Journal of Human Evolution 153 (2021) 102966

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Shivering in the Pleistocene. Human adaptations to cold exposure in Western Europe from MIS 14 to MIS 11

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ARTICLE INFO

Article history:
Received 13 August 2020
Accepted 1 February 2021
Available online xxx

Keywords:
Thermoregulation
Paleotemperature
Paleophysiology
Clothing

ABSTRACT

During the mid-Middle Pleistocene MIS 14 to MIS 11, humans spread through Western Europe from the Mediterranean peninsulas to the sub-Arctic region, and they did so not only during the warm periods but also during the glacial stages. In doing so, they were exposed to harsh environmental conditions, including low or extremely low temperatures. Here we review the distribution of archeological assemblages in Western Europe from MIS 14 to MIS 11 and obtain estimates of the climatic conditions at those localities. Estimates of the mean annual temperature, mean winter and summer temperatures, and the lowest temperature of the coldest month for each locality were obtained from the Oscillayers database. Our results show that hominins endured cold exposure not only during the glacial stages but also during the interglacials, with winter temperatures below 0 °C at many localities. The efficacy of the main physiological and behavioral adaptations that might have been used by the Middle Pleistocene hominins to cope with low temperatures is evaluated using a simple heat-loss model. Our results suggest that physiological and anatomical adaptations alone, such as increasing basal metabolic rate and subcutaneous adipose tissue, were not enough to tolerate the low winter temperatures of Western Europe, even during the MIS 13 and MIS 11 interglacials. In contrast, the use of a simple fur bed cover appears to have been an extremely effective response to low temperatures. We suggest that advanced fire production and control technology were not necessary for the colonization of northern Europe during MIS 14 and MIS 12. We propose that Middle Pleistocene European populations were able to endure the low temperatures of those glacial stages combining anatomical and physiological adaptations with behavioral responses, such as the use of shelter and simple fur clothes.

1. Introduction

Our perception of the ability of Middle Pleistocene hominins to survive in mid- and high-latitude regions has changed drastically over the last few decades. The 'short chronology' model that denied the presence of hominins in Europe before 0.5 ka, championed by R. Dennel (1983) and W. Roebroeks (Roebroeks and Kolfschoten, 1994), evolved into the 'short chronology' for northern Europe model (Dennell and Roebroeks, 1996), following the discovery of uncontroversial evidence of hominin presence in the Iberian peninsula at the end of the Early Pleistocene (Carbonell et al., 1995). Further findings at the turn of the century from Pakefield (Parfitt et al., 2005) and Happisburgh III (Parfitt et al., 2010) extended the evidence of human occupation northwards to southern Britain, and back in time to the late Early Pleistocene. It remains apparent, however, that a change in the occupation pattern of mid-latitude Europe occurred from 500 ka onward, when the number of archeological assemblages markedly increased and Acheulean technology spread throughout Western Europe (Haidle and Pawlik, 2010; Moncel et al., 2015, 2018).

There is a lack of consensus among paleoanthropologists about the phylogenetic affinities and taxonomic identities of those Middle Pleistocene European human populations. The topics under debate include the number of species that lived in Middle Pleistocene Europe, whether *Homo heidelbergensis* is a valid species, whether African fossils should be included within *H. heidelbergensis*, whether *H. heidelbergensis* is ancestral to *Homo neanderthalensis*, and if at least some Middle Pleistocene populations should be included in *H. neanderthalensis* (Rightmire, 2008; Hublin, 2009; Mounier et al., 2009; Manzi, 2011; Martinón-Torres et al., 2011;

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https://doi.org/10.1016/j.jhevol.2021.102966
0047-2484/

Stringer, 2012; Galway-Witham et al., 2019). It is beyond the scope of this article to contribute to these debates. Thus, we will avoid the use of species names when referring to the Middle Pleistocene human populations of Europe, assuming that all of them were similar in physiology and body shape (see below).

Living in mid-latitude Europe during the Middle Pleistocene involved facing a number of new challenges that did not exist in the tropical or subtropical areas where hominins originated, although also present in other areas as the Near East or northern China (MacDonald, 2017). These challenges included the long daily period of darkness in winter, marked seasonality in resource availability, and a colder climate (Moran, 1981). Confronting cold exposure is a major challenge for any species with a tropical ancestry. Thus, addressing the thermoregulatory strategies of hominins is essential to understanding their geographical expansion during the mid-Middle Pleistocene.

Thermal stress represents one of the most important constraints to which humans have had to adapt. Buffering the effects of weather to maintain homeostasis and body temperature and to avoid thermal damage is energetically expensive for any homeothermic organism (Scholander, 1955; Porter and Gates, 1969). Humans, as furless endotherms, are well adapted to dissipate heat in warm climates but poorly adapted to conserve it in the cold (Haman, 2006; Daanen and van Marken Lichtenbelt, 2016). In cold environments, the human thermoregulatory system relies on physiological responses and behavior to conserve thermal homeostasis (Leppäluotto and Hassi, 1991). These include reducing heat loss via peripheral vasoconstriction (Steegmann, 2007), increasing heat production by voluntary physical activity or involuntary shivering (Haman et al., 2010), increasing the secretion of thermogenic hormones, such as thyroid and adrenal hormones (Leonard et al., 1999, 2002, 2005), and activating non-shivering thermogenesis by mobilizing brown adipose tissue (BAT) and carbohydrates (Saito et al., 2009; van Marken Lichtenbelt et al., 2009; Yoneshiro et al., 2016). Furthermore, without protective shelter, fire, and clothing, cold exposure can rapidly result in cold-induced injuries in recent humans. These include temporary loss of function, frostbite, permanent cell damage, hypothermia, and even, death (Young et al., 1998; Van Ooijen et al., 2004; Daanen and van Marken Lichtenbelt, 2016).

Extensive investigations on the thermal responses of humans have been performed since the beginning of the 20th century (Roberts, 1952; Burton and Edholm, 1955; Erikson et al., 1956; Adams and Corvino, 1958; Barnicot, 1959; Schreider 1964, 1975; Wyndham et al., 1968). In fact, the adaptations of cold-exposed humans are an old and recurrent debate in human biology and anthropology (Hoydas and Ring, 1982; Hanna et al., 1989; Bittel, 1992; Wheeler, 1992, 1993; Frisancho, 1993; Steegmann et al., 2002; Steegmann, 2007 and references therein; Leonard and Katzmarzyk, 2010; Beall et al., 2012; Naya et al., 2016; O'Cobock, 2016; Senn et al., 2018; Wissler, 2018). The debate includes evaluating the relationship between metabolism and temperature in human populations, interpreting the ecogeographic rules for humans, and comparing body morphologies and thermal responses (Roberts 1952, 1978; Ruff 1993, 1994; Aiello and Wheeler, 2003; Dembo, 2007; Collard and Cross, 2017; Wells et al., 2019).

Anthropologists have long proposed that changes in the geometry of the human body can affect temperature regulation. Even the so-called 'cylinder model' of body form (Ruff, 1991, 1993) states that a wide body with short extremities could be adaptations to cold in hominins because it offers a smaller body surface area (BSA) for a given body mass (BM). This hypothesis highlights the efficiency of this body geometry in retaining heat and keeping warm. The thermal adaptive interpretation of Bergmann and Allen's rules (Bergmann, 1847; Allen, 1877) for humans has been accepted by many biological anthropologists and paleoanthropologists, although it has also been called into question by some researchers (i.e., Dembo, 2007; Steegmann, 2007; Beall et al., 2012; Wells et al., 2019). Their criticisms point to the physiological constraints detected in modern humans coping with cold exposure, even when they possess the alleged advantages of these morphological patterns. Furthermore, these works suggest that the human body does not respond to cold stress in a simple manner (Steegmann, 2007) and that modifications in body size and shape may not necessarily be the most efficient mechanisms in terms of thermoregulation (Dembo, 2007; Beall et al., 2012). The advantage of shortened extremities for heat conservation and the adaptive advantage of long limbs to dissipate heat are generally accepted for hominins (Trinkaus, 1981; Ruff, 1994; Holliday, 1997; Aiello and Wheeler, 2003; Tilkens et al., 2007). However, other authors consider these anatomical features to have little effect on thermoregulation (Steegmann, 2007) given that peripheral vasoconstriction and tissue insulation are basic responses to cold in humans. Certainly, the physical and geometrical differences among individuals (in terms of muscularity, adiposity, and the ratio of BSA to mass) influence their thermal responses (Anderson, 1999). Indeed, the exchange of heat by radiation, convection, and conduction and its dissipation by evaporation are more dependent on BSA, while heat production and storage rates are more closely related to breathing physiology, BM, and body composition (Giesbrecht, 1998; Anderson, 1999).

The survival of hominins in cold environments depends on their capacity to counterbalance their basal rate of heat loss, by increasing their thermogenic rate through mechanisms that prevent decrease in core temperature (~37 °C) and maintaining thermal comfort. It is well known that the thermoneutral point for a naked recent human at rest is an ambient air temperature of 27–28 °C (Erikson et al., 1956). Under these conditions, thermoregulation occurs only through vasomotor control (Kingma et al., 2012). Other physiological mechanisms of thermogenesis (e.g., metabolic heat production) are activated only when humans lose their thermoneutrality, and their temperature drops below the lower critical temperature of the core (survival limits range from 27 to 42 °C; Stocks et al., 2004).

Physiological response to cold exposure differs among individuals and is modulated by the following factors (Kingma et al., 2012): body size and BSA significantly influence the body cooling rate (Katzmarzyk and Leonard, 1998); body composition influences insulation efficiency because muscle and adipose tissues have different thermal resistances (Wells et al., 2019); heat production via shivering and non-shivering thermogenesis involve different levels of energy expenditure (Anderson, 1999); and clothing prevents heat dissipation and increases heat conservation. Moreover, the ability to maintain thermal homeostasis depends on age (i.e., age-related dysthermia) and sex. Females are more prone to heat loss, while their higher adiposity increases insulation but limits their maximum capacity for thermogenic response (Glickam-Weiss et al., 2000; Kaciuba-Uscilko and Gruzca, 2001).

