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Walking in a winter wonderland? Strategies for Early and Middle Pleistocene survival in mid-latitude Europe

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Abstract

Any occupation of northern Europe by Lower Palaeolithic hominins, even those occurring during full interglacials, must have addressed the challenges of marked seasonality and cold winters. These would have included the problems of: wind-chill and frostbite; duration, distribution and depth of snow-cover; reduced daylight hours; and distribution and availability of animal and plant foods. Solutions can essentially be characterised as a 'stick or twist' choice: i.e. year-round presence on a local scale vs. extensive annual mobility. However these options, and the 'interim' strategies that lie between them, present various problems, including maintaining core body temperature, meeting the energetic demands of mobility, coping with reduced resource availability and increasing patchiness, and meeting nutritional requirements. The feasibility of different winter survival strategies are explored with reference to Lower Palaeolithic palaeoenvironmental reconstructions and on-site behavioural evidence. Emphasis is placed upon possible strategies for (i) avoiding the excessive lean meat protein problem of 'rabbit starvation' (e.g. through exploitation of 'residential' species with significant winter body fat and/or by targeting specific body parts, following modern ethnographic examples, supplemented by the exploitation of winter plants); and (ii) maintaining body temperatures (e.g. through managed pyrotechnology, and/or other forms of cultural insulation). The paper concludes with a suggested winter strategy.

Keywords

Winter; Early and Middle Pleistocene; Mid-latitude Europe; Migration; Residency

Introduction

Recent discoveries, mostly notably the sites of Pakefield and Happisburgh III (Ashton and Lewis 2012; Parfitt *et al*. 2005, 2010; but see also Harnham: Bates *et al*. 2014), have highlighted, and extended, the range of environmental tolerances attributable to Early and Middle Pleistocene hominins in mid-latitude regions of the northern hemisphere. The inferred environmental conditions, in particular the southern Scandinavian-type environments suggested for Happisburgh III (Ashton and Lewis; 2012; Parfitt *et al*. 2010), have led to discussions about possible adaptive strategies: behavioural (e.g. fire and sheltering technologies, migration) and physiological (Ashton and Lewis 2012). Two key questions are highlighted for Lower Palaeolithic studies: how extensive were individual occupation ‘events’ in northern European landscapes, and how did hominins cope with the challenges of winter?

This paper explores both of these questions, with particular reference to meeting the winter challenges of temperature and food availability in mid-latitude Europe. While specific evidence relating to hominin solutions to the ‘winter problem’, e.g. annual migration, is frequently tenuous, possible archaeological indicators of those solutions are highlighted below, and the implications of their presence or absence reviewed. The paper thus follows the spirit of Gamble (1987) and White (2006). In exploring solutions to the winter problem, it seeks to offer an ‘on the ground’ insight into the character and chronology of the Lower Palaeolithic occupation of Europe, and by extension of middle latitudes throughout Eurasia. It builds on the classic works of Roebroeks’ (2001, 2006), Gamble (1987) and White (2006), combining Roebroeks’ and Gamble’s emphasis on the winter problem with White’s focus on solutions to the day-to-day problems of Pleistocene survival. In particular it was inspired by the recent extensions to the Lower Palaeolithic chronology of northern Europe (e.g. Parfitt *et al*. 2005, 2010) and by Roebroeks and Villa’s (2011) critique of European Palaeolithic fire evidence, which together have highlighted the intriguing question of how Europe’s earliest occupants survived, and by extension, what sort of ‘humans’ they were.

It has been widely recognised since the mid-1990s that the European record, especially in the north, shows a marked change after *c*. 500,000 years ago (e.g. Roebroeks and van Kolfschoten 1994; Dennell and Roebroeks 1996). This shift has been related to the increased encephalisation and new behaviours associated with *H. heidelbergensis* after *c*. 600,000 years ago (e.g. Gamble 2009; Ashton 2015). Nonetheless this paper’s point of departure is the entirety of the European Lower Palaeolithic, and therefore the species *H. heidelbergensis*, *H. antecessor* and, potentially, *H. erectus sensu lato* (Wood and Lonergan 2008). This choice was made in order to explore the practical challenges of winter survival without pre-judging them through the lens of one European Lower Palaeolithic hominin species or another. The potential implications of those challenges for the pre-/post-500kya pattern are explored in the Discussion.

Winter challenges in the north

The challenges presented by mid-latitude winter conditions to hunter-gatherers have been previously discussed (e.g. Gamble 1987; Roebroeks 2006) and are therefore only summarised briefly here. In short, Early and Middle Pleistocene hominins would have to cope with (i) lower, compared to summer, temperatures, including marked day/night contrasts and the problems of wind-chill and frostbite; (ii) the duration, distribution and depth of snow-cover, and other forms of precipitation; (iii) reduced daylight hours; and (iv) the distribution and availability of animal and plant foods, with associated nutritional shortfall issues.

Kelly (1995) and Roebroeks (2001, 2006) also highlight three key principles which impact on foraging strategies and mobility in the mid and higher latitudes: (i) that mammalian territory sizes increase with latitude; (ii) that resources become increasingly segregated with decreasing temperatures; and (iii) that hunter/gatherer territory sizes increase with greater dependency upon hunting.

Winter temperature estimates (T_{min}; Table 1) for Early and Middle Pleistocene north-western and north-central Europe highlight the challenges faced by non-migratory Lower Palaeolithic hominins in these regions. These estimates are based on British and German sites, as Ashton and Lewis (2012) have emphasised the comparability of British conditions with those of the near continent. Trinkaus *et al*. (1999:21–22) have previously argued that the inferred body proportions of the Boxgrove hominin

(*H. heidelbergensis*), in association with late interglacial cool temperate conditions, suggests significant biological rather than cultural solutions to the problems of conserving body heat. However minimum sustainable temperature predictions of between 11.6°C and 6.2°C for *H. erectus* (the latter adjusted for elevated BMR and increased muscle mass) do suggest limitations for purely biological solutions (Supplementary Materials: Table 1; Aiello and Wheeler 2003; this is also true for the robust and arctic body proportioned Neanderthals). Such climatic challenges become even more marked when wind-chill factors are considered (using the Stage 3 Project models as a comparative data set; van Andel and Davies 2003), although these would be reduced in closed woodland habitats, while Pettitt and White (2012:35) have noted that winter temperature estimates tend to be warmer than the reality. These figures make a strong case that the winter temperatures recorded at known occupation sites were habitually beyond the tolerances of an ‘unmodified’ Middle Pleistocene hominin. It is also likely that winter temperatures were even more challenging at sites with apparent evidence of occupation in cooler conditions, such as Cagny la Garenne (Tuffreau and Antoine 1995:151–155; Antoine *et al*. 2010), Kärlich Lower Layer H (Bosinski 1995:115), and the Boxgrove Eartham Formation (Roberts 1999:382–384).

These site-based winter temperature estimates are in notable contrast with those from Early Pleistocene sites from southern Europe (Figure 1; temperatures from Agusti *et al*. 2009). The narrow overlap range is between -1 – +6°C. Leroy, Arpe, and Mikolajewicz (2011:1461) have also suggested on the basis of palynology, from 12 southern European hominin sites, and climatic modelling, using the 9ka glacial–interglacial transition as the best currently available analogue, that the first

Europeans of the Early Pleistocene were only able to cope with a narrow winter temperature range of 0 – +6°C. In short, a northern European winter would appear to present challenges which were frequently beyond the capabilities of the earliest European hominins (*H. antecessor* and *H. erectus s.l.*), thus raising important issues with regards to the timing, duration and character of hominin range expansions into northern Europe (see also discussions by Dennell, Martinón-Torres, and Bermúdez de Castro 2011; Roebroeks 2001, 2006).

While the north-western European habitats between 0.9–0.4mya are summarised by Kahlke *et al*. (2011:1383), based on West Runton, as consisting of “temperate climate, high precipitation and low seasonality, typical of oceanic mid-latitude Europe, supporting a diverse ecosystem dominated by forest but with productive open areas as well [West Runton]”, the palaeoclimatic indicators also imply the possibility, and at times probability, of sub-freezing winter temperatures. In the broadest sense, such challenging winters can be managed by varying strategies: extensive annual mobility (i.e. migrations) or local residency (i.e. ‘toughing it out’).

Summer visitors?

The term annual migration has been adopted here to describe a long distance (e.g. 100s km) movement, distinct from the shorter (i.e. 10s km) residential moves which occur in response to changing resource distribution and availability throughout the year (e.g. Jochim 1981:148–155; Kelly 1995, fig. 4.7). Evaluating the feasibility of an annual autumn migration as a winter survival strategy requires consideration of the scale of movement necessary for the strategy to be effective (see also Ashton and Lewis 2012), and the practical factors (e.g. resource knowledge, group composition, assessment of risk) which influenced and impacted upon migratory behaviour (Kelly 1995:144–148). The key variables are identified here as: (i) gradients of climate change; (ii) gradients of habitat change; (iii) rates of hominin movement; (iv) resource knowledge; and (v) the drivers of long distance mobility. Latitudinal and longitudinal gradients of climate and habitat change are explored with reference to the Stage 3 Project data for MIS 3 'warm' intervals (van Andel and Davies 2003). Those project data are not used as exact estimates for Early and Middle Pleistocene conditions, but are used to provide insights into likely degrees of latitudinal and longitudinal change, and into differences and contrasts between multiple palaeoclimatic measures. As it is possible that these gradients of change might be influenced by changes in European palaeogeography (Barron, van Andel and Pollard 2003:58), the MIS 3 'warm' interval data was also cross-compared against the project's 'modern' simulation values (Supplementary Materials: Table 2). The gradients of change for the palaeoclimatic categories discussed below were all broadly comparable, supporting the use of the MIS 3 'warm' interval data here. Discussions of mobility to and from Britain specifically refer to either the pre-MIS 12 period when Britain and the near-Continent where permanently connected by the Weald–Artois chalk ridge, or later temporary intervals of connection. These latter intervals occurred, and permitted hominin mobility, due to a combination of (i) habitable conditions and (ii) relatively low sea-level stands and/or relatively elevated sea-bed heights which resulted in the short-lived emergence of dry land (e.g. MIS 11 stadials in the southern North Sea Basin; Ashton and Lewis 2002; Ashton, Lewis, and Hosfield 2011).

The drivers of an annual autumn migration are argued here to be a requirement for habitats with one (or more likely both) of the following characteristics: milder climatic conditions (e.g. warmer, with reduced snow cover and/or precipitation) and enhanced availability of winter foods (animal and/or plant). It is not assumed that migrations would have pre-set ‘destinations’, either settlements or specific landscape locations in the style of modern hunter-gatherers (e.g. Binford 1980) or the equivalent of the winter/summer feeding grounds and spring/early summer calving grounds that structure ungulate migrations (e.g. reindeer; Burch 1972:345). However such regular ‘destinations’ may have been a possibility if animal movements were a migration driver and herds were tracked by hominins, given the strong fidelity demonstrated by ungulate migrants to particular routes (Lendrum *et al*. 2012, and references therein). Irrespective of the above it is argued that hominin movements on a day-to-day basis would be structured by landforms (e.g. surface drainage and relief), local conditions (e.g. thickness of woodland, ground surface conditions under-foot), local resource availability (e.g. plant and animal foods, possibly fuel for fire), and environmental cues of changing conditions (e.g. vegetation characteristics and animal behaviours).

<ins>Palaeoenvironmental gradients</ins>: Mean winter air temperature data from the Stage 3 Project (Barron, van Andel, and Pollard 2003, fig. 5.7; Figure 2) emphasises the limited benefits to be gained from a simple north–south migration in north-western Europe. The temperatures vary from -4 – 0°C (at 52°N, 0°E ≈ north London) to 0 – +4°C (at 45°N, 0°E ≈ Bordeaux; a distance of *c*. 780km ‘as the crow flies’), the latter still falling within the (upper end) of the range evident at British sites (Table 1 and Figure 1). Interestingly, following a ‘coastal’ route southwards from 52°N, 0°E offers

comparable improvements in air temperature over shorter distances (reflecting the topography of western Europe and the ameliorating effects of maritime climates; see also Cohen *et al*. 2012). By contrast, the distinct northeast–southwest trend for the main temperature gradient (Barron, van Andel, and Pollard 2003:64) highlights the challenges of occupation in the northern European continental interior (e.g. the ‘zone’ of Bilzingsleben and Schöningen: Mania and Mania 2005; Thieme 2005).

The coastal/continental interior contrast is also evident in two of the Stage 3 Project’s other palaeoclimatic measures: summer and winter contrasts in mean air temperatures (Barron, van Andel, and Pollard 2003, appendix 5.1; Figure 3) and snow-cover characteristics (snow depth and the number of days with snow cover: Barron, van Andel, and Pollard 2003, fig. 5.9; Figures 4–5). The former data again highlights the ameliorating effects of coastal settings, with less marked summer/winter contrasts in the coastal west of the continent (although the day/night temperature contrasts for the winter months follow an essentially north–south trend). In the case of snow, the coastal zone offers both a shallower cover, and a reduced number of ‘snow days’. This would be relevant to migrating hominins in terms of their own movement, with regards both to the increased energetic costs of moving through snow (and the potential exposure to frostbite), and with regards to the timings of any migrations. However it is also highly significant in terms of resource distribution (and acquisition), as snow cover is a key limiting factor for particular species (e.g. 50–70cm+ for *C. elaphus* and 60cm+ for *R. tarandus*; Gamble 1986, table 3.12).

A further key factor associated with winter survival in cold landscapes concerns frostbite and hypothermia (the latter occurring in *H. sapiens* when the core body temperature falls below 35°C: Pocock, Richards, and Richards 2013:783). It is of course relevant both to migratory and residential strategies. For modern populations frostbite occurs in sub-freezing (0°C) temperatures, principally affects extremities (i.e. toes, fingers, ears and nose), and is exacerbated by high levels of heat loss. The latter can occur as a consequence of various factors, including wet clothing, over-exercise, and un-replaced calories (Golant *et al*. 2008). The avoidance of frostbite (typically achieved in modern populations through food, shelter and/or clothing) would therefore place significant demands on, at the least, the abilities of Early and Middle Pleistocene hominins to acquire resources (food and, probably, fuel) and to balance the needs for, against the risks of, high levels of daily movement. It might also impact on the timings of seasonal migrations.

However the model of mild coasts and harsh interiors suggested above is not necessarily the full picture. While there is a distinct northeast–southwest trend for the winter temperature gradient and for wind chill (Barron, van Andel, and Pollard 2003, appendix 5.1; Figure 6), precipitation shows a clear increase from the interior to the coast (Barron, van Andel, and Pollard 2003, appendix 5.1; Figure 7). Thus, the western coasts, while relatively warm and with reduced wind chill and snow cover (Figures 2 and 4–6), might also present the challenges of more regular rainfall, with its implications for the availability of dry fuel. Moreover, the Stage 3 project models of net primary productivity (gC/m2/year) and annual growing days (above 0°C and 5°C) indicate higher values (and therefore longer and more productive summer growing seasons) for inland areas of western Europe (eastern France and southern

Germany: Barron, van Andel, and Pollard 2003, appendix 5.1). This would have clear implications for plant (and therefore animal) food availability, and could potentially offer a more easily ‘reachable’ (from northern Europe) winter range (but *cf*. the comments above regarding temperature and snow cover gradients).

