Neandertal Energetics Revisited:
Insights Into Population Dynamics and Life History Evolution

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ABSTRACT

Paleoanthropologists are increasingly utilizing energetic models to provide insights into hominin ecology and evolution. Energy dynamics represent a key interface between an organism and its environment; how energy is extracted from limited resources and allocated to various somatic functions has consequences for survival and reproduction. Within the past few years, several teams of researchers have reconstructed Neandertal energy budgets to address issues such as foraging efficiency, population density and spatial utilization, cold tolerance, and the replacement of Neandertals by modern humans. In the present paper, we systematically reexamine Neandertal energy expenditure and intake through the lens of recent developments in contemporary human biology and nutritional science. We estimate Neandertal energy expenditure and dietary needs by using published sex-specific body mass estimates coupled with physiological information on contemporary high-latitude populations. Comparative data suggest that four important factors contribute to high energy requirements in Neandertals: 1) large body mass and high levels of muscularity; 2) exposure to severe cold stress; 3) consumption of high meat, high protein diets; and, 4) high levels of physical activity. Contemporary northern populations have systematically elevated basal metabolic rates (BMRs) compared to lower latitude groups, an apparent adaptation to chronic and severe cold stress. In addition, field and laboratory studies suggest high dietary protein is associated with substantially increased metabolic heat production. Further, activity patterns among contemporary northern populations and Neandertal post-cranial morphology suggest relatively high physical activity levels. Thus, multiple lines of evidence point to extremely high energy requirements and intakes among Neandertals. The high turnover of metabolic energy in Neandertals likely had important implications for key aspects of life history, such as physical growth rates, age at reproductive maturity, and lifespan. Consequently, a detailed exploration of Neandertal energetics provides insights into hominin population dynamics during the Middle to Upper Paleolithic transition.

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INTRODUCTION

The evolutionary fate of Neandertals is one of the most intensely debated topics in paleoanthropology. Despite a rich fossil record that includes thousands of specimens and dozens of well-documented archaeological sites from across western Eurasia, no consensus presently exists on the cause of Neandertal extinction. In fact, it has been suggested by several authorities (e.g., Harvati and Harrison 2008) that beyond accumulating new fossil and archaeological materials, novel techniques and new theoretical perspectives on existing fossil, archaeological, and genetic data will be required to settle the debate. Over the past several years, paleoanthropologists have begun to utilize an energetics approach to address key issues in Neandertal ecology and evolution, including foraging and locomotor efficiency (Sorensen and Leonard 2001; Weaver and Steudel-Numbers 2005), cold tolerance (Aiello and Wheeler 2003; Churchill 2008; Steegmann et al. 2002), and landscape use (Anwar et al. 2007). An energetics approach can provide important insights into human evolution, and has been increasingly utilized to study topics such as the origin of bipedalism (e.g., Leonard and Robertson 1995; Rodman and McHenry 1980; Sockol et al. 2007; Steudel-Numbers and Tilkens 2004), encephalization in *Homo* (e.g., Aiello and Wheeler 1995; Leonard et al. 2003; Leonard and Robertson 1994; Snodgrass et al. 2009), human nutritional evolution (Leonard 2002), and body size evolution (Aiello and Wells 2002; Leonard and Robertson 1997).

The basis for an energetics approach comes from the central position that energy occupies between an organism and its environment. As energy is a fundamental limiting resource in humans and other mammals, how energy is ex-

Total Energy Expenditure (TEE)

Maintenance

Basal Metabolic Rate (BMR)
Physical Activity
Thermoregulation
Thermic Effect of Food