In addition to the responses delineated above, humans may also adapt to their environment by means of behavioral and/or cultural responses. Thus, the ability of Middle Pleistocene humans to produce and control fire is central to the debate about their adaptation to cold environments (Gowlett, 2006, 2016; Roebroeks and Villa, 2011). Although the control of fire has been considered a key innovation for the survival of hominins in temperate and cold climates (Gowlett, 2006), the archeological evidence for the use of fire in Europe before 300 ka is controversial. Evidence of the use of fire at high latitudes during MIS 11 and MIS 13 has been claimed from Beeches pit, dated to 414 ± 30 ka by thermoluminescence (Preece et al., 2006) and from Menez-Dregan layer 9, dated to 465 ± 65 ka by electron spin resonance (Monnier et al., 2016;

Ravon et al., 2016), respectively. However, a younger chronology for the stratigraphic sequence of Menez-Dregan based on TL dates has been proposed by Mercier et al. (2004). In southern Europe, evidence for the early use of fire is provided from Terra Amata (de Lumley, 2016) dated to MIS 9 or MIS 11, Aroeira Cave (Sanz et al., 2020) dated to MIS 11, and Bolomor Cave dated to around 350 ka (Rosell and Blasco, 2019). Bilzingsleben and Schöningen, in Germany, have also been claimed to provide evidence of fire control by humans at around MIS 9 or MIS 11, but this interpretation has been questioned (Stahlschmidt et al., 2015; Rosell and Blasco, 2019). Rosell and Blasco (2019) suggest that fire control and the emergence of post-Acheulean technology occurred in Europe in parallel, between MIS 11 and MIS 9. In summary, evidence of fire is extremely rare before MIS 9, and it increases progressively to become frequent during MIS 4 and MIS 3 (Roebroeks and Villa, 2011). Another possible cultural response to cold is the use of clothing, a behavior that is usually assumed for Neandertals (White, 2006; Gilligan, 2007; Wales, 2012) and has also been suggested for Middle Pleistocene hominins (Hosfield, 2016; Gilligan, 2017).

In this article, we focus on cold as a constraint for hominin expansion through Western Europe from 500 ka to 350 ka and how hominins adapted to cope with it. We begin by reviewing the distribution of archeological sites dated from MIS 14 to MIS 11 and the inferred ambient temperatures with which hominins coped at those localities. We then use a simple heat-loss model (HLM) to evaluate the potential efficacy and reliability of the main physiological and behavioral strategies that might have been used by hominins to tolerate those temperatures. Our first aim is to estimate how low the temperatures were at the localities where humans were present during the MIS 14 to MIS 11 period. We estimate both summer and winter temperatures to evaluate the effect of low temperatures in the case of a seasonal occupation of northern Europe in summer, and in the case of a permanent presence of hominins in the northern localities throughout the year. We evaluate the efficacy of a number of adaptations that hominins could have developed to cope with low temperatures. We focus on thermoregulation during sleeping because it is a critical period: temperatures are usually lower at night, and heat cannot be gained from physical activity. More specifically, we will test the efficacy of metabolic responses, of the insulation provided by a subcutaneous fat layer, of the use of shelters, and of the insulation provided by simple fur covers to maintain the core temperature when sleeping. Our second aim is to test the hypothesis that hominins were able to cope with the harsh climatic conditions in Europe during the Middle Pleistocene without the frequent and controlled use of fire (for reviews of this hypothesis, see MacDonald, 2017; 2018; Hosfield, 2020).

2. Material and Methods

The paleoclimate data used in this study were obtained from a published dataset of interpolated paleoclimate maps (see below). A data set of archeological sites dated to the MIS 14 to MIS 11 period was compiled from published sources. Paleotemperatures at those localities were obtained from the paleoclimate maps. In a second step, we evaluate the efficacy of the physiological and behavioral adaptations indicated above using a simple HLM. The HLM allows us to estimate the minimum endurable temperature for a Middle Pleistocene hominin made possible by a single behavioral or physiological adaptation. Moreover, as explained below, the HLM allows us to evaluate the combined effect of several of those adaptations simultaneously. The HLM is dependent on BSA and basal metabolic rate (BMR). Thus, we estimated BMR and BSA for an average male and an average female individual from published estimations of height and weight for individuals from the Sima de los Huesos.

2.1. Paleoclimate data

A thorough bibliographic survey was performed in the Scopus Database (https:\\www.scopus.com) and in Google Scholar (https://scholar.google.com/) to locate information on archeological assemblages from Western Europe that correlate with the interval from MIS 14 to MIS 11. We searched for scientific publications containing in the Title, Abstract or keywords any combination of the terms 'MIS 11', 'MIS 12', 'MIS 13', 'MIS 14', and 'Middle Pleistocene' with the terms 'Palaeolithic', 'lithic', and 'human'. The ROAD and NQMDB databases, both accessible at https://www.roceeh.uni-tuebingen.de/roadweb/smarty_road_simple_search.php, were also searched to find sites dated to the period 0.6 to 0.3 Ma. The surveyed area included all the European territories to the west of meridian 14° E plus the entire Italian peninsula. No limit was established a priori for the latitude, but the northernmost site found was Happisburgh, at latitude 52.82° (Lewis et al., 2019a), and the southernmost was Cimitero di Atella at 40.88° (Rocca et al., 2018). The archeological assemblages were assigned to a time interval based on their numerical ages and/or their correlation with a marine isotopic (sub)stage provided by the original source.

Only archeological assemblages that could be confidently correlated to a single isotopic stage, or to one or more contiguous substages of the same isotopic stage, were retained for analyses (Fig. 1). Confidence about the accuracy of the correlation to a single isotopic stage was established as follows. When no numerical age estimates were available, we accepted the criterion of the original source, providing that no convincing evidence against that criterion was provided by other sources. When one or more numerical age estimates were available for an assemblage, we used the 95% confidence intervals of the dates to decide whether the assemblage can be confidentially correlated to a single stage, or to one or more contiguous substages. A total of 68 archeological assemblages from 46 localities (sites) fit the inclusion criteria, 33 of which could only be correlated to a specific glacial or interglacial stage, without further precision (Fig. 2C; Table 1).

Oscillayers (Gamisch, 2019a) is a global-scale, region-specific paleoclimatic database recording bioclimatic variables (Booth et al., 2014) with high temporal resolution spanning the Plio-Pleistocene. This database facilitates the study of climatic oscillations during the last 5.4 Myr at high spatial (2.5 arc-min) and temporal (10 ka time periods) resolution. The climatic oscillations between the modeled bioclim layers of the present (warm) and the last glacial maximum (cold) are computed along the $\delta^{18}O$ benthic stack of Lisiecki and Raymo (2005). Because this $\delta^{18}O$ curve dates back 5.4 million years, it is possible to estimate worldwide climate model oscillations based on this data (Gamisch, 2019b).

BIOCLIM is a model designed for species distribution modelling that defines a set of 19 bioclimatic (bioclim) variables, derived from monthly temperature and rainfall values, to obtain biologically meaningful variables that are commonly used in ecology to model species or biome distributions (Nix, 1986; Hijmans et al., 2005; Booth et al., 2014). The MIS 11 to MIS 14 stages may be subdivided into a number of substages of varying duration (Railsback et al., 2015), but most lasted more than 10 ka, the time resolution of the Oscillayers data set. Thus, in many cases it was necessary to combine the maps from several Oscillayers time slices to obtain the bioclimatic maps for a substage. In contrast, some other substages lasted less than 10 ka and were thus beyond the time resolution of the Oscillayers database. Moreover, it would be extremely difficult to correlate an archeological event to such short substages. Thus, we combined some contiguous substages

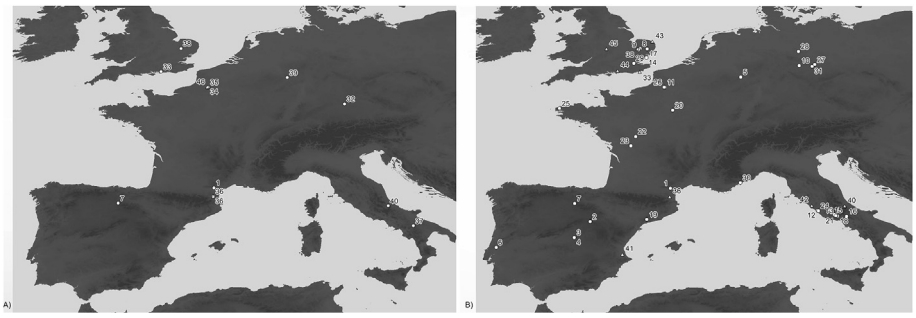

Figure 1. Spatial distribution of the archeological sites included in this study. A) Sites with assemblages dated to glacial stages MIS14 (triangles) and MIS 12 (circles). B) Sites with assemblages dated to interglacial stages MIS 13 (triangles) and MIS 11 (circles). 1, Aldéne; 2, Ambrona; 3, Aridos 1; 4, Aridos 2; 5, Ariendorf; 6, Aroeira; 7, Atapuerca Gran Dolina and Sima de los Huesos; 8, Barnham; 9, Beeches Pit; 10, Bilzingsleben II; 11, Cagny-La-Garenne II; 12, Castel di Guido; 13, Cava Pompi; 14, Clacton; 15, Fontana Ranuccio; 16, Guado San Nicola; 17, Hoxne; 18, Isoletta; 19, La Cansaladeta; 20, La Celle-sous-Moret; 21, Lademagne; 22, Le Grande Vallée; 23, Londigny; 24, Malagrotta; 25, Menez-Dregan I; 26, Saint-Acheul; 27, Schladebach/Wallendorf; 28, Schoeningen; 29, Swanscombe; 30, Terra Amata; 31, Uichteritz; 32, Attenfeld; 33, Boxgrove; 34, Cagny-Cimetière; 35, Cagny-La-Garenne; 36, Caune de l'Arago; 37, Cimitero di Atella; 38, High Lodge; 39, Kärlich; 40, Valle Giumentina; 41, Cueva de Bolomor; 42, Ficoncella; 43, Happisburgh 1; 44, Valdoe; 45, Waverly Wood; and 46, Rue du Manège.