Hominin mobility & resource acquisition: The hypothetical distance of nearly 800km outlined above prompts consideration of a key aspect of any migration ‘strategy’: group composition. If migrations involved entire groups, then how did the very young move? Were they carried? Were they walking (where able)? Either way, this would seem to impose obvious restrictions on distances covered, as would the shorter daylight hours associated with late autumn–winter–early spring periods at high latitudes (e.g. *c*. 8.0–8.5 hours/day in late November/early December at 50°N). Wall-Scheffler and Myers (2013) have modelled the impacts of the persistent reproductive loads associated with both pregnancy and child-carrying: slowing down females and reducing group speeds. This is especially noteworthy in light of pregnancy cycles, with Mussi (2007:170–173 and fig. 3) suggesting a peak in conception in late summer/early autumn, with implications for both mobility and nutritional requirements in winter/early spring. Alongside the issue of individual and group mobility, daily travel time would presumably also be shortened by the need to acquire resources — food, fresh water and potentially also fuel — and Kelly (1995:133), drawing on various sources, suggests a 20 to 30km round trip as the maximum distance that hunter/gatherers will walk comfortably in a day in a variety of habitats. This broadly tallies with Dingwall *et al*.’s (2013:565) suggestion of 1.0–2.2 miles/hour (1.6–3.5 km/hour; described as very slow walking speeds) based on the Ileret footprints. Kelly’s lower estimate of 20km/day is adopted here, partly to acknowledge group composition but also in recognition of winter day lengths. At these speeds the 780km (straight-line) distance from 52° to 45°N would still take 39 days, before taking account of local relief, vegetation cover and ground condition, and larger obstacles such as major rivers. While the ‘speed of the slowest member’ problem can be reduced by simply abandoning the slow (whether sick, old or young: see also Pettitt 2000) this would seem to be an unlikely evolutionary solution if it habitually extended to the group’s young, pregnant and infant carriers. These problems can be significantly reduced if the migrating group consists only of selected adults (e.g. a logistical summer hunting party). Such arguments have been made for the Neanderthals (e.g. with reference to the British MIS 3 record and its distinctive signature of bout coupé handaxes: White 2006), and are not unfeasible in light of Kelly (1995) and Roebroeks’ (2001, 2006) arguments concerning resource distribution, territory sizes and mobility in mid and high latitudes. However the Lower Palaeolithic archaeological record offers little clear evidence for task-specific sites and/or tool-kits, with only occasional exceptions such as Schöningen (Thieme 2005; which may itself represent behaviours more reminiscent of the Middle rather than the Lower Palaeolithic: e.g. Balter 2014; van Kolfschoten 2014).

Intra- and inter-seasonal mobility has often been discussed, for various periods and different hunter/gatherer groups, in terms of animal migrations and resource interception (e.g. Loring 1997; Spiess 1979, Ch. 4). But with regards to long distance migrations (driven at least in part by a ‘search’ for milder climatic conditions) and the question of food acquisition, then as Gamble (1987:87) has noted: “the mobility of prey far exceeded the capacity of the human predator to keep up” (see also Burch 1972, but *cf*. Spiess 1979:137–139). Practical Lower Palaeolithic alternatives might therefore include the interception of herds and other resources encountered over the course of the hominins', and potentially also the animals', migration (see Spiess 1979 for various examples), or perhaps a 'lag' pursuit of migrating herds whose summer territories overlapped with that of the hominins. Both strategies would require notable 'natural history' knowledge (after Mithen 1996): whether in terms of a knowledge base concerning the timing and locations of available animal (and plant) foods along the migration 'route' (and suitable hunting grounds, perhaps in the form of ungulate stopover sites; e.g. Sawyer and Kauffman 2011), or in the form of 'reading' the tracks of a migrating herd combined with landscape memory of traditional ungulate routes (e.g. Burch 1972:351–352; Haynes 2006). The 'lag' pursuit model would, in particular, also require the finding of alternative food sources en route.

This last point highlights a further migration issue. It would presumably involve, on each separate occasion, habitats which although essentially familiar in terms of their flora and fauna and the presence of 'readable' cues (e.g. tracks, sounds, dung), would also contain fixed resource locations which would need to be found/learned (e.g. lithic outcrops, pools for ambush hunting). This application of locational and limitational knowledge and information from existing familiar landscapes to new locations has been highlighted by Rockman (2003:4 and 19). Rockman noted that the transferability of knowledge may vary according to how fixed a resource is and to the scale of its distribution (e.g. contrast large animal ranges with plants and lithic materials, the latter of whose distributions are respectively controlled, and subject to modification, by local variations in climate and topography and geological history).

This would presumably add to the demands and costs of resource acquisition, as might the processing of those resources within a near-continuously mobile lifestyle.

Of course such movements would also not have occurred in isolation. This issue is considered in more detail in the Discussion, but long-distance autumn migrations would only have been required within a wider context of twice-yearly movements (e.g. northwards in spring and southwards in autumn). Alternatively, for a previously residential ‘northern’ group, long-distance movements could occur in response to markedly deteriorating climatic conditions and/or resource availability. In light of this, and returning to the five factors outlined above, the challenges of group mobility (iii) and resource acquisition (iv), combined with the relatively shallow gradients of climate and habitat change (i and ii), would seem to argue against the feasibility of migrations as an evolutionary strategy for coping with the challenges of mid-latitude interglacial winters in north-western Europe. This conclusion is in-keeping with Hublin and Roebroeks’ (2009) related argument that an ebb and flow model for the Neanderthal occupation of northern environments, as opposed to local extinctions, was not supported by either palaeo-ecological, archaeological or palaeogenetic evidence. This leads inevitably to the question of how those winter challenges were met by residents.

Winter residents?

The principle challenges associated with winter residency are identified here as: (i) securing sufficient fuel (and other) resources to ameliorate the effects of low temperatures; (ii) securing sufficient food resources to meet nutritional needs; (iii) managing group structure and organisation; and (iv) local mobility in a winter landscape. Factors i–iii would of course also apply during annual migrations.

<u>Cultural insulation solutions?</u> While evidence for Lower Palaeolithic pyro-technology is limited (Roebroeks and Villa 2011) there are nonetheless clear European examples from the late Middle Pleistocene (e.g. Beeches Pit, Bilzingsleben and Menez-Dregan 1: Mania and Mania 2005; Mercier *et al*. 2004; Preece *et al*. 2006; but *cf*. differing views regarding the claimed hearths at Schöningen and the chronology at Menez-Dregan 1: Balter 2014; Mercier *et al*. 2004; Monnier *et al*. 1994; Thieme 2005). It is perhaps noteworthy that the Beeches Pit and Bilzingsleben examples are from non-fluvial contexts, and the lack of a wider evidence base for fire use may well be a taphonomic consequence of the bias towards high energy river floodplain sediment traps in the European Lower Palaeolithic record (e.g. Roebroeks and van Kolfschoten 1995; Gowlett 2006). Such environments are likely to be unfavourable to both the preservation of fire traces and perhaps also to the hominin inclination to produce it in such locations, although later sites in open-air settings do produce fire traces (e.g. Neumark-Nord 2; Roebroeks and Villa 2011). The absence of fire evidence at well preserved cave site occupations such as Gran Dolina and Arago is also a possible argument against fire use in Europe's earlier Lower Palaeolithic (Roebroeks and Villa 2011). The benefits of fire have been widely discussed, spanning warmth, cooking(?), defence against predators, and extending the hominin day, both in terms of 'hearth-side' tasks such as tool-making and with regards to the maintenance of social bonds (Dunbar and Gowlett 2014; Wrangham 2009). However it is important to recognise that fire also brings demands: the challenges of locating dry fuel (a particular problem in, although not exclusive to,

winter, with implications for foraging activities) and the requirements of keeping a fire ‘in’ (with potential consequences for individual roles and group sub-divisions). The latter is particularly significant if the need for individuals to be warm and dry extended fire use beyond the dark hours, or if hominins lacked the ability to kindle fire and were reliant on gaining fire through network links or lightning strikes (Gowlett 2006:307).

Potentially complementing fire as a cultural buffer against the winter cold is the possibility of shelters. Although these have been considered with regards to European Neanderthals (e.g. Chu 2009; White 2006), their proposal in Lower Palaeolithic contexts, even terminal ones (e.g. Bilzingsleben: Mania and Mania 2005), has been contested with debates surrounding the interpretation of the material traces and questions over site integrity and taphonomy (e.g. Gamble 1999:153–172; Vollbrecht 2000. At the same time, consideration should be given as to the detectability of early structures (e.g. if constructed primarily from animal skins, wood, and other vegetation), and the bias of the sediment archive towards specific locations (see also the comments above regarding the evidence for fire). While caves might provide an alternative form of shelter (with Lower Palaeolithic European examples including Arago: e.g. de Lumley and de Lumley 1973) their availability is inevitably restricted at local and regional scales by geological history. Hominins would also face significant competition for such shelters, e.g. from spotted hyena and cave bear. Woodland settings offer both advantages (reduced wind chill, availability of fuel for fires and various raw materials for potential shelters: Met Office 2011) and disadvantages (lower temperatures) as settings for sleeping sites or even sustained permanent camps. Woodlands also offer food resources of course, although Jochim (1981) has noted that these vary between temperate and boreal forests, with the former characterised by longer growing seasons, greater diversity of plants (and animals) and a greater range of exploitable plants.

The suggestion of some form of shelter is not intended to propose the existence of an essentially modern hunter/gatherer in an Early or Middle Pleistocene context (see also Gamble's re-interpretation of the Bilzingsleben site: 1999:153–172). It is however intended to focus attention onto the simple physiological demands of surviving a northern European winter during periods of documented hominin presence. Physical adaptation remains an interesting possibility, and it is well known that human physiological changes can occur rapidly on an evolutionary timescale, e.g. the emergence of high levels of lactose digestion capacity as an adaptation to dairying during the Holocene (Holden and Mace 1997). However Ashton and Lewis (2012:59–60) have argued that physical adaptations to the cold would seem an unlikely evolutionary investment given the apparently brief nature of northern excursions during the Lower Palaeolithic and the potentially short 'occupation windows' suggested by ice core studies (e.g. Jouzel *et al*. 2007). It has also been noted that the Neanderthals, despite their well-documented physical changes, would still have required additional cultural insulation (e.g. Aiello and Wheeler 2003; White 2006).

However fire and shelter alone would not seem to solve all of the climatic challenges of a northern European winter: sub-freezing temperatures and/or snow cover would also threaten frostbite, and potentially restrict the duration of mobile foraging activities. Wales (2012) has recently modelled likely clothing coverage for

Neanderthals based on an ethnographic survey of 245 modern and historical hunter-gatherer groups. Even set against the favourable Pleistocene extremes of MIS-5e, and using southern Britain as a ‘point’-specific example, Wales (2012, figs. 3, 5, 8 and 9) suggests minimum–maximum ranges of 20/30–40/60% (of the body covered by clothing), 25–75% (probability that hands were covered by clothing) and 25–50% (probability that feet were covered by clothing). Moreover, for the warm phases of MIS-4 and 3, those figures change, respectively, to 30/40–70/80%, 50–90%, and 75–90%. Although the majority of Lower Palaeolithic occupations appear to have been in conditions closer to MIS 5e (e.g. Table 1), the latter set of figures is particularly interesting with regards to the suggested southern Scandinavian-type conditions of Happisburgh III (Parfitt *et al*. 2010), the late MIS 11 occupation of Hoxne (Ashton *et al*. 2008a), and other ‘cool’ sites (e.g. Cagny la Garenne; Tuffreau and Antoine 1995).

While tailored clothing is not being assumed (but see White 2006 for a discussion of the limitations of non-tailored Palaeolithic clothing), hand and feet ‘wraps’ would not seem to be beyond the capability (or the needs) of Lower Palaeolithic hominins. This is noteworthy in light of the range of fur-bearing animals documented on northern European Middle Pleistocene sites (Table 2). Different species would also provide pelts with different properties: thicker and warmer (e.g. fox; Hammel [1955, table 1] reported a total insulation value of 6.8 clo for *V. fulva*, compared to 6.6 clo for *C. lupus*, 5.4 clo for untanned *R. arcticus*, and 5.2 for *L. canadensis*) or durable (e.g. otter). In the case of beaver, the dense fur (12,000–23,000 hairs/cm^3 of skin) is in prime condition in the latter part of winter, while the dead wood in beaver territories, both chips from gnawing and dry wood from standing dead trees, would be a further valuable resource (Coles 2006:48 and 54). The territorial habits of the modern equivalents of selected species (excluding *C. lupus*) suggest that their furs may have been available without extensive, energetically-expensive searching (although their catching may have been rather more demanding). Many such furs would also have been best acquired in the late summer when in better condition (and when foraging activities would not face the challenges of winter snowfall, low temperatures and shorter days).

Consideration of animal resources, whether as food or sources of cultural insulation, highlights the challenges of applying modern animal behavioural data to Pleistocene ecosystems. It is true that many living European mammals evolved during the Quaternary, and their adaptations and distributions were therefore shaped by those environments (Lister 2004:237–238). However there is also clear evidence both for the non-analogue nature of Quaternary environments, and for both specialist and flexible adaptations amongst different mammal species. Non-analogue environments have been most notably emphasised by Stewart (2005) for MIS 3, with reference to the combinations of mammals living together (which are not found in the present) and the extinct faunal elements. Lister (2004:224) has highlighted the combination, within red deer, of fixed but broad-use adaptations, behavioural flexibility, and ecophenotypic plasticity, resulting in a species which is not only broadly distributed across varied habitats in the present, but also persisted through varied Quaternary habitats. By contrast, roe deer cannot consume larger quantities of grass and have both restricted present day ranges and were limited to wooded phases of the Quaternary. Lister (2004:225–226) also suggests that fine-scale spatial and temporal variability (via migratory movements and seasonality) can also lead to the evolution of flexible adaptations. In light of this, a cautionary usage of modern behavioural data is clearly appropriate. However the data are used here (Table 2, and see also Tables 3–4) solely to demonstrate both the documented presence of specific animals in Lower Palaeolithic zooarchaeological assemblages (although not of course necessarily exploited by hominins), and relative contrasts between the different species' likely distributions and potential availability for exploitation.

Finding food? The fundamental challenges of finding winter foods can be summarised under two headings: one, finding sufficient quantities of foods; and two, finding sufficient quantities of the right foods (i.e. those which meet nutritional requirements). These are especially challenging in light of the *c*. 50 nutrients required by humans for growth, maintenance and repair (Hockett and Haws 2003; it is assumed here, following these authors, that this pattern of diverse nutrient requirement evolved relatively early in hominins). They are divided between six classes (proteins, lipids [fat], carbohydrates, vitamins, minerals, and water), and their abundance varies between the primary food groups potentially available to Palaeolithic foragers (Hockett and Haws 2003, table 1; e.g. plant foods are a notable source of beta-carotene and vitamins C and E, while birds are rich sources of lipids). Critically, Hockett and Haws (2003:212) note that Palaeolithic foragers "could not have consumed a balanced intake of essential nutrients from a single animal group".

The first of the challenges (finding sufficient food, without at this stage exploring the nutritional aspects) would appear problematic for a winter residency strategy. Kelly (1995) and Roebroeks (2001, 2006) have emphasised the larger sizes of animal (and therefore hominin) territories at higher latitudes, while the risks and challenges of winter mobility, e.g. low temperatures and short days, have also been discussed above (albeit in reference to long-distance annual migrations). However animal territory sizes are also likely to have varied across a region, e.g. mid-latitude Europe, in accordance with local fluctuations in food supplies. In the case of the European wolf for example, its modern territory varies between 100–1,000km^2 (McDonald and Barrett 1993:92). Moreover the overall trend for increasing resource segregation at lower temperatures ignores the evidence for recent hunter-gatherer groups exploiting local, dispersed resources in low temperature environments (e.g. the Netsilingmiut and the Baffinland Inuit, who “hunt solitary animals, fish small streams, or, during the winter, live on the frozen surface of the ocean and hunt seals through breathing holes in the ice”: Kelly 1995:129; Figure 8). While not proposing either fishing or seal hunting in the Lower Palaeolithic, the potential for exploiting local resources in colder environments becomes especially relevant when considering the apparent evidence for distinctive, mixed landscapes in Pleistocene Europe. This is in the form of repeated associations of woodland and grassland fauna. It is evident for example at Swanscombe (Lower Gravels and Lower Loams: Schreve 1996), Hoxne (AL3 West – Lower Industry: Stuart *et al*. 1993) and Boxgrove (Unit 4c: Parfitt 1999), with combinations of fauna from river floodplains (e.g. *C. fiber*), open grasslands (e.g. *E. ferus*, *P. antiquus*) and temperate deciduous woodland (e.g. *D. dama*, *S. scrofa*). Stewart *et al*. (2003) have raised the question of whether these are genuine associations or palimpsest effects, but if genuine such locally diverse habitats and resources could result in lessened herd mobility and/or migration distances. Specifically, where food clumping is reduced and the even distribution of food is increased, then range sizes decrease (Clutton-Brock, Guinness, and Albon 1982:245). Such circumstances would appear to favour foraging over a smaller scale, and therefore partly reduce the difficulties of residential survival strategies. MacDonald *et al*. (2009) have similarly argued for a shorter effective foraging radius, and consequently a higher residential mobility, for the Neanderthals on the basis of energetics. These foraging scales would also permit a focus on specific habitats with favourable micro-climates.

