West (1969) had previously differentiated the early and late parts of the interglacial on vegetation grounds, identifying a transition from woodland to open grassland conditions. Two mammalian faunal groupings were proposed by Schreve (2001a, b) for MIS 7, on the basis of analysis of around 11,000 specimens from 24 localities in Britain: the Ponds Farm Mammal Assemblage-Zone (MAZ) of the early interglacial and the Sandy Lane MAZ of the later part. These can be readily separated from both older and younger interglacial faunal groupings on a number of criteria (Schreve, 2001a) and furthermore, the two MAZs differ markedly in their palaeoecological character, the former denoting the presence of deciduous woodland and the latter recording the spread of open grassland conditions (Schreve, 2001b). The attribution of the two MAZs to the earlier and later parts of the MIS 7 respectively was subsequently upheld by high-precision ICP-MS Uranium-series dating of tufa deposits, associated with vertebrate remains, from Marsworth in Buckinghamshire (UK) by Candy and Schreve (2007).

Here, we are concerned only with the period represented by the Sandy Lane MAZ, taken to be MIS 7a (or MIS 7c-7a combined, according to the new scheme of Berger et al., 2015). Although this interglacial period is not as warm as, for example, the Last Interglacial, the presence of European pond terrapin, *Emys orbicularis*, and of thermophilous molluscs and aquatic plants with predominantly southern and eastern European core distributions today (e.g. Green et al., 2006) imply warm summer temperatures of 18°C (Stuart, 1979; Candy et al., 2010), comparable to or slightly lower than those encountered in southern England today. Mutual climatic range estimates from beetle assemblages from sites dating to this interval suggest a mean July temperature of 15°C-16°C (comparable to southern and central England today) and winter temperatures between 0°C and -5°C (e.g. de Rouffignac et al., 1995; Murton et al., 2001)

Quantifying past precipitation levels in higher latitudes is extremely difficult, since complex pathways of isotopic fractionation in elemental or carbon isotope studies preclude their use as absolute estimates of precipitation (van Dam and Utescher, 2016). Herpetofaunal-based measures of palaeoprecipitation have been undertaken in Spain (e.g. Blain et al., 2015) but sites with rich reptile and amphibian fossil assemblages are very few in north-west Europe so further application of this methodology in this region may be limited. One possible route forward is through the development of hypsodonty index measurements in herbivorous mammals. This method has been successfully applied to Eurasian Neogene fossil data (Eronen et al., 2010; Liu et al., 2012) and correlated with palaeovegetation proxies in order to

predict palaeoprecipitation levels, thereby demonstrating increasing aridity through the Neogene.

In terms of vegetation, pollen spectra from MIS 7a sites demonstrate the overwhelming predominance of non-arboreal taxa, particularly grasses, sedges and dry ground herbs (West and Sparks, 1960; Shotton *et al*., 1962; West, 1969; Green *et al*., 1984, 1996; Buckingham *et al*., 1996; Murton *et al*., 2001), denoting open grassland habitats. Where tree pollen is present, it occurs in low proportions and is suggestive of patches of open woodland (e.g. Green *et al*., 1996). The ability of modern large herbivores to maintain and even enhance their environment through grazing is well established (McNaughton, 1985) and there is no reason why Pleistocene herbivores should have behaved differently (see Guthrie, 1990). Furthermore, the action of grazing enhances drying through a decline in residual surface plant litter and a reduction in surface water infiltration (compounded by surface compaction by grazing animals), which leads to increased evapotranspiration and continuing drying. This is not to imply that the landscape during MIS 7a in Britain was xeric (ie. too arid to support vegetation) but instead, may be summarised as one of dry, predominantly open grassland conditions.

