Energetic Competition Between Neandertals and Anatomically Modern Humans

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ABSTRACT

The effects of climate on energy expenditure, which include climatic influences on human metabolic physiology and variation in the level of physical activity required for subsistence under different environmental conditions, have been the focus of a considerable amount of research. In general, this work shows that human foragers inhabiting colder climates tend to have higher energy expenditure than those in warmer climates, both in terms of maintenance energy needs (basal metabolic rate, or BMR) and the amount of energy spent obtaining resources. Recently, several authors have applied these findings to the fossil record, with results that indicate that Neandertals would likely have had very high daily energy expenditure (DEE) as part of their adaptive response to the thermoregulatory and subsistence challenges of life in cold climates. These studies imply that anatomically modern humans would have had substantially lower energy requirements than, and thus a competitive advantage over, Neandertals in Europe. Estimates of DEE do not exist for anatomically modern humans in cold climates, however, begging the question of whether they might have required similarly high amounts of energy to survive in glacial Europe.

Here we present an exploratory analysis of climatic effects on energy expenditure in Neandertals and anatomically modern humans, using a new method. This method uses mean annual temperature along with body size, sex and age to predict BMR, thereby directly incorporating the effects of climate on metabolic physiology. We used this method to calculate BMR in a sample of Neandertals and Pleistocene modern humans, obtaining paleo-mean annual temperature values for fossil sites from data available from the Oxygen Isotope Stage 3 Project. We then estimated DEE from these BMR values, using climate-specific physical activity level (PAL) values based on extant human foragers living in different environments.

Our model suggests that Neandertals would have had substantially higher energy needs than anatomically modern humans in similar climates, on the order of 100–350 kcal per day, which corroborates the results of previous studies using different methods. This difference is in large part due to greater body mass in Neandertals, which may have related mainly to a higher proportion of muscle mass compared to anatomically modern humans. Greater muscularity in Neandertals would have provided them with greater thermoregulatory capability, may have served as insulation, and was also probably part of a subsistence strategy of close-range encounters with large mammalian prey. If greater muscle mass served these ends in Neandertals, modern humans must have used other means of dealing with insulation and subsistence in order to maintain less-massive bodies. There is archaeological evidence consistent with this interpretation, suggesting that anatomically modern humans may have brought with them into Europe improved methods of insulating themselves, as well as broadened subsistence techniques. Lower adult energy needs could have provided modern humans with reproductive advantages in the form of reduced birth spacing, greater survivorship, or both. This would likely translate into a competitive advantage over Neandertals who had higher, and thus harder to meet, energy demands.

The "Energetic Studies in Hominin Evolution" Symposium, Paleoanthropology Meetings, Philadelphia, PA, 27—28 March, 2007; symposium papers guest edited by Karen Steudel-Numbers (University of Wisconsin) and Cara Wall-Scheffler (Seattle Pacific University).

INTRODUCTION

Bioenergetics, the study of energy flow in biological systems, has become increasingly important in efforts to understand the ecology of extant hunter-gatherers, prehistoric foragers (including pre-modern members of the genus *Homo*), and extant non-human primates. The balance between the energy an individual expends on the one hand, and obtains in the form of food on the other, governs that individual's ability to maintain bodily functions and to invest in reproduction. Estimates of daily energy expenditure (DEE) can thus provide a useful tool for understanding the interactions between humans (or nonhuman primates) and

ISSN 1545-0031

their environments, along with the corresponding effects of these interactions on reproductive success.

Recently, researchers have used a variety of approaches to address the specific topic of energy expenditure in Neandertals (Aiello and Wheeler 2003; Churchill 2006; Sorensen and Leonard 2001; Steegmann et al. 2002), to better understand their subsistence and reproductive ecology as well as the nature of possible competition with anatomically modern humans. These studies have relied primarily on aspects of Neandertal body size and shape, along with assumptions about their levels of physical activity, to estimate their energy demands, with upward adjustments of the estimates to account for increased energy needs associated with living in cold climates. Such studies derive their models of Neandertal energy expenditure from physiological and behavioral data on extant subsistence-level populations inhabiting high latitudes, based on the general assumption that Late Pleistocene Eurasian environments were climatically similar to those of the Arctic today.

These studies, while differing moderately in their estimates of Neandertal DEE, unanimously conclude that Neandertal daily energy requirements would have substantially surpassed the range of the average extant modern human. This finding has been extrapolated to suggest that early anatomically modern humans in Europe likely possessed an energetic advantage over Neandertals, thanks to less-massive bodies as well as less energetically-costly behavioral solutions to adaptive challenges. Currently, however, DEE estimates for fossil modern human populations are incomplete, especially with regard to the effect of climate on energy expenditure, and thus the exact nature of the differences between Neandertals and modern humans in terms of energetic efficiency in Late Pleistocene environments remains open to question. The present study seeks to address this lingering uncertainty. Here we employ a newly developed method for estimating climate-specific energy expenditure to provide a preliminary basis for analyzing energy competition between Neandertals and anatomically modern humans.

For the most part, DEE (in kilocalories per day: $\text{kcal} \cdot \text{d}^{-1}$) in fossil humans is calculated according to the factorial method, where:

$$\text{DEE} = \text{BMR} \cdot \text{PAL}$$

BMR (in $\text{kcal} \cdot \text{d}^{-1}$) is basal metabolic rate (the energy the body uses for maintenance and growth in the absence of activity or digestion) and PAL is physical activity level, a coefficient expressing DEE as a multiple of BMR. Most often, BMR is estimated from body mass (although surface area can also be used: see Churchill 2006) with one of two commonly used predictive equations: Kleiber's (1961) general mammalian equation, or Schofield's (1985; FAO/WHO/UNU 1985) human-specific equations.

Research on recent modern humans has generally established that climate exerts an influence on BMR, although debate remains as to the exact nature of these climatic effects. In general, when other important factors such as body size, age and sex are controlled for, people living in colder climates tend to have higher BMR than people in warmer climates (see Froehle 2008, for a review). This variation in BMR may be partly heritable (Wallace 2005), but individual BMR also appears to adapt to different climates with migration (e.g. Henry et al. 1987; Ulijaszek and Strickland 1991). The adaptability of human metabolic physiology over both the long- and short- term thus appears to be part of a suite of attributes that have allowed humans to occupy a wide variety of climates.

Given the wide geographic dispersal of most members of the genus *Homo*, it seems reasonable to apply patterns of climate and BMR variation in recent humans to the fossil record. Such applications have occurred mainly in studies of Neandertals, which have employed a variety of methods to account for the effect of climate. This multiplicity of methods stems from the fact that the most commonly used equations for calculating BMR from mass (those of Kleiber and Schofield) provide no ready way to account for the effects of climate. Kleiber (1961) studied a wide variety of mammals, and included only two humans from temperate North America in his study. Schofield (1985) compiled a large database of published BMR measurements, but the vast majority of these subjects lived in the temperate climate of Western Europe. Thus, to refine estimates of energy expenditure in fossil hominins, past studies have employed a variety of methods to incorporate climatic effects, while still using the above equations as the basis for BMR values.

Rather than modifying BMR estimates from the Kleiber or Schofield equations to fit a particular climate, here we use new equations that incorporate a continuous climate variable (mean annual temperature) directly in estimating BMR. Froehle (2008) showed that mean annual temperature, to the exclusion of other continuous climate variables, significantly affects BMR. Equations derived from that study include mean annual temperature, along with standard physiologically important factors of body mass, age, and sex, as predictors of BMR, providing more consistently accurate estimates across climates than either Kleiber (1961) or Schofield (1985) (see Table 1 for equations, and Figure 1). Using these new equations along with paleontological and paleoclimate data, we generate directly comparable BMR estimates, and subsequently DEE, for fossil Neandertals and anatomically modern humans.

To estimate DEE from BMR in fossils, we use PAL as described above. The PAL coefficient acts as a potential source of error because it quantifies activity expenditures very broadly, assuming the same level of activity for different individuals rather than using detailed activity budgets to calculate individual-specific DEE. Although there is undoubtedly considerable variation in activity levels within and between foraging groups (see, for example, Jenike 2001; Panter-Brick 2002), and even in the same individual over weekly and seasonal activity cycles, one cannot observe this variation in fossil individuals. Therefore, approximating DEE based on PAL is currently the best available method. On a broad level, one can still account for some

TABLE 1. EQUATIONS FOR BASAL METABOLIC RATE[a].

Reference	Sex	Equation
Kleiber (1961)	N/A	$BMR=70\cdot(M^{0.75})$
Schofield (1985)	M	$BMR=(15.1\cdot M)+691.9$
	F	$BMR=(14.8\cdot M)+486.4$
Froehle (2008)	M	$BMR=(14.7\cdot M)-(5.6\cdot TMEAN)+735$
	F	$BMR=(9.2\cdot M)-(3.8\cdot TMEAN)+852$

[a] where BMR is in kcal · d^{-1}, M is in kg, and TMEAN is mean annual temperature in degrees C.