However there are also herd animals with generally lower levels of mobility (essentially residential species), the exploitation of which would thus also minimise hominin mobility and foraging time budgets. While Gamble (1987:87) has previously highlighted musk ok and possibly rhinoceros, a number of smaller ungulate species are today characterised by relatively minor summer/winter migrations and/or by reduced winter territoriality (Table 3). Although a Late Pleistocene sample, Julien *et al*. (2012) have also argued for non-migratory behaviour in Late Pleistocene steppe bison (*B. priscus*) on the basis of tooth enamel isotopes, in contrast to previous assumptions.

Modern animal data (Table 3) therefore suggests that at least some ungulate species might have been locally available to hominins during the winter months. However their relatively small body sizes (e.g. 16–35kg and 32–80kg for modern fallow and roe deer; MacDonald and Barrett 1993) would present different challenges in terms of the frequency of hunting required and the hominin group sizes that could be sustained. Moreover the potential problems of animal-dominated winter diets have been well-established ethnographically (e.g. Speth and Spielmann 1983), as lean animal meat carries the risk of over-dosing on protein (occurring at levels above *c*. 40%; the so-called ‘rabbit fever’; Speth 1990, 1991). This is also a particular problem for pregnant females (Hockett 2012). Ben-Dor *et al*. (2011, table 2) suggest obligatory animal fat requirements of 44–62% for *H. erectus* (based on animal fat calories divided by total calories obtained from animal sources only; the figures are reduced to 27–44% when all food sources are included). Animal fat sources (e.g. bone marrow) are of course subject to depletion, particularly in late winter and spring (e.g. Jochim 1981, fig. 3.1 for roe deer, Spiess 1979, fig. 2.2 for caribou), while carbohydrate intake is impacted by reduced winter plant food sources. Successful access to fats, marrows, carbohydrates and other vitamins and minerals is thus a critical requirement for the winter resident, working on the assumption that Lower Palaeolithic hominin metabolism was not markedly different from that of modern humans (following Buck and Stringer 2014).

Speth and Spielmann (1983) suggest three broad strategies for meeting the nutritional challenges outlined above: (i) targeting animals with higher winter and spring fat content (e.g. bear, beaver, and waterfowl, the latter of which have up to 70% fat content by edible body weight, while the hibernation and denning habits of the former create an essentially immobile resource: Jochim 1981; Walthall 1998); (ii) internal and/or external fat storage, either through body fat reserves or through the rendering of bone grease; and (iii) targeting alternative sources of carbohydrates and other minerals and vitamins, including ungulate stomachs (Buck and Stringer 2014; but *cf*. Fediuk *et al*. 2002 with regards to caribou stomachs and sources of vitamin C) and/or winter plants (e.g. seaweed/kelp, which can provide significant levels of vitamin C: Fediuk *et al*. 2002).

It is clear that there are various animals of potential ‘winter value’, which provide sources of fat, as well as, in many cases, being winter residents (Table 4; NB this paper assumes that European Lower Palaeolithic hominins were effective and skilful hunters and butchers: e.g. Parfitt and Roberts 1999; Voormolen 2008). Modern beaver tail, for example, increases its fat content from *c*. 7% (late Spring) to *c*. 60% in autumn and early winter (Coles 2006:55). Guthrie (1990:247) has also noted that more sedentary species of modern northern ungulates tend to put on larger quantities of winter fat than the long-distance migrants. Larger species (e.g. rhinoceros) would also offer a particularly valuable additional winter resource in the form of bone as a fuel source for fires (and the burning of which would result in fragmentation and their relative ‘invisibility’ in the archaeological record). A variety of modern day migratory water birds also have a documented presence in northern Europe (Peterson, Mountfort, and Hollom 1993), including Whooper swan (*c*. 8–11kg), Greylag goose (*c*. 2–4kg) and the now-extinct Great Auk (*c*. 5kg). All of these species have been recorded at Boxgrove (units 4, 4d and 4c respectively: Harrison and Stewart 1999). The particular value of such sources has been demonstrated for Canada goose, which provides enhanced levels of protein, zinc and iron, with the organs of particular value to the young and the pregnant (Belinsky and Kuhnlein 2000). Further examples of the range of specific nutritional benefits which can be gained from discrete animal body parts have been documented more widely (albeit with a specific geographical focus) in a series of Arctic hunter-gatherer-focused ethnographic studies (e.g. Fediuk *et al*. 2002; Hidiroglou *et al*. 2008; Kuhnlein *et al*. 2006; Figure 9). It would seem reasonable that at least some of these sources (or their equivalents) were known to Lower Palaeolithic hominins (through behavioural selection via trial and error). However it is also accepted here that some of the other foods in Figure 9, and their equivalents, were presumably not available (at least not as a regular or semi-regular, as opposed to occasionally scavenged, food source) due to the technological demands associated with their acquisition (e.g. marine mammals and fish or freshwater fish).

The faunal lists from a variety of Middle Pleistocene sites therefore highlight a range of species that could potentially be exploited to assist hominins in meeting the specific survival demands of a Pleistocene winter (Tables 2–4), both in regards to their lean season fat reserves (and other nutritional benefits) and coats, and in terms of their territorial sizes and ranging behaviours. However a disconnect occurs when direct evidence of the exploitation of such animals is sought. Harrison and Stewart (1999:193) explicitly note, for example, the lack of cut-marks associated with bird bones at Boxgrove, although they acknowledge that cut-marked bird bones are generally rare in prehistory and Thieme (2005) has drawn a tentative connection between the ‘throwing stick’ and goose bones at Schöningen and the hunting of birds in flight by Australian aborigines.

There are nonetheless occasional glimpses of the exploitation of residential, fat and/or fur-bearing animals (Table 5). Butchered bear remains have been recorded at Boxgrove (with skinning inferred from cut marks on a skull of *U. deningeri*; Parfitt and Roberts 1999:402–403) and Bilzingsleben (Mania and Mania 2005:108). There is also evidence for the exploitation of rhinoceros and (at Bilzingsleben) beaver. With regards to a possible winter focus on residential or locally mobile species, it is notable that wild pig, felids and roe deer were all exploited occasionally at Bilzingsleben. Interestingly, Mania and Mania (2005:108) explain this low-level usage as a consequence of inefficiency (roe deer) or danger (wild pig and felids). However an alternative interpretation is that these species were primarily only exploited during the winter (due to their relatively residential behaviour and/or valuable resources; Tables 2–4), at a time of the year when those attributes outweighed issues of danger and inefficiency. While all of these archaeological occurrences lack seasonality data, the presence of bear (and perhaps also the roe deer, felids and wild pig) at Bilzingsleben is particularly intriguing, given the claims for fires, shelters and a sustained occupation at this site (Mania and Mania 2005; but *cf*. Gamble 1999:153–172).

An alternative documented solution to periods of scarcity centres on internal storage and the accumulation of reserves of body fat. This is a common strategy in northern mammals, and in humans it has been linked with buffalo gorging by native American groups, although the duration of the benefits was not specified (Speth and Spielmann 1983:19). In this regard the quantities of butchered animals at specific sites are intriguing, particularly in light of the potentially small sizes of habitual hominin groups. These have been suggested by the scale of possible 'residential' sites such as Beeches Pit (Preece *et al*. 2006) and Bilzingsleben (Mania and Mania 2005) and have been recently argued on genetic grounds for the Neanderthal descendants of *H. heidelbergensis* (Lalueza-Fox *et al*. 2011). These suggested group sizes are also noteworthy given the general risks faced by small, dispersed hunter-gatherer groups when resources are unevenly distributed (Kelly 1995, table 6-3). However if the Schöningen horse remains, for example, are accepted to represent a series of hunting episodes (Voormolen 2008:128), then just one stallion and 2–6 mares and their foals (i.e. a horse family group) would yield approximately

400–1000kg of meat (*cf*. White's estimate of 1 reindeer-sized animal [120kg]/3 days or 1 horse-sized animal [250kg]/6 days for 10 adult Neanderthals: White 2006:563). Nutritionally-beneficial gorging by a small group of hominins, as opposed to waste (at least for the hominins) or the cognitively-demanding collaborations of multiple groups, seems a parsimonious explanation of such zooarchaeological assemblages and one with benefits in terms of aiding winter survival (Walthall 1998).

External storage of animal fats, through the production of pemmican, has also been widely documented in the case of recent hunter-gatherers (Speth and Spielmann 1983:19). Although it is commonly produced by boiling bones to extract grease, an alternative method (one not requiring cooking vessels) involves heating rocks in a fire, transferring them to a perishable container (e.g. a skin bag?) with broken-up bones, and then mixing the rendered fat with lean meat. Storage through dehydration (i.e. drying and/or smoking: Stopp 2002) is perhaps also worthy of consideration as means of managing hunting surpluses (after Bailey 1981) and potentially ensuring at least one reliable food supply through the winter months. However such a strategy has significant implications in terms of the need for stable camp-sites, controlled fire and/or the carrying capacity (of individual hominins rather than the landscape). The archaeological detection of such strategies also poses notable challenges.

Wild plant foods offer a further potential solution to the nutritional challenges of winter survival. The importance of plant foods to Neanderthals has received widespread recent discussion (e.g. Hardy 2010; Hardy and Moncel 2011; Hardy *et al*. 2012; Henry, Brooks, and Piperno 2011). In terms of seasonal availability Mabey

(2012) and Mears and Hillman (2007) have suggested a small but important range of plant foods, from roots and rhizomes [starch] and mushrooms [vitamin B] to various leafs and shoots (e.g. nettle), which could be available during the winter months. Hardy (2010) has given particular emphasis to the underground storage organs (USOs) of species such as reed mace (cattails) and wild carrot, noting their widespread distribution (albeit across the Neanderthal range), the peaks in their energy storage in late autumn and winter, and the presence of visible, above ground winter vegetation for selected species (but *cf*. Ben-Dor *et al*. 2011). Interestingly, a winter shift in plant food emphasis to the underground parts of species has also been noted for another European omnivore, the wild boar (Genov 1981, table 5). Speth and Spielmann (1983:20) have previously emphasised the higher essential fatty acid contents of many plant foods, and their potential as a means of building up storable carbohydrate reserves during the autumn. Finally Buck and Stringer (2014:164–165) have emphasised herbivore stomachs as a further source of plant food intake, with reference to the widespread ethnographic evidence for the practice, on the grounds on taste and culture alongside nutrition. Among the Greenland Inuit for example, reindeer stomachs offer the best source of carbohydrates, with the exception of more seasonally available berries. While the identification of plants to the species-level remains problematic on Early and Middle Pleistocene sites, comparison of plant family data from Hoxne (Mullenders 1993) with modern species available to winter foragers (Mabey 2012; Mears and Hillman 2007) offers insight into the range of potential resources available (Table 6). The nutritional value of seaweed/kelp (e.g. vitamin C; Fediuk *et al*. 2002, table 1 and fig. 2) and sea beet also emphasises the possible appeal of coastal sites and landscapes to early hominins (see also Ashton and Lewis 2012; Cohen *et al*. 2012).

Returning to the four factors outlined above, reduced mobility (i.e. smaller hominin foraging territories, with implications for group structure; factors iii and iv) would offer a variety of benefits in a winter landscape: reducing energy expenditure and requirements; and lessening exposure to movement through snow-covered, low temperature landscapes, and therefore reducing risk for vulnerable group members (e.g. young and old). The challenges of securing sufficient fuel (and other raw materials for cultural insulation) and food (factors i and ii) were by no means straightforward, but the fauna (and to a lesser extent flora) evident on European Middle Pleistocene sites highlights potentially locally available resources. These were perhaps combined with late summer/early autumn gorging and/or management of surpluses. This model for successful winter residency therefore requires us to at least consider behaviours (in particular rudimentary cultural insulation) which are sometimes denied to Lower Palaeolithic hominins.

Discussion

The above discussions highlight the challenges presented by mid-latitude winters to Lower Palaeolithic hominins. Yet the archaeological record (e.g. Gamble 1999; Roebroeks and van Kolfschoten 1995) confirms that these challenges were, at least on occasions, successfully met. The outstanding question concerns how they were met: whether through repeated cycles of annual migrations (effectively summer occupancy and winter abandonment of the mid-latitudes) or all-year residency.

The annual migration model would seem to present a number of significant conceptual difficulties: the gradients of palaeoenvironmental change and the distances (and therefore time and energy) involved, the implications of, and for, group membership, and the challenges of food acquisition in a series of ‘newly’ encountered habitats during periods of shortage. The drivers for any hypothetical annual spring movements into the mid-latitudes are also uncertain, although the long-distance tracking of herbivore migrations is a possible answer (but see Burch 1972). In terms of archaeological evidence, the typically local character of raw material sources in the European Lower Palaeolithic is also potentially an argument against an annual migration strategy (Féblot-Augustins 1999; although the relatively short life histories of lithic artefacts is probably a further complicating factor here: e.g. Hallos 2005; Pope and Roberts 2005). It is perhaps also noteworthy that the recently uncovered Happisburgh III footprints (Ashton *et al*. 2014) appear to include both adults and children, suggestive of an entire ‘family’ rather than a task-specific adult group (for whom seasonal migration might be more feasible). Finally, Ashton and Lewis (2012:60) have noted that such migratory behaviour would be an entirely new adaptive strategy for early hominins in northern Europe: this paper concurs that lengthy annual migrations were therefore an unlikely solution.

Alongside the challenges of migration, the need for them may also have been limited. Range expansion from southern Europe (which currently provides the widest range of early dates for a Lower Palaeolithic presence in Europe: e.g. Carbonell *et al*. 2008; Falguères *et al*. 1999; Oms *et al*. 2000) would most easily have occurred through annual, non-directional, territorial drift (in response, at least in part, to shifting resource availability) mapped onto familiar habitats (e.g. Roebroeks 2005). Expansion into the north would thus be more likely to occur incrementally, rather than through large-scale dispersals into the unknown (given the difficulties of migrating ‘alongside’ herd animals, the lack of evidence for population pressure in this period, and other mobility challenges outlined above). Under such a scenario, winter problems from year-to-year would be familiar (if not necessarily simple to overcome), becoming only gradually more challenging. In this model, the ability of the hominins to continue to meet those challenges (without resorting to long distance mobility) would seem to be the logical constraint on range expansion. Only in the event of notable and rapid environmental deterioration, for which there is of course increasingly high-resolution Pleistocene evidence (e.g. Anklin *et al*. 1993; Petit *et al*. 1999; Jouzel *et al*. 2007) might the need for major migrations become apparent. Interestingly, the demands (in terms of travelling conditions and the distances required to find improved habitats) of such long distance moves would also be increased by any behavioural conservatism which might delay departure until a survival ‘tipping point’ was reached (see also Kelly 1995:144–148).

By contrast with an annual migration model, a winter residency model (Figure 10) requires reduced mobility in snow-covered/cold landscapes (but *cf*. comments below regarding the demands of foraging), permits the sustained re-use of established sleeping sites and/or local residential mobility (MacDonald *et al*. 2009), and enables the build-up of local habitat and mobile and fixed resource knowledge. The faunal and floral records of Early and Middle Pleistocene sites are also suggestive of the availability of winter foods and other resources (e.g. fat and fur-yielding residential species, albeit often relatively small in size; Tables 2–4). However other behavioural aspects inferred by this model are currently either scarce (e.g. fire and shelters; Roebroeks and Villa 2011) or absent (e.g. ‘clothing’ or body coverings) in the archaeological record.

The residential winter strategy also has the potential to exploit and benefit from micro-climates (i.e. localised variations in temperature, rainfall, wind, humidity and resources): in short, accessing improved palaeoenvironmental conditions without the high ‘costs’ of long-distance migrations. Present-day micro-climate contrasts in the UK include upland/lowland (e.g. temperature reductions of between 5–10°C/1000m of elevation, windier upland conditions and longer upland winters/shorter summers) and inland/coastal differences (e.g. milder coastal winters but cooler coastal summers; Met Office 2011). In regard to the latter point, the coastal distributions (and potential resources) of selected early sites (Pakefield and Happisburgh I & III: Ashton *et al*. 2008b, 2014; Cohen *et al*. 2012; Parfitt *et al*. 2005, 2010) are noteworthy (although taphonomic and sampling bias should also be acknowledged). At a more local scale, Davies *et al*. (2003:210–211 & fig. 11.5) have emphasised the presence of mixed mosaics of ecotones in the Dordogne, the Ardennes and the Middle Danube, with preferential MIS 3 settlement patterns in the side valleys of the Ardennes perhaps reflecting a need for greater shelter from prevailing winds. Finally Stewart *et al*. (2003:118) noted faunal contrasts between Britain and the Ardennes which may reflect topographical variations.