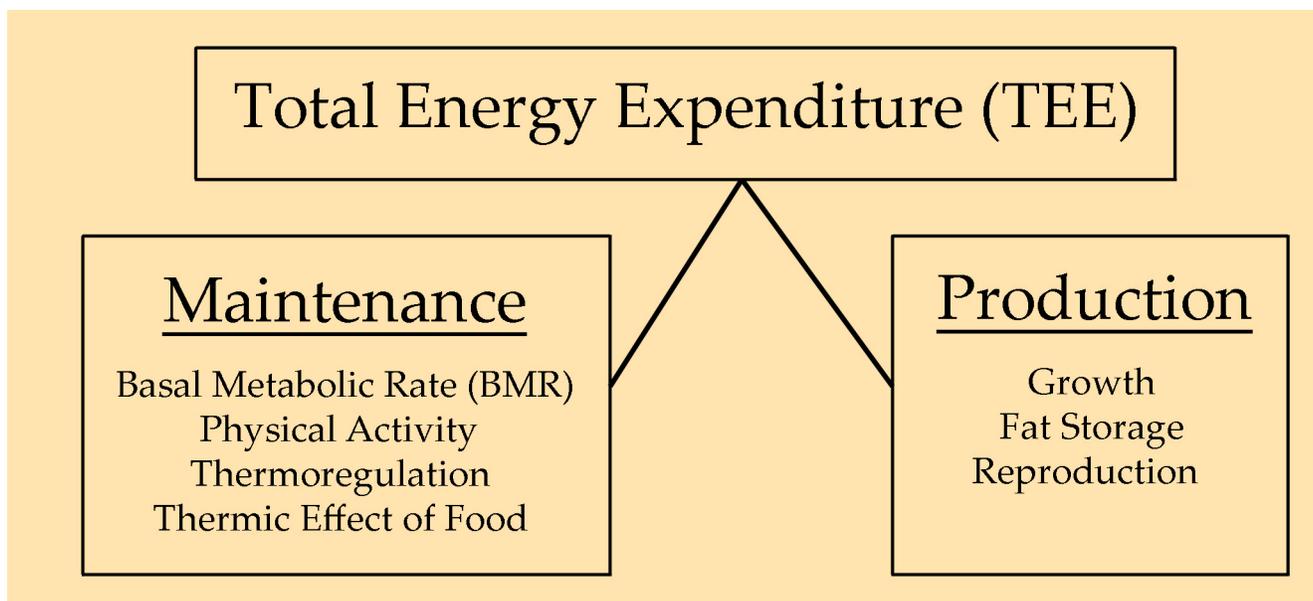Production

Growth
Fat Storage
Reproduction

Figure 1. Components of total energy expenditure (TEE), with metabolic costs associated with maintenance (i.e., energy necessary for survival on a daily basis) and production (i.e., energy costs above those needed for maintenance).

tracted from limited environmental resources and allocated to various somatic functions has consequences for survival and reproduction (Ellison 2003, 2008; Leonard et al. 2007; Leonard and Ulijaszek 2002; McNab 2002). Further, energetics provides a means by which to operationalize life history theory, the branch of evolutionary biology that focuses on trade-offs in the allocation of finite resources in order to maximize fitness in disparate environmental circumstances (Charnov 1993; Hill 1993; Hill and Hurtado 1996; Stearns 1992). Energy used for maintenance costs, such as basal metabolic rate (BMR), physical activity, thermoregulation, immune function, and diet-induced thermogenesis, cannot be used for productive costs such as growth or reproduction (Ellison 2003; Leonard 2004; Ulijaszek 1995) (Figure 1). In turn, life history theory, with its emphasis on variables such as age at maturity, growth rate, fecundity, and lifespan, provides an explanatory framework for demographic patterns (Hill and Hurtado 1996; Valeggia and Ellison 2003).

In this paper, we revisit the issue of Neandertal energetics in order to consider the evolutionary fate of Neandertals. The paper is divided into three sections. In the first section, we estimate Neandertal energy budgets by using new data on energy expenditure among contemporary northern populations and recent advances in nutritional sciences. In the second section, we systematically review evidence for Neandertal subsistence patterns in order to address energy intake and dietary composition among Neandertals. Finally, we discuss implications of Neandertal energy dynamics for reproductive ecology and life history evolution, and use this information to consider population dynamics during the Middle to Upper Paleolithic transition.

THE MIDDLE TO UPPER PALEOLITHIC TRANSITION

Neandertals evolved in Europe during the Middle Pleistocene following the split with the lineage leading to modern humans (Hofreiter et al. 2001; Hublin 1998, 2007; Klein 2003; Stringer 2008). The frequency of morphological features characteristic of Neandertals gradually increased and this distinct hominin group had fully emerged by 130,000 years ago. Neandertals evolved within the context of a European glacial environment and many skeletal features, particularly in the post-cranial skeleton, have been interpreted as reflecting the effects of cold adaptation and isolation (Coon 1962; Hoffecker 2005; Holliday 1997; Howell 1952; Hublin 1998; Klein 1999, 2003; Steegmann et al. 2002; Trinkaus 1981). Based on morphological, behavioral, and adaptive differences, most advocate a species designation, *Homo neanderthalensis* (Harvati et al. 2004; Hublin 2007; Tattersall and Schwartz 2008).

There is an emerging consensus that modern humans evolved in Africa within the past 200,000 years and later (~60,000 years ago) began a global dispersal that eventually resulted in the replacement of all other hominin species, including Neandertals (Conard 2006; Hoffecker 2005; Hublin 2007; Klein 1999, Mellars 2004; Stringer 2002). Questions remain about the extent of gene flow between Neandertals and modern humans (Templeton 2002; Trinkaus 2007), although most authorities interpret existing fossil and genetic evidence as indicative of at most minor gene flow (Bräuer 2006; Currat and Excoffier 2004; Hublin and Bailey 2006; Klein 2003; Mellars 2004; Serre et al. 2004; Stringer 2002).

While the extent of temporal and geographic overlap of Neandertals and modern humans continues to be de-

bated, there are several lines of evidence that suggest fairly extensive contact and coexistence between the species. In Europe, conservative estimates suggest that these two species coexisted for at least several millennia, with modern humans arriving before 30,000 years ago (possibly as early as 40,000-45,000 years ago) and Neandertals surviving until after 30,000 years ago (possibly as late as 28,000-24,000 years ago) (Bräuer 2006; Davies 2001; Finlayson et al. 2006; Hublin and Bailey 2006; Hublin et al. 1995; Mellars 2004; Trinkaus et al. 2003). The extent of interspecific contact likely varied regionally but this complex issue awaits further resolution. However, given evidence for extensive overlap in resource use—particularly the shared emphasis on the hunting of mammalian herbivores—there would have almost certainly been substantial resource competition (Adler et al. 2006; Bocherens and Drucker 2006; Conard 2006; O'Connell 2006; Roebroeks et al. 1992; Shea 2003). The extent of this competition is the subject of intense debate and depends on several key factors, such as hominin population density and environmental carrying capacity, both of which are presently poorly understood. Additional evidence for prolonged interaction between the species comes from the occurrence of the Châtelperronian industry, which is generally interpreted as the product of Neandertal acculturation following contact with modern humans (Hublin and Bailey 2006; Mellars 1989, 2004; Stringer 2008); if confirmed, recent evidence for the interstratification of Châtelperronian and Aurignacian artifacts (Mellars et al. 2007) would strengthen the case for prolonged interaction. Finally, following the appearance of modern humans in Europe, Neandertals experienced a geographic range contraction that limited their European presence to southern and eastern refugia (e.g., the Iberian Peninsula); within several millennia Neandertals became extinct (Hublin et al. 1995). The cause of Neandertal extinction remains unknown, although most researchers have implicated competition with modern humans as the primary factor (Mellars 1989; Shea 2003; Zubrow 1989); however, others have emphasized the role of deteriorating climate in the demise of the Neandertals, either alone (Finlayson 2004; Finlayson and Giles-Pacheco 2000) or in combination with modern human competition (Aiello and Wheeler 2003; O'Connell 2006; Stringer 2008; Stringer et al. 2003).