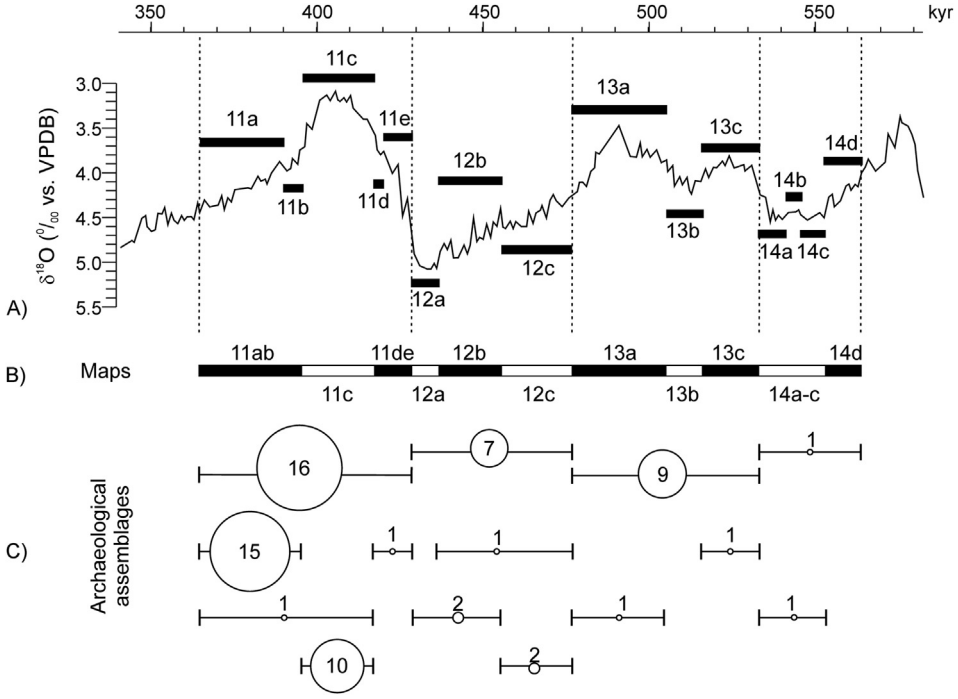

Figure 2. Summary of the data on archaeological assemblages used in this study. A) The LR04 stack of marine benthic foraminiferal $\delta^{18}O$ (Lisiecki and Raymo, 2005) is shown as a proxy for climate variation, indicating the substages defined by Railsback et al. (2015) for the MIS 11 to MIS 14 period. B) In this study, some contiguous substages were grouped into larger time intervals (Table 2) and paleoenvironmental maps computed for those intervals (see Material and Methods). C) Data for 68 archaeological assemblages reliably dated to stages MIS 11, MIS 12, MIS 13, or MIS 14 were compiled from the literature, and their temporal distribution is shown. The horizontal bars represent uncertainty about the age of the assemblages, and the size of the circle is proportional to the number of assemblages (numbers inside or above the circles).

into longer time periods, as shown in Table 1 and Figure 2. The values of the bioclim variables for the time intervals that included two or more Oscillayers time slices were obtained as the average value of the bioclim variable in the respective time slices. As an example, the value of a bioclim variable in time interval MIS 11c is the average of its values in the t39, t40, and t41 time slices (Table 2). There are 11 temperature-related bioclim variables in the Oscillayers data set, but we selected for our analyses the four variables that reflect the minimum temperatures that hominins had to endure throughout the year (Table 3). Throughout this article, we refer to the mean temperature of the warmest quarter (MTWQ) as 'summer temperature' and to the mean temperature of the coldest quarter (MTCQ) as 'winter temperature'. All of the maps and the Python scripts, version 2.7.18 (Python Software Foundation. Amsterdam) used to compute them are available from Willmes et al. (2020).

We obtained the values of the bioclim variables at each locality from the corresponding Oscillayers map. For the archeological assemblages that were correlated to an entire MIS without further precision, we computed an interval defined by the mean, maximum and minimum values of the variable during that stage. We proceeded in a similar way with those assemblages dated to a period that included more than one Oscillayers map. For the archeological assemblages correlated to a single substage we obtained point estimates of the bioclim variables from the paleoclimate maps corresponding to that substage. Thus, we acquired single-value

Table 1
Archeological assemblages from Western Europe dated from MIS 14 to MIS 11.

Code	Locality	Unit	Long.[a]	Lat.[b]	Age	References
1	Aridos 1	–	−3.53	40.15	MIS 11a	Sesé and Soto (2002); Yravedra et al. (2010)
2	Cagny-La-Garenne II	Levels I and H	2.34	49.87	MIS 11	Auguste (2009)
3	Barnham	5c	0.75	52.37	MIS 11c	Ashton (2016); Ashton et al. (1994)
4	Swanscombe	Lower loam	0.32	51.42	MIS 11c	Ashton (2016); Ashton et al. (1994)
5	Swanscombe	Upper loam	0.32	51.42	MIS 11a	Ashton (2016)
6	Ariendorf	1	7.28	50.53	MIS 11	Koenigswald and Heinrich (1999); Turner (1990)
7	Schoeningen	Scho 12	11.03	52.18	MIS 11	Haidle and Pawlik (2010) Conard et al. (2015); Kolfschoten (2014); Richter and Krbetschek (2015)
8	Bilzingsleben II	II	11.07	51.28	MIS 11	Koenigswald and Heinrich (1999); Mania (1998) Haidle and Pawlik (2010)
9	Atapuerca Gran Dolina	TD10-3	−3.52	42.35	MIS 11	Rodríguez et al. (2011)
10	Atapuerca Gran Dolina	TD10-1	−3.52	42.35	MIS 11a−b	Rodríguez et al. (2011)
11	Atapuerca Gran Dolina	TD10-2	−3.52	42.35	MIS 11c	Rodríguez et al. (2011)
12	Fontana Ranuccio	FR 4	13.35	41.63	MIS 11a−b	Palombo et al., 2000–2002; Pereira et al. (2018); Sala and Masini (2007)
13	Castel di Guido	–	12.28	41.9	MIS 11d−e	Ceruleo et al. (2019); Palombo et al., 2000–2002
14	Malagrotta	–	12.33	41.88	MIS 11	Ceruleo et al. (2019)
15	Aridos 2	–	−3.53	40.15	MIS 11a	Sesé and Soto (2002); Yravedra et al. (2010)
16	La Celle-sous-Moret	Tufa	2.85	48.38	MIS 11c	Auguste (2009); Limondin-Lozouet et al. (2010)
17	Clacton	Freshwater beds	1.09	51	MIS 11c	Ashton (2016)
18	Terra Amata	C1a	7.25	43.7	MIS 11	Valensi (2009)
19	Terra Amata	C1b	7.25	43.7	MIS 11	Palombo and Valli, 2003–2004; Valensi (2009)
20	Ambrona	AS1	−2.508	41.166	MIS 11a−b	Falguères et al. (2006); Santonja et al. (2018)
21	Ambrona	AS2	−2.508	41.166	MIS 11a−b	Falguères et al. (2006); Santonja et al. (2018)
22	Ambrona	AS1–4	−2.508	41.166	MIS 11	Falguères et al. (2006); Santonja et al. (2018)
23	Guado San Nicola	SU A*B, SU B, SU B*C, SU C, and SU C	14.16	41.52	MIS 11a−b	Pereira et al. (2016)
24	Isoletta	GA6Z	13.57	41.53	MIS 11a	Pereira et al. (2018)
25	Lademagne	102 m a.s.l.	13.48	41.53	MIS 11c	Pereira et al. (2018)
26	Cava Pompi	Level 5	13.44	41.56	MIS 11a−b	Pereira et al. (2018)
27	Saint-Acheul	Tufa	2.31	49.87	MIS 11a−b	Antoine and Limondin-Lozouet (2004)
28	Beeches Pit	3b	0.64	52.3	MIS 11c	Preece et al. (2006)
29	Beeches Pit	6	0.64	52.3	MIS 11	Preece et al. (2006)
30	Beeches Pit	5	0.64	52.3	MIS 11	Preece et al. (2006)
31	Beeches Pit	7	0.64	52.3	MIS 11	Preece et al. (2006)
32	Aroeira	Layer X	−8.62	39.51	MIS 11c	Daura et al. (2017); Daura et al. (2018)
33	La Cansaladeta	A, B, C, D	1.18	41.31	MIS 11a	Ollé et al. (2016)
34	La Cansaladeta	I–J	1.18	41.31	MIS 11b	Preece et al. (2006)
35	La Cansaladeta	K	1.18	41.31	MIS 11c	Preece et al. (2006)
36	Hoxne	A	1.19	52.35	MIS 11a	Ashton et al. (2016); Ashton et al. (2008)
37	Hoxne	B	1.19	52.35	MIS 11a	Ashton et al. (2016); Ashton et al. (2008)
38	Le Grande Vallée	U5a–U5e	0.46	46.68	MIS 11	Hérisson et al. (2016)
39	Menez-Dregan I	Layer 7	−4.49	48.5	MIS 11	Mercier et al. (2004); Monnier et al. (2016); Ravon et al. (2016)
40	Aldéne	TU II	2.7	43.35	MIS 11	Rossoni-Notter et al. (2016)
41	Uichteritz	Middle gravel	11.91	51.21	MIS 11a−c	Lauer et al. (2020)
42	Schladebach/ Wallendorf	–	12.09	51.33	MIS 11	Lauer and Weiss (2018)
43	Londigny	IIBt horizon	0.15	46.08	MIS 11c	Connet et al. (2020)
44	Kärlich	Level H	7.47	50.47	MIS 12	Haidle and Pawlik (2010); Kolfschoten and Turner (1996)
45	Boxgrove	6b, 8a, 8b,	−0.72	50.85	MIS 12	García -Medrano et al. (2019)
46	Atapuerca Gran Dolina	TD10-4	−3.52	42.35	MIS 12	Rodríguez et al. (2011)
47	Caune de l'Arago	CM_III	2.66	42.79	MIS 12	Falguères et al. (2015); Hanquet and Desclaux (2011); Magniez et al. (2013)
48	Cagny-La-Garenne	–	2.34	49.86	MIS 12a−b	Auguste (2009)
49	Cagny-Cimetière	Basal gravels	2.33	49.86	MIS 12a−b	Limondin-Lozouet et al. (2010); Tuffreau (1980)
50	Cimitero di Atella	L	15.66	40.88	MIS 12	Abruzzese et al. (2016); Rocca et al. (2018)
51	Valle Giumentina	VV1 LABM	14.02	42.18	MIS 12b−c	Nicoud et al. (2016); Villa et al. (2016)
52	Aldène	TU I	2.7	43.35	MIS 12	Rossoni-Notter et al. (2016)
53	Attenfeld	–	11.2	48.78	MIS 12c	Haidle and Pawlik (2010)
54	High Lodge	Bed E	0.56	52.35	MIS 12c	Lewis et al. (2019b)
55	Atapuerca Sima de los Huesos	LU 6	−3.52	42.35	MIS 12	Aranburu et al. (2017); Carbonell et al. (2003); Demuro et al. (2019)
56	Cueva de Bolomor	Fase I	−0.42	39.07	MIS 13	Fernández et al. (2000); Rivals and Blasco (2008)
57	Boxgrove	4b	−0.72	50.85	MIS 13	García -Medrano et al. (2019); Roberts and Parfitt (1999)
58	Boxgrove	5a	−0.72	50.85	MIS 13	García -Medrano et al. (2019); Roberts and Parfitt (1999)