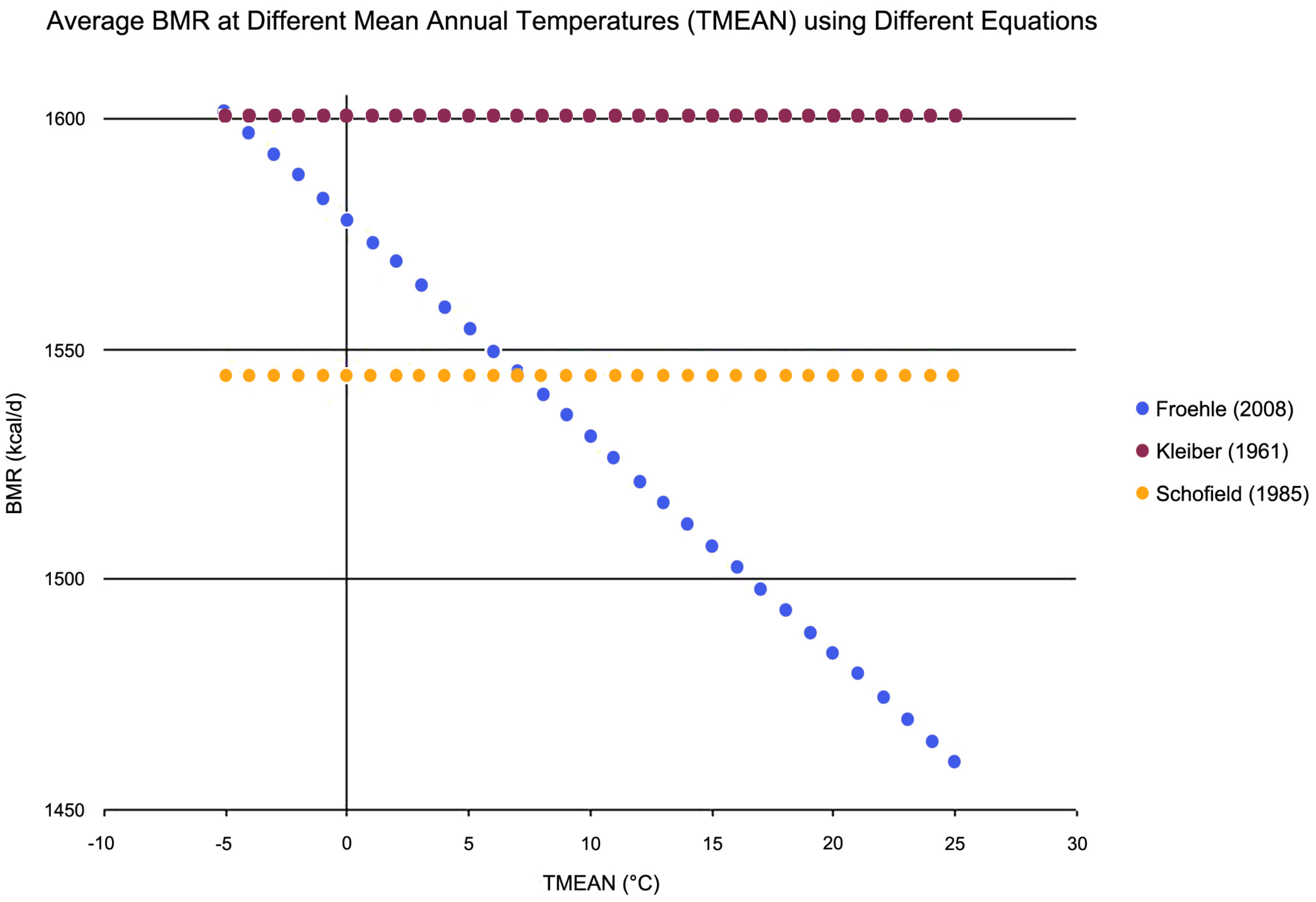

Figure 1. Basal metabolic rate (BMR) as estimated from body mass using three different methods, plotted against mean annual temperature (TMEAN). We used average body mass for anatomically modern human males (68.5kg) and females (59.2kg) in our fossil sample (see Table 2). Average male and female BMR values were calculated at every mean annual temperature value between -5 °C and 25 °C (based on Froehle 2008). The sexes were combined to arrive at mid-sex average values, which we present in the figure. In comparison, the Kleiber (1961) and Schofield (1985) equations take no account of climate. Clearly, the different equations' estimates diverge from one another in different climates.

variation in activity, since the value of PAL can differ between sexes, and also between different populations based on subsistence strategies and for cultural reasons.

We outline in detail our choice of PAL values in the Methods section of this paper, but it is instructive to review the available data here first. As a general guideline for assessing human energy expenditure, the World Health Organization (WHO) considers PALs of 1.55–1.77 for men and 1.56–1.63 for women as constituting light activity, 1.78–2.09 (men) and 1.64–1.81 (women) as moderate activity, and greater than 2.09 (men) and 1.81 (women) as representing heavy activity (FAO/WHO/UNU 1985). Behavioral data on extant foraging groups can, to some degree, provide an estimate of where hunting and gathering fall in the above ranges of exertion, and indicate the most appropriate PAL values to use with fossil Neandertals and anatomically modern humans. Data on extant forager activity levels are few (Panter-Brick 2002), and are currently based on empirical data from only three groups—the Igloolik of circumpolar Canada, the Ache from the tropical forest of Paraguay, and the !Kung of the Kalahari Desert in Botswana.

Energy expenditure was not measured in the Ache and !Kung, but Leonard and Robertson (1992) derived PAL values for these groups by estimating BMR from body mass and calculating DEE using published daily activity budgets (Hill et al. 1984, 1985; Hurtado et al. 1985; Lee 1979) along with standard cost-of-activity formulae (Leslie et al. 1984). Godin and Shephard (1973) directly measured Igloolik oxygen consumption during normal activities, producing typical DEE values for both males and females. Others have subsequently compared those DEE values to BMR estimates to arrive at PAL (Katzmarzyk et al. 1994). For the Ache, both sexes would be considered to have heavy levels of activity according to the WHO standards (PAL of 2.15 and 1.88 for men and women, respectively). Igloolik men have heavy activity levels (2.5—Snodgrass, pers. comm.), while Igloolik women are right at the border between moderate and heavy levels (1.8). In contrast, !Kung men engage in moderate levels of activity (PAL=1.71), while !Kung women engage in light activity (PAL=1.51).

Variation in PAL between the three groups, and the degree to which males and females differ in each society, may in part reflect ecological differences related to climate. The heavy activity level of the Igloolik can be considered representative of the high mobility necessary to obtain sufficient calories in a cold, relatively unproductive environment. Males in this case tend to focus on big-game hunting, while females, though less mobile and mainly engaged in household activities, also expend energy at a level well above BMR in laborious tasks such as processing animal skins (Panter-Brick 2002). The Ache and !Kung, though both resident in the tropics, live in very different environments (tropical forest vs. desert), which likely underlies the considerable divergence in the energy they expend on foraging, and in their rates of reproduction (Panter-Brick 2002). Thus, these two groups may represent opposite ends of the range of variation in PAL among hunter-gatherers, providing low-energy (!Kung) and high-energy (Ache) models of foraging in tropical humans (Jenike 2001). The PAL values we use to calculate DEE in fossil Neandertals and anatomically modern humans are based in part on the above data for extant foragers, with which we account for variation between sexes and due to environmental conditions.

In employing the factorial approach to estimate DEE in Neandertals and modern humans, we draw on a wide variety of data sets, each with its own inherent sources of error. Our methodology thus compounds error from estimates of body mass, geological age, mean annual temperature, BMR, and PAL. This very compounding of error has led to criticism of energetic studies of fossils as "highly relative, gross and oft-revised." (Kuhn and Stiner 2006: 971). We wish to be clear that our intent is not to produce exact estimates for individual fossil specimens. Rather, we intend to provide a quantitative platform that allows for the comparison of different groups based on relative energetic expenditures. Because the assumptions and sources of error are the same for each group we compare, any relative differences we find can tell us something meaningful about each group's relationship to its ecological setting in terms of energy. These relative differences, and their implications, should hold, despite the fact that we cannot account for a great deal of idiosyncratic variation between individuals.

Thus, while we caution the reader to keep in mind that our DEE results have a relatively low degree of precision, this study's value lies in its direct comparison of Neandertals and anatomically modern humans using a single set of methods. The energetic advantages associated with certain body sizes or shapes or with certain climatic preferences should be apparent in this type of analysis, regardless of the exact number of calories expended by one group or another. We also note that, despite the use of different methods and varying assumptions, previous studies of Neandertal energetics have all produced largely concordant results (compare Aiello and Wheeler 2003; Churchill 2006; Sorensen and Leonard 2001; Steegmann et al. 2002). Thus, previous studies can provide a basis for evaluating our Neandertal results, and also the results for modern humans relative to Neandertals.

In this study we will determine whether differences in energy expenditure were likely to have existed between Neandertals and anatomically modern humans in similar climates. We will examine the potential sources of any differences in energy ecology, within the constraints of the study's assumptions. We interpret such differences in terms of potential reproductive advantages, in light of available paleontological and archaeological data.

METHODS

We obtained body mass estimates, sex, and geological age for a sample of adult Neandertal (n=26) and anatomically modern human (n=39) fossils (Table 2). Most of the body mass estimates (55 of 65) were determined by Ruff et al. (1997: supplemental material), who estimated mass from femoral head dimensions, and stature plus bi-iliac breadth. In order to expand the sample, we also estimated mass in the remaining ten specimens using other methods (see

TABLE 2. FOSSIL SAMPLE DATA.