The vegetation record is is consistent with the evidence from the mammalian record for late MIS 7. Sites in Britain are generally dominated by what have informally been referred to as "mammoth-horse" assemblages. These are characterised by the presence of a late morphotype of steppe mammoth (*Mammuthus trogontherii*), first co-existing with, and then giving way to, woolly mammoth (*Mammuthus primigenius*) (Lister and Sher, 2001), in association with wild horse, *Equus ferus*. Narrow-nosed rhinoceros (*Stephanorhinus hemitoechus*), bison (*Bison priscus*), aurochs (*Bos primigenius*), red deer (*Cervus elaphus*) and giant deer (*Megaloceros giganteus*) are well-represented, highlighting the predominantly open character of the vegetation, whereas species generally associated with woodland (straight-tusked elephant, *Palaeoloxodon antiquus*, and Merck's rhinoceros, *Stephanorhinus kirchbergensis*) are reduced in number, and fallow deer (*Dama dama*) is entirely absent (Schreve, 2001a). Overall, the assemblages are consistent with the concept of Kahlke's (1999) *Mammuthus-Coelodonta* faunal complex, which expanded into dry, steppic environments after the Saalian glaciation, although it is not necessary to infer that open habitats equate with cold climate, as is often misunderstood from the palynological and other proxy records. The possibility of a warm, dry steppic environment has therefore been largely overlooked.

The addition of other taxa to the Sandy Lane MAZ gives it a further pronounced dry and/or continental flavour not seen in other interglacial assemblages. In particular, this period sees the presence in Britain of woolly rhinoceros (*Coelodonta antiquitatis*) and wild ass (*Equus hydruntinus*), both suited to dry and open habitats, irrespective of temperature inferences (Kahlke, 1999; Abbazzi *et al*., 1996; Bonfiglio *et al.,* 2001). The small mammal assemblages are equally distinctive when compared to those from immediately preceding and succeeding interglacials, including taxa such as the common hamster, *Cricetus cricetus*, *Allocricetus bursae* (possibly conspecific with the living grey dwarf hamster, *Cricetulus migratorius*) and *Citellus citellus* (probably conspecific with the living long-tailed ground squirrel, *Spermophilus undulatus*) representing a pronounced westwards movement of taxa that are today distributed in

dry grasslands, steppes and semi-deserts (Kryštufek *et al.*, 2008a,b; Shar and Lkhagvasuren, 2008).

The Sandy Lane MAZ therefore comprises a distinctive group of taxa that can be traced more widely across NW Europe. In France, mammalian assemblages from Vassincourt (Meuse), Moru and Sempigny (Oise), Tourville-la-Rivière (Seine-Maritime), Biache-Saint-Vaast and Arques (Pas-de-Calais) and levels 20-18 at Achenheim (Bas-Rhin) contain characteristic taxa such as the late morphotype of *Mammuthus trogontherii* and have been attributed, on mammalian faunal grounds, to the later part of MIS 7 by Auguste (1995). In Germany, the Lower and Upper Travertines at the site of Weimar-Ehringsdorf, historically correlated with the Eemian interglacial, have been attributed to the MIS 7 interglacial on the basis of the mammalian assemblages (summarised in Schreve, 2002) and Uranium-series and ESR dating (Blackwell and Schwarcz, 1986; Mallik *et al.*, 2000; Schüler, 2004). New In particular, aspects of the Upper Travertine faunal assemblage compare closely with the Sandy Lane MAZ, including the abundant presence of the late morphotype of steppe mammoth and the absence of straight-tusked elephant and fallow deer. This characteristic mammalian faunal suite is therefore widespread across NW Europe, highlighting the extensive development of warm, dry steppic habitats during this interglacial.

This was a landscape in which Neanderthals thrived. By way of illustration, early Middle Palaeolithic sites of late MIS 7 age in Britain include those from the Taplow/Mucking Gravel Formation of the Thames terrace sequence, such as the upper beds at Aveley in Essex (Schreve, 2004) and Crayford in Kent (Spurrell, 1880), Maidenhall and Stoke Tunnel in Suffolk (Layard, 1912) and Pontnewydd in Dyfed (Green, 1984). In France, assemblages have come from Osiers à Bapaume (Pas-de-Calais, Koehler, 2008), Biache-Saint-Vaast (Tuffreau and Sommé, 1988) and Therdonne (Oise) (Locht *et al.*, 2000) amongst others, whereas the Upper Travertines at Ehringsdorf have yielded a hearth and associated artefacts (Steiner and Steiner, 1975). Many more sites with rich lithic assemblages exist, although to date, it has not been possible to specify which part of MIS 7 they belong to. Nevertheless, on the basis of what *is* currently known, it is clear that Neanderthal distribution across NW Europe was more widespread in MIS 7 than during the Last Interglacial. This observation would appear to scotch any suggestion that Neanderthals were unable to cope with relatively dry conditions and in fact, one might suggest that the reverse (high precipitation) might present them with more significant problems, especially as climatic conditions deteriorated at the end of the interglacial.