(*continued on next page*)

Table 1 (*continued*)

Code	Locality	Unit	Long.[a]	Lat.[b]	Age	References
59	Boxgrove	4c	−0.72	50.85	MIS 13	García -Medrano et al. (2019); Roberts and Parfitt (1999)
60	Caune de l'Arago	CM_II	2.66	42.79	MIS 13	Falguères et al. (2015); Hanquet and Desclaux (2011); Magniez et al. (2013)
61	Valdoe	Slindon sands	−0.72	50.94	MIS 13	Roberts et al. (2009); Voinchet et al. (2015)
62	Ficoncella	FIC 1	11.88	42.22	MIS 13a	Aureli et al. (2016)
63	Valle Giumentina	VV1 LAN	14.02	42.18	MIS 13c	Nicoud et al. (2016); Villa et al. (2016)
64	Happisburgh 1	Organic mud and gray sands	1.54	52.82	MIS 13	Gibbard et al. (2019); Lewis et al. (2019a)
65	High Lodge	Bed C	0.56	52.35	MIS 13	Gibbard et al. (2019); Lewis et al. (2019a); Lewis et al. (2019b)
66	Waverly Wood	–	−1.46	52.34	MIS 13	Keen et al. (2006)
67	Caune de l'Arago	CM_I	2.66	42.79	MIS 14	Falguères et al. (2015); Hanquet and Desclaux (2011); Magniez et al. (2013)
68	Rue du Manège	–	2.28	49.88	MIS 14a −c	Antoine et al. (2015)

[a] Long., longitude.
[b] Lat., latitude.

estimates of the bioclim variables for 31 assemblages, and interval estimates for the remaining 37 assemblages.

2.2. The heat-loss model

Several homeostatic mechanisms enable homeothermic organisms to maintain a constant core temperature across a generally wide range of ambient temperatures. Human strategies for adapting to cold include lowering the body temperature (hypothermic response), minimizing heat loss (insulative response), and increasing heat production (metabolic response; Mäkinen, 2007). Several models have been developed to accurately describe thermoregulation in humans (Stolwijk, 1971; Fiala et al., 2001, 2012; Huizenga et al., 2001; Cheng et al., 2012; Foster and Collard, 2013), but most of them are excessively complex and would require making numerous assumptions if applied to a fossil hominin. Aiello and Wheeler (2003) made a first attempt to describe thermoregulation in Neandertals using a simple model, later applied by MacDonald (2018) and Hosfield (2020) to Middle Pleistocene hominins. Sørensen (2009) applied an improved version to describe thermoregulation in Neandertals during the Eemian. The model used by Sørensen (2009) is based on the following equation to estimate heat loss in humans:

$$L = \frac{BSA(T_c - T_a)}{R + \frac{1}{C}} \quad (1)$$

where L is the heat loss in watts (W), BSA is the body surface area (m^2), T_c is the body core temperature, which is assumed to be 37 °C in humans, and T_a is the ambient temperature. Temperatures are expressed in the model in Kelvin degrees (K). R is the summed thermal resistance of all the isolating layers (including clothes, hair, subcutaneous fat, or any other isolating item), and C is a wind-related convection term expressed in $W/m^2 \cdot K$. The thermal resistance of a particular isolating layer is the ratio of the layer thickness (s_i) in m, and the heat conductivity of the layer (k_i), expressed in W/m·K. Thus, the summed thermal resistance (R) is measured in $m^2 \cdot K/W$ and obtained as:

$$R = \sum_{i=1}^{n} \frac{s_i}{k_i} \quad (2)$$

Sørensen (2009) used the value of 2 W/m·K as the heat conductivity of fat. However, Hatfield and Pugh (1951) experimentally measured the heat conductivity of human fat and obtained an average value of 0.000488 cal $cm/cm^2 \cdot s \cdot °C$, equivalent to 0.2 W/m·K. In adult modern humans, the thickness of the subcutaneous adipose tissue (SAT) varies between 0.0025 m and 0.0077 m in males and females reported to be within normal limits for weight, although in obese individuals SAT thickness may reach 0.03 m (Störchle et al., 2017, 2018). In our analyses we assumed a SAT thickness of 0.005 m for the average male and female individuals because it is the mean value for modern humans within normal weight limits. Moreover, since an increased subcutaneous fat layer has been proposed as a possible adaptation to cold in Middle

Table 2
Time intervals used in the analyses and their correlation with the Oscillayers time slices (Gamisch, 2019b).[a]

Time interval	Chronology (ka)	Oscillayers time slices
MIS 11 ab	370–390	t37, t38
MIS 11c	390–420	t39,t40, t41
MIS 11de	420–430	t42,
MIS 12a	430–440	t43
MIS 12b	440–460	t44, t45
MIS 12c	460–480	t46, t47
MIS 13a	480–500	t48, t49, t50
MIS 13b	500–510	t51
MIS 13c	520–530	t52, t53
MIS 14a-c	530–550	t54, t55
MIS 14d	550–560	t56

[a] The naming of the substages follows Railsback et al. (2015). The computations of the bioclim variables for the MIS stages from the Oscillayers data are based on the definitions in Table 3 and were conducted using Python v. 2.7.18 (Python Software Foundation, Amsterdam) and GRASS GIS v. 7.4 (GRASS Development Team c/o OSGeo., Beaverton). The relevant scripts and GIS data are available from Willmes et al. (2020).

Table 3
Bioclim variables used in this study and definitions from O'Donnell and Ignizio (2012), where T_{avg} represents mean temperature and T_m represents minimum temperature of the current month.

BIOCLIM variable	Description	Definition
BIO1	Mean annual temperature	$\frac{\sum_{i=1}^{i=12} T_{avg_i}}{12}$
BIO6	Minimum temperature of the coldest month	$min(Tm_1, \ldots, Tm_{12})$
BIO10	Mean temperature of the warmest quarter	Maximum of each three consecutive months (Jan.–Mar., Feb.–Apr., to Dec.–Feb.) averaged temperature
BIO11	Mean temperature of the coldest quarter	Minimum of each three consecutive months (Jan.–Mar., Feb.–Apr., to Dec–Feb) averaged temperature

Pleistocene hominins (see discussion in MacDonald, 2018), we tested the thermal insulation effect of a thicker SAT, in the range of 0.005 m–0.03 m.

The heat conductivity of animal fur was taken by Sørensen (2009) to be k_i = 0.035 W/m·K. However, thermal conductivity varies among species. In carnivore pelts, the thermal conductivity ranges from 0.045 ± 0.030 W/m·K in mustelids to 0.069 ± 0.015 W/m·K in ursids (Liwanag et al., 2012). Fur thickness ranges between 0.045 and 0.060 m in the Arctic fox (*Alopex lagopus*), 0.035–0.055 m in reindeer (*Rangifer tarandus*), and 0.055–0.065 m in wolves and bears (Scholander et al., 1950). Moreover, White (2006) reported that reindeer fur, highly appreciated by modern Arctic people for its thermal insulation properties, has a clo value of 7, equivalent to a thermal resistance of R = 1.085 m^2 K/W. The clo is the unit of clothing insulation, equivalent to a thermal resistance of 0.155 m^2 K/W (Owen, 2017). In our analyses, unless otherwise stated, we used an average thickness of 0.05 m and an average thermal conductivity of 0.055 W/m·K for animal fur, since these are the average values of thickness and conductivity, respectively, reported for the fur of mammals similar in size and phylogenetically close to the species available to the Middle Pleistocene hominins in Europe.

The wind convection term C was determined from wind velocity (V) expressed in m/s, according to the following equation:

$$C = 5 + 3.95V^{0.6} \quad (3)$$

Since the Oscillayers data set does not provide information on wind velocity, we tested the effects of wind under a variety of conditions (see below).

Long-term human survival in a given environment is only possible when heat production is in equilibrium with heat loss. If heat loss permanently exceeds the heat production capacity of the individual, the organism enters hypothermia (core temperature below 35 °C), and death occurs within a few hours (Collins, 1983). Sleeping is a critical period for the survival of humans in cold environments (Scholander et al., 1958). For a sleeping or resting individual, heat production is equal to their BMR if physiological thermoregulatory mechanisms are not activated. Thus, the minimum endurable ambient temperature (T_{min}) for a resting or sleeping human may be obtained by substituting L for BMR in Eq. (1), and solving for T_a:

$$T_{min} = T_c - \frac{BMR}{BSA}\left(R + \frac{1}{C}\right) \quad (4)$$

BMR is expressed in W in Eq. (4) following the international system of units; however, in physiology and nutrition it is customary to express BMR in kcal/day, and the equations used to estimate BMR from BM usually also express BMR in kcal/day (see below). Thus, we expressed BMR in W in our computations, but in the text, we also report BMR in kcal/day. Critical temperature is defined as the lowest ambient temperature at which a homeothermic organism can maintain its BMR without losing body temperature (Scholander et al., 1957), it is equivalent to the lower critical temperature in Aiello and Wheeler (2003) and Hosfield (2020). Since thermogenesis is fundamentally dependent on BMR, increasing BMR is a direct way to elevate heat production. Shivering also increases heat production, but in energetic terms it is an acute physiological mechanism to enhance thermogenesis. In our analyses we tested the effect on T_{min} of raising the BMR of hominins by different factors, up to three times the estimated BMR value, since this is the limit to which BMR may be raised on a permanent basis (Burton and Edholm, 1955; Hammond and Diamond, 1997; Westerterp, 2001; Aiello and Wheeler, 2003). Thus, the minimum endurable temperature is the lowest ambient temperature at which a human being at rest can maintain its normal core temperature without elevating its metabolic rate, considering the insulating effect of clothing and heat loss by air convection. In contrast, the minimum sustainable temperature in Aiello and Wheeler (2003) and Hosfield (2020) is the minimum temperature at which a human can maintain normal body temperature by raising its BMR to its maximum sustainable level, which is assumed to be three times the normal BMR.