NEANDERTAL ENERGY BUDGETS

ESTIMATING BASAL METABOLIC RATE (BMR)
Basal metabolic rate (BMR) is defined as the minimum amount of energy necessary to sustain basic biological functions; BMR is measured in a thermoneutral environment with the subject in a post-absorptive condition (after a 12-hour fast) (Blaxter 1989; Leonard 2004; Ulijaszek 1995). In most contemporary human populations, BMR is the single largest component of energy expenditure and thus occupies a central role in estimates of population-level energy needs (FAO/WHO/UNU 1985, 2004; FNB/IOM 2002; Schofield 1985). Fat-free mass, in particular, is highly correlated with BMR, explaining approximately 70-80% of BMR

variation (Nelson et al. 1992; Sparti et al. 1997; Weinsier et al. 1992). There is considerable interpopulation variation in BMR independent of body size and composition, with relatively depressed values in tropical populations and elevated values in northern groups (Henry and Rees 1991; Leonard et al. 2002; Roberts 1978). The hypothesis that BMRs are elevated among indigenous northern populations as an adaptation to chronic and severe cold stress has generated controversy for decades, primarily because early metabolic studies relied on small sample sizes and often did not adequately control for the potentially confounding effects of anxiety, diet, and body composition (see review in Snodgrass et al. 2005). However, more recent studies with controlled measurement conditions have confirmed earlier findings by documenting relatively high BMRs among native circumpolar groups compared to lower latitude reference populations and non-indigenous individuals living in the same communities (Galloway et al. 2000; Leonard et al. 2002, 2005; Rode and Shephard 1995a; Snodgrass et al. 2005).

Our research among three indigenous Siberian populations (the Evenki of central Siberia, the Buryat of southern Siberia, and the Yakut [Sakha] of eastern Siberia) has demonstrated systematically elevated BMRs relative to lower latitude norms for body mass, fat-free mass, and surface area (Galloway et al. 2000; Leonard et al. 2002, 2005; Snodgrass et al. 2005, 2007, 2008; Sorensen et al. 1999). Among the pooled Siberian sample, BMR among males (n = 115) is 15% above and females (n = 169) 18% above predicted values based on the Cunningham (1991) fat-free mass standards (Snodgrass et al. 2008) (Table 1; Figure 2). BMR is also significantly elevated among males (+10%) and females (+7%) according to the Oxford age- and sex-specific body mass predictive equations (Henry 2005) (see Table 1). This metabolic elevation is unlikely to reflect body composition differences between circumpolar populations and lower latitude groups since fat-free mass facilitates comparisons between different populations with diverse body sizes and composition. Further, the mixed diets of all three Siberian groups, which include their major energy component from carbohydrates (~45–60% of calories) and a modest consumption of protein (~12–17% of calories) (Leonard et al. 2002, 2005; Snodgrass 2004; Sorensen 2003), make it unlikely that BMR elevation documented in recent studies is the result of extreme levels of dietary protein (see discussion below). Metabolic elevation appears to reflect a physiological adaptation to chronic and severe cold stress experienced in the circumpolar environment; this relationship with climate is supported by geographic studies that demonstrate a strong negative association between BMR and mean annual temperature, which remains when controlled for differences in body size (Leonard et al. 1999, 2005; Roberts 1952, 1978). Present evidence suggests that genetic factors play an important role in structuring metabolic adaptation among indigenous northern populations but that short-term functional responses to acute cold stress, mediated at least in part by thyroid hormones (particularly triiodothyronine [T3] and thyroxine [T4]), further elevate metabolic rate dur-

TABLE 1. MEASURED BMR (means and standard error of the mean [SEM]) VERSUS PREDICTED BMR[1] IN THREE INDIGENOUS SIBERIAN POPULATIONS.

	Females (n=169)	Males (n=115)
BMR vs. Fat-Free Mass[2]		
Measured (*kcal/day*)	1378 (16) ***	1720 (26)***
Predicted (*kcal/day*)	1173.4 (9)	1490 (13)
Percent Deviation (%)	+ 17.7	+ 15.2
BMR vs. Body Mass[3]		
Measured (*kcal/day*)	1378 (16)***	1720 (26)***
Predicted (*kcal/day*)	1289 (10)	1575 (17)
Percent Deviation (%)	+ 7.1	+ 9.5

[1]Differences between measured and predicted are statistically significant at: ***$P < 0.001$.
[2]Measured BMR was compared with predicted values for fat-free mass according to the General predictive equation of Cunningham (1991).
[3]Measured BMR was compared with predicted values for body mass according to the sex- and age-specific Oxford predictive equations (Henry 2005).

ing winter months (Leonard et al. 1999, 2005; Mishmar et al. 2003; Ruiz-Pesini et al. 2004; Snodgrass et al. 2005; Wallace 2005).