4. Continuation

Neanderthals were apparently further excluded from Britain (along with much of NW Europe) by severe climatic deterioration, for example during MIS 6 and MIS 4, and by the proposed persistence of high sea levels during the early Devensian interstadials (MIS 5c and 5a) (Currant and Jacobi, 2011). During these interstadials, however, there is evidence of Neanderthal occupation in north-west France, coming from colluvial sediments infilling karstic depressions, superimposed first by a grey 'forest soil' attributed to MIS 5c, and subsequently by thin steppic soils of brief duration, attributed to MIS 5a (Locht, 2002). The Neanderthal range, however,

reached its maximum extent in Eurasia during MIS 3, the middle part of the last cold stage, stretching from western Britain to the Middle East and Siberia (Krause *et al.*, 2007).

The "Mammoth Steppe" environment of NW Eurasia during MIS 3 consisted of a broad belt of steppe-tundra that has no precise modern analogue today. In contrast to today's high-latitude tundra, which is relatively poor in nutrients and supports only low herbivore biomass, the Mammoth Steppe was much drier, with increased evaporation, higher seasonality and deeper summer thaws than prevail today (Guthrie, 1990). Estimates of animal biomass and plant productivity (10.5 tons/km^2), based on evidence from northern Siberia, are close to those of modern African savannas, some of the most biodiverse environments on earth (Zimov *et al.*, 2012). Climatic controls on the growth of woody plants instead favoured the development of rich grasslands that supported the many millions of herbivores, the grazing and dunging actions of which in turn maintained an open landscape and contributed to nutrient recycling. This was not a truly xeric environment, since perennial bodies of water existed, together with rich vegetation cover, but it was certainly a dry one. Estimates of annual precipitation for the Mammoth Steppe range from 150-300mm (Velichko and Zelikson, 2001; Zimov *et al.*, 2012), somewhat less than experienced (for example) in the modern short-grass steppe of the Great Plains of North America (mean 310mm, range 115-595mm; Milchunas *et al.*, 1989).

The Middle Devensian (MIS 3), although a relatively warmer part of the last glaciation compared to MIS 4 and MIS 2, was a period subject to rapid (often millenial-scale) stadial-interstadial climatic oscillations, as seen in the Greenland ice cores (e.g. NGRIP, 2004). Presumably Neanderthal occupation of the far north-west of Europe occurred only during the interstadial periods, although even with improved radiocarbon dating precision, standard errors on the age estimates may make this difficult to verify in all cases. What is also difficult to determine is the extent to which Neanderthals were able to withstand winter temperatures (estimated, for example at Lynford, Norfolk, to be as low as -15°C for January, Coope, 2012), perhaps necessitating seasonal occupation only of the far north-west. In contrast, mean summer temperatures in the region of 12°C to 14°C at Lynford (Coope, *ibid*) presumably posed no such problem but some interstadials were even warmer than this, with palaeoclimatic reconstructions based on wider coleopteran evidence for this period indicating summer temperatures reaching 17ºC at certain points (Coope, 2002).

For the Late Pleistocene Neanderthals in the north-west of Europe, this would have been highly familiar turf, especially looking back at the environments of MIS 7 in which they had previously flourished. The suite of mammalian species present in MIS 3 indicates extremely close parallels with those of MIS 7c-7a, notably in terms of potential prey species and carnivore competitors. Although the temperate-adapted rhinoceroses of MIS 7 were by now long extinct and the presence of reindeer (*Rangifer tarandus*) marks a significant new Late Pleistocene component, the large herbivore guilds of MIS 3 and MIS 7c-7a are remarkably similar, with mammoth, woolly rhinoceros, horse, bison, giant deer and red deer common to both, the last present in the south of Britain during MIS 3. As suggested by Currant and Jacobi (2011), in the light of apparent significant consumption of woolly mammoth and woolly rhinoceros by Neanderthals (Drucker and Bocherens, 2004), it is perhaps no

coincidence that Britain was reoccupied when those two species became re-established. Key elements of the carnivore guild are also identical, namely brown bear, spotted hyaena, lion and wolf (Schreve, 2001a; Currant and Jacobi, 2011). In the small mammal assemblages, the presence of elements such as ground squirrel in Britain (Currant and Jacobi, 2011) recalls the earlier, westwards movement of dry, continental taxa during late MIS 7. It was under these conditions that Neanderthals reached their maximum range and scale of activities.