2.3. Estimating basal metabolic rate and body surface area

We based our estimations about the physiology of European Middle Pleistocene hominins on data from the Sima de los Huesos (SH) sample, which constitutes the most complete sample of a biological population from this period (Carretero et al., 2012; Arsuaga et al., 2015; Demuro et al., 2019). Estimates of BM and stature (H) for the adult specimens from the SH population were obtained from Will et al. (2017). We used the average BM and H values for the six male and six female specimens with paired BM and H values in Will et al. (2017; see also Supplementary Online Material [SOM] Table S1).

It is well appreciated that BMR in homeotherms is strongly correlated with BM (White and Seymour, 2003; Craig, 2011). Humans conform to the general mammalian scaling law that scales BMR as a function of BM raised to 0.75 (Kleiber, 1947, 1961). Although this general equation has been used to estimate the BMR of hominins (Aiello and Wells, 2002; Aiello and Wheeler, 2003), only two human individuals from North America were included by Kleiber (1947) in the study. Thus, we estimated BMR as recommended by the FAO/WHO/UNU (1985, 2004) reports on human energy requirements, applying the equations reported in Schofield (1985), and the equations provided by the Oxford Brooke Database (Cole and Henry, 2005; Henry, 2005) for adult males and females.

The Schofield equations Schofield (1985) for individuals aged 18–29 years are as follows:

$$\text{BMR Males} = 15.1\text{BM} + 692 \quad (5)$$

$$\text{BMR Females} = 14.8\text{BM} + 487 \quad (6)$$

where BM is body mass in kg, and BMR is measured in kcal/day.

The Oxford equations (Cole and Henry, 2005; Henry, 2005) for individuals aged 18–30 years are as follows:

$$\text{BMR Males} = 16.0\text{BM} + 545 \quad (7)$$

$$\text{BMR Females} = 13.1\text{BM} + 558 \quad (8)$$

where BM is body mass in kg, and BMR is measured in kcal/day.

We selected the equations for those age intervals because the longevity estimated for the SH population is no more than 40 years and less than 15% of the population lived more than 30 years (Bermúdez de Castro et al., 2004). Moreover, we assume that the paleodemography of the SH population is representative of the paleodemography of any contemporaneous hominin population in Western Europe (Bermúdez de Castro et al., 2004). It may be argued that the SH population was a demographic outlier and does not represent the structure of a Middle Pleistocene living population. However, using the Oxford equations for individuals aged 30–60 years only reduces the estimated BMR by a 5%, both for males and females. Thus, considering other age structures for the hominin populations would have little effect on our results. Although these equations have been criticized (Weekes, 2007; Heyes and MacDonald, 2015), they have been widely tested and generally accepted by researchers and remain the standard reference for the

estimation of BMR in living populations (but see Froehle, 2008). Thus, we estimated the BMR of an average male and female using the Schofield equation and the Oxford equation, and then computed the average of both estimates (SOM Table S2).

Several equations have been proposed to estimate BSA in humans (Verbraecken et al., 2006), and they are commonly used in medicine to calculate doses of chemotherapeutic agents and in other clinical applications. Most of these regression equations estimate BSA from the height and weight of the individual. Churchill (2006) used several of these clinical equations to estimate BSA in a Neandertal individual from La Ferrasie 1 (see Table 3 in Churchill, 2006), and compared the results with an estimate obtained using a 3D model of the same Neandertal individual. All the equations underestimated BSA by 4–7% relative to the Neandertal model, but the most similar results were obtained with the equations of Boyd (1935), Gehan and George (1970), and Haycock et al. (1978). Although many authors use the Du Bois and Du Bois (1916) formula, we used the equation provided by Haycock et al. (1978), as it is applicable to a wide range of human body shapes:

$$BSA = 0.024265\ H^{0.3964}\ x\ BM^{0.5378} \quad (9)$$

where BSA is the body surface area in cm^2, H is height in cm, and BM is body mass in kg. However, according to a comparison by Churchill (2006), the Haycock et al. (1978) equation shows similar performance to the Gehan and George (1970) equation, which is a refinement of the equation in Boyd (1935), and all produce similar results (SOM Table S3).

To estimate the proportions of the different body tissues in average male and female individuals from the SH population, we use the equations for fat-free mass (FFM) provided by Wells (2009) for males and females. Finally, fat mass was calculated as the difference between lean mass (FFM) and BM.

$$\ln(FFM) = -0.979 + 0.731\ln(BM) + 0.375\ln(H) \quad \text{males} \quad (10)$$

$$\ln(FFM) = -0.316 + 0.507\ln(BM) + 0.389\ln(H) \quad \text{females} \quad (11)$$

where FFM and BM are measured in kg and H in cm, respectively.

2.4. Estimating minimum endurable temperature

As noted above, resting and sleeping are critical activities for thermoregulation in a cold environment, since thermogenesis is reduced in the absence of muscular activity. The minimum endurable ambient temperature during sleeping is a good proxy for the minimum ambient temperature for long-term human survival because sleeping is a mandatory daily activity, temperatures are usually lower at night than during daylight hours, and thermogenesis by muscular activity is absent. Thus, we used Eq. (4) to estimate the minimum endurable ambient temperature during sleep. Following (Sørensen, 2009), we use the HLM to estimate T_{min} under different conditions (Table 4). First, we explored the effect of increasing SAT thickness up to an unrealistic value of 3 cm, similar to the subcutaneous fat thickness observed in obese recent humans. For this first simulation, we assumed the individual was naked and protected from wind. In a second simulation, the sleeping individual was allowed to increase BMR up to three times the estimated value for an average Middle Pleistocene hominin, while sleeping naked and protected from the wind. In the third simulation the individual was assumed to be sleeping in a shelter, lying on an animal fur and covered also with animal furs of varying thickness (0–0.65 m). Finally, we evaluated the effect of wind on the heat loss of a hominin sleeping in the open over a layer of animal furs and under a fur bed cover. In this fourth simulation, wind intensity varied from low (2 m/s) to moderate (20.0 m/s). A wind velocity of 2 m/s corresponds to a number 2, or a 'light breeze', on the Beaufort scale, while 20.0 m/s is the velocity of a number 6 wind or 'strong breeze' (Oliver, 2005). As a comparison, the average monthly wind velocity in Western Europe nowadays is between 2 and 5 m/s (Fick and Hijsman, 2017). The four simulations were computed for one average adult male and one average adult female.

3. Results

3.1. Estimated temperatures during the glacial/interglacial stages from MIS 14 to MIS 11

The climate data estimated for the localities with evidence of human presence suggest that hominins were able to cope with a wide range of ambient temperatures (Fig. 3). During the MIS 11 and MIS 13 interglacial stages, considering only the 31 assemblages with point estimates, humans lived in localities with estimated mean annual temperatures (MATs) between 5.1 °C and 15.3 °C, minimum temperature of the coldest months (MTCMs) between −8.0 °C and 6.5 °C; MTCQs between −3 °C and 4 °C; and MTWQs between 12.3 °C and 20.4 °C. The temperature ranges are even wider if the uncertainty concerning the remaining 37 assemblages is taken into account. Considering the maximum and minimum values of the climate variables during the entire interglacial stage at the localities of those 37 assemblages, the MAT was between 0.7 °C and 16.0 °C, the MTCM between −11.9 °C and 5.1 °C, the MTCQ between −7.5 °C and 10.3 °C, and MTWQ between 12.0 °C and 22.7 °C.

Interestingly, the range of temperatures at the localities inhabited by humans increased markedly during the MIS 14 and MIS 12 glacial stages. Considering the 31 assemblages that were more accurately dated, the MAT was between 2.8 °C and 6.4 °C, MTCM between −11.9 °C and −5.9 °C, MTCQ between −7.2 °C and −1.5 °C and MTWQ between 10.5 °C and 14.0 °C. With respect to the 37 assemblages dated with less accuracy, the estimated interval for MAT was between 2.8 and 11.3 °C, MTCM was between −12.0 °C and −0.4 °C, MTCQ was between −7.1 °C and 4.3 °C, and MTWQ was between 10.8 °C and 18.2 °C. However, these

Table 4
Summary of the four simulations performed with the heat-loss model to estimate the minimum endurable temperature for an average adult female and an average adult male Middle Pleistocene hominin.

	Shelter	Wind	BMR[a]	SAT[b] (m)	Animal fur cover (m)
Simulation 1	Yes	0	1x	0.005 to 0.03	No
Simulation 2	Yes	0	1x to 3x	0.005	No
Simulation 3	Yes	0	1x	0.005	0–0.065
Simulation 4	No	2 m/s to 20 m/s	1x	0.005	0.05

[a] BMR = basal metabolic rate.
[b] SAT = subcutaneous adipose tissue.