More speculatively, the potential and evidence for winter residency, and by extension a relatively local annual mobility, is perhaps also supported by Middle Palaeolithic studies (as direct data on Lower Palaeolithic mobility is currently very limited). Britton *et al*. (2011) have documented the availability and exploitation of both migratory and residential herbivores at the site of Jonzac, in the form of reindeer and bison. These could form the basis of a locally-focused strategy, exploiting seasonally-predictable but also seasonally-restricted migrants alongside year-round residents. Relatively local mobility, over at least *c*. 20km during a lifetime, was also suggested by Richards *et al*.'s (2008) strontium isotope study, albeit on a single Neanderthal tooth. Both offer interesting perspectives against the need for annual, long-distance migration as a strategy.

A winter residency strategy is therefore the favoured model here. This is not to suggest however that winter residency is straightforward. Hominins would have to cope with mid-latitude winter climates (whether locally ameliorated by micro-habitats or not), and the potential depletion of local resources (e.g. residential species and plant foods). A locally or perhaps regionally shifting range would presumably be a requirement of any residential strategy, although the absence of task-specific Lower Palaeolithic sites might suggest a 'drifting' pattern (on a yearly basis?) as opposed to the more logistical approaches described by Binford (1980). Such range shifts are envisaged at a larger scale (annual?) than the equally-important seasonal or sub-seasonal local residential mobility described by MacDonald *et al*. (2009). The relationships between range size and habitat 'quality' (e.g. for deer; Putman 1988) would be a further complicating factor, as wider ranging prey would place greater demands on hominin foraging mobility.

Nonetheless it is certainly evident from selected sites that hominins were sometimes capable of survival in cooler phases of mid-latitude interglacial episodes (e.g. Ashton *et al*. 2008a; Parfitt *et al*. 2010; Roberts 1999). What is less clear is how widely distributed or sustained such survival was. In geographical terms, the challenges of mid-latitude interglacial winters may define mid-latitude Europe as, at best, a zone of disjunct distribution, if not a zone of periodic extinction (after Roebroeks 2006, fig. 2). Certainly Roebroeks and van Kolfschoten's (1994) short chronology, although since modified (e.g. Dennell and Roebroeks 1996), remains broadly valid in terms of the identified distinction between the archaeological records of northern Europe pre- and post-500/600kya. Dennell, Martinón-Torres, and Bermúdez de Castro (2011) have subsequently argued for frequent local extinctions of "sink" populations in northern Europe. Ashton and Lewis (2002; and subsequently Ashton and Hosfield 2010; Ashton, Lewis, and Hosfield 2011) have proposed gradual population decline between MIS 13 and MIS 7, related both to changing landscape preferences of hominins during the early Middle Palaeolithic and to the changing 'windows of access' that developed in response to the evolving palaeogeography of the English Channel region. The winter challenges outlined here may provide a potential explanation for those demographic trends and local extinctions: in short, winter survival was a challenging task, the success of which could be adversely effected by relatively minor climatic shifts, resource shortages and/or 'historical events'. The latter would seem especially likely in the event of small group sizes (e.g. Lalueza-Fox *et al*. 2011; albeit for Neanderthals), which would be particularly prone to individual deaths. The northern European record as it stands is perhaps suggestive that post-500/600kya hominins (*H. heidelbergensis*) were able to buffer those adverse effects somewhat more successfully than their predecessors (as reflected in the richer lithic records and in behavioural 'innovations' such as fire and shelter; e.g. Mania and Mania 2005; Roebroeks and van Kolfschoten 1995; Roebroeks and Villa 2011; Wymer 1999). However even after 500kya the limited evidence for such innovations, and the possible evidence for MIS-level patterns in handaxes (Pettitt and White 2012, table 4.4; White 2015), may also be indicating that cyclical glaciations were not the only cause of Middle Pleistocene extirpations.

This paper has, throughout, walked a tightrope familiar to Lower Palaeolithic researchers. It is not the intention to re-cast Lower Palaeolithic hominins as essentially modern hunter-gatherers with a slightly smaller brain, or to retreat to notions of marginal scavenging (e.g. Binford 1985; 1987). It is however seeking to acknowledge the likely practicalities, difficulties and requirements of mid-latitude winter living.

Conclusion

The recent discoveries at Happisburgh III (Parfitt *et al*. 2010), combined with palaeoenvironmental evidence from a range of other sites (e.g. Ashton and Lewis 2012) have highlighted the potential challenges to Lower Palaeolithic hominins of an all-year round presence in mid-latitude northern Europe. Yet consideration of the available resources (e.g. fur and fat-bearing winter residents, winter plant foods) highlights the potential for successful local residency, so long as we are willing to accept the need for, and possible presence of, ‘survival behaviours’ (e.g. rudimentary cultural insulation, internal and perhaps external food storage) amongst the repertoire of Middle, and perhaps also Early, Pleistocene hominins.

However the demands of survival, and the limited evidence for key components in the archaeological record, may also suggest that such strategies had a mixed success rate, although perhaps becoming more reliable after *c*. 500–600kya and the appearance of *Homo heidelbergensis* (e.g. Dennell and Roebroeks 1996; Ashton 2015).

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Comments

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The discovery of 800,000-year-old flint artefacts at Happisburgh III places Early Pleistocene hominins in unfamiliar territory both geographically and conceptually. In the widely accepted scenario, Lower Palaeolithic hominins were largely restricted to latitudes below 45°N, with only brief expansions northward during warm climate phases. At Happisburgh, hominins lived in an environment similar to modern-day southern Scandinavia. Hosfield has taken this and other recent findings as motivation to explore solutions to the “winter problem”; that is, did the challenges of low temperatures and reduced resource availability during the winter force annual migrations, or were Lower Palaeolithic hominins able to live at these northern latitudes year-round?

I appreciate the contrasting phrases that Hosfield uses to frame hominin survival in mid-latitude Europe: “winter wonderland” and “winter problem.” While low temperatures and heavy snow cover might be welcomed as a “wonderland” by those living at mid-latitudes, people who live in more temperate climates might view those same conditions as a “problem.” This is a matter of personal opinion, but there is actually a wide gap between how modern Europeans living at different latitudes cope with low temperatures. Psychological factors may have as much to do with feelings of comfort as the actual physiological responses to outdoor temperature. People are willing to tolerate a certain level discomfort if day-to-day or seasonal temperatures meet their expectations[1]. Nevertheless, Hosfield’s wonderland can quickly deteriorate into a legitimate problem as extremely low temperatures bring increased risk of frostbite and hypothermia, not to mention heart attacks, strokes, and a host of other respiratory ailments (especially among older segments of the population). But again, populations living at more northern latitudes expect cold temperatures and are better prepared. In a study of excess winter mortality across eight European regions, a given fall in temperature leads to higher rates of death in regions with warm

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[1] For example, residents of Sheffield, UK (53°N), report an annual outdoor neutral temperature of 13.3°C, whereas the people of Athens (38°N) feel neither warm nor cool, but neutral, at 22.8°C (Nikolopoulou and Lykoudis 2006:1462) — an impressive comfort gap of nearly 10°C.

winters[2]. Interestingly, mortality increased among people who were less active outdoors during periods of low outdoor temperatures.

Of course, these measures of comfort and winter mortality reflect contemporary buffers against the cold (socio-economic factors and also play a considerable role), or what Hosfield and others refer to as cultural insulation, i.e., fire, clothing, and shelter. A related "winter problem" is the undeniable rarity of these insulating behaviours in the Lower Palaeolithic record. For that, Hosfield's recipe for a successful winter residency "requires us to at least consider behaviours (in particular rudimentary cultural insulation) which are sometimes denied to Lower Palaeolithic hominins". This statement echoes White's (2006:559) earlier appeal to "speculate just a little beyond actual data and grant Neanderthals a few simple habits." If we are willing to do so, winter at Happisburgh 800,000 years ago transforms from an altogether hostile and forbidding environment into a manageable few months during the regular seasonal cycle. While it is tempting to allow for such speculation, most, if not all, of the Lower Palaeolithic sites under consideration by Hosfield lack any seasonality data.

Yet, if we bring data from Schöningen 13II-4 into the discussion[3], we can arrive at some conclusions about winter residency in mid-latitude Europe during the Middle Pleistocene. I can report here that the *Equus mosbachensis* assemblage from the

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[2] In southern Finland (including Helsinki, 60°N), each 1°C decrease in temperature resulted in a 0.27% increase in mortality, while the same 1°C temperature drop in Athens (38°N), however, was met with a 2.17% rise in mortality (The Eurowinter Group 1997:1343).

[3] Based on an analysis of the available lithic assemblage, Serangeli and Conard (2015) classify the site within the late Lower Palaeolithic, although obvious arguments can be made for inclusion in the Middle Palaeolithic. Recent TL age estimates of 337-300 ka (Richter and Krbetschek 2015) and palaeoenvironmental reconstruction (Urban and Bigga 2015) place the site toward the end of the MIS 9 interglacial.

Schöningen “Spear Horizon” does, in fact, represent multiple hunting episodes, and, more importantly, includes juvenile horses that died during all seasons of the year (see Villaluenga *et al.* 2015). As most of the assemblage shows clear evidence for all stages of butchery, we do not have to allow for much speculation to place hominins at Schöningen during the winter at the end of the MIS 9 interglacial[4]. From the Schöningen evidence, it would appear that elements of Hosfield’s winter residency model were in practice among Middle Pleistocene hominins, at least by 300,000 years ago. In many ways, the mosaic lakeshore environment at Schöningen is reminiscent of most Lower Palaeolithic sites mentioned by Hosfield—indications for open grasslands, with forests nearby, and the presence of some body of water. It is in these types of environments where we are likely to find indications for winter and year-round residency.

On offer is a detailed winter survival strategy, but a couple of important issues regarding winter residency at mid-latitude Europe during the Lower Palaeolithic are still up for debate: how far beyond 300,000 years ago and to which hominin species are we willing to extend these winter strategies without robust seasonal data or evidence for cultural insulation; or, at what point did winter become less of a problem and more of a wonderland? Hosfield seems willing to establish a provisional “winter problem/winter wonderland” boundary with the arrival of *Homo heidelbergensis* at 500-600kya. I am willing to keep an open mind, but it will require more than speculation to push the boundary back any further than that based on current evidence.

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[4] Mean January temperatures at Schöningen (52°N) during the Middle Palaeolithic are estimated between −4°C and −1°C (see Urban and Bigga 2015:69), slightly lower than the winter temperature estimates for Happisburgh (−3°C and 0°C).

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Hominins were present in Eurasia from at least 1.8 mya, and by 1 mya this presence is documented at highly dispersed points between about 30 and 40 degrees north, from China to Spain. In north-western Europe, hominins were present (at this time or not so long after) as far as 53 degrees north, at locations where winter conditions were considerably cooler than those encountered in Spain. Hosfield's thought-provoking paper addresses the implications of this challenging environmental context for the changing niches of these hominins.

Archaeological evidence for one of the key technologies in the niche of current and prehistoric humans living in cool conditions, fire, is scarce in the European Lower Palaeolithic. This may represent a real absence before c. 350 kya, especially given the lack of evidence from well-preserved sites in a range of depositional conditions (Roebroeks and Villa 2011). Further, the number of later Lower Palaeolithic sites providing persuasive evidence for fire use (including multiple types of evidence) is small. A recent multi-analytical, micro-contextual examination of a putative hearth and burnt wooden artifact from Schöningen showed no trace of controlled combustion (Stahlschmidt et al. In press), raising questions about the outcome of the application of a similar range of techniques to other sites. This scarce evidence for fire use makes it even more important to identify (or rule out) other strategies that could be used to cope with cold temperatures and obtain adequate nutrition, in order to understand the how fire fitted into the niches of the early occupants of Europe (or not).

Hosfield identifies a range of possible survival strategies, and explores the costs, benefits and trade-offs involved. Below, I will focus on a small selection of these suggestions which may point to plausible ‘fire-free’ strategies.

Following the calculations of Aiello and Wheeler (2003), Hosfield shows that increased hominin metabolic heat production and muscular insulation would not have been sufficient to cope with north-western winter temperatures. Even taking into account a more cold-adapted body form and the raised winter metabolism suggested by data from current Siberian populations (Leonard, Snodgrass, and Sorensen 2005), this remains true. Further, this is also the case in southern Europe, to a lesser extent. At the same time, this analysis highlights the extremely high benefits of even very light clothing; 1 clo of clothing, equivalent to a business suit, would minimise the risk of dying of cold, while clo values of roughly 5-7 are given by Hosfield for pelts of likely co-residential animals. (Actually growing a personal coat of fur could be more effective still!) Nevertheless, even with cultural insulation, or in southern European temperatures, hominins would have needed to burn extra metabolic energy to keep warm.

The question of how hominins got enough to eat becomes even more important when we consider the possible absence of fire, because of fuel needed for metabolic up-regulation to keep warm, and because humans today are dependent on the additional energy obtained from food that has been cooked (Carmody et al. 2009).

Hosfield identifies several fat-rich animals and birds and edible plants that were probably available and would have contributed to a nutritionally balanced diet. Various low-tech forms of preserving food and maintaining supplies are highlighted; it would be interesting to know how these processes affect energy and nutrient gain, whether negatively or positively. The suggestion that hominins could have reduced foraging travel distances and hence food requirements is interesting, but the loss of the heat-producing benefits of foraging activity could be problematic without fire.

Hosfield highlights the high costs of a strategy of annual migration in terms of time spent travelling, particularly in a mixed group, and searching for key resources in unfamiliar locations, and limited benefits in terms of degrees of winter temperature. This discussion greatly improves our understanding of what long-distance migration involves, and also highlights the potential benefits to be gained by a coastal migration. By moving a third of the distance south-east along rivers and the French coast hominins could have obtained similar thermal benefits to that involved in a long-distance migration to the Aquitaine region. Such a travel route could extend the locally diverse habitats and resources and favourable microclimates that Hosfield highlights in UK sites (Cohen et al. 2012). Depletion of coastal resources would drive further movement, including movement further north in the summer (Cohen et al. 2012). Seasonal migration along predominantly coastal and fluvial routes may have been a plausible strategy for coping with winter cold.

As Hosfield concludes, given the limited evidence for key behaviours in the archaeological record, and the challenging conditions at middle latitudes in Europe, it seems very likely that overwintering strategies were not always successful.

Interestingly, in the Nihewan Basin of China multiple sites dated to the Early Pleistocene document hominin presence in a region where winter temperatures during interglacials could have dropped to –15 degrees Celsius (Dennell 2012). Would the ‘winter residential strategies’ suggested by Hosfield work in these more severe conditions? If not, perhaps we need to consider the possibilities that ‘annual migration’ was an option for some hominin populations, that we are seeing the traces of multiple tentative and ill-fated expansions, and/or that we are missing some biological or cultural options – with possible implications for how we interpret the north-west European evidence.

This paper takes an important step in going beyond discussions of the timing and nature of colonization in western Europe, to consider the implications for changing hominin niches. Hosfield develops a constructive approach to this problem, drawing on a very wide range of comparative sources, and building up a coherent picture involving multiple aspects of hominin strategies. Given the scarcity of evidence for key material culture solutions, especially fire, and the evidence for occupation of even more severe conditions in other parts of Eurasia, understanding the niches of these early occupants of Eurasia may ultimately require further consideration of a very wide range of solutions, particularly biological and cultural solutions falling outside the variety employed by recent humans.

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Hosfield is to be congratulated on providing a thoughtful and necessary consideration of the hominin record of mid-European latitudes. It’s a paper that brings into focus all those regions at continental margins which offered only punctuated, limited windows of colonisation potential. Certainly Hosfield has identified issues we should continue to engage with and refocus on, addressing what were the environmental/climatic tolerances of hominin groups?, how did anatomy, behaviour and technology evolve through time to extend these tolerances?, and how can we identify and investigate this trajectory in the archaeological record?