	Specimen	Sex[a]	Mass (kg)[b]	Age (kya)	Period[c]	References[d]
Neandertals	La Quina 5	F	71.2	50	cold-temperate	a,b
	Spy 1	F	67.5	50	cold-temperate	a,b
	La Ferrassie 2	F	67.0	72	glacial	a,b
	Grotte du Prince	F	74.8	100	cold-temperate	a,b
	Shanidar 6	F	59.4	100	cold-temperate	a,b
	Krapina 208	F	68.4	130	interglacial	a,b
	Krapina 209	F	63.7	130	interglacial	a,b
	Krapina 214	F	62.2	130	interglacial	a,b
	Tabun C1	F	63.2	150	glacial	a,b
	Saint-Césaire 1	M	78.9	36	glacial	a,c
	Amud 1	M	75.3	45	cold-temperate	a,b
	Fond-de-Forêt 1	M	83.9	50	cold-temperate	a,b
	Kiik-Koba 1	M	78.1	50	cold-temperate	a,b
	Neandertal 1	M	78.9	50	cold-temperate	a,b
	Shanidar 1	M	80.5	50	cold-temperate	a,b
	Shanidar 3	M	79.9	50	cold-temperate	a,b
	Shanidar 5	M	68.5	50	cold-temperate	a,b
	Spy 2	M	83.6	50	cold-temperate	a,b
	La Chapelle 1	M	77.3	52	cold-temperate	a,b
	Kebara 2	M	75.6	60	glacial	a,b
	La Ferrassie 1	M	85.0	72	glacial	a,b
	Lezetxiki 1	M	73.9	75	cold-temperate	a,b
	Régourdou 1	M	72.1	75	cold-temperate	a,b
	Shanidar 2	M	75.2	100	cold-temperate	a,b
	Shanidar 4	M	72.0	100	cold-temperate	a,b
	Krapina 213	M	80.6	130	interglacial	a,b
Anatomically Modern Humans	Bruniquel 24	F	58.8[†]	20	glacial	b,d,e
	Abri Pataud 5	F*	60.9	21	glacial	a,b
	Cap Blanc I	F	56.3[†]	21	glacial	b,d,e
	Nahal Ein Gev	F	51.7	21	glacial	a,b
	Paglicci 25	F	60.6	24	glacial	a,b
	Dolní Věstonice 3	F	54.8	26	glacial	a,b
	Předmostí 1	F	55.4	27	glacial	a,b
	Předmostí 10	F	70.6	27	glacial	a,b
	Předmostí 4	F	65.1	27	glacial	a,b
	Předmostí 9	F	57.7	27	glacial	a,b
	Grottes des Enfants 5	F	52.8	28	glacial	a,b
	Batadomba Lena 2	F	59.1[‡]	29	glacial	f,g,h,i
	Cro Magnon 2	F	59.2	30	glacial	a,b
	Mladeč 1	F	62.7[$]	31	glacial	j,k,l
	Qafzeh 9	F	62.3[†]	90	cold-temperate	b,e,m

TABLE 2. FOSSIL SAMPLE DATA (continued).

	Specimen	Sex[a]	Mass (kg)[b]	Age (kya)	Period[c]	References[d]
Anatomically Modern Humans	Kubbaniya	M	69.6	20	glacial	a,n
	Abri Pataud 4	M	63.0	21	glacial	a,b
	La Rochette 1	M*	64.7	24	glacial	a,b,o
	Baousse de Torre 2	M	75.4	25	glacial	a,b
	Caviglione 1	M	65.2	25	glacial	a,b
	Pavlov 1	M	79.0	26	glacial	a,b
	Paviland	M	72.9	26	glacial	a,b
	Předmostí 14	M	65.9	27	glacial	a,b
	Předmostí 3	M	70.8	27	glacial	a,b
	Dolní Věstonice 13	M	68.0	27	glacial	a,b
	Dolní Věstonice 14	M	72.0	27	glacial	a,b
	Dolní Věstonice 16	M	71.0	27	glacial	a,b
	Grottes des Enfants 4	M	83.8	28	glacial	a,b
	Batadomba Lena 1	M	61.7‡	29	glacial	f,g,h,i
	Cro Magnon 1	M	67.6	30	glacial	a,b
	Cro Magnon 3	M	65.3	30	glacial	a,b
	Mladeč 21	M	62.7	31	glacial	a,k,l
	Mladeč 22	M	76.5	31	glacial	a,k,l
	Mladeč 24	M	76.8	31	glacial	a,k,l
	Nazlet Khater 1	M	52.2	33	glacial	a,p,q
	Tianyuan	M*	71.9‡	39	cold-temperate	h,i,r
	Liujiang	M	53.1†	67	glacial	a,s,t
	Skhul IV	M	66.2†	98	cold-temperate	b,u,v
	Skhul V	M	69.7†	98	cold-temperate	b,u,v

[a] Sex as reported with mass estimate, where available. Starred entries indicate sex inderterminate. For these specimens, sex was assigned based on z-scores in comparison to average males and females in the sample of Ruff et al. (1997).

[b] Mass estimated from stature and bi-iliac breadth except where noted:

†From femoral head diameter. Average of three methods in Ruff et al. (1997). Femoral head diameter was estimated from acetabular height for Liujiang using equation in Rosenberg (1988).

‡From stature (Henneberg et al. 1989; Feldesman et al. 1990; Mathers and Henneberg 1995).

$From orbital area (Kappelman 1996).

[c] General global climate regime under which each fossil lived, using oxygen isotope stages. "Glacial" includes OIS 6 (>130 ka), OIS 4 (74-59 ka) and the cold portion of the late Pelniglacial and early Last Glacial Maximum (37 ka in OIS 3 to 20 ka in OIS 2). "Cold-temperate" includes the later stages of the Last Interglacial (OIS 5d-5a: 110-74 ka) and the early portion of the Pleniglacial (first half of OIS 3: 59-37 ka). "Interglacial" corresponds to OIS 5e (130-110 ka). These designations determined the climate maps that were used to derive mean annual temperature values.

[d] References: a. Ruff et al. 1997, supplemental data; b. Oakley et al. 1971, 1975, *Catalogue of Fossil Hominids* vol. 2 & 3; c. Site geography from coordinates for the town of Saint-Cesaire, France; d. Mathers and Henneberg 1995; e. Femoral head measured by S. Churchill; f. Baernstein and Kennedy 1990; g. Kennedy and Deraniyagala 1989; h. Feldesman et al. 1990; i. Henneberg et al. 1989; j. Kappelman 1996; k. Beals et al. 1983; l. Wild et al. 2005; m. Valladas et al. 1998; n. Site geography from coordinates for the town of El'Aqaba el Saghira, Egypt; o. Orschiedt 2002;p. Vermeersch et al. 1982; q. Vermeersch 2002; r. Shang et al. 2007; s. Rosenberg 1988; t. Rosenberg 2002; u. Grün et al. 2005; v. Vandermeersch 1981.

Table 2): from femoral head diameter in six specimens (using the average of the three equations provided Ruff et al. 1997); from femur length and stature estimates in three specimens (following Feldesman et al. 1990; Henneberg et al. 1989; Mathers and Henneberg 1995); and from orbital area in one specimen (from Kappelman 1996).

For all but three modern human specimens, we followed the sex designations reported with published mass estimates or other morphometric data. For the three specimens in which sex was indeterminate (Abri Pataud 5, La Rochette 1, and Tianyuan), we assigned sexes by comparing body mass for each specimen to the sample of modern human mass estimates in Ruff et al. (1997). To determine the utility of published fossil body mass estimates in assigning sex to unknown specimens, we first tested for sexual dimorphism in the comparative data, finding a significant difference between males and females (two sample t-test, $p<0.001$). Mass estimates were distributed normally in both sexes (Shapiro-Wilk test: M: $p=0.949$; F: $p=0.777$), which allowed us to calculate sex-specific z-scores for mass in each of our three specimens of unknown sex. We assigned sexes to those specimens based on the smaller of the two z-scores (indicating mass closer to the mean of one sex than the other), resulting in two specimens being designated male (Tianyuan, La Rochette 1), and one female (Abri Pataud 5) for the purposes of this study.

We obtained paleoclimate data from the Oxygen Isotope Stage (OIS) Three Project's websites. The websites provide "snapshot" isotherm maps depicting climate in Europe (Phase 4 output: ftp://ftp.essc.psu.edu/pub/emsei/pollard/Stage3/PLOT) and worldwide (ftp://ftp.essc.psu.edu/pub/emsei/pollard/Stage3/PLOTGCM), for three broad categories of global climate: 1) modern, or interglacial; 2) typical cold event, from the last glacial maximum (LGM); and, 3) typical warm event during OIS 3. The typical cold and typical warm maps represent end-members (i.e., cold and warm peaks, respectively) of millennial-scale fluctuations in climate that occurred throughout the OIS 3 glaciation. Such fluctuations in climate also occurred throughout other large-scale oxygen isotope periods, as evidenced by Greenland ice cores (Barron et al. 2003). Ideally, in order to obtain the best estimates for the climate conditions under which our fossil specimens lived, we would use geochronological dates to locate each specimen within both the larger OIS climate periods, and also within these smaller-scale fluctuations. Unfortunately, however, the error of age estimates for fossils generally is on the order of at least 1000 years, nearly the same scale as the fluctuations from cold to warm end-members. This precluded our precise placement of fossils within these smaller fluctuations, and forced us to categorize them according to broader standards as defined by the larger OIS periods.

