



Neandertal growth: What are the costs?



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ABSTRACT

Energetic approaches have been increasingly used to address key issues in Neandertal palaeoecology and palaeobiology. Previous research has focused exclusively on the energy requirements of adults and highlights the high energy demands of these individuals compared with modern humans. Less attention has been paid to the energy requirements of sub-adult Neandertals, even though this age group could provide clues for a better understanding of Neandertal life history. Accordingly, herein, we estimate the energy costs of maintenance and growth in Neandertal infants and children from one to six years of age and compare these costs with values for modern humans. Statural growth models for two modern human populations (Beasain and Evenki) and an average Neandertal model population are used to establish weight growth models. In turn, these models of body weight growth are used to estimate key components of energetic variables (basal metabolic rate, total energy expenditure, energy of growth and daily energy requirements). Between three and six years of age, Neandertal children have slightly lower basal and growth energy costs than do modern humans of the same age, due primarily to their smaller body mass and slower growth rates. The reduction in energy allocated to growth is likely the result of metabolic adaptations to other somatic factors and thermal stress. Data from contemporary human infants and children suggest that even mild cold stress increases non-shivering thermogenesis, thus elevating metabolic needs by 50% or more. These results suggest that thermal stress likely played a strong role in shaping the delayed developmental patterns and lower energy allocated to growth during early life in Neandertals relative to *Homo sapiens*.

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Introduction

The most obvious difference between the life history patterns of modern humans and those of other primates is the duration of the growth and developmental period (Leigh, 2001). Chimpanzees, as well as some other primates, pass through three differentiated stages (infancy, juvenescence, and adolescence) before reaching adulthood at the age of 13–15 years (Pusey, 1978; Goodall, 1986; Sugiyama, 2004; Hamada and Udono, 2006; Zihlman et al., 2007). In contrast, humans spend approximately 18–20 years in immaturity, a period that is divided into four stages (infancy, childhood, juvenescence, and adolescence) (Bogin, 1990; Bogin and Smith, 1996). A bioenergetic perspective, which considers the relative allocation of energy to basal maintenance, activity, growth, and

reproductive costs, can provide important insights into our peculiar ontogenetic cycle.

Energy balance has been studied in various hominin species (Leonard and Robertson, 1997; Aiello and Key, 2002; Aiello and Wells, 2002; Steudel-Numbers, 2006). *Homo neanderthalensis*, one of the best represented species in the hominin fossil record, has attracted the greatest attention from researchers. Previous studies have suggested high metabolic rates for adult Neandertals compared with the standards for modern human adults. Energy expenditure of adult Neandertals has been estimated through predictive equations relating basal metabolic rate, activity levels and body mass (Sorensen and Leonard, 2001; Churchill, 2006; Froehle and Churchill, 2009; Macdonald et al., 2009). The findings are the results of several factors, such as the estimated high body mass, the high activity levels assumed, and the impact of cold stress on thermoregulation. Approaches based on energy budget have been used to address key issues in Neandertal ecology and fitness, including thermoregulation and cold adaptation (Stegmann et al., 2002; Aiello and Wheeler, 2003; Churchill, 2006; Froehle and

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Churchill, 2009), locomotion (Weaver and Steudel-Numbers, 2005) and foraging efficiency (Sorensen and Leonard, 2001; Verpoorte, 2006). Different methods used to estimate total energy expenditure produce significantly different results for Neandertal adults. Sorensen and Leonard (2001) estimate total energy expenditure (TEE) using sex-specific mean Neandertal masses and World Health Organization (WHO) equations to predict basal metabolic rates (BMR) and eventually adjusting for the effects of cold climate on BMR. Other estimations are based on the observed caloric consumption of arctic foragers, while adjusting for the larger size of Neandertals (Stegmann et al., 2002), or on calculations of BMR based on skin surface area (Churchill, 2006). These studies produced TEE values for an average adult Neandertal living in cold conditions in the range between 3500 and 5000 kcal/day.

Previous research has focused on adult specimens. There have been no studies conducted to examine the energy costs among immature individuals with respect to basal metabolic rate (BMR), energy deposited during growth (E_d), total energy expenditure (TEE), and daily energy requirements (DER), although it is noted that only during early infancy do the energy costs of growth represent a sizable portion of the TEE (Butte et al., 1995). Several studies indicate that the BMR per unit body mass during growth differs from adult values and that the greater quantity of metabolically active organs in infants compared with children and adults contributes to their higher metabolic rates (Holliday et al., 1967).

Among human populations, not only do climatic factors exert an important influence on body mass, morphology, and proportions, but these relationships change in response to socioeconomic and ecological shifts (Bielski, 1986; Martorell and Habicht, 1986; Eveleth and Tanner, 1990; Katzmarzyk and Leonard, 1998). Comparative physiological data from around the world indicate that BMRs are higher in populations living in cold environments due to the adaptation necessary to increase metabolic heat production (FAO, 1957; Roberts, 1978; Leonard et al., 2002, 2005; Froehle, 2008). Compared with adults, infants and young children are at much greater metabolic risk of thermal stress because of their small total body masses, high surface area/weight ratios and higher thermoneutral zone: that is, the environment in which body temperature is maintained with the lowest energy expenditure and oxygen consumption (5–7 °C higher than in adults) (Frisancho, 1993; WHO, 1996; Leonard et al., 2002). Consequently, human infants display a broad array of physiological and morphological responses to combat thermal stress. The most notable of these is the presence of high levels of brown adipose tissue (BAT or brown fat), which contributes to substantial increases in metabolic rate due to non-shivering thermogenesis (Cannon and Nedergaard, 2004). As BAT is present in many mammals (Cannon and Nedergaard, 2004), it can be considered an ancient thermal adaptation that has been preserved in some primates such as *Macaca fuscata* and *Macaca mulatta* (Chaffee and Allen, 1973; Chaffee et al., 1975; Tokura et al., 1975, 1981) and also in humans. It would be reasonable to assume that metabolic plasticity, based on BAT metabolism, is a key primate cold adaptation. This physiological plasticity is greater during early ontogenesis when the offspring must face their new environment (Wells and Stock, 2007). Research by Adamsons et al. (1965) has shown that exposure of human infants to even mild cold stress results in a doubling of the resting metabolic rate due to non-shivering thermogenesis. It is further reasonable to assume that Neandertals had biological cold defences similar to those noted in modern humans and primates: that is, the maintenance of BAT into adulthood. Consequently, it may be assumed that such somatic factors may have played a particularly important role in shaping the developmental patterns and energy demands of Neandertal infants and children.