It is the last of these aspects that I’d like to consider in this comment. The archaeological record of Northern Europe, which Hosfield has justifiably focused on, is important in terms of its depth and intensity of research history. While regions of eastern Europe and central, eastern Asia (Dennell and Roebroeks 2005), and also to a degree South Africa, provide important regions to consider this subject, North Western Europe is perhaps the only one with a data set large enough to consider any systematic study at this point in time. Even so this a region where new sites, often based on minimal finds, can transform our known understanding of distribution in time rapidly, the discoveries at Pakefield (Parfitt et al 2005) and Happisburgh Parfitt et al 2010) for example, and it is also a region where our understanding is developed enough to consider the considerable taphonomic challenges to identifying behavioural change over time. I want to focus on four of these: artefact visibility, the landscape distribution of artefacts, the question of ‘home bases’ and identifying associated climate signatures.

Artefact Visibility: As the Early Pleistocene discoveries from East Anglia have shown, the archaeological record for the earliest occupation episodes is sparse and, more significantly, characterised by Mode 1 flake tool signatures preserved in fluvial sediment systems. While we might expect this record to be sparse and resulting from punctuated episodes of occupation, between the environmental signatures of Happisburgh and Pakefield we have temperatures both colder and warmer than those of today presented, suggesting a wide degree of tolerance, at least seasonally for regional populations. We must also consider, after 600,000 years populations in northern Europe are using Mode 2 Acheulean tool kits including large and recognisable bifaces. As a result we still have a lingering 'Short Chronology' effect to contend with (Dennell and Roebroeks 1996). We need to filter the degree to which the increase of sites through the Mid Pleistocene relate to the visibility of these artefacts and their historical identification in the field. In order to build a robust picture of occupation tolerance we need to be able to calibrate the anticipated under-presentation of pioneer Mode 1 using populations in our records.

Landscape Distribution: We have a record so dependent on stone artefacts that we must always bear in mind our distribution of archaeological sites reflects tool discard patterns in the first instance, not hominin behaviour. Through to the end of the Early Middle Pleistocene at least we have a record dominated by river valley distribution patterns, dominated by large accumulations of either bifaces or large robust Mode 1 Clactonian tools (Ashton et al. 2006). Where preservation allows, we can see these are often associated with butchery activities. In order to assess the associated climatic and environmental context of these key sites we need to be mindful of a) the potential separation in time and space of occupation and secondary accumulation of archaeological material through transportation and b) how records proven to be in primary context might be recording only part of the landscape range of a hominin population (Pope et al 2016). Adaptations essential to broadening environmental tolerance may not be taking place in all parts of the landscape equally.

Home Bases: Taking this term with a great deal of caution we need to consider the appearance and presence in the record of locales we might consider habitation as opposed to butchery/extraction sites. Very few of our recorded archaeological localities, often in open low-lying areas involving butchery residues, would be very safe as camp sites. This is especially the case prior to the use of fire or shelter construction. Given these are the main technological adaptations beyond clothing which we might be looking for in the record to evidence responses to climate change, we have to consider where in the landscape these are most likely to appear and whether preservation asymmetries might be prejudicing their discovery. Hosfield points out the interfluve position of the Beeches Pit site, providing the earliest evidence for fire in the region. Only systematic investigation of similar contexts could begin to answer whether the rarity of such sites is due to lower levels of preservation and discovery when compared to fluvial landscape contexts.

Finally, we are left to consider how closely we can associate an archaeological signature with a climatic or environmental one. We should consider why so many of our Palaeolithic records come from the transition between glacial and interglacial periods when l landsurfaces are likely to be destabilised and moved down slope or sealed under mobile sediment. The more stable paleosol contexts of interglacials might relate to relatively prolonged periods of landscape stability enabled by larger degrees of vegetation cover and reduced or absent high energy fluvial/ or periglacial erosion. Indeed considering full interglacial environments again, and the effects low raw material availability and dense vegetation cover might have on both occupation patterns and archaeological visibility needs to be readdressed as part of this discussion (Roebroeks 1992). Alongside cycles of colonisation and depopulation controlled just by the presence/absence of cold temperatures, we could consider more specific wonderlands of opportunity occurring within transitional phases between climatic extremes.

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Hosfield asks a question rarely addressed: how did lower Paleolithic people survive the freezing temperatures of mid-latitude regions of the Ice Age, or even interglacial Europe? The winters were extremely cold, with temperatures frequently dropping below what has been understood as the survival range of humans. But yet, we find the remains of human activity in central and northern Europe during the Lower Paleolithic. The simple answer would be that they had the technology. We remain reluctant, however, to attribute to Lower Paleolithic people the technologies necessary to survive harsh winters, among them control of fire, clothing, shelter construction and food storage. We lack archaeological evidence for such behavior in sites 500,000 years old and older. Hence, in light of the current knowledge in paleoanthropology, Hosfield’s question is usually met with conjecture. I would like to comment on some of his arguments.

The first is Hosfield's refutation of the annual migration theory. Hosfield brings solid arguments against this theory and I would like to add one. He notes that such annual migration does not occur in a vacuum. The people who returned from colder to warmer habitats during the winter had to cross rivers, mountains, and unknown terrain with changing fauna and flora. Moreover, they most likely faced an additional obstacle. When cranes or reindeer migrate, the entire population relocates annually. There are no cranes in Africa during the summer. However, humans do not migrate as a species. Some groups may have moved into northern regions during the summer but others remained in the south. Such groups most likely did not welcome significant number of migrating groups returning from the north into their territory in the winter. This is an additional argument against annual migration as a solution to the mid-latitude winter survival challenges.

My second comment relates to the existence of food storage technology, frequently underestimated in discussions of survival strategies. In warmer areas, such as the Levant, lack of food storage limits any long-term survival strategy. Meat spoils within hours in the hot climate and vegetarian food is vulnerable to rodents, insects, and even humidity. These obstacles all but disappear in the freezing conditions of a cold environment. One need only pile the meat or bulbs and they will remain preserved as long as low temperatures persist. Of course, the inhabitants needed to protect their food from predators, but they also needed to protect themselves from the same. The hominins also had to warm their food before consumption. Here, I agree with Hosfield's unstated conclusion that they must have controlled fire in order to survive the cold northern winters.

My principal comment is that we tend to forget that central and northern Europe are not the only cold regions along the route leading out of Africa. In Africa, itself, there are very cold regions, with the temperature dropping below freezing during the cold desert nights of the Sahara and the Kalahari. The East African Rift Valley has moderate temperatures year round but when you climb up to the Ethiopian highlands it is cold. Even today, in interglacial conditions, the average temperature in Dmanisi during the month of January is minus 3.8^{O}C. It is difficult to remember at the end of the searing hot Jordan Valley summer of 2015 that it snowed the previous winter with temperatures dropping to minus 5 ^{O}C during an interglacial winter. The point is that hominins encountered cold, even freezing conditions long before they reached central and northern Europe. They could not have survived the winter conditions of the Turkish plateau without suitable technology such as clothing, fire, and, most likely, shelter. This does not mean that the Dmanisi hominins of 1.8 million years ago controlled fire or produced clothing. However, their presence in this cold environment should be considered in the context of the subject at hand. For example, when we consider Early and, in particular, Middle Pleistocene hominins, we assume that the loss of body hair is a fact of human evolution. But fur may have been an important survival factor for earlier hominins in cold environments. However, once you no longer have fur, you need technology to survive. The hominins occupying the mid-latitude regions of the northern hemisphere after 500,000-600,000 years ago had seen cold winters previously. They were most likely experienced survivors of the cold and had the technology needed to survive such extreme conditions.

The freezing winter regions of Europe were almost certainly marginal environments for hominin groups due to the harsh conditions and survival challenges. But as John Speth (2010) noted, anthropologists rarely ask themselves the question “marginal with respect to what?” Regions that appear marginal and unsuitable to us, the modern farmers, may have offered good survival conditions to people with the suitable technology and knowledge. Given their long history of overcoming the challenges of cold environments on their way to Europe, the straightforward explanation for the survival of Mid-Pleistocene hominins during the frozen winters of the mid-latitude region is that they possessed the necessary knowledge and technology.

Reply

I thank my colleagues for their thoughtful and constructive comments, and for responding to the paper in the spirit in which it was intended. I hope my responses below are similarly framed. The question, raised by Hutson and Sharon, of how climatic conditions are perceived is an important one, and Hutson’s distinction between psychological and physiological responses offers a potentially valuable insight into how winters were managed. The notion of being acclimatized, prepared and tolerating a few months of seasonal discomfort is feasible, not least in light of the demands of large-scale annual movements, and the potential ‘resistance’ to such movements from other hominin groups in the ‘destinations’, a point highlighted by Sharon. Wintering in coastal regions, emphasised by MacDonald as offering favourable and diverse habitats, resources and micro-climates, might have been a key means of reducing the seasonal discomfort and, in north-west Europe, have been compatible with intra-regional, annually repeated, mobility strategies. I think the critical issue here concerns how, at the scale of individual hominin lives, annual mobility, range expansion and dispersal actually happens. I think we don’t currently know the answers and that this is a critical knowledge gap. What is likely to have influenced mobility decisions are the distances and benefits involved. Taking a broader view, MacDonald stresses the severe interglacial winter temperatures of the Nihewan Basin (present-day average January figures are -10–-15°C; Dennell 2013) and, like Dennell, favours non-winter occupation and high mobility. Given those temperatures I would certainly agree, but still wonder if the milder winters of Europe may have sometimes enabled residency over inter-regional mobility.

Sharon offers potential support to residency in emphasising the cold, sometimes freezing, conditions encountered both within and closer to Africa (e.g. the East African Rift Valley and the uplands of southern Georgia), and the possibility that the early northerners were experienced survivors of the cold. This wider context is key, and in stressing the Ethiopian Highlands and the Turkish Plateau Sharon reminds us that climatic and ecological conditions are significantly impacted by altitudinal, as well as latitudinal, change, although significant changes in one’s altitude can of course be achieved through much shorter movements. While the caveats associated with modern data are fully acknowledged, a brief comparative survey of present-day climates for selected locations, including some of those discussed by Sharon (Table 1 & Figure 1), highlights a further point. The demanding Dmanisi winter estimates emphasise the question of when, not least in terms of glacial/interglacial cycles and changing coastal palaeogeography, and in which directions hominin ranges expanded into Europe. While weather patterns and altitudinal impacts have been modified since the Early Pleistocene as a result of uplift (e.g. Demir *et al*. 2009), the substantial elevated relief in parts of Turkey (the climate regime at Erzurum, in the east of the country, is comparable to Dmanisi) and Georgia are still likely to have presented significant winter challenges in comparison to areas such as the Jordan valley, and been a potentially significant obstacle to north-westward range expansion. It may therefore be unsurprising that the Dmanisi climate associated with the Lower Palaeolithic occupations has been described as notably warmer and drier than the present, and of Mediterranean type (Gabunia *et al*. 2000). Nonetheless, as Sharon suggests, if upland landscapes were successfully survived through winter conditions broadly comparable to those of the present, rather than avoided, then those lowland European winters may not have been all that difficult a proposition.

MacDonald rightly emphasises that a need for elevated winter food intake, as fuel to maintain body temperature, would remain even if cold-adapted bodies, raised winter metabolism and insulation through clothing/coverings were part of the hominins' biological and behavioural repertoire. She also notes that a possible absence of fire would further raise dietary demands. Sharon's emphasis on the benefits of cold conditions for food storage, in contrast to those of warmer areas such as the Levant, highlights a possible means of securing winter food supplies. However Sharon also adds, echoing Gamble (1987), that natural 'cold storage' places demands on pyro-technological knowledge and skills. Fisher's (1995) discussion of the meat preservation potential of cold water storage offers a further possible option, albeit one with extremely low archaeological visibility in this period, for meeting the dietary demands of winter survival. MacDonald wonders how low-technology methods of preservation would impact the energy and nutrient gain from stored foods. Further research is certainly needed, but Health Canada (1995) suggest enhanced energy and various nutrient levels in dried as opposed to roasted caribou (Table 2), while Morris *et al*. (1981) noted that the drying of bison meat to make jerky only eliminated the moisture content, with fat, protein, mineral and trace elements all remaining. Finally, MacDonald's emphasis on the benefits of foraging activity for the maintenance of body temperature is also noteworthy, and offers an interesting contrast to my own (and Hutson's) emphasis on the perils of mobility in low temperature landscapes (e.g. frostbite and hypothermia).

Pope rightly highlights the significant taphonomic complications which we face when exploring the behavioural characteristics of the early Europeans, and stresses four key issues: artefact visibility, landscape distributions of artefacts, the 'home base' issue, and the associating of archaeological and climatic signals. I agree with Pope's argument that the scope of the pre-600kya occupation in north-western Europe may well be under-represented due to the visibility of core and flake artefacts, especially in fluvial contexts, and associated historical collecting issues. Along similar lines I wonder if the apparent *c*. 600kya shift in the scale of the European record, especially in the north, might also be semi-illusory, influenced by the widespread shift to Acheulean technology in the west and occasional 'headliner' sites such as Boxgrove. Might the real transformation in the occupation of the north come at MIS 11 (Cole and Hosfield in prep.)? Much more work can usefully be done along the lines of the settlement history modelling of Ashton and Lewis (2002; see also Ashton and Hosfield 2010; Ashton *et al*. 2011) and the Unified Palaeolithic Landscape Approach of Pope *et al*. (in press). I also agree with Pope's observation that the adaptations that broadened environmental tolerances may not have occurred equally in all parts of the landscape, and further add that specific and archaeologically visible behaviours, such as butchery, may be incorporated within very different hominin strategies or lifeways at different times and places, while still leaving rather similar traces (e.g. note the similarities in the range of exploited animals and the categories of butchery marks at the early European sites of Gran Dolina TD-6 and Sima del Elefante, and at later sites such as Boxgrove: Huguet *et al*. 2013; Parfitt and Roberts 1999; Saladie *et al*. 2011). I have no easy answers to these taphonomic problems to present here, but certainly concur with Mark White's recent observation that "Without a substantial increase in new discoveries, an enhancement of our current database or very significant new analytical techniques or trust-worthy dating methods, the British Palaeolithic [in the context of my paper White's call for new discoveries and enhanced data-sets crosses national boundaries] will decline in significance, and cease to have anything new to say on a European scale" (White 2016:132). Pope *et al*.'s (in press) emphasis on process will be critical in meeting these needs, as a means of enhancing our understanding of where we find material and which periods, landscape settings and behaviours are best represented within that data. Such new approaches, combined with different methodologies and strategies from across Europe (e.g. the contrasts between Palaeolithic research strategies in the chalk landscapes of Britain and France; Pope *et al*. in press), is one potential route to (i) sampling those landscape settings and contexts in which campsites *sensu lato* may have been more likely to be sited and have the potential to be preserved, and (ii) enhancing our understanding of the spatio-temporal separations that undoubtedly occurred between occupation activities, the climatic conditions that were actually *experienced*, and the subsequent accumulations of archaeological material.

As all my commentators have in different ways rightly noted, I have speculated in places, for example with regards to the capacity for fire production or the paucity of seasonality data. It may well be that sustained year-round residency in mid-latitude Europe was only a regular feature towards the end of the Middle Pleistocene, and Hutson emphasises the strong supporting evidence from Schöningen in MIS-9. However there have been interesting developments since the initial submission of this paper, including Walker *et al*.'s (2016) claims for anthropogenic fire at Cueva Negra at *c*. 800 kya (but see Jiménez-Arenas *et al*. 2011 for a critique of the site dating), albeit a tended fire rather than a heat-controlled hearth fire. This supports the potential for fire manipulation ability amongst the earliest Europeans, as do other early 'fire sites' such as Gesher Benot Ya'aqov (Alperson-Afil 2008) and Gowlett's (2016) emphasis on fire awareness and intensification and the Alaskan natural fire record. It does not necessarily suggest fire production however, nor does it address the question of where the evidence is in the north. Finally, as MacDonald notes, the previously claimed hearths at Schöningen have also been strongly critiqued recently (Stahlschmidt *et al*. 2015), with potential methodological and interpretive implications for other sites as well.