5. Crossing the Threshold

Inferences of Neanderthal habitat preferences based on evidence from Iberia may well be appropriate for examining the context of Neanderthal extinction in the Late Pleistocene of southern Europe but they are atypical of the majority of the record, failing to capture the range of environments occupied in other parts of Europe and at other times. While Neanderthals were evidently able to survive in the locally-open forests of central Germany during the Last Interglacial, it is difficult to keep arguing for successful and sustained colonisation of the rest of north-west Europe during the warm and oceanic conditions of MIS 5e. Although rapid sea level rise may explain Neanderthal absence from Britain at this time, preservational bias cannot account for the lack of sites (even isolated or scattered finds) elsewhere, especially when one considers the abundance of Last Interglacial palaeoenvironmental records and indeed those of older interglacials across the region, seemingly spared from the forces of erosion.

In many respects, early Neanderthals crossed a threshold as early as 220,000 years ago, during the MIS 7c-7a interglacial, a period that marked their initial successful occupation of north-west Europe, a level of accomplishment that was not repeated again until MIS 3, when they attained their maximum geographical range. This does not mean that Neanderthals were becoming progressively used to cold, open conditions (*contra* Ashton, 2002), since as seen above, summer temperatures during the interstadials of MIS 3 were similar to and sometimes even exceeded those reconstructed for MIS 7c-7a. A crucial point here is that these open grasslands were (frequently) warm and dry habitats, a fact that has been all too often overlooked in cases where vegetation records dominated by grasses and herbs have been simplistically equated with cold-climate conditions. It is clear that Neanderthals were far from marginalised by such environments, given their widespread presence at times when such dry, productive habitats prevailed. Obtaining direct measurements of past rainfall is difficult given the range of proxies available, but ongoing development of new modern training sets for herbivore hypsodonty may allow better quantification of exactly how dry these environments were, thereby allowing more nuanced comparison with established refugial areas in the Mediterranean.

Neanderthals could still be forced out by extremes of cold but the MIS 7c-7a and MIS 3 environments are unified by their dry and open character. The singular conditions of the Last Interglacial may therefore be viewed as something of a brief reversal (quite literally a set-back) for Neanderthals in an otherwise consistent trend of preference. It is an interesting aside to note that even today, modern human aesthetic preferences favour savanna-like settings with relatively uniform length grasses, scattered trees and water, and that those preferences are cross-cultural in studies of North Americans, Europeans, Asians, and Africans (Frumkin, 2001), perhaps revealing a deep-rooted affinity for those habitats. Open environments

would have offered superior opportunities for identifying resources, shelter and predator avoidance but a relatively treeless landscape presents its own challenges, in terms of requiring greater mobility, enhanced social flexibility and more developed hunting techniques. The last links clearly to the dietary stable isotope evidence for hyper-carnivory in Neanderthals (Bocherens *et al*., 1999, 2001) but the openness of the environment may have accelerated other developments, for example the use of concealment and ambush hunting techniques, where animals were manipulated into places where they could be disadvantaged before being dispatched (White *et al*., 2016). Such techniques had been practised and indeed perfected for almost 200,000 years.

Acknowledgements

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List of Figures:

Figure 1: Comparison of the climatic structure of MIS 7 (LR04 stack and EPICA) with insolation curves for 65°N and orbital parameters over the last 800ka.

Figure 2: Detail of the structure of MIS 7, highlighting peaks of different magnitude depending on geographic location and latitude (North Atlantic and Atlantic), shown against the LR04 stack and SPECMAP.

LR04 stack

1 5 7 9 11 13 15 17 19

EPICA EDC3

"warm" interglacials

mid-Brunhes Event

"cool" interglacials

Insolation 21 June 65°N

Eccentricity

Precession

Obliquity

Time (kyr BP)

Time (kyr BP)

a) N Atlantic ODP 982 (57.5 N)

Mean SST (°C)

b) Atlantic Core DSDP 607 (41 N)

SST summer (°C)

c) LR04 stack

δ¹⁸O ‰ (PDB)

7a

7c

7e

7b

7d

d) SPECMAP

Ice Volume (s.d. units)

Time (kyr BP)