Most past energetic modeling studies (e.g., Sorensen and Leonard 2001) have concluded that Neandertals were similar to contemporary northern populations in having elevated BMRs based on several lines of evidence. First, well-controlled metabolic studies described above have documented systematically elevated BMRs among indigenous northern populations from both Siberia and North America. Second, Neandertals evolved in Europe in the Middle Pleistocene within the context of a glacial environment and show morphological features (e.g., large body size and relatively short limbs and elongated trunks) likely related to cold adaptation (Coon 1962; Hoffecker 2005; Holliday 1997; Klein 1999, 2003; Ruff 1993; Trinkaus 1981). Third, in contrast to Upper Paleolithic modern human sites, Middle Paleolithic sites have not produced evidence for the use of sophisticated cold weather technology (e.g., tailored clothing) (Hoffecker 2005; Klein 1999). This has generally been interpreted as indicative of dependence by Neandertals on biological mechanisms for coping with chronic and severe cold stress (Coon 1962; Hoffecker 2005; Holliday 1997; Klein 1999; Ruff 1993). It should, however, be noted that several authors have recently suggested that Neandertal dependence on biological means of cold adaptation has been overstated (Aiello and Wheeler 2003; Gilligan 2007; White 2006). Others (e.g., Steegmann et al. 2002) have made the opposite claim and argue that the extent of Neandertal cold adaptation has been underappreciated; this view is based in part on the conclusion that Neandertals had functional stores of brown adipose tissue, which would have given them an enhanced ability to generate heat and contributed to their ability to resist cold stress. While the presence of brown fat in Neandertal adults is controversial, it is

supported by several lines of evidence, including the presence of brown fat in human newborns and non-human primates (e.g., *Macaca mulatta* exposed to chronic cold stress), its retention in some cold exposed human adults (e.g., outdoor workers in Finland), and recent biomedical imaging research suggesting that the amount of active brown adipose tissue in adult humans is greater than previously recognized (Beall and Steegmann 2000; Chaffee et al. 1975; Himms-Hagen 1984; Huttenen et al. 1981; Himms-Hagen and Ricquier 1998; Lean 1989; Nedergaard et al. 2007; van Marken Lichtenbelt et al. 2009). In sum, the conclusion that Neandertals had relatively high BMRs is well supported.

In the present study, we estimate Neandertal energy expenditure and dietary needs by using published sex-specific body mass estimates coupled with metabolic information on contemporary indigenous Siberian populations. We used the body mass estimates of Ruff et al. (1997; provided by Churchill 2008) for Neandertal males (77.6 kg [170.7 lbs]) and females (66.4 kg [146.1 lbs]) to estimate BMR from our Siberian regression equations (Leonard et al. 2005; Snodgrass et al. 2007, 2008). Given the presence of pronounced metabolic elevation and other biological adaptations to the cold among contemporary northern groups and evidence for adaptation among Neandertals to the extreme glacial conditions of Late Pleistocene Europe, we feel that estimation of BMR for Neandertals using these data is appropriate and almost certainly underestimates the magnitude of Neandertal long-term metabolic elevation. We also used a second approach to estimate Neandertal BMR, in this case using fat-free mass estimates to predict BMR based on the Siberian regression equations. Fat-free mass was estimated from body mass data assuming that Neandertals had a similar body fatness as traditionally living Inuit adults (14% fat for males and 25% fat for females [Rode and Shephard 1994; Shephard 1974]); this value is similar to traditionally-
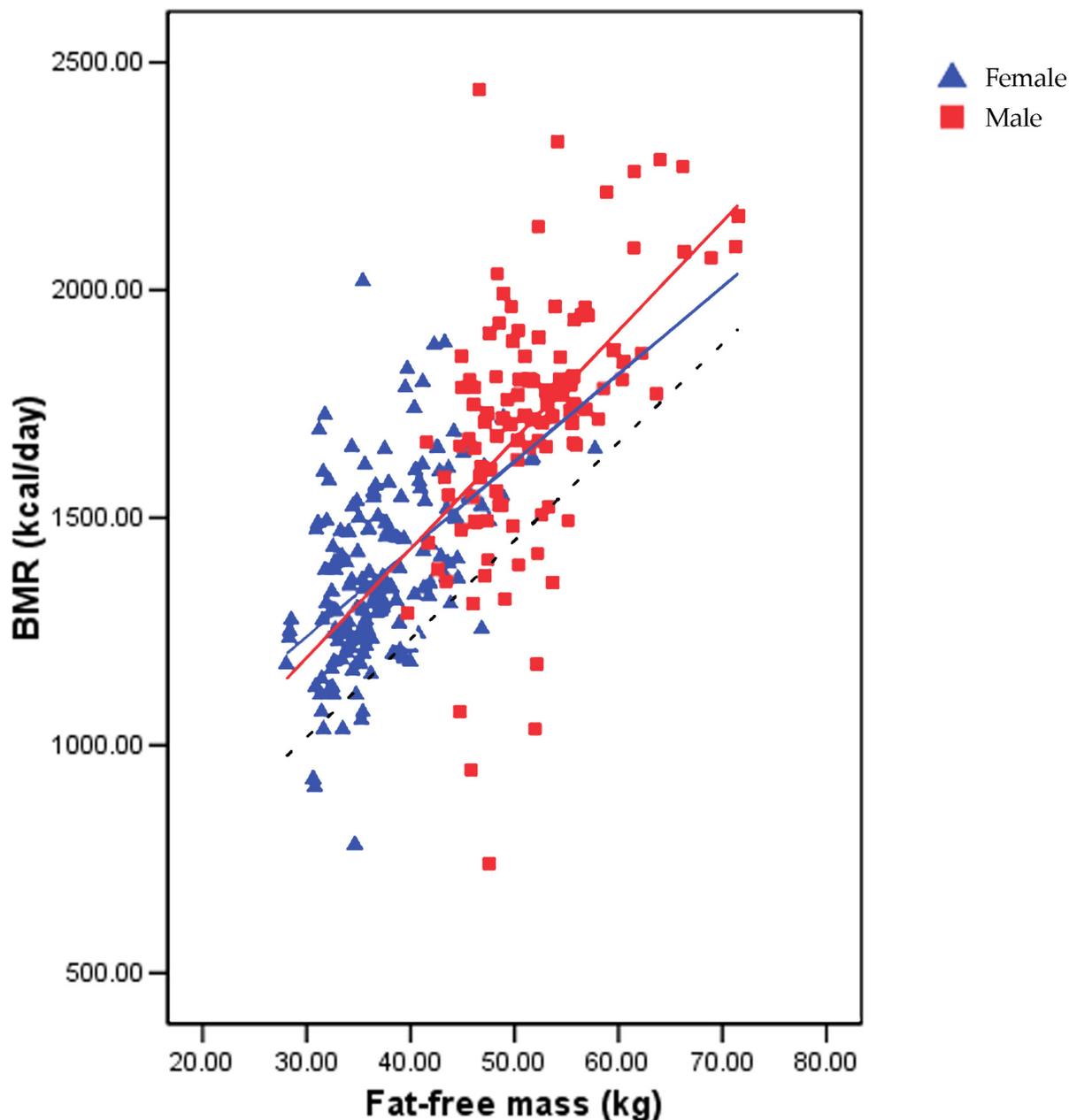
Figure 2. Relationship between basal metabolic rate (BMR; kcal/day) and fat-free mass (kg) among indigenous Siberian men (red squares) and women (blue triangles) compared to the general predictive equation of Cunningham (1991) for lower latitude populations (dashed line). Siberian men average 1720 kcal/day (7,400 kJ/day), 15.2% higher than predicted values. Siberian women average 1,378 kcal/day (5,766 kJ/day), 17.7% higher than predicted values.