Ultimately I am in agreement with MacDonald's emphasis on considering a wider range of biological and cultural solutions, and by extension a wider range of models for 'being human', when exploring the early occupations of the north – these are exciting times to be thinking about Early and Middle Pleistocene hominins beyond Africa, whoever they may ultimately prove to be…

References

Agustí, Jordi, Hugues-Alexandre Blain, Gloria Cuenca-Bescós, and Salvador Bailon. 2009. Climate forcing of first hominin dispersal in Western Europe. *Journal of Human Evolution* 57:815–821.

Aiello, Leslie, and Peter Wheeler. 2003. Neanderthal Thermoregulation and the Glacial Climate. In *Neanderthals and modern humans in the European landscape during the last glaciation*. Tjeerd H. van Andel, and William Davies, eds. Pp. 147–166. Cambridge: MacDonald Institute for Archaeological Research.

Alperson-Afil, Nira. 2008. Continual fire-making by hominins at Gesher Benot Ya‘aqov, Israel. *Quaternary Science Reviews* 27(17):1733–1739.

Andrews, Peter, and Barbara Ghaleb. 1999. Taphonomy of the Westbury Cave bone assemblages. In *Westbury Cave: The Natural History Museum Excavations, 1976–1984*. Peter Andrews, Jill Cook, Andrew Currant, and Christopher Stringer, eds. Pp. 87–126. Bristol: Western Academic & Specialist Press Limited.

Anklin, Martin, Jean-Marc Barnola, J. Beer, T. Blunier, J. Chappellaz, H.B. Clausen, D. Dahl-Jensen, *et al*. 1993. Climate instability during the last interglacial period recorded in the GRIP ice core. *Nature* 364:203–207.

Antoine, Pierre, Patrick Auguste, Jean-Jaques Bahain, Christine Chaussé, Christophe Falguères, Bassam Ghaleb, Nicole Limondin-Lozouet, *et al*. 2010. Chronostratigraphy and palaeoenvironments of Acheulean occupations in Northern France (Somme, Seine and Yonne valleys). *Quaternary International* 223–224:456–461.

Ashton, Nick. 2015. Ecological niches, technological developments and physical adaptations of early humans in Europe: the handaxe-*Heidelbergensis* hypothesis. In *Settlement, Society and Cognition in Human Evolution: Landscapes in Mind*. Fiona

Coward, Robert Hosfield, Matt Pope, and Francis Wenban-Smith, eds. Pp. 138–153. New York: Cambridge University Press.

Ashton, Nick M., and Robert Hosfield. 2010. Mapping the human record in the British early Palaeolithic: evidence from the Solent River system. *Journal of Quaternary Science* 25(5):737–753.

Ashton, Nick, and Simon G. Lewis. 2002. Deserted Britain: Declining Populations in the British Late Middle Pleistocene. *Antiquity* 76(292):388–396.

Ashton, Nick, and Simon G. Lewis. 2012. The environmental contexts of early human occupation of northwest Europe: The British Lower Palaeolithic record. *Quaternary International* 271:50–64.

Ashton, Nick, Simon G. Lewis, Simon Parfitt, and Mark White. 2006. Riparian landscapes and human habitat preferences during the Hoxnian (MIS 11) Interglacial. *Journal of Quaternary Science* 21(5):497–505.

Ashton, Nick, Simon G. Lewis, Simon A. Parfitt, Kirsty E.H. Penkman, and G. Russell Coope. 2008a. New evidence for complex climate change in MIS 11 from Hoxne, Suffolk, UK. *Quaternary Science Reviews* 27(7–8):652–668.

Ashton, Nick M., Simon A. Parfitt, Simon G. Lewis, G. Russell Coope, and Nigel Larkin. 2008b. Happisburgh Site 1 (TG 388307). In *The Quaternary of Northern East Anglia Field Guide*. Ian Candy, Jonathan R. Lee, and Anna M. Harrison, eds. Pp. 151–156. London: Quaternary Research Association.

Ashton, Nick, Simon G. Lewis, and Robert Hosfield. 2011. Mapping the human record: population change in Britain during the Early Palaeolithic. In *The Ancient Human Occupation of Britain*. Nick M. Ashton, Simon G. Lewis, and Chris B. Stringer, eds. Pp. 39–51. Amsterdam: Elsevier.

Ashton, Nick, Simon G. Lewis, Isabelle De Groote, Sarah M. Duffy, Martin Bates, Richard Bates, Peter Hoare, *et al*. 2014. Hominin Footprints from Early Pleistocene Deposits at Happisburgh, UK. *PLoS ONE* 9(2):e88329.

Bailey, Geoff N. 1981. Concepts of Resource Exploitation: Continuity and Discontinuity in Palaeoeconomy. *World Archaeology* 13(1):1–15.

Balter, Michael. 2014. The killing ground. *Science* 344(6188):1080–1083.

Barron, Eric, Tjeerd H. van Andel, and David Pollard. 2003. Glacial Environments II: Reconstructing the Climate of Europe in the Last Glaciation. In *Neanderthals and modern humans in the European landscape during the last glaciation*. Tjeerd H. van Andel, and William Davies, eds. Pp. 57–78. Cambridge: MacDonald Institute for Archaeological Research.

Bates, Martin R., Francis F. Wenban-Smith, Silvia M. Bello, David R. Bridgland, Laura T. Buck, Matthew J. Collins, David H. Keen, *et al*. 2014. Late persistence of the Acheulian in southern Britain in an MIS 8 interstadial: evidence from Harnham, Wiltshire. *Quaternary Science Reviews* 101:159–176.

Belinsky, Devorah L., and Harriet V. Kuhnlein. 2000. Macronutrient, Mineral, and Fatty Composition of Canada Goose (*Branta canadensis*): An Important Traditional Food Resource of the Eastern James Bay Cree of Quebec. *Journal of Food Composition and Analysis* 13:101–115.

Bello, Silvia M., Simon A. Parfitt, and Chris Stringer. 2009. Quantitative micromorphological analyses of cut marks produced by ancient and modern handaxes. *Journal of Archaeological Science* 36:1869–1880.

Ben-Dor, Miki, Avi Gopher, Israel Hershkovitz, and Ran Barkai. 2011. Man the fat hunter: the demise of *Homo erectus* and the emergence of a new hominin lineage on the Middle Pleistocene (ca. 400 kyr) Levant. *PLoS ONE* 6(12):e28689.

Binford, Lewis R. 1980. Willow Smoke and Dogs' Tails: Hunter-Gatherer Settlement Systems and Archaeological Site Formation. *American Antiquity* 45:1–17.

Binford, Lewis R. 1985. Human Ancestors: Changing Views of Their Behaviour. *Journal of Anthropological Archaeology* 4:292–327.

Binford, Lewis R. 1987. Were there elephant hunters at Torralba? In *The Evolution of Human Hunting*. Matthew H. Nitecki, and Doris V. Nitecki, eds. Pp. 47–105. New York: Plenum Press.

Bosinski, Gerhard. 1995. The earliest occupation of Europe: Western Central Europe. In *The Earliest Occupation of Europe: Proceedings of the European Science Foundation Workshop at Tautavel (France), 1993*. Wil Roebroeks and Thijs van Kolfschoten, eds. Pp. 103–128. Leiden: University of Leiden Press.

Britton, Kate, Vaughan Grimes, Laura Niven, Teresa E. Steele, Shannon McPherron, Marie Soressi, Tegan E. Kelly, Jacques Jaubert, Jean-Jaques Hublin, and Michael P. Richards. 2011. Strontium isotope evidence for migration in late Pleistocene *Rangifer*: implications for Neanderthal hunting strategies at the Middle Palaeolithic site of Jonzac, France. *Journal of Human Evolution* 61:176–185.

Buck, Laura T., and Chris B. Stringer. 2014. Having the stomach for it: a contribution to Neanderthal diets? *Quaternary Science Reviews* 96:161–167.

Burch, Ernest S. 1972. The Caribou/Wild Reindeer as a Human Resource. *American Antiquity* 39(3):339–368.

Carbonell, Eudald, José M. Bermúdez de Castro, Josep M. Parés, Alfredo Pérez-González, Gloria Cuenca-Bescós, Andreu Ollé, Marina Mosquera, *et al*. 2008. The first hominin of Europe. *Nature* 452:465–469.

Carmody, R.N., E. Cone, R.W. Wrangham, and S.M. Secor. 2009. Cooking and the net energy value of meat: implications for human evolution. *Integrative and Comparative Biology* 49:E27-E27.

Chu, Wei. 2009. A functional approach to Palaeolithic open-air habitation structures. *World Archaeology* 41(3):348–362.

Clutton-Brock, Tim H., F.E. Guinness, and S.D. Albon. 1982. *Red Deer: Behaviour and Ecology of Two Sexes*. Edinburgh: Edinburgh University Press.

Cohen, Kim M., Katharine MacDonald, Josephine C.A. Joordens, Wil Roebroeks, and Philip L. Gibbard. 2012. The earliest occupation of north-west Europe: a coastal perspective. *Quaternary International* 271:70–83.

Coles, Bryony. 2006. *Beavers in Britain's Past*. Oxford: Oxbow Books.

Coope, G. Russell. 1993. Late-Glacial (Anglian) and Late-Temperate (Hoxnian) Coleoptera. In *The Lower Palaeolithic Site at Hoxne, England*. Ronald Singer, Bruce G. Gladfelter, and John J. Wymer, eds. Pp. 156–162. Chicago: University of Chicago Press.

Coope, G. Russell. 2006. Insect faunas associated with Palaeolithic industries from five sites of pre-Anglian age in central England. *Quaternary Science Reviews* 25:1738–1754.

Davies, William, Paul Valdes, Cheryl Ross, and Tjeerd H. van Andel. 2003. The Human Presence in Europe during the Last Glacial Period III: Site Clusters, Regional Climates and Resource Attractions. In *Neanderthals and modern humans in the European landscape during the last glaciation*. Tjeerd H. van Andel, and William Davies, eds. Pp. 191–220. Cambridge: MacDonald Institute for Archaeological Research.

Demir, Tuncer, Ali Seyrek, Hervé Guillou, Stéphane Scaillet, Rob Westaway, and David Bridgland. 2009. Preservation by basalt of a staircase of latest Pliocene terraces of the River Murat in eastern Turkey: Evidence for rapid uplift of the eastern Anatolian Plateau. *Global and Planetary Change* 68(4):254–269.

Dennell, Robin. 2013. The Nihewan Basin of North China in the Early Pleistocene: Continuous and flourishing, or discontinuous, infrequent and ephemeral occupation? *Quaternary International* 295:223–236.

Dennell, Robin W., and Wil Roebroeks. 1996. The earliest colonization of Europe: the short chronology revisited. *Antiquity* 70(269):535–542.

Dennell, Robin W., and Wil Roebroeks. 2005. An Asian perspective on early human dispersal from Africa. *Nature* 438(7071):1099–1104.

Dennell, Robin W., María Martinón-Torres, and José M. Bermúdez de Castro. 2011. Hominin variability, climatic instability and population demography in Middle Pleistocene Europe. *Quaternary Science Reviews* (Special Issue: Early Human Evolution in the Western Palaearctic: Ecological Scenarios) 30(11–12):1511–1524.

Dingwall, Heather L., Kevin G. Hatala, Roshna E. Wunderlich, and Brian G. Richmond. 2013. Hominin stature, body mass, and walking speed estimates based on 1.5 million-year-old fossil footprints at Ileret, Kenya. *Journal of Human Evolution* 64:556–568.

Dunbar, Robin I.M., and John A.J. Gowlett. 2014. Fireside Chat: the Impact of Fire on Hominin Socioecology. In *Lucy to Language: the Benchmark Papers*. Robin I.M. Dunbar, Clive Gamble, and John A.J. Gowlett, eds. Pp. 277–296. Oxford: Oxford University Press.

Falguères, Christophe, Jean-Jaques Bahain, Yuji Yokoyama, Jean Luis Arsuaga, Jose Maria Bermudez de Castro, Eudald Carbonell, James L. Bischoff, and Jean-

Michel Dolo. 1999. Earliest humans in Europe: the age of TD6 Gran Dolina, Atapuerca, Spain. *Journal of Human Evolution* 37(34):343–352.

Féblot-Augustins, Jehanne. 1999. Raw material transport patterns and settlement systems in the European Lower and Middle Palaeolithic: continuity, change and variability. In *The Middle Palaeolithic Occupation of Europe*. Wil Roebroeks, and Clive S. Gamble, eds. Pp. 194–214. Leiden: University of Leiden.

Fediuk, Karen, Nick Hidiroglou, René Madère, and Harriet. V. Kuhnlein. 2002. Vitamin C in Inuit Traditional Food and Women's Diets*. Journal of Food Consumption and Analysis* 15:221–235.

Fisher, Daniel C. 1995. Experiments on subaqueous meat-caching. *Current Research in the Pleistocene* 12:77–80.

Gabunia, Leo, Abesalom Vekua, and David Lordkipanidze. 2000. The environmental contexts of early human occupation of Georgia (Transcaucasia). *Journal of Human Evolution* 38:785–802.

Gamble, Clive S. 1986. *The Palaeolithic Settlement of Europe*. Cambridge: Cambridge University Press.

Gamble, Clive S. 1987. Man the Shoveler: Alternative Models for Middle Pleistocene Colonization and Occupation in Northern Latitudes. In *The Pleistocene Old World: Regional Perspectives*. Olga Soffer, ed. Pp. 81–98. New York: Plenum Press.

Gamble, Clive S. 1999. *The Palaeolithic Societies of Europe.* Cambridge: Cambridge University Press.

Gamble, Clive S. 2009. Human Display and Dispersal: A Case Study from Biotidal Britain in the Middle and Upper Pleistocene. *Evolutionary Anthropology* 18:144–156.

Genov, Peter. 1981. Food Composition of Wild Boar in North-eastern and Western Poland. *Acta Theriologica* 26(10):185–205.

Golant, Alexander, Russell M. Nord, Nader Paksima, and Martin A. Posner. 2008. Cold exposure injuries to the extremities. *Journal of the American Academy of Orthopaedic Surgeons* 16(12):704–15.

Gowlett, John A.J. 2006. The early settlement of northern Europe: Fire history in the context of climate change and the social brain. *C. R. Palevol* 5:299–310.

Gowlett, J.A.J. 2016. The discovery of fire by humans: a long and convoluted process. *Philosophical Transactions of the Royal Society B* 371(1696):20150164.

Guthrie, R. Dale. 1990. *Frozen Fauna of the Mammoth Steppe*. Chicago: University of Chicago Press.

Hallos, Jane. 2005. "15 Minutes of Fame": Exploring the temporal dimension of Middle Pleistocene lithic technology. *Journal of Human Evolution* 49(2):155–179.

Hammel, H.T. 1955. Thermal Properties of Fur. *American Journal of Physiology* 182:369–376.

Hardy, Bruce L. 2010. Climatic variability and plant food distribution in Pleistocene Europe: implications for Neanderthal diet and subsistence. *Quaternary Science Reviews* 29:662–679.

Hardy, Bruce L., and Marie-Hélène Moncel. 2011. Neanderthal Use of Fish, Mammals, Birds, Starchy Plants and Wood 125-250,000 Years Ago. *PLoS ONE* 6(8):e23768.

Hardy, Karen, Stephen Buckley, Matthew J. Collins, Almudena Estalrrich, Don Brothwell, Les Copeland, Antonio García-Tabernero, *et al*. 2012. Neanderthal medics? Evidence for food, cooking, and medicinal plants entrapped in dental calculus. *Naturwissenschaften* 99:617–626.

Harrison, Colin J.O., and John R. Stewart. 1999. Arvifauna. In *Boxgrove: A Middle Pleistocene hominin site at Eartham Quarry, Boxgrove, West Sussex*. Mark B. Roberts, and Simon A. Parfitt, eds. Pp. 187–196. London: English Heritage.

Haynes, Gary. 2006. Mammoth landscapes: good country for hunter-gatherers. *Quaternary International* 142–143:20–29.

Health Canada. 1995. *Native Foods and Nutrition: An Illustrated Reference Manual*. Medical Services Branch.

Henry, Amanda G., Alison S. Brooks, and Dolores R. Piperno. 2011. Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq; Spy I and II, Belgium). *Proceedings of the National Academy of Sciences* 108(2):486–491.

Hidiroglou, Nick, Robert W. Peace, Penny Jee, Donna Leggee, and Harriet Kuhnlein. 2008. Levels of folate, pyridoxine, niacin and riboflavin in traditional foods of Canadian Arctic Indigenous Peoples. *Journal of Food Composition and Analysis* 21:474–480.