Having recognized this problem, Stage Three Project researchers cautiously recommended that the cold LGM maps could be used for the entire glacial period from 37–20 ka, and the typical warm maps for the entire pleniglacial period from 59–37 ka (Barron et al. 2003). We adopted this approach here, and also extended it to cover the earlier OIS periods for which we have specimens, applying the typical cold event maps to earlier glacial periods (OIS 6: >130 ka; OIS 4: 74–59 ka; recognizing that OIS 6 was more uniformly cold than the LGM, while OIS 4 was somewhat warmer: Frenzel 1973; van Andel and Tzedakis 1996), the typical warm event maps to earlier pleniglacial periods (OIS 5d–-5a: 110–74 ka; recognizing that OIS 3 generally was both colder and less stable than the latter part of OIS 5: see Guiot 1989; van Andel and Tzedakis 1996), and the modern map to the last interglacial (OIS 5e: 130–110 ka; while recognizing that OIS 5e at its *peak* was warmer than anything experienced during the Holocene: Butzer 1975; Gamble 1986; van Andel and Tzedakis 1996).

We gave each fossil in our sample a climate designation based on the above criteria, using geological age estimates from Ruff et al. (1997) with some revisions based on newer publications (Grun et al. 2005; Valladas et al. 1998; Vermeersch 2002; Wild et al. 2005—see Table 2). Specimens were designated as "glacial," "cold-temperate" (corresponding to pleniglacial above), or "interglacial." These categories do not necessarily describe any site's local climate, but rather denote the global climate regime in the time period during which each individual may have lived. Using these climate designations, we located each fossil's site on the appropriate OIS 3 maps. The maps of Europe depict isotherms of mean air temperature at 2m above the surface during summer (June, July, August) and winter months (December, January, February). The worldwide maps provide similar depictions of seasonal mean temperature, but at a lower resolution than the Europe-specific maps (grid of ca. 223x134km for world vs. 60x60km in Europe, when at latitude of 53.0°).

For each fossil site we obtained mean winter and mean summer temperatures. Since each isotherm on the maps represented a range of temperatures, we took the middle value for the isotherm in which each site fell. If a site fell on the border between two isotherms, the middle value for the entire range of temperatures was used. Summer and winter seasonal temperatures were averaged to arrive at a rough approximation of mean annual temperature.

There are a number of caveats to this approach. One is that the climate models appear to be more accurate in some regions than others. For example, van Andel (2003) cautions that while the models generally provide an accurate picture of Western Europe and the western Mediterranean, they are less accurate with regard to central, southern, and southeastern Europe. Likewise, the comparability of European and non-European climates is somewhat limited by the difference in scale between the two sets of models. Furthermore, as noted above, the use of single models for time periods covering many millennia ignores substantial smaller-scale variation in climate. Finally, the amount of error introduced by using the mean of average summer and winter temperatures from the OIS 3 maps as a proxy for mean annual temperature is not known. For example, using the OIS 3 modern simulation and the above methods, mean annual temperature for modern day San Diego, CA, is predicted to be 21.3°C, whereas from World Meteorological Organization weather stations, the actual value is probably closer to 17.7°C.

This aspect of our approach may under- or over-estimate mean annual temperature for these fossil sites, perhaps on the order of ca. 3° C, the effect of which on BMR we would predict to be ca. 17 $\text{kcal} \cdot \text{d}^{-1}$ in males and ca. 11 $\text{kcal} \cdot \text{d}^{-1}$ in females. These values would be magnified in estimates of DEE, but even with the highest PAL value (2.5), would only amount to ca. 30–40 $\text{kcal} \cdot \text{d}^{-1}$ in either sex. From earlier estimates of Neandertal DEE that range between 3300–5500 $\text{kcal} \cdot \text{d}^{-1}$, the error produced by our mean annual temperature estimates appears very small (up to 1.2%) and is likely to be unimportant. Considering that the same error is inherent in our calculations for both Neandertals and anatomically modern humans, comparisons between the two should likewise be relatively unaffected by this error.

For each fossil specimen, we used the body mass estimate and the associated mean annual temperature estimate to calculate BMR using the predictive equations from Froehle (2008) (see Table 1). Using these BMR values, we then estimated daily energy expenditure (DEE) as:

$$\text{DEE } (\text{kcal} \cdot \text{d}^{-1}) = \text{BMR } (\text{kcal} \cdot \text{d}^{-1}) \cdot \text{PAL}$$

where PAL = the coefficient for physical activity level. We made no assumptions about the impact of cultural differences between Neandertals and modern humans (where they existed) on PAL—in other words, we assumed that Neandertals and modern humans would have required the same level of energy expenditure above basal levels, at least within the sexes and within climate zones. We revisit this assumption below.

We assigned PAL values depending on the local climate of each site during occupation, and the sex of each individual. The assumption that different climate regions require different levels of exertion in foraging is based on observations of extant foragers in the Arctic vs. the tropics, and also on the reduced productivity (and hence greater mobility costs for foragers) of glacial Europe (Huntley and Allen 2003). Each specimen was classified as coming from a cold, temperate, or tropical climate, based on a z-score comparison of their mean annual temperature data to a large modern sample divided between circumpolar/high altitude (corresponding to cold above), temperate, and tropical populations (from Froehle 2008). Note that these local climate classifications are based on site-specific mean annual temperature as obtained from the OIS 3 maps, and are distinct from the previous time-dependent climate designations that we used to determine which map to use for each fossil in the first place.

We assigned each fossil to a local climate group based on the smallest mean annual temperature z-score obtained for each site, in comparison to the extant climate groups (Table 3). This resulted in the classification of 23 modern humans (13 M, 10 F) and 9 Neandertals (7 M, 2 F) as cold, 13 modern humans (9 M, 4 F) and 16 Neandertals (9 M, 7 F) as temperate, and 3 modern humans (2 M, 1 F) and 1 Neandertal (M) as tropical (see Table 3). Based on these local climate designations, we assigned a PAL value corresponding to expected foraging effort based on relative productivity of the environment. Our study diverges from previous reconstructions of Neandertal DEE in that we assume a sex difference in activity levels. We drew PAL values for tropical/temperate hominins from Panter-Brick (2002), using the average of Ache and !Kung foragers (PAL=1.70 in females, 1.93 in males).

For cold climates, however, the values for the Igloolik (female=1.8; male=2.2) reported in Panter-Brick (2002) are probably too low, based on the relatively sedentary nature of that population accompanying adoption of "western" technologies (Godin and Shephard 1973). For males, we used the slightly higher PAL value of 2.5 (Snodgrass, pers. comm.), which is consistent with the energy Igloolik males expend hunting terrestrial herbivores (caribou: Godin and Shephard 1973), and is probably a reasonable approximation of foraging realities in Late Pleistocene European glacial climates. For females, however, we expect that Neandertals and anatomically modern humans would have had considerably higher activity levels than the more sedentary Igloolik women. Despite having overall high-moderate to heavy workloads, and engaging in some household activities requiring considerable exertion (such as scraping furs and chewing skins—possibly relevant to hominins in cold climates), Igloolik women did not forage. In contrast, there is some evidence that Neandertal females may have regularly hunted large game (Kuhn and Stiner 2006). Meanwhile, the absence of sex differences in lower limb robusticity in anatomically modern human fossils (Holt 2003) indicates similar levels of mobility (Stock 2006) in males and females, consistent with modern forager women who travel long distances in search of resources and/or transport heavy loads (Carlson et al. 2007). Thus, we used a higher PAL value of 2.2 for cold-climate females. This we derived by dividing the male cold-climate PAL of 2.5 by the male/female PAL ratio in the !Kung and Ache (1.14), where both sexes actively forage.

RESULTS

Fossil site climate data are summarized in Table 3. Of the sites designated as having cold local climates, mean annual temperature at all Neandertal sites was 6° C, towards the warmest end of the cold climate range (and also falling just within the lower 95% confidence interval of the temperate climate range). In contrast, modern humans from cold-designated sites lived at much lower mean annual temperature values, averaging 2.2°C (range: -2.0–6.0°C). Interestingly, of the sites we included in this study, more of the Neandertal sites qualified as temperate than cold (8 vs. 6, respectively), while the opposite was true for modern human sites (9 vs. 11, respectively). These findings are consistent with previous indications that Neandertals tended to inhabit warmer locations than early European modern humans (Aiello and Wheeler 2003). Within the temperate and tropical sub-samples we found no substantial differences in mean annual temperature between Neandertals and anatomically modern humans (average temperate mean annual temperature:

TABLE 3. PALEO-TMEAN (MEAN ANNUAL TEMPERATURE).