living nGanasan reindeer herder/hunters (11% in males and 30% in females [Rode and Shephard 1995b]) and an average for non-Western populations (13% in males and 25% in females [Norgan 1994]).

Our results suggest that Neandertal BMRs were on average approximately 1800–1900 kilocalories (kcal)/day in males and 1500–1600 kcal/day in females (Table 2), with somewhat higher estimates obtained from fat-free mass estimates.

All previous Siberian studies and nearly all among Alaskan and Canadian natives were conducted during the warm summer months and the early fall when the study populations were not exposed to acute cold stress. As a result, it is difficult to ascertain the magnitude of seasonal metabolic fluctuations among indigenous northern populations and even more uncertain when extrapolating to past populations. However, several lines of evidence suggest significant metabolic upregulation in response to acute

TABLE 2. ESTIMATED ENERGY EXPENDITURE (kcal/day) MEANS FOR NEANDERTALS.*

	BMR (kcal/d)	Winter (kcal/d)	PAL	TEF (kcal/d)	TEE (kcal/d)
Females					
Summer—Low Activity	1465	-	1.82	267	2933
Summer—High Activity	1465	-	2.50	366	4029
Winter—Low Activity	1465	293	1.82	640	3840
Winter—High Activity	1465	293	2.50	879	5274
Males					
Summer—Low Activity	1876	-	1.98	371	4085
Summer—High Activity	1876	-	2.50	469	5159
Winter—Low Activity	1876	375	1.98	891	5348
Winter—High Activity	1876	375	2.50	1126	6754

* including basal metabolic rate (BMR), thermic effect of food (TEF), and total energy expenditure (TEE)

cold would have occurred seasonally in Neandertals. First, seasonal studies of metabolism among industrialized European and Japanese populations have documented metabolic increases of approximately 5–15% during winter months compared to summer measurements, with metabolic upregulation negatively tracking temperature (Kashiwazaki 1990; Osiba 1957; Plasqui et al. 2003; but see Haggarty et al. 1994). Second, thyroid hormone profiles of northern populations suggest substantial seasonality in BMR, given that thyroid hormones increase rates of oxidative metabolism throughout the body upon exposure to chronic cold temperatures and play an important role in structuring short-term cold-induced metabolic upregulation during winter months (Itoh 1980; Leonard et al. 1999, 2005; Osiba 1957). Exposure to cold temperatures and shifts in photoperiod lead to hormonal changes that increase the circulating concentration of T_3 and T_4 and boost thermogenesis and ATP turnover (Levine et al. 1995; Silva 2003; Tkachev et al. 1991). Thyroid hormone levels are closely associated with BMR through their direct effects on rates of oxidative metabolism (Danzi and Klein 2003; Guyton and Hall 2006). Indigenous northern populations appear to have a greater propensity for seasonal thyroid elevation than non-indigenous residents of northern latitudes, which likely structures functional BMR upregulation in response to acute cold stress (Tkachev et al. 1991). Our research among the Evenki, for example, has documented a link between free T_4 levels and BMR, as well as overall elevated levels of free T_4 compared to non-indigenous Russian residents living in the same communities (Leonard et al. 1999).