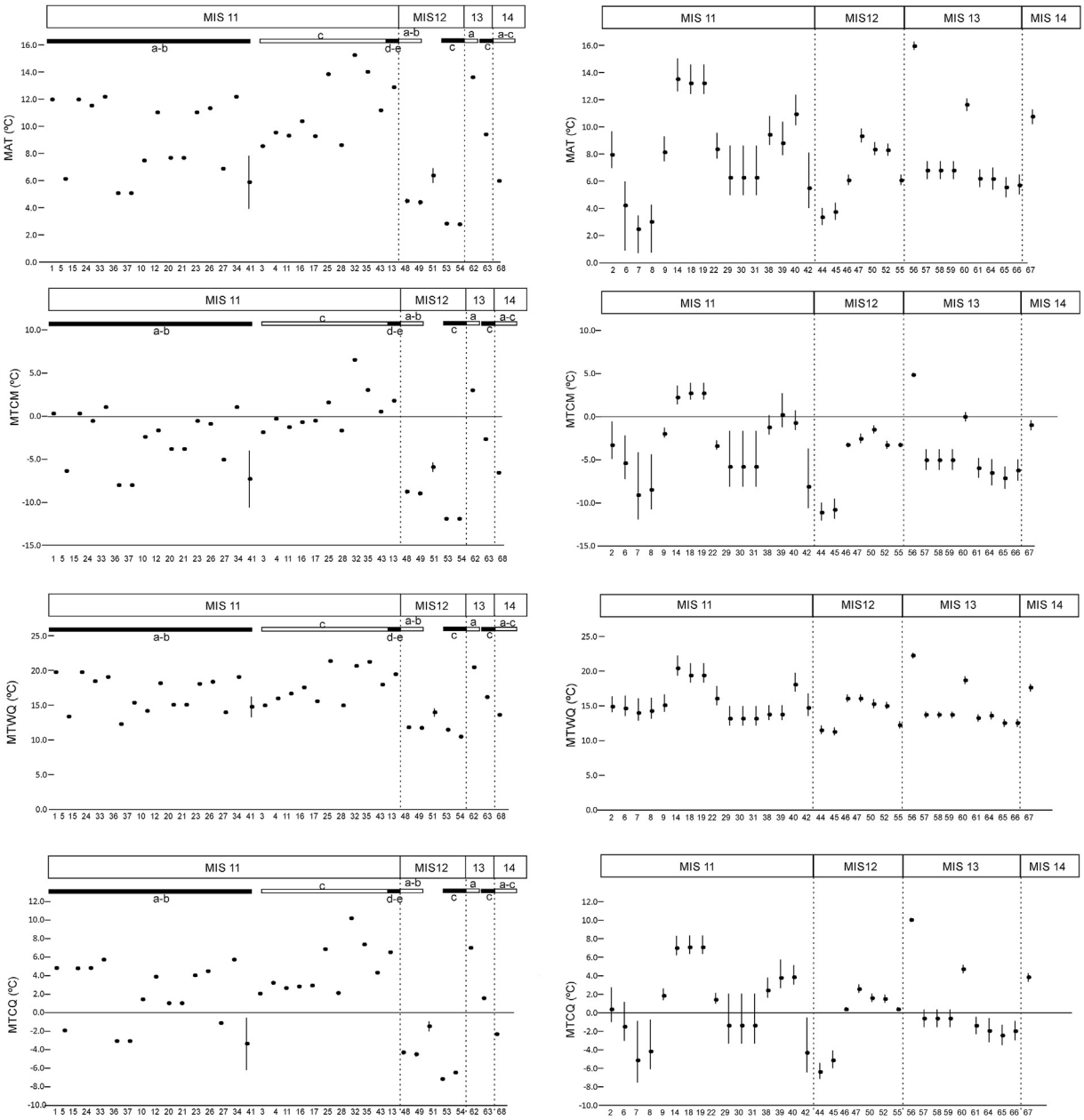

Figure 3. Estimated mean annual temperature (MAT), minimum temperature of the coldest month (MTCM), mean temperature of the coldest quarter (MTCQ), and mean temperature of the warmest quarter (MTWQ) at the localities included in this study. The numbers correspond to the codes of the assemblages shown in Table 1. The figures in the left column include the archeological assemblages that have been correlated to a substage or to two substages of the same stage. The figures in the right column include assemblages dated to an isotopic stage, without further precision. The vertical bars represent the maximum and minimum value of the target variable at the locality during the isotopic stage, and the dots represent the average.

estimates should be interpreted with caution. Most of the substages considered here lasted more than 10 kyr, while the MIS stages lasted 30–60 kyr. Climatic oscillations occurred during both stages and substages, and it is not possible to pinpoint the time interval during which hominins were present at a locality. Thus, our interpretation of these results remains conservative.

In summary, a conservative estimation is that hominins inhabited areas with mean winter temperatures between −3.0 °C and 4 °C during the interglacials, and between −7.2 °C and −1.5 °C during the glacial stages. Moreover, the minimum temperatures of the coldest month at some of those localities were as low as −8 °C during the interglacials and −11.9 °C during the glacial stages. More interestingly, our results suggest that during the winter, hominins endured temperatures close to 0 °C, or below 0 °C, even in the southernmost localities and even during the interglacials (Fig. 3).

3.2. Estimated minimum endurable temperatures

The estimated BMR was 1828 kcal day (88.6 W) for an average male of the SH population and 1440 kcal/day (70 W) for an average female. The estimated BSA was 1.94 m^2 for the average male and 1.74 m^2 for the average female (SOM Table S2). With regard to body composition, an average male weighing 77.8 kg is estimated to have had 15.4 kg of fat mass and 62.4 kg of lean mass, while an average female weighing 66.08 kg is estimated to have had 21.78 kg of fat mass and 44.29 kg of lean mass (SOM Table S1).

Using our estimated values of BMR and BSA in Eq. (4), the minimum endurable temperature for a naked male sleeping in a rock shelter, or in the absence of wind, without activating thermogenesis would be 26.3 °C, and for a female sleeping under the same conditions it would be 27.7 °C. These values are very similar to the critical temperatures reported for recent humans, which range between 25 and 27 °C (Scholander et al., 1957), and to the minimum endurable temperatures estimated by Sørensen (2009) for Neandertals using the same HLM. However, using the model by Aiello and Wheeler (2003), and considering the insulation effect of an increased muscularity, Hosfield (2020) estimated a markedly lower minimum sustainable temperature (7.6 °C) for the SH individuals. The minimum endurable temperatures estimated here are not only markedly warmer than the mean winter temperatures at all the localities inhabited by hominins in Western Europe from MIS14 to MIS 11 (Fig. 3); they are also warmer than the mean summer temperatures at all those localities. Consequently, hominins living in Europe during this period would have needed to raise their metabolic rate and/or employ some kind of bed cover to survive, even in summer. Notably, the use of a simple fur cover over the body makes a great difference. Hominins sleeping under the same conditions, but covered by furs, would be able to endure temperatures of −16.5 °C in the case of females and −25 °C in the case of males (Table 5). These temperatures are markedly lower than the minimum sustainable temperatures estimated by Hosfield (2020) for a SH individual wearing simple clothing (−12.6 °C). These differences can be explained by the fact that Hosfield (2020) modelled the effect of light clothes providing 1 clo of insulation, equivalent to a modern business suit (Owen, 2017), while here we simulated the effect of animal pelts covering the entire body. Increasing the metabolic rate is also an effective response, although much more energetically costly. Multiplying the BMR by a factor of 2 would allow the male and female hominins to sleep naked at temperatures of 15.5 °C and 18.5 °C, respectively (Table 5).

3.3. The effects of cold-endurance strategies on heat loss

The effect on heat loss of increasing SAT thickness to 3 cm is shown in Figure 4A. The effect of increasing SAT thickness is linear, and it decreases T_{min} up to a value of 21 °C for a naked male and up to 23 °C for a naked female. However, these temperatures are only similar to the mean summer temperatures at the warmer localities (Fig. 3), and they assume that the SAT thickness of Middle Pleistocene hominins was similar to the value observed in obese recent humans. Raising the metabolic rate has an even greater effect (Fig. 4B). As mentioned above, multiplying the BMR by a factor of 2 lowers the minimum endurable temperature of a naked sleeping male to 15.5 °C, and in the case of a female it decreases it to 18.5 °C (Table 5). These temperatures are similar to the mean summer temperatures at the coldest localities but are still above the average winter temperatures at the warmest localities. Only by multiplying their BMR by a factor of 3 would Middle Pleistocene hominins have been able to endure temperatures of 5 °C (males) and 9 °C (females), while sleeping naked and sheltered from the wind. With such an extreme increase in BMR, the hominins would have been able to tolerate the mean winter temperatures at some localities during the interglacials, but not during the glacial stages (Fig. 3).

We tested the effect of an animal fur with an average thickness of 5 cm. However, even the use of the thinnest animal furs (3.5 cm) would have provided sleeping hominins with enough thermal insulation to resist ambient temperatures below 0 °C (Fig. 4C). This would be enough to resist the mean winter temperatures at most localities during the interglacials (Fig. 3), although to endure the winter temperatures at the coldest localities an improved fur cover, and/or its combination with other adaptations to cold, would be necessary.

The three preceding simulations were computed assuming that the hominins were sheltered from the effects of wind. Although this assumption is likely to be valid for those archeological sites located in rock shelters or karstic areas, most hominins probably lacked natural protection against wind at many localities. Thus, we tested the effect of wind on T_{min} for a hominin sleeping in an open field under a fur cover. The results in Figure 4D show that even a light breeze provokes a drastic reduction in T_{min}, although the effect is not linear and T_{min} remains relatively stable under winds of more than 5 km/h. Therefore, even when sleeping in the open under the influence of wind, a hominin well protected by animal furs would be able to endure temperatures of around −10 °C, similar to the lowest temperatures of the coldest month at the coldest localities during the glacial stages (Fig. 3).

4. Discussion

There is a general agreement between our estimates and those reported by other authors for some the archeological sites included in the present study and based on the Mutual Climatic Range of different organisms (SOM Table S4). However, there are also discrepancies in some cases. Winter temperatures based on coleopterans (Coope, 2006; Ashton and Lewis, 2012) tend to be lower than our MTCQ estimates, and summer temperatures tend to be higher than our MTWQ estimates, although the intervals overlap in most cases. Interestingly, it has been shown that the MCR method applied to coleopterans tends to produce winter temperature estimates too warm (Pettitt and White, 2012), suggesting that our estimates of the lowest winter temperatures endured by hominins are conservative. MATs based on reptiles and amphibians (Rodríguez et al., 2014; Blain et al., 2018) show a good agreement with our estimates for the Gran Dolina, Aridos-1, and Ambrona assemblages when the 95% confidence intervals for the MCR estimates are taken into account. However, the MAT estimated by

Table 5
Estimated minimum endurable temperatures (T_{min}) for an average female and an average male Middle Pleistocene hominin while sleeping sheltered from wind (V = 0 m/s), naked, and with a standard fur bed cover. The effect of multiplying the basal metabolic rate by a factor of 2 is also shown.[a]

	BMR (W)	BSA (m^2)	R (m^2·K/W)	C (W/m^2· K)	SAT		Fur		V (m/s)	T_{min} (°C)
					s_i (m)	k_i (W/m·K)	s_i (m)	k_i (W/m·K)		
Naked female	70.0	1.74	0.03	5	0.005	0.2	0	0.05	0	27.7
Naked male	88.6	1.90	0.03	5	0.005	0.2	0	0.05	0	26.3
Naked female 2x BMR	140.0	1.74	0.03	5	0.005	0.2	0	0.05	0	18.5
Naked male 2x BMR	177.2	1.90	0.03	5	0.005	0.2	0	0.05	0	15.6
Female with fur	70.0	1.74	1.13	5	0.005	0.2	0.055	0.05	0	−16.5
Male with fur	88.6	1.90	1.13	5	0.005	0.2	0.055	0.05	0	−25.0

[a] SAT = subcutaneous adipose tissue; BMR = basal metabolic rate; BSA = body surface area; R = thermal resistance; C = wind convection term; s_i = thickness of the isolating layer; k_i = thermal conductivity of the isolating layer; V = wind.