With respect to the role of body composition in metabolic responses to growth, we must be aware that changes in body composition at different ages may differ between Neandertals and *Homo sapiens*. Similarly, populations of colder climates tend to have lower levels of body fat for a given body mass index (i.e., North American Inuit) in contrast with tropically adapted populations (i.e., Australian Aborigines) (Leonard and Katzmarzyk, 2010). Such differences could emphasise the role of body mass and shape as well as the nutritional and climatic constraints necessary to provide an accurate picture of body composition. During the long occupation of Eurasia by Neandertals in the Late Pleistocene (van Andel and Tzedakis, 1996; van Andel and Davies, 2003), there were sustained periods of climatic cold (Aiello and Wheeler, 2003) as well as warmer periods (Finlayson and Carrion, 2007; Wales, 2012). However, during an enormous time span, Neandertals were under the selection pressure of confronting the thermal stress caused by low environmental temperatures, at least during the winter season (Stegmann et al., 2002). Even in the southern refugia, where the last Neandertal populations lived (Finlayson et al., 2006), winter temperatures were probably below 6 to 8 °C (Barron and Pollard, 2002). Several aspects of Neandertal body morphology (so-called hyper-arctic body form, Holliday, 1997) may have had developmental effects related to a highly active childhood spent in seasonal environments (Churchill, 1998, 2006). Taking into account their body shape and the notion that some Neandertal populations appear to have lived in similar climatic conditions to those faced by recent Arctic populations (Froehle and Churchill, 2009), circumpolar populations could be the best analogue for modelling the relationship between height and weight in Neandertals, assuming our lack of knowledge regarding their body composition.

According to the study of Martín-González et al. (2012), linear growth rates (cm/year) of Neandertal children (<6 years) were much slower than those of modern human children. Thus, the aim of the present study is to explore the energetic trade-offs and consequences of these different patterns of physical growth between Neandertals and modern humans. Our approach focuses on the differences in energetic costs between Neandertals and modern humans due to somatic factors and other external factors such as living in different environmental conditions. Possible dissimilarities due to other external factors and/or behavioural constraints, such as different activity levels or diets, are not considered herein.

Goikoetxea et al. (2012) first attempted to estimate Neandertal basal metabolic rate (BMR) and total energy expenditure (TEE) based on data of individuals between birth and five years of age collected from the literature. However, due to the uncertainty in the age estimations of these specimens (Martín-González et al., 2012), it was not possible to calculate weight gain (g/d), energy deposited during growth (E_d), or daily energy requirements (DER). In the present work, we overcome this problem by using a new approach, employing the linear growth model developed in Martín-González et al. (2012) for an average Neandertal individual from birth to six years old, constructed using primary data on long bone lengths, then converting it into a weight growth model. This conversion was performed using the height-weight relationship observed in contemporary human circumpolar populations. Daily energy costs for BMR, growth and activity are then estimated from the weight growth model and compared with those of recent circumpolar populations and a southern European reference population with complete longitudinal available data. We then estimate the energy costs associated with thermal stress to evaluate the influence of these costs on the energy budget. Because it is difficult to discriminate sex in young, immature skeletal remains, the models for growth in height and weight are built for a hypothetical average Neandertal individual, without considering differences related to sex. This approach is justified because the growth pattern in

modern children (CDC, 2002; Sobradillo et al., 2004; WHO, 2004; Ferrández, 2005) shows only small differences between boys and girls during these early years of life.

Materials and methods

Two recent populations, Beasain and Evenki, were selected for comparison with the average Neandertal growth model. The Beasain sample, representing a European population from a temperate environment, includes longitudinal data from infants and children born in the late 1990s and thereafter whose clinical records were housed in the Beasain Health Centre (Gipuzkoa, Spain). The height and weight measurements were collected regularly until the subjects were 12–14 years old. Although the age, height, and weight were monitored for 125 boys and 125 girls, only 212 individuals are included in the study because individuals with less than 14 measurements before the age of six years were excluded (see Martín-González et al., 2012). The Evenki sample, representing a cold-adapted population (Leonard et al., 1994), comprises cross-sectional height and weight data from 207 subjects (91 boys and 116 girls). Because we lack longitudinal data for the Neandertal sample and must make the growth models for the three samples comparable, the Beasain data were treated as cross-sectional by re-sampling them (see Martín-González et al., 2012). Moreover, we use a sample of six circumpolar populations to obtain a model to estimate weight from height in Neandertal infants and children (see below). This set includes Northwestern Alaskan Eskimos, Foxe Basin Eskimos, Norwegian Lapps, Finnish Lapps (Auger et al., 1980), Southwestern Alaskan Eskimos (Heller et al., 1967), and Evenki (Leonard et al., 1994), hereafter, the circumpolar set. The circumpolar set was selected to build the Neandertal height-weight model on the premise that Neandertals shared a similar body morphology with modern circumpolar groups, as claimed by several authors (Ruff et al., 1993; Holliday, 1997), particularly in circumpolar populations with notably heavy weight and height relationships (see Leonard et al., 1994; Shephard and Rode, 1996; Leonard et al., 2005).

Weight and weight gain estimations

To obtain a sub-adult average weight gain model from the average height growth model of Martín-González et al. (2012) (Fig. 1), we ascertained the relationship between height and weight for each of the three human samples (Beasain, Evenki, and Neandertals) by fitting an exponential model to estimate weight from height in each population. In the case of the two modern populations (Beasain and Evenki), raw height and weight data were used as inputs in the models. To estimate Neandertal mass, we regressed weight on height in the circumpolar set. Weight was transformed to natural logarithms and several linear and polynomial models were fitted for each sample, with weight as the dependent variable and stature as the independent variable. Eventually, the best model describing the height-weight relationship for each sample was selected after a regression analysis. The analyses were performed using MATLAB version 7.10.0.

To study the variability and reliability of our results, the 95% confidence interval (CI) for the Neandertal height-weight model based on the circumpolar set was computed and a sensitivity analysis was conducted. Variations in weight gain and in BMR based on the extreme values of the confidence interval for weight were also computed. In addition, we developed a sensitivity analysis to evaluate the effect of errors in the height estimates of Neandertals on our estimates of BMR, TEE and DER (see Appendix A, Supplementary Online Material (SOM) Table S1).

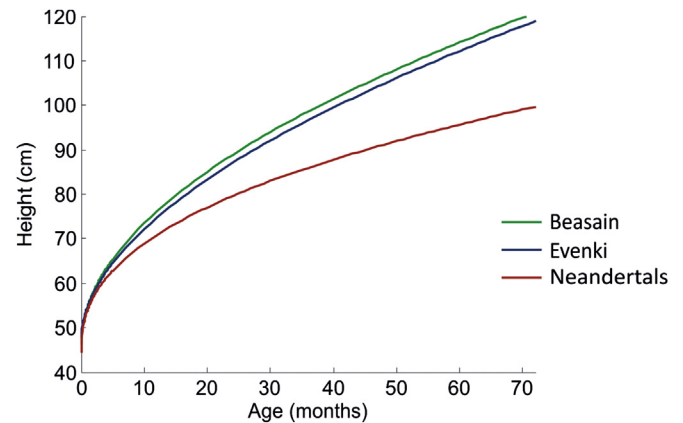


Figure 1. Average stature growth model for Beasain, Evenki, and Neandertal infants and children from birth to six years old (data from Martín-González et al., 2012). Note the slower height growth pattern of the Neandertal population compared with modern humans.