Given the generally severe winter climatic conditions reconstructed for most European Neandertal sites and that Neandertals were likely more dependent on biological adaptations than contemporary northern populations, we conservatively estimate a seasonal BMR increase in Neandertals of 20%.

ESTIMATING PHYSICAL ACTIVITY
In order to estimate physical activity levels among Neandertals, we looked to energy expenditure data from contemporary subsistence-level human populations. We concentrated on physical activity data measured using the doubly labeled water technique, since it measures energy over a relatively long period (~7–10 days) and is generally accepted as the most accurate technique for measuring free-living energy costs in humans and other vertebrates (Nagy et al. 1999; Schoeller 1999; Speakman 1997). Data are expressed as the physical activity level (or PAL), which reflects activity levels as multiples of BMR; further, PAL is a useful measure as it adjusts for the effects of body size.

A large dataset published by FNB/IOM (2002) indicates that healthy, normal-weight adults in the United States and other developed nations have PALs that average 1.73 for males and 1.72 for females (Leonard 2008). Available data are scarce for subsistence populations but generally show PALs that are substantially higher than among industrialized, urbanized nations; however, there is variation by type of subsistence economy, season, and measurement technique (Leonard 2008; Schulz and Schoeller 1994; Snodgrass 2004). The best data on activity patterns among subsistence groups come from studies conducted among Bolivian Aymara agropastoralists (Kashiwazaki et al. 1995) and Gambian agriculturalists (Heini et al. 1991, 1996; Singh et al. 1989); no doubly labeled water data are available for hunter-gatherers. Gambian men had PALs of 2.4, which reflects intense physical activity associated with harvesting activities, while Gambian women had somewhat lower PALs (1.9). Both Aymara men and women had fairly high PALs (2.0), which reflects the important roles that both sexes play in the subsistence herding and agricultural economy; however, given that the Aymara study was conducted during the pre-harvest season the values likely do not reflect yearly activity peaks. Although no doubly labeled water stud-

ies have been conducted among Arctic hunter-gatherers, a study using the time allocation method among the Igloolik Inuit during the early stages of economic development (Godin and Shephard 1973) gives us some indication of energy patterns in a northern forager population. Inuit males had PALs of 1.8–2.2, with the highest values among individuals most involved in the traditional hunting economy. Inuit women at the time of the study were already less involved in the subsistence economy and had PALs that averaged 1.8. However, the study may have underestimated physical activity costs (especially among men), since it relied on the time allocation method, which can significantly underestimate total energy expenditure, especially at high levels of physical activity (Durnin 1990; Leonard et al. 1997; Snodgrass 2004; Spurr et al. 1996).

A meta-analysis by Leonard (2008) calculated an average for contemporary subsistence populations of 1.98 for males and 1.82 for females, although this likely underestimates PALs since some of the data were obtained from time allocation studies. A PAL of approximately 2.5 appears to be the upper bounds of sustainable population-level energy expenditure (Black et al. 1996; Shetty 2005), although PALs obtained using doubly labeled water have been found to be considerably higher among other groups, including athletes in training (~2.0–3.5; Black et al. 1996) and individuals involved in heavy physical labor (~2.8–3.1; Diaz et al. 1991).

In the present study, we estimated the contribution of physical activity to Neandertal total energy expenditures using two approaches: 1) PAL means for subsistence populations (1.98 in males, 1.82 in females) from Leonard (2008); and, 2) the high end of the sustainable activity range in contemporary human populations (PAL=2.5). The activity levels documented among contemporary subsistence populations almost certainly underestimates Neandertal energy patterns given that all values were obtained from populations not fully dependent on subsistence activities (i.e., all the contemporary human populations are to a certain extent integrated into larger economies). The intensive foraging niche occupied by Neandertals was largely focused on the hunting of terrestrial herbivores (Bocherens et al. 1999, 2001; Burke 2004; Chase 1989; Gaudzinski and Roebroeks 2000; Hoffecker 2005; Kuhn and Stiner 2006; Lieberman and Shea 1994; Marean and Kim 1998; Richards 2007; Richards et al. 2000; Stiner 1994) and would have entailed very high activity costs associated with prey search and capture. Further support for extremely high costs of physical activity among both Neandertal males and females comes from the species' distinctive post-cranial morphology, which likely in part reflects a highly physically active and strenuous lifestyle (Kuhn and Stiner 2006; Pearson et al. 2008; Ruff et al. 1993, 1994; Trinkaus 1986, 1987, 1989; Trinkaus and Churchill 1999). In fact, the high activity estimate used here (i.e., PAL=2.5) may actually underestimate Neandertal energy expenditure; this was the conclusion of Sorensen and Leonard (2001), who used a PAL of 3.0 as the high end of their activity estimate.