Hockett, Bryan, and Jonathan Haws. 2003. Nutritional ecology and diachronic trends in Palaeolithic diet and health. *Evolutionary Anthropology* 12:211–216.

Hockett, Bryan. 2012. The consequences of Middle Palaeolithic diets on pregnant Neanderthal women. *Quaternary International* 264:78–82.

Holden, Clare, and Ruth Mace. 1997. Phylogenetic Analysis of the Evolution of Lactose Digestion in Adults. *Human Biology* 69(5):605–628.

Holman, J. Alan. 1998. The herpetofauna. The interglacial mammalian fauna from Barnham. In *Excavations at the Lower Palaeolithic Site at East Farm, Barnham, Suffolk 1989–94*. Nick M. Ashton, Simon G. Lewis, and Simon A. Parfitt, eds. Pp. 101–106. London: The British Museum (Occasional Paper No. 125).

Holman, J. Alan. 1999. Herpetofauna. In *Boxgrove: A Middle Pleistocene hominin site at Eartham Quarry, Boxgrove, West Sussex*. Mark B. Roberts, and Simon A. Parfitt, eds. Pp. 181–187. London: English Heritage.

Holmes, Jonathan A., Tim Atkinson, D.P. Fiona Darbyshire, David J. Horne, José Joordens, Mark. B. Roberts, Katharine J. Sinka, and John E. Whittaker. 2009. Middle Pleistocene climate and hydrological environment at the Boxgrove hominin site (West Sussex, UK) from ostracod records. *Quaternary Science Reviews* 29(13–14):1515–1527.

Hublin, Jean-Jacques, and Wil Roebroeks. 2009. Ebb and flow or regional extinctions? On the character of Neandertal occupation of northern environments. *C. R. Palevol* 8:503–509.

Huguet, Rosa, Palmira Saladié, Isabel Cáceres, Carlos Díez, Jordi Rosell, Maria Bennàsar, Ruth Blasco, *et al*. 2013. Successful subsistence strategies of the first humans in south-western Europe. *Quaternary International* 295:168–182.

Jiménez-Arenas, Juan M., Manuel Santonja, Miguel Botella, and Paul Palmqvist. 2011. The oldest handaxes in Europe: fact or artefact? *Journal of Archaeological Science* 38(12):3340–3349.

Jochim, Michael A. 1981. *Strategies for survival: cultural behaviour in an ecological context*. London: Academic Press.

Jouzel, J., V. Masson-Delmotte, O. Cattani, G. Dreyfus, S. Falourd, G. Hoffmann, B. Minster, *et al*. 2007. Orbital and millennial Antarctic climate variability over the past 800 000 Years. *Science* 317:793–796.

Julien, Marie-Anne, Hervé Bocherens, Ariane Burke, Dorothée G. Drucker, Marylène Patou-Mathis, Oleksandra Krotova, and Stéphane Péan. 2012. Were European steppe bison migratory? ^{18}O, ^{13}C and Sr intra-tooth isotopic variations applied to a palaeoethological reconstruction. *Quaternary International* 271:106–119.

Kahlke, Ralf-Dietrich, Nuria García, Dimitris S. Kostopoulos, Frédéric Lacombat, Adrian M. Lister, Paul P.A. Mazza, Nikolai Spassov, and Vadim V. Titov. 2011. Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. *Quaternary Science Reviews* (Special Issue: Early Human Evolution in the Western Palaearctic: Ecological Scenarios) 30(11–12):1368–1395.

Kelly, Robert L. 1995. *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways*. Washington: Smithsonian Institution Press.

Kleiber, Max. 1961. *The Fire of Life*. New York: Wiley.

Kuhnlein, Harriet V., V. Barthet, A. Farren, E. Falahi, Donna Leggee, O. Receveur, and P. Berti. 2006. Vitamins A, D, and E in Canadian Arctic traditional food and adult diets. *Journal of Food Composition and Analysis* 19:495–506.

Lalueza-Fox, Carles, Antonio Rosas, Almudena Estalrrich, Elena Gigli, Paula F. Campos, Antonio García-Tabernero, Samuel García-Vargas, *et al*. 2011. Genetic evidence for patrilocal mating behavior among Neandertal groups. *Proceedings of the National Academy of Sciences* 108(1):250–253.

Lendrum, Patrick E., Charles R. Anderson, Jr., Ryan A. Long, John G. Kie, and R. Terry Bowyer. 2012. Habitat selection by mule deer during migration: effects of landscape structure and natural-gas development. *Ecosphere* 3(9):art82.

Leonard, W.R., J.J. Snodgrass, and M.V. Sorensen. 2005. Metabolic adaptation in indigenous Siberian populations. *Annual Review of Anthropology* 34:451–471.

Leroy, Suzanne A.G., Klaus Arpe, and Uwe Mikolajewicz. 2011. Vegetation context and climatic limits of the Early Pleistocene hominin dispersal in Europe. Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. *Quaternary Science Reviews* (Special Issue: Early Human Evolution in the Western Palaearctic: Ecological Scenarios) 30(11–12):1448–1463.

Lister, Adrian M. 2004. The Impact of Quaternary Ice Ages on Mammalian Evolution. *Philosophical Transactions: Biological Sciences* 359(1442):221–241.

Loring, Stephen. 1997. On the trail to the caribou house: Some reflections on Innu caribou hunters in northern Ntessinan (Labrador). In *Caribou and Reindeer Hunters of the Northern Hemisphere*. Lawrence J. Jackson and Paul T. Thacker, eds. Pp. 185–220. Aldershot: Avebury.

de Lumley, Henry, and Marie-Antoinette de Lumley. 1973. Pre-Neanderthal remains from Arago cave in southwestern France. *Yearbook of Physical Anthropology* 17:162–168.

MacDonald, David, and Priscilla Barrett. 1993. *Mammals of Britain and Europe*. London: Collins.

MacDonald, Katharine, Wil Roebroeks, and Alexander Verpoorte. 2009. An energetics perspective on the Neandertal Record. In *The Evolution of Hominin Diets*. Jean-Jaques Hublin and Michael P. Richards, eds. Pp. 211–220. Dordrecht: Springer.

Mania, Dietrich. 1995. The earliest occupation of Europe: the Elbe–Saale region (Germany). In *The Earliest Occupation of Europe*. Wil Roebroeks and Thijs van Kolfschoten, eds. Pp. 85–101. Leiden: Leiden University Press.

Mania, Dietrich, and Ursula Mania. 2005. The natural and socio-cultural environment of *Homo erectus* at Bilzingsleben, Germany. In *The Hominin Individual in Context: Archaeological investigations of Lower and Middle Palaeolithic landscapes, locales and artefacts*. Clive S. Gamble and Martin Porr, eds. Pp. 98–114. London: Routledge.

Mabey, Richard. 2012. *Food for Free*. London: Collins.

Mears, Ray, and Gordon Hillman. 2007. *Wild Food*. London: Hodder & Stoughton.

Mercier, Norbert, Laurence Froget, Didier Miallier, Thierry Pilleyre, Serge Sanzelle, and Chantal Tribolo. 2004. Nouvelles données chronologiques pour le site de Menez-Dregan 1 (Bretagne): l'apport de la thermoluminescence. *Quaternaire* 15(3):253–261.

The Meteorological Office. 2011. *Microclimtes*. Exeter: Met Office. http://www.metoffice.gov.uk/media/pdf/n/9/Fact_sheet_No._14.pdf.

Mithen, Steven. 1996. *The Prehistory of the Mind*. London: Thames & Hudson.

Monnier, Jean-Laurent, Bernard Hallégouët, Stéphan Hinguant, Michel Laurent, Patrick Auguste, Jean-Jacques Bahain, Christophe Falguères, *et al*. 1994. A new regional group of the Lower Palaeolithic in Brittany (France), recently dated by Electron Spin Resonance. *C. R. Acad. Sci. Paris, Ser. II* 319:155–160.

Morris, Elizabeth A., W. Max Witkind, Ralph L. Dix, and Judith Jacobson. 1981. Nutritional content of selected aboriginal goods in northeastern Colorado: buffalo (*Bison bison*) and wild onions (*Allium* spp.). *Journal of Ethnobiology* 1(2):213–220.

Mullenders, William W. 1993. New Palynological Studies at Hoxne. In *The Lower Palaeolithic Site at Hoxne, England*. Ronald Singer, Bruce G. Gladfelter, and John J. Wymer, eds. Pp. 150–155. Chicago: University of Chicago Press.

Mussi, Margherita. 2007. Women of the Middle Latitudes. The Earliest Peopling of Europe from a Female Perspective. In *Guts and Brains: an Integrative Approach to the Hominin Record*. Wil Roebroeks, ed. Pp. 165–183. Leiden: Leiden University Press.

Nikolopoulou, Marialena, and Spyros Lykoudis. 2006. Thermal comfort in outdoor urban spaces: analysis across different European countries. *Building and Environment* 41:1455–1470.

Oms, Oriol, Josep Maria Parés, Bienvenido Martínez-Navarro, Jordi Agustí, I. Toro, G. Martínez-Fernández, and Alain Turq. 2000. Early human occupation of Western Europe: Paleomagnetic dates for two Paleolithic sites in Spain. *Proceedings of the National Academy of Sciences* 97(19):10666–10670.

Parfitt, Simon A. 1998. The interglacial mammalian fauna from Barnham. In *Excavations at the Lower Palaeolithic Site at East Farm, Barnham, Suffolk 1989–94.* Nick Ashton, Simon G. Lewis, and Simon A. Parfitt, eds. Pp. 111–147. London: The British Museum (Occasional Paper No. 125).

Parfitt, Simon A. 1999. Mammalia. In *Boxgrove: A Middle Pleistocene hominin site at Eartham Quarry, Boxgrove, West Sussex*. Mark B. Roberts and Simon A. Parfitt, eds. Pp. 197–290. London: English Heritage.

Parfitt, Simon A., and Mark B. Roberts. 1999. Human modification of faunal remains. In *Boxgrove: A Middle Pleistocene hominin site at Eartham Quarry, Boxgrove, West Sussex*. Mark B. Roberts and Simon A. Parfitt, eds. Pp. 395–415. London: English Heritage.

Parfitt, Simon A., René W. Barendregt, Marzia Breda, Ian Candy, Matthew J. Collins, G. Russell Coope, Paul Durbridge, *et al*. 2005. The earliest record of human activity in northern Europe. *Nature* 438:1008–1012.

Parfitt, Simon A., Nick M. Ashton, Simon G. Lewis, Richard L. Abel, G. Russell Coope, Mike H. Field, Rowena Gale, *et al*. 2010. Early Pleistocene human occupation at the edge of the boreal zone in northwest Europe. *Nature* 466:229–233.

Peterson, Roger T., Guy Mountfort, and P.A.D. Hollom. 1993. *Birds of Britain and Europe*. 5th edition. London: Collins.

Petit, J.R., J. Jouzel, D. Raynaud, N.I. Barkov, J.-M. Barnola, I. Basile, M. Bender, *et al*. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* 399:429–436.

Pettit, Paul. 2000. Neanderthal lifecycles: developmental and social phases in the lives of the last archaics. *World Archaeology* 31(3):351–366.

Pettitt, Paul, and Mark. J. White. 2012. *The British Palaeolithic*. London: Routledge.

Pocock, Gillian, Christopher D. Richards, and David A. Richards. 2013. *Human Physiology*. 4th edition. Oxford: Oxford University Press.

Pope, Matt, and Mark B. Roberts. 2005. Observations on the relationship between Palaeolithic individuals and artefact scatters at the Middle Pleistocene site of Boxgrove, UK. In *The Hominin Individual in Context: Archaeological investigations of Lower and Middle Palaeolithic landscapes, locales and artefacts*. Clive S. Gamble and Martin Porr, eds. Pp. 81–97. London: Routledge.

Pope, Matt, Lesley Blundell, Beccy Scott, and Hannah Cutler. In press. Behaviour and process in the formation of the North European Acheulean record: Towards a Unified Palaeolithic Landscape Approach. *Quaternary International*.

Preece, Richard C., John A.J. Gowlett, Simon A. Parfitt, David. R. Bridgland, and Simon G. Lewis. 2006. Humans in the Hoxnian: habitat, context and fire use at Beeches Pit, West Stow, Suffolk, UK. *Journal of Quaternary Science* 21(5):485–496.

Putman, Rory. 1988. *The natural history of deer*. Bromley: Christopher Helm.

Richards, Michael, Katerina Harvati, Vaughan Grimes, Colin Smith, Tanya Smith, Jean-Jaques Hublin, Panagiotis Karkanas, and Eleni Panagopoulou. 2008. Strontium isotope evidence of Neanderthal mobility at the site of Lakonis, Greece using laser-ablation PIMMS. *Journal of Archaeological Science* 35(5):1251–1256.

Richter, Daniel, and Matthias Krbetschek. 2015. The age of the Lower Paleolithic occupation at Schöningen. *Journal of Human Evolution* 89:46–56.

Roberts, Mark B. 1999. 6.3 Flintwork from other contexts. In *Boxgrove: A Middle Pleistocene hominin site at Eartham Quarry, Boxgrove, West Sussex*. Mark B. Roberts and Simon A. Parfitt, eds. Pp. 378–384. London: English Heritage.

Rockman, Marcy. 2003. Knowledge and learning in the archaeology of colonization. In *Colonization of Unfamiliar Landscapes: the archaeology of adaptation*. Marcy Rockman and James Steele, eds. Pp. 3–24. London: Routledge.

Roebroeks, Wil. 2001. Hominin behaviour and the earliest occupation of Europe: an exploration. *Journal of Human Evolution* 41:437–461.

Roebroeks, Wil. 2005. Life on the Costa del Cromer. *Nature* 438:921–922.

Roebroeks, Wil. 2006. The human colonisation of Europe: where are we? *Journal of Quaternary Science* 21(5):425–436.

Roebroeks, Wil, and Thijs van Kolfschoten. 1994. The earliest occupation of Europe: a short chronology. *Antiquity* 68:489–503.

Roebroeks, Wil, and Thijs van Kolfschoten, eds. 1995. *The Earliest Occupation of Europe*. Leiden: Leiden University Press.

Roebroeks, Wil, and Paola Villa. 2011. On the earliest evidence for habitual use of fire in Europe. *Proceedings of the National Academy of Sciences* 108(13):5209–5214.

Roebroeks, Wil, Nicholas J. Conard, and Thijs van Kolfschoten. 1992. Dense forests, cold steppes, and the Palaeolithic settlement of Northern Europe. *Current Anthropology 33*(5):551–586.

Ruff, Christopher B. 1994. Morphological adaptation to climate in modern and fossil hominids. *Yearbook of Physical Anthropology* 37:65–107.

Saladié, Palmira, Rosa Huguet, Carlos Díez, Antonio Rodríguez-Hidalgo, Isabel Cáceres, Josep Vallverdú, Jordi Rosell, *et al*. 2011. Carcass transport decisions in *Homo antecessor* subsistence strategies. *Journal of Human Evolution* 61(4):425–446.

Sawyer, Hall, and Matthew J. Kauffman. 2011. Stopover ecology of a migratory ungulate. *Journal of Animal Ecology* 80(5):1078–1087.

Schreve, Danielle C. 1996. The mammalian fauna from the Waechter excavations, Barnfield Pit, Swanscombe. In *Excavations at Barnfield Pit, Swanscombe, 1968–1972*. Bernard Conway, John McNabb, and Nick Ashton, eds. Pp. 149–162. London: British Museum (Occasional Paper No. 94).

Serangeli, Jordi, and Nicholas J. Conard. 2015. The behavioral and cultural stratigraphic contexts of the lithic assemblages from Schöningen. *Journal of Human Evolution* 89:287–297.

Shotton, Frederick W., David H. Keen, G. Russell Coope, Andrew P. Currant, Philip L. Gibbard, M. Aalto, Sylvia M. Peglar, and J.E. Robinson. 1993. The Middle Pleistocene deposits of Waverley Wood Pit, Warwickshire, England. *Journal of Quaternary Science* 8(4):293–325.

Speth, John D. 1990. Seasonality, resource stress, and food sharing in so-called ‘egalitarian’ foraging societies. *Journal of Anthropological Archaeology* 9:148–188.