Estimation of metabolic rates

Basal metabolic rate and energy expenditure We estimated the BMR in the three human samples using the equations for birth to three years of age and for three to 10 years of age as reported in the FAO/WHO/UNU (1985) statement on human energy requirements (Table 1), as derived from Schofield (1985). The BMR was estimated using equations for each sex, and the mean was then calculated to obtain an average value for an individual of each population. We are aware of the limitations of the estimations derived from the Schofield equation (1985). Henry (2005) emphasises the underestimation of the BMR for the lower age groups (birth to three years) in both males and females, the underestimation of the BMR in males, and the overestimation of the BMR in females at three to 10 years of age. To evaluate the influence of this bias on our results, we compared the measured values of BMR in some recent populations obtained from the literature (SOM Table S2), with the estimations obtained for the same populations using the FAO/WHO/UNU (1985) equations.

Total energy expenditure (TEE) is estimated using two methods: multiplying the BMR by the physical activity level (TEE1) (Sorensen and Leonard, 2001; Churchill, 2006; Froehle and Churchill, 2009; Macdonald et al., 2009) and using equations that estimate this parameter from body mass (TEE2) (FAO/WHO/UNU, 2004). Consequently, the equation used to estimate TEE1 for infants and children is as follows:

$$\text{TEE1} = \text{BMR} \times \text{PAL} \quad (\text{FAO/WHO/UNU, 1985, 2004}) \quad (1)$$

In the second method, we used equations that estimate TEE2 directly from body mass in kg. There are two equations, one for each sex (FAO/WHO/UNU, 2004) for infants and for children older than one year:

$$\text{TEE2} = 263.4 + 65.3 W - 0.454 W^2 \quad \text{for females} \quad (2)$$

$$\text{TEE2} = 310.2 + 63.3 W - 0.263 W^2 \quad \text{for males} \quad (3)$$

Table 1

Equations used to estimate the basal metabolic rate (BMR) in Beasain, Evenki, and Neandertal infants and children (FAO/WHO/UNU, 1985).

Age	♀	♂
0–3 years	BMR = 61.0 W – 51	BMR = 60.9 W – 54
3–10 years	BMR = 22.5 W + 499	BMR = 22.7 W + 495

BMR in kcal/day; W (weight) in kg.

Table 2

Physical activity levels (PAL) for modern infants and children (male and female).

Age (months)	♀	♂	Source
12	1.29	1.31	Data for healthy children at Children's Nutrition Research Center, Houston (USA) (Butte et al., 2000)
24	1.40	1.40	Data for healthy children at Children's Nutrition Research Center, Houston (USA) (Butte et al., 2000)
24–36	1.40	1.45	FAO/WHO/UNU, 2004, from Torun et al., 1996; Torun, 2005
36–48	1.45	1.45	FAO/WHO/UNU, 2004, from Torun et al., 1996; Torun, 2005
48–60	1.50	1.50	FAO/WHO/UNU, 2004, from Torun et al., 1996; Torun, 2005
60–72	1.55	1.55	FAO/WHO/UNU, 2004, from Torun et al., 1996; Torun, 2005

where TEE2 is in kcal/day and W (weight) is in kg. In this case, both equations are used to obtain the TEE2 values, and an average value is then calculated.

Physical activity Energy expenditure for daily physical activity is expressed as a multiple of the BMR (see FAO/WHO/UNU, 1985, 2004). Thus, the physical activity level (PAL) index is calculated as $PAL = TEE/BMR$. Recent analyses of energy expenditure from studies using the doubly labelled water technique (Butte et al., 2000; Torun, 2005) provide a better picture of activity-related energy costs among children around the world and resulted in marked changes in the WHO's recommended energy (FAO/WHO/UNU, 2004). These data suggest that between-population variation in activity energy expenditure among infants and young children is less than that observed among adults. Thus, for all three of our samples, we estimated activity energy costs based on the age- and sex-specific PAL values from Butte et al. (2000) and Torun (2005) (see Table 2). As we modelled from one to six years of age, we used the average PAL factors for both sexes for those ages (Table 2).

Growth The energy cost of growth is related to the nature of weight gain during growth. In infancy, weight gain is 40% fat, 10% protein and 50% water (Holliday, 1978). The energy needs for growth have two different but related components: the energy used to synthesise new tissues in anabolic processes (as part of the BMR and, consequently, included in the TEE calculations) and the energy deposited in those tissues as part of fat and protein catabolism (FAO/WHO/UNU, 2004). This second component is called E_d and is calculated by multiplying the weight gain (g/d) by the energy accrued during normal growth (FAO/WHO/UNU, 2004). The daily weight gain is obtained by subtracting the estimated weight at age $t - 1$ from the estimated weight at age t and dividing it by 365 days (one year) for ages of one to six years. The value of energy accrued, defined as the energy needed to gain one gram of weight, is obtained from data published in the FAO/WHO/UNU report for normal growth in modern children (FAO/WHO/UNU, 2004). That value is determined to be 2.0 kcal/g for females and males older than one year. As the value of energy accrued has not been measured in the Evenki and Beasain populations, we assume that this value is the same in the three samples (Evenki, Beasain and Neandertals). Given that our null

hypothesis is that the three samples have the same energy requirements, this assumption favours the null hypothesis.

The daily energy requirements (DERs) can be defined as the sum of the metabolic costs associated with maintenance (TEE) and those associated with production (growth, fat storage) and reproduction (Leonard and Ulijaszek, 2002; Snodgrass and Leonard, 2009). The DER is equal to the TEE in adult men and non-pregnant and non-lactating women; however, in the case of pregnant and lactating women and in growing infants and children, the energy required for those processes must be added to the TEE to estimate the DER (FAO/WHO/UNU, 2004). Consequently, the daily energy requirements of infants and children are estimated as follows:

$$DER = TEE + E_d \text{ (FAO/WHO/UNU, 2004)} \quad (4)$$

We calculated two different DER values: DER1 based on TEE1 and DER2 based on TEE2. In the cases in which equations for each sex can be used to estimate metabolic rates (BMR, TEE, and DER), we used both and then calculated the mean value because these rates do not show large differences between modern boys and girls during their early years (FAO/WHO/UNU, 2004).

Thermal stress Human infants and young children are particularly vulnerable to the effects of thermal stress as neonatal cold injury represents an important cause of morbidity and mortality among populations living in high latitude/altitude regions (WHO, 1997; Mance, 2008). Consequently, in response to cold challenges, human infants show a tremendous capacity to increase metabolic heat production. As shown in Table 3, early studies by Adamsons et al. (1965) and Dawkins and Scopes (1965) found that even mild cold stress (i.e., temperatures of 25–26 °C) resulted in metabolic increases of 71%–121% above resting levels. The ability to increase metabolic rate in response to cold is reduced with age, as body mass increases and levels of BAT decrease (Frisancho, 1993; Cannon and Nedergaard, 2004; Kingma et al., 2012). Nonetheless, even by late childhood (ages eight to 12 years), mild to moderate thermal stress produced metabolic increases of 11%–56% (see Table 3). As Neandertals lived in a broad range of environments during their long occupation of Europe in the Late Pleistocene, they sustained periods of intense climatic cold and it is likely that Neandertal children showed

Table 3

Comparative data on changes in metabolic rate (kcal/kg/day) in response to thermal stress among infants and children.