ESTIMATING THERMIC EFFECT OF FOOD

Recent studies in nutritional sciences guide our estimates of the thermic effect of food in Neandertals. The thermic effect of food averages approximately 6–10% of total energy costs in Western populations, virtually all of which consume diets with carbohydrates as the largest source of energy (Leonard 2004; Wright et al. 2004). Carbohydrates and fats induce metabolic increases of less than 5% for the first few hours after a meal and thus contribute minimally to overall energy costs. Protein, however, substantially influences metabolic rate following a meal, inducing metabolic elevations of up to 30%, which may not return to normal for 12 hours (Guyton and Hall 2006; Reed and Hill 1996; Soares et al. 1988). A study conducted in the 1950s among traditionally living Alaskan Inuit (Rodahl 1952) showed that the most elevated BMR values were found among those populations with the highest intake of protein (approximately 130–200 g/day), even though BMR was measured under standard conditions (i.e., $\geq$12 hours after the last meal). The Anaktuvuk Pass (Alaska) Inuit at the time of the study had a diet composed almost exclusively of land mammals (primarily caribou) and consumed approximately 200 g/day of protein; this group had BMRs 10–15% higher than Inuit consuming a so-called White man's diet. Other early dietary studies of traditionally living Inuit in Alaska, Canada, and Greenland showed an even greater consumption of protein, which in some groups exceeded 300 g/day (DuBois 1928; Kemp 1971; Krogh and Krogh 1913; Rodahl 1952; Schaefer 1981). Most studies of northern populations also have documented substantial seasonal fluctuations in protein consumption among traditionally living northern groups, with a 20% higher protein intake during March as compared to August (Rodahl 1952).

Given that Neandertals consumed a high-protein diet primarily composed of animal source foods, and protein consumption may have been as high as that documented among historically-known Inuit, we made adjustments to Neandertal total energy expenditure estimates by an additional 10% and 20% to reflect summer and winter values, respectively.

ESTIMATING TOTAL ENERGY EXPENDITURE (TEE)

Our TEE estimates indicate that Neandertals would have had extremely high total energy costs that were on the order of 4000–7000 calories per day in males and 3000–5000 calories per day in females (see Table 2). These estimates show considerable overlap with those calculated in other studies (e.g., 3000–5000 kcal/day in Neandertal females and 4000–6000 kcal/day in Neandertal males [Sorensen and Leonard 2001]; 3360–4480 kcal/day for Neandertal males [Steegmann et al. 2002]). However, our estimates suggest that Neandertal energy expenditure may have been even higher than estimated in other studies, which reflects our inclusion of the energy costs associated with seasonal metabolic upregulation in response to acute cold stress and the consumption of a diet extremely high in protein. Although we can never be certain of the exact energy costs of life as

a Neandertal, we can safely conclude that their energy expenditures were extremely high.

Based on our estimates, Neandertal energy costs would have been at the very high end of the range for TEEs in human subsistence-level populations, such as those measured in Gambian agriculturalists and Aymara agropastoralists (Heini et al. 1991, 1996; Kashiwazaki et al. 1995; Singh et al. 1989), but within the range of measurements from endurance athletes in training (Black et al. 1996), soldiers during training exercises (Hoyt et al. 1991), and heavy manual laborers (Diaz et al. 1991).

Our estimates of Neandertal energy expenditures follow present evidence from contemporary human populations and include a seasonal adjustment for increased energy usage during winter months in response to acute cold stress and a high protein diet. This heightened energy expenditure would have occurred at precisely the time that energy availability would have been most limited in most of the Neandertal range. The consequences of this seasonal energy imbalance are discussed below.

ENERGY INTAKE AND DIETARY COMPOSITION

The energy expenditures calculated in the present study are surprisingly high but are even more extraordinary when considering that in order to sustain these expenditures long-term, energy returns from foraging must be even higher to account for wastage, provisioning of dependents, and the energy costs of growth and reproduction. Data compiled by Sorensen and Leonard (2001) for ten contemporary hunter-gatherer groups document population-level foraging returns that are generally two-and-a-half times that needed simply for TEE, with approximately 1.3–1.4 as minimum sustainable. Neandertals were clearly capable of effective resource extraction, given their high energy requirements and the fact that the species survived for over 100,000 years including through repeated climatic oscillations during the Late Pleistocene. This raises the question: How were Neandertals able to obtain adequate calories to maintain their extraordinarily high energy expenditures?

Based on evidence from archaeological and isotopic studies, Neandertals consumed a diet focused primarily on hunted animal foods; this diet emphasized medium- and large-bodied terrestrial herbivores and shows little evidence across most of the range for a sizeable contribution of vegetable foods, aquatic resources, or small-bodied animals (Bocherens et al. 1999, 2001; Burke 2004; Chase 1989; Gaudzinski and Roebroeks 2000; Hoffecker 2005; Kuhn and Stiner 2006; Marean and Kim 1998; Richards 2007; Richards et al. 2000; Stiner 1994). There was some regional variation in diet across the Neandertal range—for example, Neandertals in southern parts of their range included some fish, marine mammals, shellfish, small animals, and plant foods in their diets (Finlayson 2004; Kuhn and Stiner 2006; Lev et al. 2005; Richards 2007; Stiner et al. 1999; Stringer et al. 2008)—but what is truly extraordinary is the remarkable dietary homogeneity in the species over space and time. Even at sites that would have allowed access to marine or freshwater aquatic resources, no major contribution of aquatic foods to Neandertal diets has been detected (Richards 2007).

Neandertals occupied a very high trophic position that was focused on the consumption of medium- and large-bodied terrestrial herbivores, yet this raises important questions related to the macronutrient composition of the diet and seasonal patterns of resource availability. In regards to the macronutrient composition of the diet, available evidence discussed earlier suggests that Neandertals consumed a high protein diet that would have required high metabolic costs associated with the thermic effect of food. Further, if Neandertal physiology was similar to modern humans, they may have encountered problems stemming from their extreme protein consumption. Contemporary humans are limited in the amount of protein that can be regularly consumed without detrimental health effects that result from physiological limitations in our ability to metabolize amino acids (Cordain et al. 2000; Speth 1989, 1991); present data suggest that the protein (combined animal and plant) ceiling is approximately 50% of total calories with certain segments of the population, such as pregnant women, having a considerably lower protein ceiling (~25%).