	Site	Latitude[a]	Longitude[a]	TMEAN (°C)[b]	Climate Group[c]
Neandertals	Amud	32.87	35.50	20.0	tropical
	Fond-de-Forêt	50.57	5.70	6.0	cold
	Grotte du Prince	43.78	7.62	11.0	temperate
	Kebara	32.55	34.95	15.0	temperate
	Kiik-Koba	45.05	34.30	12.5	temperate
	Krapina	46.17	15.87	12.3	temperate
	La Chapelle	44.98	1.72	6.0	cold
	La Ferrassie	44.95	0.93	6.0	cold
	La Quina	45.50	0.32	8.0	temperate
	Lezetxiki	43.07	-2.50	6.0	cold
	Neandertal	51.23	6.95	6.0	cold
	Régourdou	45.05	1.18	7.0	temperate
	Saint-Césaire	45.75	-0.50	6.0	cold
	Shanidar	36.83	44.22	12.5	temperate
	Spy	50.48	4.72	6.0	cold
	Tabun	32.67	35.08	11.3	temperate
Anatomically Modern Humans	Abri Pataud	44.93	1.02	6.0	cold
	Baousse de Torre	43.78	7.62	8.0	temperate
	Batadomba Lena	6.77	80.20	12.5	temperate
	Bruniquel	44.03	1.57	4.0	cold
	Cap Blanc	44.95	1.13	5.0	cold
	Caviglione	43.78	7.62	8.0	temperate
	Cro Magnon	44.93	1.02	8.0	temperate
	Dolní Věstonice	48.88	16.67	-1.0	cold
	Grottes des Enfants	43.78	7.62	8.0	temperate
	Kubbaniya	24.09	32.90	18.8	temperate
	La Rochette	45.03	1.13	5.0	cold
	Liujiang	24.18	109.43	16.3	temperate
	Mladeč	49.00	17.00	2.0	cold
	Nahal Ein Gev	32.78	35.63	11.3	temperate
	Nazlet Khater	26.75	31.25	18.8	temperate
	Paglicci	41.67	13.62	5.0	cold
	Paviland	51.55	-4.25	0.0	cold
	Pavlov	48.87	16.67	-1.0	cold
	Předmostí	49.50	17.42	-2.0	cold
	Qafzeh	32.68	35.30	20.0	tropical
	Skhul	32.67	35.08	20.0	tropical
	Tianyuan	39.65	115.87	1.3	cold

[a] Decimal scale degrees (as opposed to using minutes and seconds), where positive values refer to N latitude and E longitude, and negative values refer to S latitude and W longitude. Positive/negative divisions occur at the equator (latitude) and the prime meridian (longitude).

[b] Average of winter and summer mean surface temperatures from OIS3 Project maps. For European sites, winter temperatures were obtained from December-January-February maps, and summer temperatures from June-July-August maps. For sites outside Europe, winter temperatures came from February maps, and summer from August maps.

[c] Based on z-score comparison with mean annual temperatures for worldwide extant human tropical, temperate, and circumpolar/high altitude (cold) samples from Froehle (2008).

11.3 vs. 12.2° C, respectively; all tropical mean annual temperature values: 20° C).

Individual fossil BMR and DEE estimates are provided in Table 4, and mean values by sample are given in Table 5. Among the individuals living in cold climates, Neandertal males had 7% higher BMR and DEE than modern human males. Neandertal females also were higher by 3%, although this finding is based on an extremely small Neandertal sample (n=2). Under temperate conditions, male Neandertal BMR and DEE were both 9% higher than for modern human males, while in females, the Neandertal values were 7% higher than for their anatomically modern counterparts. Samples sizes for Late Pleistocene hominins living in tropical conditions were very small, but the single Levantine Neandertal deriving from relatively warm conditions (Amud 1) had estimated BMR and DEE values that were 7% larger than the mean of two Levantine modern human males (Skhul IV and V). This is consistent with the pattern seen in the cold- and temperate-climate comparisons, suggesting that under all climatic conditions and in both sexes, Neandertals tended to have higher energy requirements than their early modern human counterparts (Figure 2).

Our absolute DEE values for Neandertal males in cold climates are generally consistent with those of previous studies (Figure 3). For female Neandertals in cold climates, our estimates are within the low range or lower than those of other studies. This is mainly a function of our assumption that females were somewhat less active than males, and thus had lower PAL values. Not surprisingly, our DEE estimates in tropical and temperate Neandertals are much lower than the ranges given in previous studies. Our incorporation of mean annual temperature as a predictor of BMR is partly responsible for this result, as is our assumption that PAL values were lower in temperate and tropical populations.

In both Neandertals and modern humans living in cold climates, DEE was higher than for populations living in temperate and tropical climates. In males, the average difference is on the order of 1200 kcal · d^{-1} higher in cold climates, or 1.4 times as high as the average DEE in temperate/tropical males. The average female living in a cold climate would have required approximately 800 kcal · d^{-1} more than temperate or tropical females, or roughly 1.3 times average DEE in the warm climates. The differences between climate regions result in part from small variations in metabolic rate due to climate, with cold-climate groups having expected BMR values 2–9% higher than temperate and tropical groups. The initially higher BMR values are then further magnified by the assumed differences in PAL between the climate categories. In general, these divergent DEE values illustrate the substantial energetic pressure we expect Neandertals and anatomically modern humans to have experienced in cold, less productive environments.

Within the same climates, we find that Neandertals tended to have higher DEE than modern humans. In general, Neandertal male DEE exceeded that of modern human males in the tropical climate zone by roughly 200 kcal · d^{-1}, and in temperate and cold climate zones by about 275 kcal · d^{-1}. In temperate and cold-climate females (no tropical comparison was possible), Neandertal DEE was greater than in modern humans by only 100–150 kcal · d^{-1}. Higher energy requirements in Neandertals appear to result mainly from larger body size, and not from climate differences. This is particularly important in males, where there is a larger discrepancy between Neandertal and anatomically modern human average body size (entire sample, Neandertals vs. anatomically modern humans: males: 77.6 vs. 68.5 kg; females: 66.4 vs. 59.2 kg).

Within the cold climate group, mean annual temperature actually appears to limit differences in DEE between the two groups. This is a result of our finding that Neandertals occupied sites only at the extreme warm end of the cold-climate range, while mean annual temperature from anatomically modern human sites included many colder values. Indeed, if Neandertals occupied regions that were as cold as the coldest modern human sites (-2.0°C, which findings in the Altai Mountains in Siberia suggest they sometimes did: Krause et al. 2007), we would predict correspondingly higher BMR and DEE values. In that case, Neandertal DEE would exceed that of modern humans by approximately 350 kcal · d^{-1} in males, and 150 kcal · d^{-1} in females. The effect of mean annual temperature within the temperate group is negligible, since there is little variation in average mean annual temperature at Neandertal and anatomically modern sites (11.3 vs. 12.2° C, respectively).

DISCUSSION

This study has produced methodologically consistent estimates of DEE in both Neandertals and anatomically modern humans, incorporating the likely effects of climate into those estimates. Our results are largely concordant with previous studies that indicate higher energy requirements in Neandertals as compared to modern humans, although we find that the basis for those differences lies in body mass, rather than climate. Given the way we incorporate mean annual temperature into our calculations, and the geographical/temporal distribution of the fossils, if modern humans and Neandertals were of similar body mass we would actually anticipate higher DEE in the former provided the site-specific mean annual temperature values we derived. This is in part a result of our assumption of physiological parity between Neandertals and anatomically modern humans, in that we expect similar metabolic responses to cold climate in such closely related taxa. In addition, because we assume the same levels of physical activity in both groups, body size becomes the major explanatory factor of the energetic differences we observe between Neandertals and modern humans.

Because large Neandertal body mass appears to have been in part related to their climatic adaptation, it is necessary to examine how anatomically modern humans were able to maintain smaller bodies while occupying even colder regions. Again, since we assume physiological parity, we must rely on behavioral interpretations to explain this difference. It remains possible that important differ-

TABLE 4. ENERGETIC ESTIMATES FOR FOSSIL SPECIMENS.

Neandertals							Anatomically Modern Humans						
Climate	**Sex**		**Specimen**	**Mass (kg)**	**BMR (kcal · d^{-1})[a]**	**DEE (kcal · d^{-1})[b]**	**Climate**	**Sex**		**Specimen**	**Mass (kg)**	**BMR (kcal · d^{-1})[a]**	**DEE (kcal · d^{-1})[b]**
Cold	F		La Ferrassie 2	67.0	1446	3180	Cold	F		Abri Pataud 5	60.9	1389	3057
			Spy 1	67.5	1450	3190				Bruniquel 24	58.8	1378	3031
										Cap Blanc I	56.3	1351	2972
										Dolní Věstonice 3	54.8	1360	2992
										Mladeč 1	62.7	1421	3127
										Paglicci 25	60.6	1391	3059
										Předmostí 1	55.4	1369	3012
										Předmostí 4	65.1	1459	3209
										Předmostí 9	57.7	1390	3059
										Předmostí 10	70.6	1509	3320
		Mean	(n=2)	67.3	1448	3185			Mean	(n=10)	60.3	1402	3084
	M		Fond-de-Forêt 1	83.9	1935	4837		M		Abri Pataud 4	63.0	1628	4069
			La Chapelle 1	77.3	1838	4594				Dolní Věstonice 13	68.0	1740	4351
			La Ferrassie 1	85.0	1951	4877				Dolní Věstonice 14	72.0	1799	4498
			Lezetxiki 1	73.9	1788	4469				Dolní Věstonice 16	71.0	1784	4461
			Neandertal 1	78.9	1861	4653				La Rochette 1	64.7	1658	4145
			Saint-Césaire 1	78.9	1861	4653				Mladeč 21	62.7	1645	4114
			Spy 2	83.6	1930	4826				Mladeč 22	76.5	1848	4621
										Mladeč 24	76.8	1853	4632
										Paviland	72.9	1807	4517
										Pavlov 1	79.0	1902	4755
										Předmostí 3	70.8	1787	4467
										Předmostí 14	65.9	1715	4287
										Tianyuan	71.9	1785	4462
		Mean	(n=7)	80.2	1881	4701			Mean	(n=13)	70.4	1766	4414

TABLE 4. ENERGETIC ESTIMATES FOR FOSSIL SPECIMENS (continued).