Group/Reference	Metabolic rate (kcal/kg/day)				
	Sex	n	Thermoneutral environment	Cold environment	%Change*
Newborn infants (Adamsons et al., 1965)	M/F	50	32.0	70.2 (at 25 °C)	+120
Newborn infants (Dawkins and Scopes, 1965)	M/F	10	33.4	57.0 (at 25 °C)	+71
Boys, 8 years (Inoue et al., 1996)	M	11	41.7	46.5 (at 15 °C)	+11
Boys, 10–13 years (Wagner et al., 1974)	M	9	39.8	44.9 (at 16–17 °C)	+13
Boys, 11–12 years (Smolander et al., 1992)	M	8	36.9	57.7 (at 5 °C)	+56

*All changes are significant at $P < 0.01$.

Note that the thermoneutral zone for infants and children is established in the interval from 36.5 °C to 37.5 °C (normothermia) (WHO, 1996; Mance, 2008). The cold environment is indicated in the data for the different group references. The thermoneutral zone (TNZ) is the environment in which body temperature is maintained with the lowest expenditure of energy and oxygen consumption.

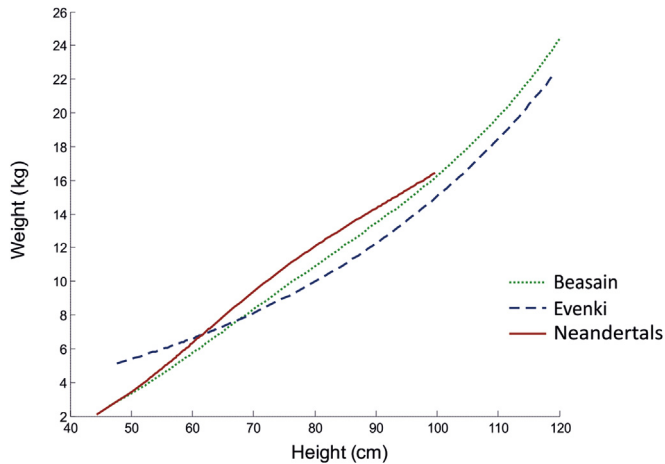


Figure 2. Comparison of the models for body weight and height fitted to the three human samples.

increased metabolic heat production in response to thermal stress. Accordingly, we introduce a highly conservative thermal correction by increasing the value of the BMR by 20% for Neandertal and Evenki infants (<2 years) and by 10% for Neandertal and Evenki children two to six years of age.

Results

Weight and weight gain estimations

The exponential models relating height and weight in the three human samples (Fig. 2) show unreliable results for individuals younger than one year old due to the scarcity or lack of data for this age interval. Consequently, the models produce large estimation errors for this period (SOM Figures S1, S2, S3), and are not suitable for estimating the weight of individuals from birth to one year old. In addition, the data structure is different for the Evenki and the other two human samples with regard to the smaller statures (younger individuals) because data on individuals shorter than 57 cm are not available for the Evenki population. Thus, the best fit for the circumpolar set and the Beasain sample is obtained with 4th-degree polynomials, while a linear model provides the best fit for the Evenki sample (Table 4 and SOM Figure S1, S2 and S3). In summary, we adopt a conservative position by assuming that our weight estimations are not reliable for individuals younger than one year old. We have found that height explains 98.2% of the variation in weight for the Beasain population, 89.4% for the Evenki population and 98.4% for the circumpolar set.

A sensitivity analysis was conducted to evaluate the effect of error in the Neandertal height estimation on weight, weight gain and BMR estimates. An error of $\pm 5\%$ in height estimation produces deviations in BMR estimates between 3% and 10% (SOM Table S1). Thus, an acceptable sensitivity to the initial conditions (errors in

Table 5

Uncertainty in the predictions of weight, weight gain, and basal metabolic rate (BMR) for Neandertal infants and children between one and six years old.

Age (Months)	Weight ^a (kg)	Weight gain (g/d)	BMR (kcal/d)
12–24	11.92 (11.62–12.23)	6.22 (6.35–6.49)	655.81 (674.11–692.87)
24–36	13.41 (13.10–13.72)	4.04 (4.07–4.09)	745.74 (764.60–783.90)
36–48	14.54 (14.23–14.85)	3.10 (3.10–3.10)	818.52 (825.52–832.67)
48–60	15.50 (15.18–15.82)	2.62 (2.63–2.64)	840.11 (847.21–854.44)
60–72	16.37 (16.05–16.70)	2.37 (2.40–2.43)	859.69 (867.03–874.52)

The 95% confidence interval for weight (in parentheses) is used to obtain uncertainty intervals for weight gain and BMR estimations (see text).

^a Weight values correspond to the one at the end of each interval.

height estimation) is observed along the entire process of the estimation. In addition, the 95% confidence intervals for the Neandertal height-weight model and their influence on the weight gain and BMR estimates are presented in Table 5. According to these results, the uncertainty in the estimation of the BMR due to the error in the estimation of Neandertal weight is less than 5% (Table 5). In summary, although our method involves several sequential estimations, the sensitivity analyses indicate that errors are moderately amplified throughout the process.

The estimated weights (weight at the end of each interval) of the Beasain, Evenki, and Neandertal samples (Table 6) are compared in Fig. 3. The Beasain average individual is heavier compared with the other two groups during the entire period from one to six years of age. In contrast, while the Evenkis and Neandertals appear to be similar in weight during the 12–24 month interval, Neandertals exhibit lower weights than their Evenki peers after that age interval. Fig. 4 shows weight gain in the Beasain, Evenki, and Neandertal groups. Weight gain is estimated as fairly stable during the entire period for the two modern groups (Table 6). Conversely, in Neandertals, the highest values are attributed to the youngest individuals, and these values then decrease with age (Table 6).

Estimations of metabolic rates

When the BMR estimated for Neandertals older than two years is compared with the BMR for the Beasain and Evenki individuals (Table 6), both modern human groups appear to have slightly higher BMRs than the Neandertals, with the differences increasing as the individuals age (Fig. 5). In the Evenki and Beasain samples, TEE1 and TEE2 show similar values at all age intervals (Table 6). In contrast, TEE1 produces higher estimates than TEE2 for Neandertals from 48 months onward (Table 6 and Fig. 6). From two years to six years, both TEE1 and TEE2 values are higher in the Beasain and Evenki individuals than in the Neandertals (Fig. 6A and B). Definitively, the differences are greater when TEE is estimated using the FAO/WHO/UNU (2004) equations (TEE2).

The estimated energy deposited during growth (E_d) values is presented in Table 6 and Fig. 7. The two modern human samples demonstrate similar and fairly constant E_d values during the entire period, while the values for Neandertals are similar to values for

Table 4

Regression equations relating height and weight in modern humans. The equation for six circumpolar recent populations was used to fit the Neandertal model (see text).

Population	Equation	R-square	SSE	Adjusted R-square	RMSE
Beasain (Temperate)	$\ln(W) = -5.237e - 8 * h^4 + 2.397e - 5 * h^3 - 0.004023 * h^2 + 0.3139 * h - 7.104$	0.982	38.85	0.982	0.099
Evenki (Circumpolar)	$\ln(W) = 0.02054 * h + 0.6567$	0.894	2228.00	0.893	0.104
Circumpolar Set	$\ln(W) = -5.933e - 8 * h^4 + 2.845e - 5 * h^3 - 0.004939 * h^2 + 0.3857 * h - 8.892$	0.984	2043.00	0.984	0.086

W = weight (kg) and H = height (cm).