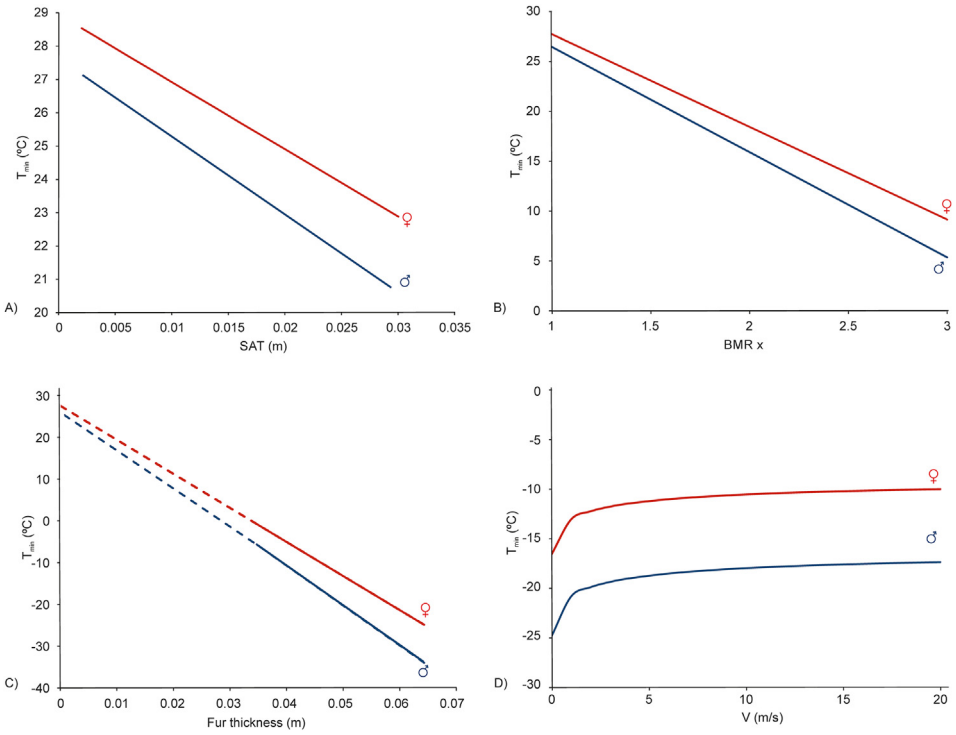

Figure 4. Effect of different thermoregulatory mechanisms on the minimum endurable temperature (T_{min}) for an average Middle Pleistocene male and female during sleeping. A) Effect of increasing the thickness of the subcutaneous adipose tissue assuming that the individual is sleeping naked and sheltered from the effect of wind (V = 0). B) Effect of increasing the basal metabolic rate by a factor of 1–3, assuming the individual is sleeping naked and sheltered from the effect of wind. C) Effect of covering the body with furs of different thickness while sleeping in a place sheltered from the effect of wind; the solid portion of the line corresponds to the actual thickness of the animal furs. D) Effect of different wind velocities on the minimum endurable temperature of an individual sleeping covered by a fur with a thickness of 5 cm.

Rodríguez et al. (2014) for TD10-4 based on reptiles and amphibians is much higher than the MAT reported here for that assemblage (SOM Table S4). Likely, those discrepancies are explained by the combination of a number of factors. In some cases, estimates are not entirely comparable. For example, the summer and winter temperatures based on amphibians and reptiles represent the mean temperature of the warmer and coldest month, respectively, while our estimates represent the mean values for a quarter of the year (MTWQ and MTCQ). Moreover, the reliability of the MCR methods relies on the assumption of 'niche conservation', that is, that the climatic requirements of the species remained constant from the Pleistocene to the present. However, that is not always the case (Varela et al., 2009), and disharmonious assemblages composed by species whose climatic ranges do not overlap today have been identified (Polly and Eronen, 2011). Finally, at least in some cases, hominin occupation might have occurred during short-term climatic oscillations that are not captured within the 10 kyr blocks of the Oscillayers model.

Our results show that Middle Pleistocene hominins endured cold stress even in southern Europe and during warm intervals. The results presented above suggest that mean winter temperatures in the Iberian and Italian localities inhabited by hominins during MIS 11 and MIS13 were lower than 10 °C. Importantly, these were mean temperatures. Thus, it may be reasonably assumed that at these localities, the air temperature dropped to values close to or below 0 °C on many winter nights. As shown by the HLM, a naked hominin would be unable to endure such low temperatures without the help of physiological thermoregulatory mechanisms and/or behavioral responses.

However, hominins were able to cope at that time with much lower temperatures in Britain and Central Europe, especially during MIS 12. Hosfield (2016) thoroughly discusses the evidence and feasibility of seasonal occupation of northern Europe during the interglacial stages. It is important to note that, even if these human populations migrated southward in winter during a glacial stage, they had to cope with very harsh temperature conditions. During MIS 12 the minimum temperatures of the coldest month were well below 0 °C even at the southernmost localities like Atapuerca, Caune de L'Arago, and Valle Giumentina. Indeed, Lewis et al. (2019a) suggested that survival at these southern European localities would have led to physiological and behavioral adaptations to cold environments that were critical for the colonization of more northern areas. Moreover, during MIS 12 mean winter temperatures of the warmest areas of Europe, located along the coasts of the southern peninsulas, were not higher than 10 °C, and they were markedly lower toward the centers of the peninsulas. If hominins were permanent residents in the northernmost localities during cold periods, they regularly endured winter temperatures below −10 °C and probably endured much lower temperatures on occasion. Even during relatively warm periods, like the MIS 11a–MIS 11b substages, mean winter temperatures were as low as −1.2 °C at Saint Acheul and 1 °C at Ambrona. All of these observations suggest that the Middle Pleistocene hominins were physiologically and/or behaviorally well adapted to cope with cold stress. Pleistocene hominins may have adapted to cold exposure through a combination of physiological, anatomical and/or behavioral mechanisms that reduce heat loss by increasing thermal insulation or increase heat gain (Steegmann et al., 2002; Aiello and Wheeler, 2003; Mäkinen 2010; Daanen and van Marken Lichtenbelt, 2016; MacDonald, 2018).

Thermal insulation may be improved by increasing the number of insulating layers or by improving the effectiveness of the existing layers. However, as shown by our results, increasing the thickness of SAT only has a moderate effect on the minimum endurable

temperature and thermal comfort, questioning its real value as an insulating layer. Indeed, despite the comparatively extremely low thermal conductivity of fat, other tissues may also contribute to insulation. It has been suggested that muscle may contribute no less than 50% to total body insulation (Anderson, 1999). Moreover, according to the HLM, the 3-cm thick SAT necessary to decrease the minimum endurable temperature by 5–6 °C is equivalent to the value observed in obese recent humans. Moreover, it is extremely unlikely that Middle Pleistocene humans had a SAT thickness of 2 or 3 cm, because of the serious physiological and mobility disadvantages associated to largely increased subcutaneous fat thickness (MacDonald, 2018). Thus, while Middle Pleistocene hominins may have thickened their SAT layer to improve their thermal insulation, it seems unlikely they increased their SAT to the extent observed in obese modern humans. As suggested both by the estimated proportion of FFM (SOM Table S1) and the assumed high levels of daily physical activity for paleolithic hunter-gatherers (Sorensen and Leonard, 2001), Middle Pleistocene hominins likely had remarkable muscle mass. This high muscle mass could also provide efficient thermal protection (see Table 2 in Steegmann et al., 2002).

Importantly, recent cold-adapted human populations do not show a marked increase in SAT thickness. Anthropometric data on Alaskan Inuits, for example, show that they are leaner and have relatively little subcutaneous fat compared with other populations (Alaskans, Aleuts and native North Americans; Shephard et al., 1973; So, 1980; Risica et al., 2000). Inuit SAT thickness is, on average, only 1.5 mm while it is 6.5 mm for other recent populations (Rennie et al., 1962). Therefore, it has been suggested that their high level of physical activity coupled with cold exposure and greater peripheral blood flow may be responsible for the lean body composition in Inuits (Milan et al., 1963).

In recent humans, a body composition with a high percentage of fat mass is frequently associated with an increased probability of cardiovascular and metabolic diseases (Kyle et al., 2003). The Middle Pleistocene hominins might have been partially protected from the negative effects of increased fat deposits by certain metabolic adaptations and their high levels of daily physical activity. A thick layer of body hair would also add protection against cold temperatures. David-Barrett and Dunbar (2016) modeled the insulation effect of body hair in australopithecines, and MacDonald (2018) and Hosfield (2020) thoroughly reviewed the arguments in favor and against a thick winter fur cover in Middle Pleistocene hominins. Convincing evidence against the presence of a dense body hair cover in Middle Pleistocene hominins has been presented based on genetic data (Rogers and Wooding, 2004; Reed et al., 2007). However, it has been suggested that natural fur cover might have been an important survival factor for more primitive species of the genus *Homo* living in cold environments (Sharon, 2016). As demonstrated by our results, and already highlighted by several authors (Stenton, 1991; Sørensen, 2009; Wales, 2012; Hosfield, 2016; Gilligan, 2017), animal fur has superb insulation properties. A simple pelt from a large animal, or several smaller pelts, used as a bed cover are enough to provide proper thermal insulation to a hominin under very low temperatures during the critical sleeping period. Simple, non-tailored clothing would be less efficient during physical activity, since it would not be snugly fitted to the body, allowing for large amounts of heat loss (White, 2006). Thus, our results cannot be directly transferred to active hominins covered with simple non tailored clothes.

Although indirect evidence of tailoring technology, such as bone needles or piercing implements, is absent from the lower paleolithic record, indirect evidence for the acquisition and processing of animal pelts exists. For example, evidence of the hunting of a lion at Atapuerca TD10.1 has been reported by Blasco et al. (2010), and microwear analyses suggest the use of stone tools for hide processing at Hoxne (Keeley, 1993), Schöningen (Rots et al., 2015), Atapuerca TD10.1 (Pedergnana and Ollé, 2020), and Qesem (Lemorini et al., 2006).