Neandertals							Anatomically Modern Humans						
Climate	Sex		Specimen	Mass (kg)	BMR (kcal · d-1)[a]	DEE (kcal · d-1)[b]	Climate	Sex		Specimen	Mass (kg)	BMR (kcal · d-1)[a]	DEE (kcal · d-1)[b]
Temperate	F		Grotte du Prince	74.8	1498	2547	Temperate	F		Batadomba Lena 2	59.1	1348	2292
			Krapina 208	68.4	1435	2439				Cro Magnon 2	59.2	1366	2323
			Krapina 209	63.7	1391	2365				Grottes des Enfants 5	52.8	1307	2223
			Krapina 214	62.2	1378	2342				Nahal Ein Gev	51.7	1285	2184
			La Quina 5	71.2	1477	2510							
			Shanidar 6	59.4	1351	2297							
			Tabun C1	63.2	1391	2364							
		Mean	(n=7)	66.1	1417	2409			Mean	(n=4)	55.7	1327	2256
	M		Kebara 2	75.6	1762	3401		M		Baousse de Torre 2	75.4	1799	3471
			Kiik-Koba 1	78.1	1813	3499				Batadomba Lena 1	61.7	1572	3034
			Krapina 213	80.6	1851	3572				Caviglione 1	65.2	1649	3182
			Régourdou 1	72.1	1756	3388				Cro Magnon 1	67.6	1683	3249
			Shanidar 1	80.5	1848	3567				Cro Magnon 3	65.3	1650	3185
			Shanidar 2	75.2	1770	3417				Grottes des Enfants 4	83.8	1922	3710
			Shanidar 3	79.9	1840	3550				Kubbaniya	69.6	1653	3190
			Shanidar 4	72.0	1723	3326				Liujiang	53.1	1424	2749
			Shanidar 5	68.5	1672	3227				Nazlet Khater 1	52.2	1397	2696
		Mean	(n=9)	75.8	1782	3439			Mean	(n=9)	66.0	1639	3163
Tropical	F		N/A				Tropical	F		Qafzeh 9	62.3	1349	2294
		Mean	N/A						Mean	(n=1)	N/A	N/A	N/A
	M		Amud 1	75.3	1730	3339		M		Skhul IV	66.2	1596	3081
										Skhul V	69.7	1648	3180
		Mean	(n=1)	N/A	N/A	N/A			Mean	(n=2)	68.0	1622	3131

[a] Using Equation Set B from Froehle (2008).

[b] DEE = BMR x PAL, where PAL is physical activity level ratio. PAL based on climate designation (see Table 3). For periglacial climates, male PAL=2.50, female=2.20; for temperate and tropical climates, male=1.93, female=1.70.

TABLE 5. MEAN ESTIMATED BMR AND DEE (kcal · d^{-1}) FOR NEANDERTALS AND EARLY ANATOMICALLY MODERN HUMANS (AMH) [mean ± 1SD, (n), range].

		Climate Group					
		Cold		Temperate		Tropical	
		BMR	DEE	BMR	DEE	BMR	DEE
Neandertals	Males	1881 ± 60 (7) 1788-1951	4701 ± 150 (7) 4469-4877	1782 ± 62 (9) 1672-1851	3439 ± 118 (9) 3227-3527	1730 (1)	3339 (1)
	Females	1448 ± 3 (2) 1446-1450	3185 ± 6 (2) 3180-3190	1417 ± 54 (7) 1351-1498	2409 ± 92 (7) 2297-2547	--	--
Anatomically Modern Humans	Males	1766 ± 84 (13) 1628-1902	4414 ± 211 (13) 4069-4755	1639 ± 165 (9) 1397-1922	3163 ± 318 (9) 2696-3710	1622 ± 37 (2) 1596-1648	3131 ± 70 (2) 3081-3180
	Females	1402 ± 49 (10) 1351-1509	3084 ± 88 (10) 2972-3320	1327 ± 37 (4) 1285-1366	2256 ± 63 (4) 2184-2323	1349 (1)	2294 (1)

ences in thermogenesis and brown fat metabolism existed between Neandertal and modern humans (see Steegman et al. 2002; Wallace 2005), which may have given modern humans a physiological adaptation to cold that was effective in the context of less-massive body size. Such variation may eventually be detected through ancient DNA research, but these differences have not as yet been established. Instead, we suggest that various lines of evidence from the paleontological and archaeological records can help explain how modern humans could maintain lighter bodies in colder environments, and reap the concomitant energetic benefits. We will examine these benefits in light of the potential reproductive advantages they may have conferred upon anatomically modern humans relative to Neandertals.

Morphological indicators suggest the Neandertals were heavily muscled, which may have provided them with both a greater thermogenic capacity and greater insulation against the cold (Aiello and Wheeler 2003; Churchill 2006; Steegmann et al. 2002), and which was part of a close-range, confrontational hunting strategy focused on terrestrial herbivores (Bocherens et al. 1999, 2001, 2005; Churchill 1998; Churchill and Rhodes 2006; Fizet et al. 1995; Miracle 2005; Patou-Mathis 2000; Richards et al. 2000, 2001; Valensi and Psathi 2004; Vaquero et al. 2001; Villa and d'Errico 2001). Greater body mass in Neandertals compared to anatomically modern humans results mainly from reduced muscularity in the latter (Churchill 1998; Trinkaus 1986), suggesting that modern humans could not sustain Neandertal-like thermoregulatory and subsistence strategies.

Considerable evidence suggests that important differences existed in the ways that Neandertals and European modern humans fended off the cold and obtained food. In discussing this evidence, we acknowledge that considerable debate exists as to the timing, nature, and meaning of the transition from the Middle to the Upper Paleolithic in Europe, and we recognize the problems of assigning particular lithic industries to particular biological taxa (a problem that is particularly acute for initial and early Upper Paleolithic industries, such as the early Aurignacian: Churchill and Smith 2000; Conard et al. 2004). Nevertheless, some relevant distinctions exist between the behavior of Neandertals (for the majority of their tenure in Europe) and that of Upper Paleolithic modern humans, which may have allowed smaller body mass, and thus lower energetic requirements, in the latter.

With respect to keeping warm, Late Pleistocene modern *H. sapiens* may have replaced insulating muscle with clothing that was better-tailored than that of the Neandertals. This is suggested by the appearance of bone awls dating to 45–40 ka in western Russia (Anikovitch et al. 2007) and in central and Western Europe (Conard and Bolus 2003; Mellars 2006), and eyed needles from Eastern European modern human sites by 35–30 ka (Hoffecker 2005). Such implements are absent from Mousterian assemblages, although bone awls appear in the late Neandertal-associated Châtelperronian (d'Errico et al. 1998). The development