SSE = Sum of squares for error.

RMSE = Root mean squared error.

Table 6

Estimates of weight, weight gain, basal metabolic rate (BMR), total energy expenditure (TEE), energy deposited during growth (E_d), and daily energy requirements (DER) for Beasain, Evenki and Neandertal infants and children between one and six years old.

Sample	Age (Months)	Weight ^a (kg)	Weight gain (g/d)	BMR (kcal/d)	TEE1 ^b (kcal/d)	TEE2 ^c (kcal/d)	E_d (kcal/d)	DER1 ^d (kcal/d)	DER2 ^e (kcal/d)
Beasain	12–24	13.14	8.81	749	1067	1070	18	1084	1088
	24–36	15.84	7.38	913	1301	1215	15	1315	1230
	36–48	18.55	7.44	916	1329	1356	15	1343	1371
	48–60	21.50	8.08	983	1474	1504	16	1490	1520
	60–72	24.77	8.97	1057	1638	1660	18	1656	1678
Evenki	12–24	11.52	7.04	650	926	980	14	940	994
	24–36	14.40	6.90	803	1145	1119	14	1159	1133
	36–48	16.63	7.08	873	1266	1257	14	1280	1271
	48–60	19.33	7.39	934	1401	1396	15	1415	1410
	60–72	22.17	7.78	998	1547	1536	16	1562	1551
Neandertals	12–24	11.92	6.35	674	957	1002	13	970	1015
	24–36	13.41	4.07	765	1086	1085	8	1094	1093
	36–48	14.54	3.10	826	1197	1146	6	1203	1152
	48–60	15.50	2.63	847	1271	1197	5	1276	1203
	60–72	16.37	2.40	867	1344	1243	5	1349	1248

^a The weight values correspond to the end of each interval.

^b TEE1 was calculated as $BMR \times PAL$.

^c TEE2 was calculated using the equations from [FAO/WHO/UNU \(2004\)](#).

^d DER1 was calculated as $TEE1 + E_d$.

^e DER2 was calculated as $TEE2 + E_d$.

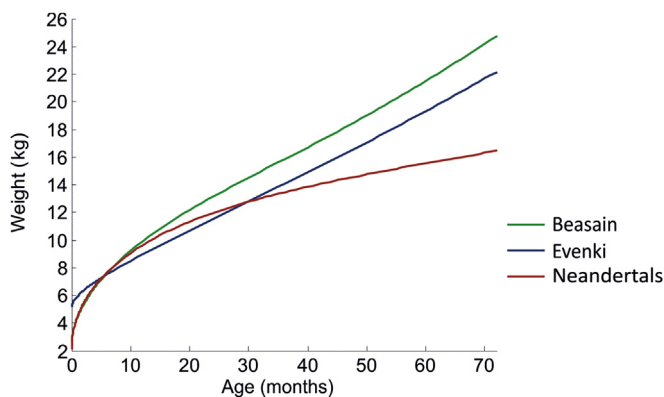


Figure 3. Average weight growth model for Beasain, Evenki, and Neandertal infants and children from birth to six years of age.

youngest modern humans and become markedly lower for the oldest individuals. The estimated daily energy requirements for the three groups are shown in [Table 6](#) and [Fig. 8A and B](#). From the age of 12–24 months until the age of 60–72 months, Beasain and Evenki

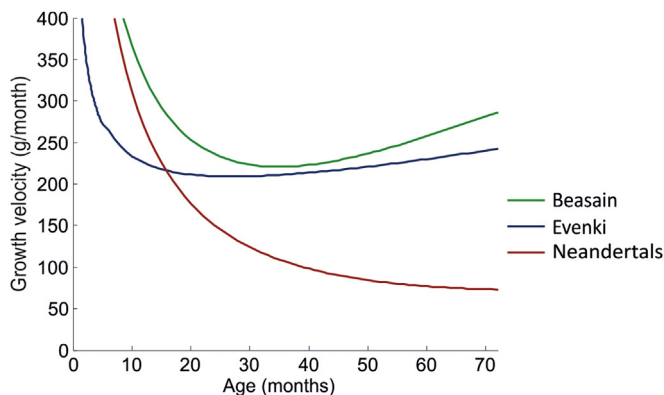


Figure 4. Mean weight gain (g/month) for Beasain, Evenki, and Neandertal infants and children from one to six years of age.

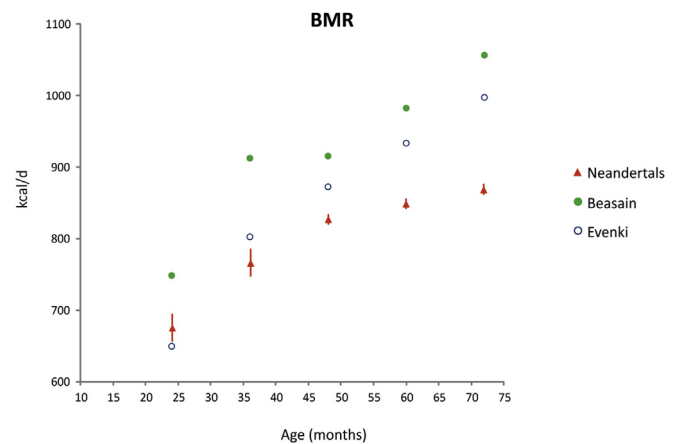


Figure 5. Basal metabolic rate (BMR) values for Beasain, Evenki, and Neandertals.

infants and children exhibit higher DER1 and DER2 values than Neandertals ([Table 6](#)), with the difference increasing as the individuals age, although Evenkis show slightly lower values than Beasain individuals during the entire period. The energetic pattern resulting from the application of the thermal correction in the BMR for the Evenki and Neandertal populations is presented in [Fig. 9](#). Both modern human groups, the Evenki and Beasain populations (the latter without thermic correction), appear to have slightly higher BMRs than Neandertals, with the differences becoming larger as the individuals age from 24 months onward.

Discussion

Reliability of the estimations

We are aware of the limitations of the approach presented herein. Some shortcomings regarding the study of past populations deserve comment. First, it has been suggested that the comparison of growth curves between recent human populations and archaeological fossil populations is awkward ([Wood et al., 1992](#); [Humphrey, 2003](#); [Vercellotti et al., 2014](#); but see; [Stringer et al., 1990](#)). The