Another key factor related to thermal insulation is wind protection, as a light breeze is enough to produce a drastic increase in heat loss by convection. The frequent occupation of rock shelters and cave entrances, in regions where they were available, seems clearly related to a preference for wind and rain protection during resting and sleeping. Ethnographic data show that recent hunter-gatherers sleeping in open areas build temporary windbreaks to protect themselves at night (Scholander et al., 1958). These may be extremely simple structures, made with the materials at hand that would not be preserved in the archeological record. A simple snow wall would provide adequate protection against wind if built with the proper orientation (Densmore, 1929; Chu, 2009). Additionally, heat loss during resting and sleeping may also be reduced through nestled group sleeping. This is a widespread behavior among social mammals exposed to cold environments (Hanya et al., 2007; Ueno and Nakamicho, 2016). The individuals of the group cluster tightly during the night, or while resting during the day, gaining heat from each other and reducing heat loss. Internal heat production may be increased by raising BMR, by increasing muscular activity by shivering, or activating the non-shivering BAT thermogenesis. However, these mechanisms are energetically expensive. As shown in this study, increasing BMR is an effective mechanism to cope with low temperatures during cold exposure. By multiplying their BMR by a factor of 2, Middle Pleistocene hominins would be able to endure the mean summer temperatures at the coldest localities without using bed covers or activating other adaptive responses. However, it would be necessary to increase their BMRs by a factor of 3 to endure the mean winter temperatures at the warmest localities under the same conditions. Notably, those increments of BMR are markedly higher than the values observed in recent human populations living in cold environments. Early studies of the Inuit populations of Alaska and Canada reported an increase of 25%–35% in BMR in these Arctic groups and showed a negative correlation between BMR and MAT (Heinbecker, 1928; Crile and Quiring, 1939; Roberts, 1952, 1978). More recent research confirmed the systematic elevation of BMR among indigenous Arctic populations, but to a lesser extent. Values ranging from 7% to 19% above the predicted values for males, and from 3% to 17% for females, have been reported by several authors (Katzmarzyk et al., 1994; Galloway et al., 2000; Leonard et al., 2002, 2005; Snodgrass et al., 2005). This metabolic response is shaped by elevating the production of thyroid hormones and sensitivity to them, through short-term acclimatization and genetic adaptations (see Leonard et al., 2005 and references therein).

Moreover, increasing the BMR estimated for a Middle Pleistocene hominin by a factor of 2 implies an energetic cost of 3650 kcal/day for males and 2880 kcal/day for females. Raising the BMR to three times the estimated value requires 5480 kcal/day for males and 4320 kcal/day for females. It should be noted that these are estimates of basal energy consumption and that the total daily energy expenditure would be much higher. Individuals with a moderate level of physical activity would multiply their BMR by a factor of 1.5 (Sorensen and Leonard, 2001) leading to daily energetic expenditures of 5480 kcal/day for males and 4320 kcal/day for females if their BMRs were increased by a factor of two, and 8220 kcal/day for males and 6480 kcal/day for females if their BMRs were increased by a factor of three. Maintaining such high levels of energy expenditure would require equally high levels of energy intake to maintain energetic balance. Large game, a food resource rich in fat tissues of high caloric value, and edible plants were abundant in Mediterranean Europe during the Middle Pleistocene (Rodríguez et al., 2014) and they were probably also available in

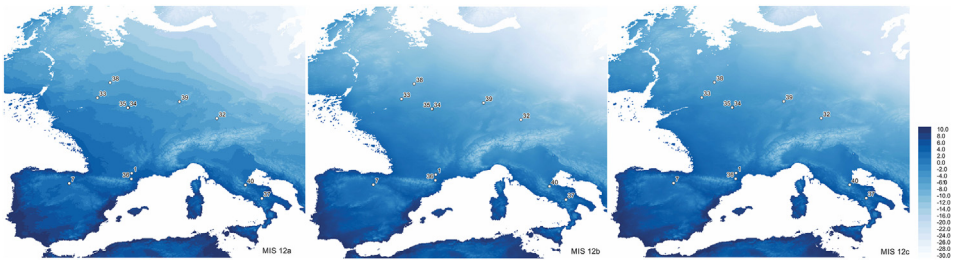

Figure 5. Mean winter temperatures (mean temperatures of the coldest quarter; MTCQ) during the three substages of MIS12 and localities with archaeological assemblages correlated to this glacial stage. The sites numbers are the same as those in Figure 1.

high latitude regions, even during the cold periods (Hosfield, 2016). Although a detailed analysis of the availability of food resources in Western Europe during the Middle Pleistocene is beyond the scope of this article (but see Hosfield, 2016), we suggest that maintaining such extremely high levels of energy intake long term seems unlikely. Humans can activate two cold-induced physiological mechanisms to produce heat and keep warm in cold environments: shivering thermogenesis and non-shivering thermogenesis. Shivering consists of the involuntary contraction of skeletal muscles to produce heat, raising the metabolism by up to five times the BMR at peak intensity (Eyolfson et al., 2001). Although shivering is extremely effective as a short-term response to cold exposure, it cannot be sustained for long periods, and it certainly cannot be sustained overnight. When core and skin temperatures surpass a certain threshold, vasoconstriction begins (at skin temperature below 35 °C), after which shivering occurs and its intensity becomes maximal at a skin temperature of 34–35 °C, stopping at 31 °C (Castellani and Young, 2016). Several studies of shivering have shown that humans are able to sustain these rates of heat production for up to 2 h (Haman et al., 2004), but because of the high metabolic cost, shivering is time-limited depending on the exhaustion of glycogen storage in the body (Benzinger, 1969; Haman et al., 2010; Daanen and van Marken Lichtenbelt, 2016; Haman and Blondin, 2017). BAT combustion (non-shivering thermogenesis) is another effective but acute metabolic response to activate heat production in severely cold environments (Cannon and Nedergaard, 2004). As BAT is present in many mammals, it can be considered an ancient thermal adaptation in cold-adapted primates such as *Macaca fuscata* (Tokura et al., 1981) and humans (van Marken Lichtenbelt et al., 2009). We can speculate that Middle Pleistocene hominins had similar physiological cold defenses maintained into adulthood, as suggested elsewhere for Neandertals (Steegmann et al., 2002; Mateos et al., 2004).

It is well documented ethnographically that recent hunter-gatherers use fire as a source of heat, especially during the night. Aboriginal Australians sleep naked in the open at temperatures close to 0 °C, under the protection of a windbreak made for the occasion and between two camp fires that are stoked overnight (Scholander et al., 1958). The San people of the Kalahari sleep at temperatures of around 10 °C under a leather cloak, lying radially around a fire which they keep burning overnight (Wyndham and Morrison, 1958). However, evidence of fire in Europe older than 300 ka is scarce and controversial. Nevertheless, as highlighted by several authors (Gowlett, 2016; Hosfield, 2016), evidence of the use of fire by hominins does not imply the existence of advanced pyrotechnology, such as the ability to kindle fires. Indeed, the scarce evidence of fire use prior to MIS 9 might be explained by a lack of kindling technology and a reliance on natural fires from lightning strikes (Gowlett, 2006). Moreover, the lack of fire evidence from almost all the sites in Western Europe older than 400 ka (Roebroeks and Villa, 2011) is a strong argument against the frequent and controlled use of fire before MIS 11 or MIS 10. Recent indigenous populations present cold adaptation strategies that can be considered both phenotypic and genotypic (Leonard et al., 2005; Mäkinen, 2010). The main response varies from one population to another and depends on the intensity of cold exposure. Intermittent exposure to cold that produces minimal body heat loss and a blunted thermal response will promote short-term habituation (Leppäluoto and Hassi, 1991). However, prolonged and/or severe cold exposure with important heat losses, counterbalanced by increases in thermogenesis, will promote acclimatization (insulative or metabolic) in both the short and long term (Mäkinen, 2010). It has been documented ethnographically that different indigenous populations have different cold tolerances and activate distinct physiological adjustments and behaviors, from hypothermic and hypometabolic acclimatization in aboriginal Australians (Scholander et al., 1958), to insulative acclimatization in Kalahari San populations (Whydham ad Morrison, 1958), and metabolic acclimatization in Kawésqar (Hammel et al., 1960), Inuit, and Siberian populations (Leonard et al., 2005). Behavioral responses are equally variable: Lapps rely on shelter and highly effective clothing protection (Scholander et al., 1957), while aboriginal Australians and Kawésqar people use few or no clothes but use fire as a very effective heat source (Scholander et al., 1958; Mäkinen, 2010). In the case of Middle Pleistocene hominins, our results suggest that a combination of physiological and behavioral responses (metabolic and insulative acclimatization) was a successful strategy to maintain homeostasis during cold exposure (Fig. 5).

5. Conclusions

Considering the temporal and spatial distribution of archeological assemblages during the Middle Pleistocene and the evidence provided here, it is apparent that hominins were able to tolerate cold exposure and expand their distribution toward central and northern Europe, without controlling fire production. This apparent paradox is easily solved when considering the different physiological and behavioral responses to cold stress outlined above. Although elevating the BMR by a factor of 2 or 3 is probably not sustainable in the long run, more moderate increases are observed as adaptive responses to cold in recent humans. Combining that metabolic response with the use of simple fur bed covers, the other physiological mechanism commented above, and some simple behavioral adaptations, Middle Pleistocene hominins could endure air temperatures several degrees below freezing.

Acknowledgments

We are grateful to Nick Ashton and Paula García Medrano for inviting us to participate in the WEAP Final Conference “Humans in Transition: The occupation of Western Europe, 500–400 ka.” An anonymous editor from Elsevier’s Language Services improved the

English of the original manuscript. This research was supported by the MICINN project PID2019-105101 GB-I00. The funding source was not involved in the study design, nor in the collection, analysis, or interpretation of data, the writing of the report, or in the decision to submit the article for publication. The research of C.W. was funded by the German Research Foundation (DFG) through the Collaborative Research Centre 806 (DFG project number 57444011).

Supplementary Online Material

Supplementary online material to this article can be found online at https://doi.org/10.1016/j.jhevol.2021.102966.

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