Speth, John D. 1991. Nutritional constraints and Late Glacial adaptive transformations: the importance of non-protein energy sources. In *The Late Glacial in north-west Europe: human adaptation and environmental change at the end of the Pleistocene*. Nick Barton, Alison J. Roberts, and Derek A. Roe, eds. Pp. 169–178. London: Council for British Archaeology (Research Report No. 77).

Speth, John D. 2010. *The Paleoanthropology and Archaeology of Big-Game Hunting: Protein, Fat, or Politics?* New York: Springer.

Speth, John D., and Katherine A. Spielmann. 1983. Energy source, protein metabolism, and hunter-gatherer subsistence strategies. *Journal of Anthropological Archaeology* 2:1–31.

Spiess, Arthur E. 1979. *Reindeer and Caribou Hunters: an Archaeological Study*. New York: Academic Press.

Stahlschmidt, Mareike C., Christopher E. Miller, Bertrand Ligouis, Ulrich Hambach, Paul Goldberg, Francesco Berna, Daniel Richter, *et al*. 2015. On the evidence for human use and control of fire at Schöningen. *Journal of Human Evolution* 89:181–201.

Stewart, John R., Thijs van Kolfschoten, Anastasia Markova, and Rudolf Musil. 2003. The Mammalian Faunas of Europe during Oxygen Isotope Stage 3. In *Neanderthals and modern humans in the European landscape during the last glaciation*. Tjeerd H. van Andel, and William Davies, eds. Pp. 103–130. Cambridge: MacDonald Institute for Archaeological Research.

Stewart, John R. 2005. The ecology and adaptation of Neanderthals during the non-analogue environment of Oxygen Isotope Stage 3. *Quaternary International* 137(1):35–46.

Stopp, Marianne. 1993. Taphonomic analysis of the faunal assemblage. *The Lower Palaeolithic Site at Hoxne, England*. In Ronald Singer, Bruce G. Gladfelter, and John J. Wymer, eds. Pp. 139–149. Chicago: University of Chicago Press.

Stopp, Marianne. 2002. Ethnohistoric analogues for storage as an adaptive strategy in northeastern subarctic prehistory. *Journal of Anthropological Archaeology* 21:301–328.

Stuart, Anthony J. 1992. The High Lodge mammalian fauna. In *High Lodge: Excavations by G. de G. Sieveking 1968–68 and J. Cook 1988*. Nick M. Ashton, Jill Cook, Simon G. Lewis, and James Rose, eds. Pp. 120–123. London: British Museum Press.

Stuart, Anthony J., Ronald G. Wolff, Adrian M. Lister, Ronald Singer, and Jane M. Egginton. 1993. Fossil vertebrates. In *The Lower Palaeolithic Site at Hoxne, England*. Ronald Singer, Bruce G. Gladfelter, and John J. Wymer, eds. Pp. 163–206. Chicago: University of Chicago Press.

The Eurowinter Group. 1997. Cold exposure and winter mortality from ischaemic heart disease, cerebrovascular disease, respiratory disease, and all causes in warm and cold regions of Europe. *The Lancet* 349:1341–1346.

Thieme, Hartmut. 2005. The Lower Palaeolithic art of hunting: the Case of Schöningen 13 II-4, Lower Saxony, Germany. In *The hominid individual in context: Archaeological investigations of Lower and Middle Palaeolithic landscapes, locales and artefacts*. Clive Gamble and Martin Porr, eds. Pp. 115–132. London: Routledge.

Trinkaus, Erik, Christopher B. Stringer, Christopher B. Ruff, Robin J. Hennessey, Mark B. Roberts, and Simon A. Parfitt. 1999. Diaphyseal cross-sectional geometry of the Boxgrove 1 Middle Pleistocene human tibia. *Journal of Human Evolution* 37:1–25.

Tuffreau, Alain, and Pierre Antoine. 1995. The earliest occupation of Europe: Continental Northwestern Europe. In *The Earliest Occupation of Europe: Proceedings of the European Science Foundation Workshop at Tautavel (France), 1993*. Wil Roebroeks and Thijs van Kolfschoten, eds. Pp. 147–163. Leiden: University of Leiden Press.

Urban, Brigitte, and Gerlinde Bigga. 2015. Environmental reconstruction and biostratigraphy of late Middle Pleistocene lakeshore deposits at Schöningen. *Journal of Human Evolution* 89:57–70.

van Andel, Tjeerd H., and William Davies, eds. 2003. *Neanderthals and modern humans in the European landscape during the last glaciation*. Cambridge: MacDonald Institute for Archaeological Research.

van Kolfschoten, Thijs. 2014. The Palaeolithic locality Schöningen (Germany): A review of the mammalian record. *Quaternary International* 326–327:469–480.

Villaluenga Aritza, Jarod M. Hutson, Alejandro García-Moreno, Elaine Turner, and Sabine Gaudzinski-Windheuser. 2015. A site for all seasons: reconstructing the occupational history of the Middle Pleistocene Schöningen 13 II-4 "Spear Horizon." *Proceedings of the European Society for the Study of Human Evolution (PESHE)* 4:231.

Vollbrecht, Jürgen. 2000. The antler finds at Bilzingsleben, excavations 1969–1993. *Internet Archaeology* 8. http://dx.doi.org/10.11141/ia.8.1

Voormolen, Boudewijn. 2008. *Ancient hunters, modern butchers: Schöningen 13II–4, a kill–butchery site dating from the northwest European Lower Palaeolithic*. PhD thesis, University of Leiden.

Wales, Nathan. 2012. Modelling Neanderthal clothing using ethnographic analogues. *Journal of Human Evolution* 63:781–795.

Walker, Michael J., D. Anesin, Diego E. Angelucci, Azucena Avilés-Fernández, F. Berna, A. T. Buitrago-López, Y. Fernández-Jalvo, *et al*. 2016. Combustion at the late Early Pleistocene site of Cueva Negra del Estrecho de Río Quípar (Murcia, Spain). *Antiquity* 90(351):571–589.

Wall-Scheffler, Cara M., and Marcella J. Myers. 2013. Reproductive costs for everyone: How female loads impact human mobility strategies. *Journal of Human Evolution* 64:448–456.

Walthall, John A. 1998. Overwinter strategy and early Holocene hunter-gatherer mobility in temperate forests. *Midcontinental Journal of Archaeology* 23(1):1–22.

White, Mark J. 2006. Things to do in Doggerland when you're dead: surviving OIS3 at the northwestern-most fringe of Middle Palaeolithic Europe. *World Archaeology* 38(4):547–575.

White, Mark J. 2015. 'Dancing to the rhythms of the biotidal zone': Settlement history and culture history in Middle Pleistocene Britain. In *Settlement, Society and Cognition in Human Evolution: Landscapes in Mind*. Fiona Coward, Robert Hosfield, Matt Pope, and Francis Wenban-Smith, eds. Pp. 154–173. New York: Cambridge University Press.

White, Mark J. 2016. Lost Landscapes of Palaeolithic Britain: where do we go from here? In *Lost Landscapes of Palaeolithic Britain.* Mark White, Martin Bates, Matt Pope, Danielle Schreve, Beccy Scott, Andy Shaw, and Elizabeth Stafford, eds. Pp. 131–136. Oxford: Oxford Archaeology.

Wood, Bernard, and Nicholas Lonergan. 2008. The hominin fossil record: taxa, grades and clades. *Journal of Anatomy* 212(4):354–376.

Wrangham, Richard. 2009. *Catching Fire: how cooking made us human*. New York: Basic Books.

Wymer, John. 1999. *The Lower Palaeolithic Occupation of Britain*. Salisbury: Wessex Archaeology and English Heritage.

Main Text

Table 1: Winter and summer temperature estimates for Early and Middle Pleistocene north-western and north-central European sites. [1]Sensitivity tests on coleoptera-based MCR procedures suggest that winter temperature estimates are usually too warm (Pettitt and White 2012:35); [2]Ashton and Lewis 2012 (Pakefield listed as -4 – +6°C); [3]Ashton *et al*. 2008a; [4]Coope 1993; [5]Coope 2006; [6]Holman 1998; [7]Holman 1999; [8]Holmes *et al*. 2009; [9]Mania 1995 (the specific source of the palaeo-temperature estimates is not stated, but the fauna includes molluscs and ostracods); [10]Parfitt *et al*. 2010; [11]Shotton *et al*. 1993.

Table 2: Fur-bearing animals, with modern distribution data for comparison, documented on northern European Middle Pleistocene sites. Other documented species include: *V. vulpus; M. putorius; M. erminea; M. lutreola; and L. lutra.* [1]Macdonald and Barrett 1993 (modern European data; it is fully acknowledged that Early and Middle Pleistocene species' ecology would not have been identical to their modern equivalents); [2]Mania and Mania 2005; [3]Parfitt 1999; [4]Schreve 1996; [5]Stuart *et al*. 1993. Site units: Swanscombe (LL): Lower Loam; Swanscombe (LG): Lower Gravels.

Table 3: Modern home range, density and mobility data for selected ungulate species, documented on Middle Pleistocene sites. [1]Bello, Parfitt, and Stringer 2009; [2]Clutton-Brock, Guinness, and Albon 1982; [3]Macdonald and Barrett 1993 (modern European data; it is fully acknowledged that Early and Middle Pleistocene species' ecology would not have been identical to their modern equivalents); [4]Mania and Mania 2005; [5]Parfitt 1998; [6]Parfitt 1999 (notes that the fallow deer's late rut results in males' poor condition during winter); [7]Putman 1988; [8]Schreve 1996; [9]Stuart 1992; [10]Stuart *et al*. 1993; [11]Thieme 2005; [12]Voormolen 2008. Site units: Swanscombe (LL): Lower Loam; Swanscombe (LG): Lower Gravels.

Table 4: Fat-bearing and/or residential winter animals, with modern distribution data for comparison, documented on Middle Pleistocene sites. [1]Jochim 1981; [2]Macdonald and Barrett 1993 (modern European data); [3]Mania and Mania 2005; [4]Parfitt 1998; [5]Parfitt 1999; [6]Schreve 1996; [7]Stuart 1992; [8]Stuart *et al*. 1993.

Table 5: Butchery by species and technique, from selected Lower Palaeolithic sites. [1]Andrews and Ghaleb 1999; [2]Ashton *et al*. 2008b; [3]Bello, Parfitt, and Stringer 2009; [4]Parfitt 1998; [5]Parfitt and Roberts 1999; [6]Stopp 1993; [7]Voormolen 2008.

Table 6: Plant families identified at Hoxne, with comparison to modern plant species available to winter foragers. [1]Mabey 2012; [2]Mears and Hillman 2007; [3]Mullenders 1993, table 6.3 & figs. 6.1–6.3.

Reply

Table 1: Present day average temperatures (°C), by month, for selected locations (data source: Climate-Data.org [http://en.climate-data.org/]). [1]Addis Ababa elevation: 2,355m asl; [2]Dmanisi elevation: 1,225m asl; [3]Erzurum elevation: 1,904m asl; [4]Estimates for Gesher Benot Ya'aqov based on data for Hulata.

Table 2: Energy and nutrient values for dried and roasted caribou (Health Canada 1995:120). [1]RE: *retinol equivalents;* [2]*NE:* niacin equivalents, where 1mg niacin equivalent is equal to 1mg niacin or 60mg tryptophan.

Main Text

Figure 1: Comparison of winter temperature ranges for Spanish (Early Pleistocene; EP) and British (Early Pleistocene and Middle Pleistocene; EP & MP) sites. Number of sites calculated according to the temperature ranges for each site (e.g. 7 sites have a T_{min} range which spans -3°C). Spanish site data (Almenara-Casablanca 3; Cal Guardiola; Cúllar Baza 1; Barranca León 5; Fuente Nueva 3; Trinchera Dolina (TD6); Trinchera Elefante (TERc)) from Agusti *et al*. (2009); British site data (Boxgrove, Brooksby, Happisburgh I, Happisburgh III, High Lodge, Hoxne, Pakefield) from Ashton *et al*. 2008a; Ashton and Lewis 2012; Coope 1993, 2006; Holman 1998, 1999; Holmes *et al*. 2009; Mania 1995; Parfitt *et al*. 2010.

Figure 2: Mean winter air temperature data (°C) from the Stage 3 Project's MIS-3 'warm' simulation (Barron, van Andel, and Pollard 2003, fig. 5.7 [Stage 3 Warm Phase DJF]). Dashed white line: Modern European coastline.

Figure 3: Summer/winter contrasts in mean air temperature data (°C) from the Stage 3 Project's MIS-3 'warm' simulation (Barron, van Andel, and Pollard 2003, appendix 5.1). Dashed white line: Modern European coastline.

Figure 4: Snow depth (cm) data from the Stage 3 Project's MIS-3 'warm' simulation (Barron, van Andel, and Pollard 2003, fig. 5.9). Dashed white line: Modern European coastline.

Figure 5: Number of days with snow cover data from the Stage 3 Project's MIS-3 'warm' simulation (Barron, van Andel, and Pollard 2003, fig. 5.9). Dashed white line: Modern European coastline.

Figure 6: Wind chill (°F) data from the Stage 3 Project's MIS-3 'warm' simulation (Barron, van Andel, and Pollard 2003, appendix 5.1). Dashed white line: Modern European coastline.

Figure 7: Precipitation (mm/day) data from the Stage 3 Project's MIS-3 'warm' simulation (Barron, van Andel, and Pollard 2003, appendix 5.1). Dashed white line: Modern European coastline.

Figure 8: Relationship between effective temperature and average distance/residential move (after Kelly 1995, fig. 4-7). Note the examples (circled) for groups making relatively short mean residential moves in low effective temperature environments (see Kelly 1995:128–130 for details). Effective Temperature (*ET*) is derived from the mean temperatures (°C) of the warmest and coldest months (*W* and *C*; where $ET = \frac{18\,W - 10\,C}{(W - C) + 8}$), and its value varies from 26 (equator) to 8 (poles). High *ET* values are associated with tropical, non-seasonal environments (in terms of temperature, not precipitation) with long growing seasons. Low *ET* values are associated with cold, seasonal environments with short growing seasons (Kelly 1995:66–69).

Figure 9: Selected sources of vitamins in Arctic hunter-gatherer diets (data from Hidiroglou *et al*. 2008; Kuhnlein *et al*. 2006). Values per 100g of fresh raw caribou

liver (e.g. 1.58mg for Riboflavin) compared against alternative food sources (e.g. raw moose liver [6.51mg] and raw beluga muktuk [0.02mg] for Riboflavin). G&D: growth and development.

Figure 10: A winter residency model.

Reply

Figure 1: Present day average temperatures (°C), by month, for selected locations (data source: Climate-Data.org [http://en.climate-data.org/]).

Supplementary Materials

Table 1: Lower critical and minimum sustainable ambient temperatures for *H. erectus* and *H. sapiens* (after Aiello and Wheeler 2003, tables 9.1–9.3). [1]*H. erectus* data from KNM-WT 15000 (Ruff 1994); [2]*H. sapiens* data from Předmost 3 & 9, Skhul 4 and Grotte des Enfants 4 (Ruff 1994); [3]BMR = 3.4 x mass $(\text{kg})^{0.75}$ (Kleiber 1961); [4]Elevated BMR = BMR raised by 15% to account for climatic and dietary-induced increases (after Aiello and Wheeler 2003:150); [5]Body surface area (m^2) = 0.00718 x mass $(\text{kg})^{0.425}$ x stature $(\text{cm})^{0.725}$; [6]Typical human conductance = 5 $\text{W.m}^{-2}.°\text{C}^{-1}$; [7]Total conductance = typical human conductance x surface area (m^2); [8]Critical temperature (°C) = 37°C – (BMR/Total conductance); [9]Minimum sustainable ambient temperature (°C) = 37°C – ((3 x BMR)/Total conductance); [10]Typical human conductance reduced by 5% to account for hominin muscularity (after Aiello and Wheeler 2003:150); [11]Typical human conductance reduced by c. 44% to account for 1 clo of insulation (after Aiello and Wheeler 2003:150). 1 clo is roughly equivalent to the insulation provided by a western business suit.

Table 2: Selected palaeoclimate simulation data for three point-specific locations, for an MIS 3 ‘warm’ interval and the present day. Data from Barron, van Andel, and Pollard (2003). [1]Descriptions of palaeoclimate measures from Barron, van Andel, and Pollard (2003:78).