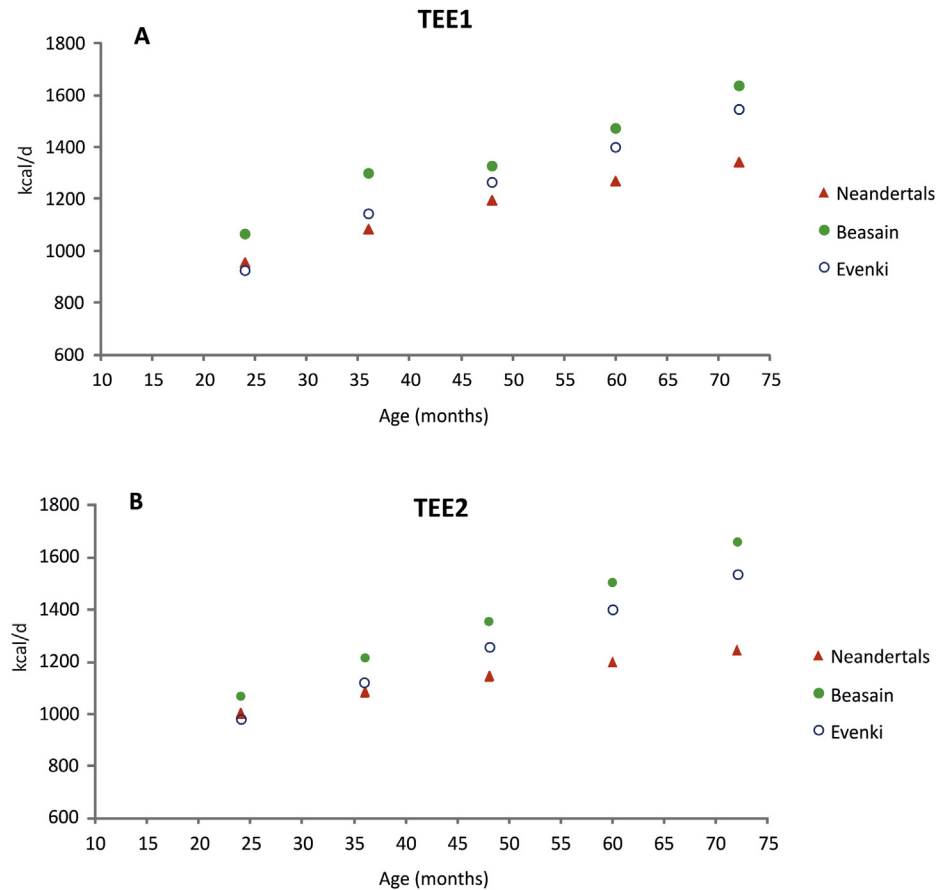


Figure 6. Total energy expenditure (TEE) values for Beasain, Evenki, and Neandertals. (A) TEE calculated using the BMR*PAL equation (TEE1) and (B) TEE calculated using the FAO/WHO/UNU (2004) equations (TEE2).

methodological problems that make this comparison difficult are related to the small sample size of the fossil populations, the bias regarding the age of the individuals, and the inaccuracy of age, height, and weight estimations. Indeed, the inaccuracy of age and height estimations is a methodological constraint addressed by Martín-González et al. (2012) when computing their Neandertal height growth model. Accordingly, they selected the combination of age and height for each individual that favoured the null hypothesis that Neandertals and modern humans share the same growth model. With respect to sample size, the sample size used to

create the Neandertal growth model in Martín-González et al. (2012) was small (10 specimens, Table 3:142), but it was reasonably distributed along the birth to six years interval, and our comparisons are based on average height and weight growth models that provide continuous data.

The approach presented herein is based on a number of sequential estimates of metabolic variables. Each of these estimates has its own error and uncertainty, which is transmitted, and perhaps amplified, in the subsequent estimation steps. Therefore, it is necessary to evaluate the uncertainty in the estimates of the

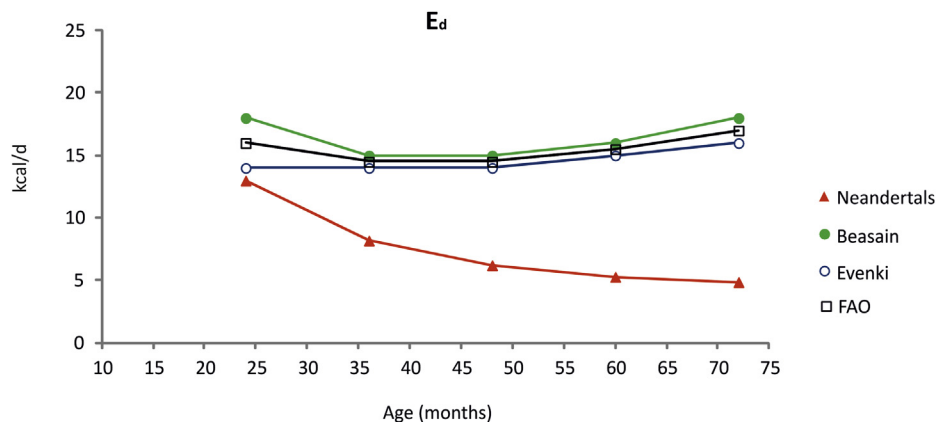


Figure 7. Energy deposited during growth (E_d) values for Beasain, Evenki, and Neandertals and FAO/WHO/UNU (2004) data.

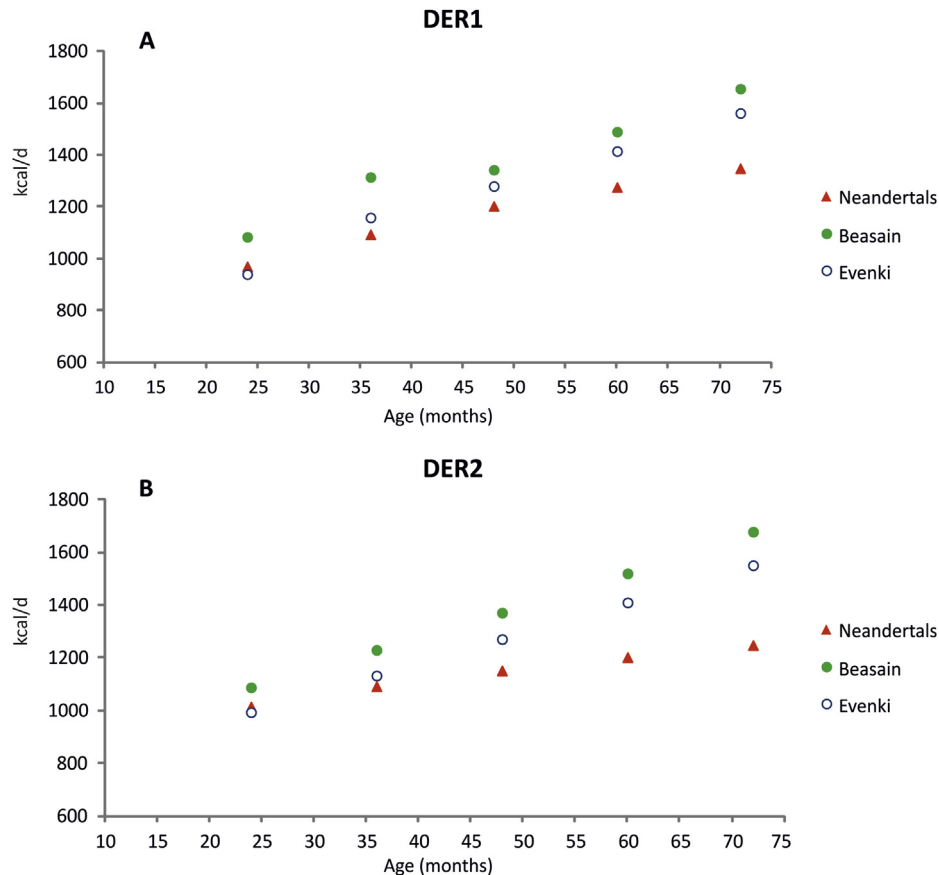


Figure 8. Daily energy requirements (DER) for Beasain, Evenki, and Neandertals. (A) DER1 using TEE1 and (B) DER2 using TEE2.