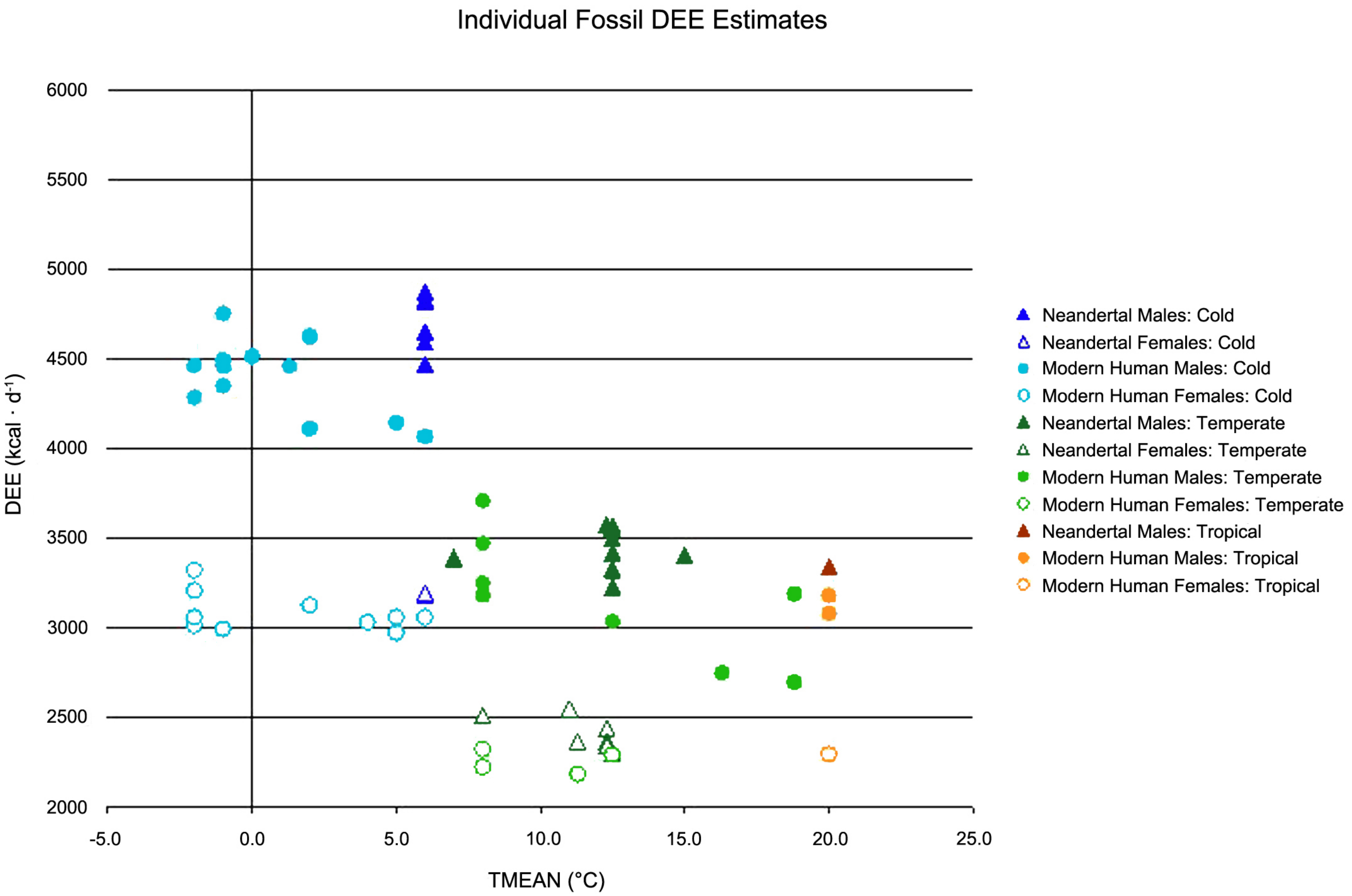

Figure 2. Daily energy expenditure (DEE) estimates for Neandertal (triangles) and anatomically modern human (circles) males (filled symbols) and females (open symbols), in cold (blue), temperate (green) and tropical (orange) climates. DEE data were plotted against mean annual temperature for each fossil's site, to illustrate the association between climate and DEE in our model (note that the DEE values are in part dependent on mean annual temperature, because our equations incorporate this climate variable to estimate BMR, and subsequently, DEE). We estimated DEE by multiplying basal metabolic rate (BMR) by physical activity level (PAL). We used higher PAL values for cold/periglacial individuals (males=2.5, females=2.2) than for temperate/tropical fossils (males=1.93, females=1.7). Groups living in cold climates tend to have higher DEE than those in warmer climates. In all regions, Neandertals have higher average DEE than AMH.

of better-tailored clothing may have allowed anatomically modern humans to occupy sites intolerable to Neandertals (Aiello and Wheeler 2003) despite their less-massive bodies. Greater cultural buffering in the form of more efficient hearths and shelters may have also helped modern humans deal with glacial climates (references in Holliday 1997). These cultural proclivities may have obviated the need for heavy musculature for heat production and insulation.

In the realm of resource acquisition, many lines of evidence suggest a substantial difference between Neandertals and Upper Paleolithic modern humans. In general, it appears that modern humans employed a more diverse range of foraging behaviors than Neandertals. The flexible and stratified type of foraging observed in recent hunter-gatherers and apparent in Upper Paleolithic modern humans may have originated in more productive tropical environments (Kuhn and Stiner 2006), with subsequent adaptation and honing in the cold plains of Central Asia (Finlayson and Carrión 2007). In general, the anatomically modern human foraging strategy may have been characterized by a reduced reliance on direct confrontation with large game compared to Neanderthals, achieved through the use of long range projectile weaponry and an expansion of diet breadth.

Projectile points may date back to 77 ka in Africa (McBrearty and Brooks 2000; Brooks et al. 2005), and are present in the Near East by roughly 50–40 ka (Shea 2006). This means that modern humans entering Europe could have brought this technology and associated hunting techniques (Churchill 1993) with them, although there is also evidence for insular development of projectile technology within Europe (Shea 2006). Morphological aspects of the scapula, humerus, and ulna may indicate regular use of projectiles by middle Upper Paleolithic modern humans (by Gravettian times), but not by Neandertals (Churchill and Rhodes n.d.; Rhodes and Churchill 2009). Nevertheless, some of the

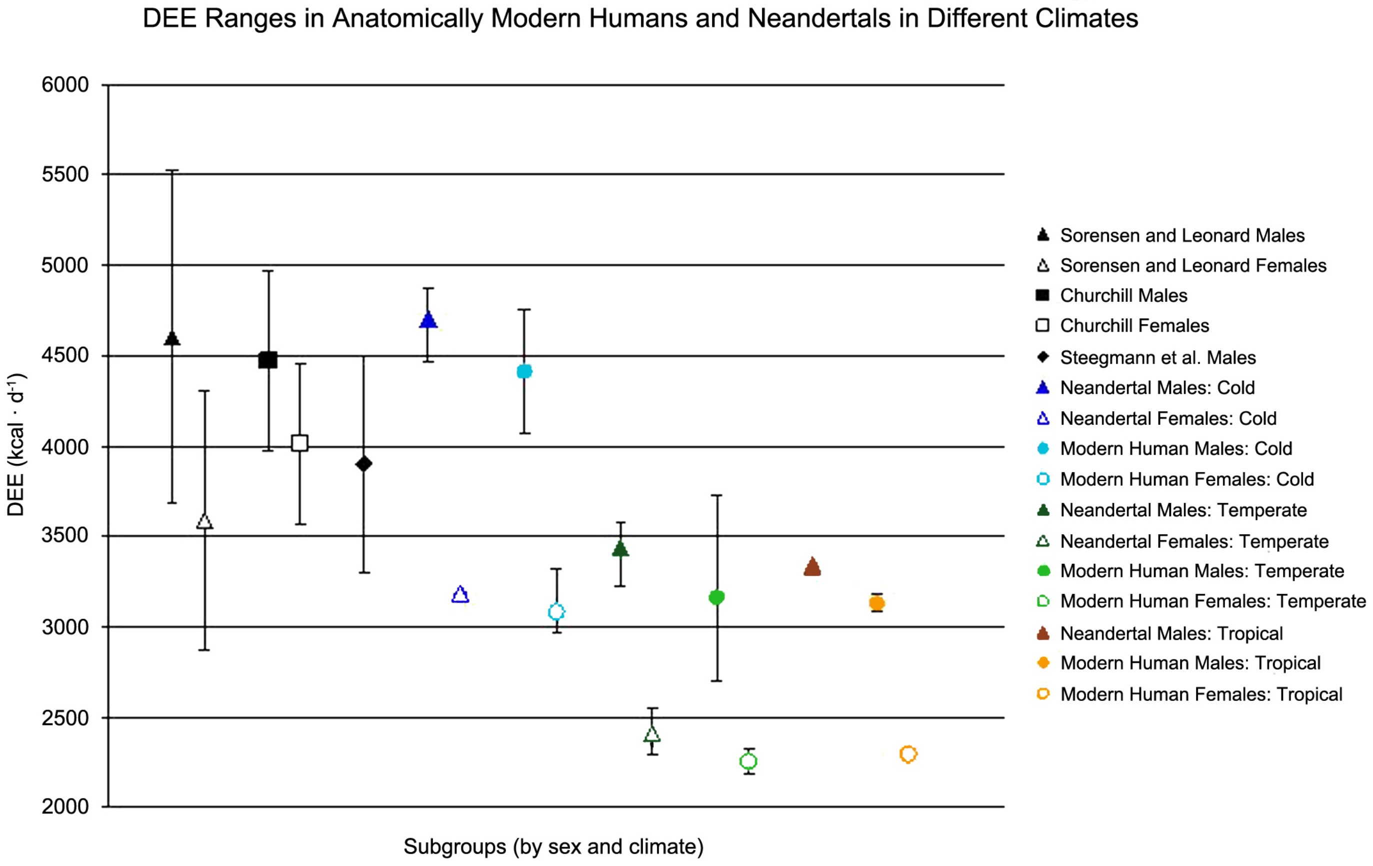

Figure 3. Our results compared to previous studies of Neandertal DEE (Sorensen and Leonard 2001; Steegmann et al. 2002; Churchill 2006). Our results are divided by hominin group (Neandertal: triangles; anatomically modern human: circles), sex (males: filled symbols; females: open symbols), and climate (cold: blue; temperate: green; tropical: orange). Each symbol represents mean DEE for that particular group (e.g. cold-dwelling Neandertal females), and the error bars denote the full range of our DEE estimates within that group. For the previous studies, again, the error bars denote the range of DEE estimates for each sex, and the symbols represent the middle values between the extremes of those ranges. Both Neandertals and anatomically modern humans living in cold climates fall within the range of DEE values proposed in earlier studies, whereas temperate and tropical populations have considerably lower DEE estimates.

earliest potential projectile points in Europe come from the Châtelperronian (Shea 2006).

Stable isotope evidence indicates a higher incidence (relative to the Neandertals) of aquatic resource exploitation in modern humans by 28–20 ka (Richards et al. 2001), though this is not universally the case (Drucker and Bocherens 2004). As with projectile points, it is possible that anatomically modern humans brought the methods and technology for aquatic resource acquisition with them into Europe, as barbed points associated with fish remains appear in the African Middle Stone Age by as early as 90 ka (Yellen et al. 1995). Both the Mousterian and Châtelperronian lack such implements (Villa and d'Errico 2001; Hoffecker 2005); they are similarly absent, however, from Upper Paleolithic industries until after 24 ka (Hoffecker 2005). Most evidence of Neandertal aquatic resource exploitation in Europe consists of shellfish remains (Stiner et al. 1999), although some late Neandertal populations appear to have consumed marine mammals (Stringer et al. 2008). This is in contrast to isotopic signals indicative of consumption of fish and their mammalian and avian predators in modern humans (Richards et al. 2001).