target variables and compare the uncertainty to the amplitude of the differences among the three human samples. With respect to the BMR estimations, there are two possible sources of error: deviations in height and weight estimates and an estimating error associated with the FAO/WHO/UNU equations. With respect to the first source, the sensitivity analysis indicates that a deviation of $\pm 5\%$

in height estimate produces a moderate variation in the BMR estimate (3%–10%). Moreover, when a 95% confidence interval for the weight estimate is taken into account, the effect on the BMR estimate is less than 5%. Such uncertainty is relatively low when compared to the amplitude of differences between Neandertals and modern humans, which is in the range of 4%–22%. The reliability of the FAO/WHO/UNU equations has been questioned by Henry (2005), who recommends the use of an alternative set known as the Oxford equations. We tested the reliability of the FAO/WHO/UNU equations using data obtained from the literature on BMR and weight as measured in certain recent infant and children populations (SOM Table S2). The FAO/WHO/UNU equations underestimate the BMR in the age interval considered herein by 13%, on average, in comparison to the measured values. Thus, our estimates of the BMR for Neandertals and modern humans likely underestimate the actual values. However, a comparison of the BMR estimated values among these three samples is justified as they have been computed using the same methodology.

The two methods used to estimate TEE have different sources of error. Both methods are affected by errors in Neandertal height and weight estimates similar to the way in which BMR is affected. Specifically, the error in TEE1 is determined by errors in the estimate of the BMR, as it is the result of $TEE1 = BMR \times PAL$. Moreover, TEE2 is also affected by the error associated with the FAO/WHO/UNU, 2004 equation. The reliability of the estimations provided by this equation has been tested by comparing the estimations with measured values of TEE in recent populations (SOM Table S3). This comparison indicates small differences (approximately 1%) between measured and estimated values when using this equation. The differences between the values obtained using the TEE1 and

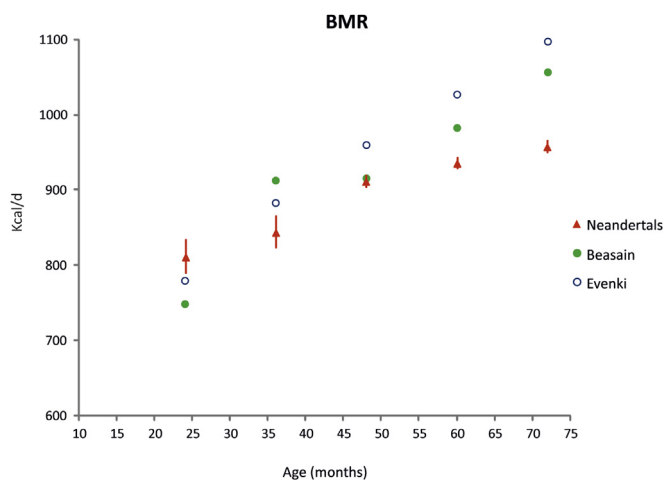


Figure 9. Basal metabolic rates (BMRs) for Beasain, Evenki, and Neandertals after applying the thermal correction in the rates for Neandertals and Evenki, thus increasing the BMR values for infants (<2 years) by 20% and by 10% for children two to six years of age.

TEE2 equations ($TEE = BMR \times PAL$ or [FAO/WHO/UNU, 2004](#), respectively) could be partly because TEE1 does not include the effect of thermoregulation or the thermic effect of food and partly because the values of PAL used herein underestimate the actual PAL values for infants younger than 24 months ([Table 2](#)). Interestingly, TEE2 produces larger differences between Neandertals and modern humans than TEE1.

Other factors influencing energy requirements

The results obtained in this study suggest that the daily energy requirements of Neandertals were lower than those of modern European humans (Beasain sample) between the ages of one to six years. Regarding the Evenki sample, these differences are emphasised in individuals older than two years of age until the end of the interval at six years. While the variations are slight at the beginning of the period, they are markedly different at the end of the interval ([Fig. 8A and B](#)), even when thermal correction was applied to BMR ([Fig. 9](#)). The relatively low BMRs for the Evenki children are largely the product of their small size, rather than their low mass-specific metabolic rate. [Leonard et al. \(1994\)](#) suggested that the short stature of native Siberians is a function of their high activity and metabolic rates on their dependence to acclimatise to the colder environments.

These results with respect to the energetics of Neandertal children are consistent with the distinct evolutionary developmental patterns of Neandertals and modern humans or, at least, they are evidence of the modularity of development in body systems as recently proposed ([Green et al., 2010](#); [Smith et al., 2010](#); [Gunz et al., 2010, 2012](#); [Martín-González et al., 2012](#); [Gokhman et al., 2014](#)). Furthermore, dissociations among dental development, somatic growth, and life-history variables are present in Neandertals. Thus, the faster growth rate proposed for Neandertals may be restricted to the teeth or the cranium and thus may not be applicable to the entire body ([Guatelli-Steinberg, 2009](#)). Consequently, the slow linear growth of Neandertals might be an adaptation to allow for faster growth of the brain. Nevertheless, several factors (brain growth, body composition and diet) that could affect metabolic rates (BMR, TEE, and DER) have not been taken into account in our calculations. The positive correlation between BMR and brain size in primates is well known, as is the potential trade-off between growth and the metabolic budget ([Navarrete et al., 2011](#)). Based on works by Ponce de León and colleagues (2008) and [Gunz et al. \(2010, 2012\)](#), Neandertal infants had cranial capacities at birth similar to those of modern human infants (≈ 400 cc) (this value is also obtained if the birth cranial capacity for Neandertals is estimated using the equation of [DeSilva and Lesnik, 2008](#)) even when taking into account the fetopelvic dilemma, which maintains that the postnatal brain growth rate is close to the prenatal growth rate ([Rosenberg, 1988](#); [Friedlander and Jordan, 1994](#); [Weaver and Hublin, 2009](#), but see; [Dunsworth et al., 2012](#)). This is notable because the cranial capacities of adult Neandertals (1200 cc to 1626 cc) are, on average, larger than those of modern humans. These findings indicate that the rates of brain growth in early life among Neandertals may have been faster than those observed in modern humans because Neandertals achieved more postnatal brain growth over a shorter period of development ([Dean et al., 1986](#); [Trinkaus, 1986](#); [Trinkaus and Tompkins, 1990](#); [Ramírez Rozzi and Bermúdez de Castro, 2004](#); [Smith et al., 2007](#); [Ponce de León et al., 2008](#); [Smith et al., 2010](#); [Thompson and Nelson, 2011](#)) or, at least, within the same amount of time ([Kondo and Ishida, 2003](#); [Guatelli-Steinberg et al., 2005, 2007a,b](#)). If the analyses of Ponce de León and colleagues (2008) are correct and Neandertals

had higher rates of brain growth than modern humans during early infancy, this would likely increase their BMR values postnatally.

Another factor not included in our estimations is the role that body composition plays in bioenergetics. It is known that body composition changes with age ([Wilmer, 1940](#); [Holliday, 1978](#); [Forbes, 1987](#); [Shephard, 1991](#)) and that different tissues have different effects on metabolic rates (particularly on BMR) ([Holliday, 1978](#)). Furthermore, even though the brain is the most expensive tissue during early life, the proportion of lean body mass to fat body mass is extremely important in metabolic processes. Despite the impossibility of making accurate estimations of the body composition of fossil individuals, the analysis of fossil bones could lead to the proposal of rough hypotheses regarding muscle mass in Neandertals. Some researchers have highlighted the greater muscle masses of adult Neandertals in comparison with average modern humans ([Ruff et al., 1994](#); [Aiello and Wheeler, 2003](#); [Churchill, 2006](#); [Stock, 2006](#)). There could be a relationship between muscle mass and the huge robusticity evident in postcranial skeletons. The different distribution of skeletal robusticity in the limbs is influenced by bone strength and mass and is also related to biomechanics, behaviour, genetics and climatic factors ([Stock, 2006](#)). However, few data on robusticity and bone strength during growth in immature Neandertal individuals are available. Previous research (see [Ruff et al., 1994](#); [Cowgill, 2010](#)) suggests that though postcranial robusticity was slightly higher in immature Neandertals than in average modern humans, it was within the range of values observed in recent children.

Taking into account the key role played by adiposity in postnatal metabolism as a factor in development ([Wells, 2010](#)), it may be assumed that an important amount of adipose tissue was also present in immature Neandertals. As previously mentioned, infants are more vulnerable to cold stress than adults because of their small mass and higher thermoneutral temperatures ([Frisancho, 1993](#)). Furthermore, it is widely recognised that BAT plays an important role in thermoregulation. To combat cold stress, human infants are born with significant amounts of BAT deposited at the nape of the neck and between the scapulae. In response to cold, BAT is activated by the secretion of noradrenaline, resulting in increased cellular heat production ([Ravussin and Galgani, 2011](#)). Research on the metabolic responses of infants has shown that BAT is activated with the exposure to even mild-moderate cold stress (15°C ; 59°F), resulting in more than a doubling of the metabolic rate ([Adamsons et al., 1965](#)). This thermal adaptation is conserved in some primates, such as *M. fuscatta* and *M. mulatta*, during cold exposure ([Chaffee et al., 1975](#); [Tokura et al., 1975](#)). The role of BAT, however, is usually neglected in the works on Neandertal bioenergetics ([Aiello and Wheeler, 2003](#); [Churchill, 2006](#); [Froehle and Churchill, 2009](#); [Macdonald et al., 2009](#); [Snodgrass and Leonard, 2009](#); however, see; [Steegmann et al., 2002](#)). Previously, it has been assumed that BAT is lost after infancy and that it has no influence on thermoregulation and energy balance in later childhood and adulthood. However, over the last five years, studies using positron emission tomography (PET) have documented significant levels of active BAT in healthy adults ([Nedergaard et al., 2007](#); [van Marken Lichtenbelt et al., 2009](#); [Virtanen et al., 2009](#)), thus confirming insights from earlier anatomical studies ([Lean et al., 1986](#); [Lean, 1989](#)). It is reasonable to assume that BAT responses to thermal stress could be conserved in hominins as a paedomorphic retention into adulthood. For Neandertal infants and children inhabiting cold regions, the importance of BAT for raising metabolic heat production would likely represent an advantage in relation to climate. Taking into account the effects that brain growth rate, BAT and diet thermogenesis might have on metabolism, we are aware that our estimations of the metabolic rates of Neandertal infants and children

might be underestimated. It may be argued that, if we take these internal and external constraints into consideration, the daily energy requirements of immature Neandertals would be similar to, or slightly higher than, those of their modern human counterparts.

The high metabolic rates estimated for adult Neandertals have been compared with modern human adult standards (Sorensen and Leonard, 2001; Steegmann et al., 2002; Churchill, 2006; Froehle and Churchill, 2009; Macdonald et al., 2009; Snodgrass and Leonard, 2009). Despite the fact that these estimated values for the daily energy requirements are within the range observed among modern human populations, they are, in some cases, almost 2000 kcal/day higher than those observed for a typical, healthy adult with moderate activity levels (FAO/WHO/UNU, 2004; IOM, 2005). Some important factors could contribute to the increase in these energy requirements in Neandertals, the most important being the estimated large body mass, high skeletal robusticity, the attributed huge physical activity level, the exposure to climate stress in groups inhabiting colder areas, and the protein-rich diet (Snodgrass and Leonard, 2009). In contrast to adults, our results show that Neandertal infants and children three to six years of age are estimated to have had lower daily energy requirements than their modern human counterparts. Therefore, one question arises: when did the shift from lower to higher metabolic costs occur during Neandertal ontogeny? We may speculate that this change did not occur before immature Neandertals attained an almost adult body mass and adult proportions. According to Nelson and Thompson (2002), bone robusticity increased dramatically at the time that Neandertals attained their final body mass, which implies that Neandertals put on weight very quickly after completing their linear growth. While this period of weight gain would be a very stressful stage, it would occur at an age at which the individual was self-sufficient with respect to food resource management.

The distinct energy demands of Neandertal infants and children, along with their slower linear growth velocities (Martín-González et al., 2012), also have important implications for evolutionary life history trade-offs and for the nutritional and reproductive biology of Neandertal mothers. If we assume that our results are correct, Neandertal mothers appear to have borne infants and children that might have had slightly lower daily energy demands from the ages of three to six years than modern humans. Nevertheless, if brain growth rate was higher in Neandertals (Zollikofer and Ponce de León, 2013) or if Neandertals inhabiting colder regions had higher BMRs and/or increased activity of BAT, then we might expect the energy demands of Neandertal infants and children to be higher than those reported herein. Finally, it is known that cold-acclimated animals show retardation in increased skeletal growth, weight gain, and body length compared with heat-acclimated animals (Chaffee and Allen, 1973) and that these significant changes in skeletal metabolism (loss of bone calcium) are related to significant endocrine changes (Cohn et al., 1961). Some metabolic adaptations due to somatic factors and thermal stress might have markedly increased the metabolic rates in Neandertals and likely reduced the energy available to them for growth in stature and mass.

Conclusions

The energy costs of maintenance and growth in Neandertal infants and children from one to six years of age have been estimated and compared with the values for modern humans. Our results suggest that Neandertals differ from modern humans in their daily energy requirements during infancy and childhood. Between three and six years of age, Neandertal children had lower basal and growth energy costs than modern humans of the same age, mainly due to their smaller body mass and slower growth rates. The

reduction in energy allocated to growth is likely the result of metabolic adaptations to other somatic factors and thermal stress. Comparative data from contemporary human infants and children show that even mild cold stress may elevate metabolic needs by 50% or more. These results suggest that thermal stress likely played a strong role in shaping the delayed developmental patterns and lower energy allocated to growth during early life in Neandertals relative to *H. sapiens*.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jhevol.2014.09.003>

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