Zooarchaeological data also suggest a gradual increase in exploitation of small mammals and birds beginning with the early Aurignacian, by about 36–32 ka (Stiner et al. 2000; Stewart 2004), further indicating decreased reliance on muscular force production in obtaining animal protein. Meanwhile, isotope data show that Neandertals occupied a top-predator trophic position, focusing on large game (Bocherens et al. 2001, 2005). The more frequent inclusion of lower-ranked prey items may have reduced modern human foraging efficiency in comparison to Neandertals, since smaller prey can have high post-encounter handling costs relative to caloric returns. This may have attenuated the energetic advantage of small body size in modern humans somewhat, either by indicating higher PAL, or by reducing the "surplus" calories netted for a given level of physical exertion. Nevertheless, increased diet breadth probably provided modern humans greater flexibility in obtaining sufficient calories to maintain reproductive levels, which, coupled with lower overall caloric needs, would likely have provided substantial demographic payoffs (Stiner 2001; Stiner et al. 2000; O'Connell 2006).

Increased handling costs may have also been partially offset by more efficient locomotion, resulting from modern humans having narrower trunks and longer limbs than Neandertals (Steudel-Numbers and Tilkens 2004; Weaver and Steudel-Numbers 2005). More efficient locomotion would have been especially important if anatomically modern humans and Neandertals were similarly mobile, as recent strontium isotope evidence may suggest (Richards et al. 2008). Furthermore, the reduced muscular force production associated with killing and possibly transporting small mammals as opposed to large ones might have provided further energetic benefits, meanwhile requiring less-muscular and therefore less-massive bodies.

If the above behavioral mechanisms did indeed allow anatomically modern humans to maintain less-massive bodies in colder climates, what might the attendant lower energy requirements have meant for reproduction and demographic competition with Neandertals? We assume that an energetic advantage generally translates into a reproductive advantage. The efficient capture and effective allocation of calories to competing energetic demands underlies reproductive success (McNab 2002), since producing and raising offspring requires a great deal of calories, particularly in large-brained hominins (Rosenberg 1992; Martin 2007). For example, among extant subsistence-level human populations, gestation and lactation costs reach maximums of approximately 175 kcal · d^{-1} and 500 kcal · d^{-1}, respectively (Butte et al. 1997; Dufour and Sauther 2002; Thongprasert et al. 1987). Differences between groups in energy expenditure, assuming comparable rates of calorie capture from foraging, can mean differences in the amount of energy above maintenance levels that can be allocated to gestation and lactation.

Assuming that reproductive energy values from modern-day populations also applied to fossil modern human and Neandertal foragers, we can construct a heuristic model to illustrate the effect that lower DEE might have had on reproduction. Based on very broad generalizations drawn from modern-day foragers, we set the modal social group size (for the purposes of the model) at eight reproductive-aged adult, full-time foragers, evenly split between males and females (Kelly 1995) for both the Neandertal and anatomically modern human groups. This is a rough approximation, as modern day forager group size and composition vary considerably, both between groups and within groups seasonally. It also ignores the presence of weaned juveniles and post-reproductive adults, all of whom forage to some degree, but for whom we lack good models of energy expenditure or productivity. Relying on reproductive-age adults alone can, however, provide some idea of energy "savings" in modern humans vs. Neandertals on an economic, as opposed to individual, scale. Based solely on these eight adults, and averaged across environments, a group of anatomically modern humans would require roughly 1500–2000 kcal · d^{-1} less than a similar Neandertal group.

Very crudely, 1500–2000 kcal · d^{-1} represents the daily gestation costs of up to 8–11 near-term fetuses, or the energy needed to nurse 3–4 infants. With similar levels of foraging returns in Neandertals and modern humans, reduced energy expenditure in the latter could have had large payoffs in terms of greater offspring survivorship and/or reduced inter-birth intervals. This assumes, however, a relatively major male contribution to adult female/offspring energy needs, since males account for about 70–75% of reduced energy expenditure (compared to Neandertals) in adult anatomically modern human full-time foragers. The energy savings for modern human vs. Neandertal females are comparably much lower than for males, based mainly on a smaller difference in average female body size (cold-climate sample: 67.3 kg vs. 60.3 kg) and lower PAL.

Modern-day foragers exhibit a wide variety of food-sharing patterns, especially with regard to female access to male-procured resources (Kelly 1995). If, in the extreme case, Neandertal and anatomically modern human males contributed no calories to offspring production, lower DEE in modern human vs. Neandertal females would have conferred a noticeably smaller reproductive advantage of roughly 400–600 kcal · d^{-1} (this ignores any potential caloric contributions from post-reproductive foragers or other childcare helpers). Thus, the above quantities of additional offspring should be taken as an extreme maximum, and the reproductive implications of reduced DEE interpreted conservatively. Nonetheless, any caloric surplus could have been used to promote even small reductions in birth-spacing, or to improve offspring survivorship rates, both with potentially large long-term demographic consequences.

If anatomically modern humans were not able to obtain as many calories per unit time as Neandertals, then lower DEE may not have resulted in relative caloric "surpluses." With absolutely lower caloric requirements, however, modern humans would have needed to obtain an absolutely smaller amount of resources in order to satisfy those requirements. Thus, even in the absence of surpluses, lower energy requirements may have given modern humans an advantage in comparison to Neandertals with higher absolute needs. In other words, the greater one's energy needs, the higher one's chances of failing to meet those needs, especially in a limited-productivity environment with seasonal caloric shortfalls and substantial competition for resources. Less-massive bodies with proportionately lower caloric demands are advantageous in calorie-poor environments (see discussion and references in Bogin 1999), as one is more likely to satisfy individual energy demands on a daily basis. If the production of offspring is included in those individual demands, then a failure to obtain sufficient resources could mean the inability to sustain offspring development. If by having lower caloric requirements anatomically modern humans experienced fewer daily caloric shortfalls, they may have also had lower infant mortality and higher survivorship rates than Neandertals.

CONCLUSIONS

This study employs a new method for systematically incorporating climate into energetic estimates, with the goal of providing a direct comparison of energy needs in Neandertals and anatomically modern humans living under similar climate regimes. The higher predicted energy expenditure values we find for Neandertals result mainly from larger body size, and are in fact minimized by the fact that modern humans were able to occupy sites that were colder than the Neandertal sites for which data were available. Lower energy expenditure in modern humans likely provided a reproductive and demographic advantage relative to the Neandertals, which may have played an important role in evolutionary competition between the two groups. Even the most conservative interpretation of our results suggests that modern human groups may have been able to convert their energetic "savings" into a slight reproductive advantage.

Recent studies suggest that this situation may have been exacerbated by differences in juvenile growth between Neandertals and anatomically modern humans. Neandertal brain growth appears to have proceeded at a more rapid pace than in modern humans, but did not reach completion any earlier (Ponce de León et al. 2008). A similar principle applies to body mass (Hou et al. 2008), and is also relevant to the Neandertal/modern human comparison. These findings suggest that Neandertal infants and juveniles would have had higher daily energy assimilation rates, and would have potentially taken longer to mature than modern human juveniles (Ponce de Leon et al. 2008). Increased daily energy needs, and a longer period of dependence on adults for sustenance, would have placed a considerable burden on Neandertal groups, one that may have been comparatively reduced in anatomically modern humans. In other words, every extra unit of energy modern humans could devote to reproduction may have been "worth" more in terms of how much offspring growth it could fund. Even if our results are interpreted very conservatively, an increase in population growth rate can follow from a relatively minor increase in energy allocated to reproduction (Ricklefs 1973; Sorensen and Leonard 2001). Such small energetic differences could have given modern humans a demographic advantage over Neandertals in periods of climatic crisis, that may have upset any established equilibrium between the two (Hublin 2000).

Since massive, more muscular bodies appear to have been part of the Neandertal adaptation to climate, lighter, less-muscular bodies in anatomically modern humans would have required alternative modes of adjustment to cold. Various lines of evidence provide support for the idea that modern humans were able to adapt to cold via behavioral rather than anatomical means, thereby allowing smaller body size and concomitantly lower adult energy needs. Given the preliminary nature of this study, however, we expect that future research could improve the quality of the energetic data, and thus the robustness of the comparison between anatomically modern humans and Neandertals. In particular, a more thorough evaluation of subsistence patterns in Neandertals and fossil modern humans, as compared to extant foraging groups, might provide more reliable physical activity level (PAL) values, thus enhancing the reliability of daily energy expenditure (DEE) estimates.

ACKNOWLEDGEMENTS

We thank Karen Steudel-Numbers and Cara Wall-Scheffler for inviting us to submit this paper, and we thank Margaret Schoeninger, Karen Rosenberg, Alyssa Crittenden, Josh Snodgrass, and Deb Olszewski for their comments. We also wish to acknowledge Maciej Henneberg and Chris Ruff for supplying fossil data. Climate data for the Late Pleistocene are from maps available on the OIS Stage 3 Project website. Climate data for living humans (for derivation the BMR equations) are from the online databases of the Data Support Section of the Scientific Computing Division, National Center for Atmospheric Research (supported by the National Science Foundation).

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