There is a huge amount of dietary variation in historically-known human forager populations, with extreme variation in habitual protein consumption (~20–50% of calories; Cordain et al. 2000). As discussed above, a number of traditionally-living northern populations studied during the early 20th century obtained over 40% of their calories from protein and some acquired upwards of 50% of their calories from protein (DuBois 1928; Rodahl 1952; Schaeffer 1981). However, other northern groups in the past and virtually all high-latitude populations today consume lower levels of protein; in some traditionally living groups this was achieved through the consumption of a high-fat, marine mammal dominated diet, while in more economically developed populations, carbohydrates provide the largest share of dietary energy (Ho et al. 1972; Leonard et al. 2005; Schaeffer 1981; Shephard and Rode 1996).

Further insights into Neandertal dietary composition come from our knowledge of the geographic patterning of diet among contemporary human foragers. These studies show that the contribution of plant foods is generally lower in more northern regions and there is a corresponding increase in the dependence on aquatic resources (e.g., fish and marine mammals) (Cordain et al. 2000; Kelly 1995; Marlowe 2005). This pattern suggests that fish and other aquatic resources would have been a major contributor to Neandertal diets, especially in northern parts of the range, yet available archaeological evidence and stable isotope data suggest that aquatic resources were only taken opportunistically and were only a minor dietary item (Kuhn and Stiner 2006; Richards 2007; Stiner et al. 1999). Although there is some evidence for the use of plant foods among Neandertals, especially from lower latitude sites (e.g., Lev et al. 2005), there is presently no solid evidence that plant foods comprised a major part of the Neandertal diet. While preservation issues likely bias our reconstruction of Nean-

dertal diets by underestimating the contribution of plant foods, the lack of evidence for intensive plant processing technology supports the conclusion that plant foods played at most a minor role in the diet (Kuhn and Stiner 2006). Taken together, this evidence suggests a relatively minor role for carbohydrates in Neandertal diets.

Fats, with their high energy density and near universal desirability (Speth and Spielmann 1983), must have played a critical role in Neandertal diets, an idea advanced by several authors (e.g., Cachel 1997). However, given the extremely limited and geographically localized evidence for marine mammal use by Neandertals, the primary fat source would have been terrestrial mammals. Consequently, fats would have been available in limited quantities during certain seasons as a result of yearly changes in the body composition of prey foods (Cordain et al. 2002; Speth 1991). Several strategies could have maximized fat acquisition in Neandertals, including focusing on large-bodied mammals (larger mammals typically have a relatively high fat content compared to smaller mammals [Calder 1984; Pitts and Bullard 1968]), consuming fat-rich tissues (e.g., marrow and brains) (Finch and Stanford 2004), and the selective targeting of prey species and individuals for high fat content. Still, one cannot escape the conclusion that Neandertals, especially those in northern and eastern areas, would have experienced pronounced seasonal limitations in fat availability that would have forced their reliance on protein and would have led to periods of intense energy stress.

IMPLICATIONS OF ENERGY DYNAMICS FOR NEANDERTAL EXTINCTION

The high turnover of metabolic energy reconstructed for Neandertals, combined with severe limitations on energy availability, would have almost certainly shaped Neandertal life history traits, including growth rate, reproductive patterns (e.g., age at first birth and interbirth interval), and lifespan. Here, we consider the issue of how Neandertal energy dynamics may have shaped reproductive ecology and population dynamics in the Middle Pleistocene. Although much of this section is highly speculative, we believe that our interpretations and extrapolations are well supported by the available evidence. The following section is divided into two parts. In the first, we focus on Neandertal reproductive ecology and consider the effects of climatic deterioration on Neandertal population dynamics. In the second, we review and contrast energy patterns between modern humans and Neandertals, and consider the role that modern humans could have played in the extinction of Neandertals.

Recent research in human biology has revealed that multiple energetic variables, not just the size of energy stores (i.e., body fat), influence female reproductive physiology and shape reproductive capacity (i.e., fecundity) (see review in Ellison 2008). Studies of athletes and subsistence populations have consistently shown that in addition to fat stores, both energy balance (i.e., whether gaining or losing weight, and how fast) and energy flux (i.e., the rate of energy turnover) influence ovarian function and affect fecundity (Bullen et al. 1985; Ellison 2001, 2003, 2008; Jasienska and Ellison 1998; Panter-Brick et al. 1993). Research on Polish farmers by Jasienska and Ellison (1998, 2004), for example, demonstrates that even with adequate nutritional intake, seasonally-increased physical activity associated with the harvest season can lead to downregulation of ovarian function and a reduced probability of conception. Ovarian function has been shown to be highly sensitive to energetic conditions and, in particular, energy expenditure; relatively small changes in energy expenditure, energy intake, or energy stores have been linked to rapid alterations in ovarian hormone levels which affect fecundity (Ellison 2001, 2003, 2008; Ellison et al. 1993; Jasienska and Ellison 1998; Lipson and Ellison 1996; Panter-Brick et al. 1993). This continuum of ovarian function, with facultative modulation of ovarian hormones and fecundity in response to energetic parameters, serves to optimize the energy allocated to reproduction (Ellison 2001, 2003, 2008; Jasienska and Ellison 2004). In fact, seasonal shifts in energy patterns among contemporary humans, which result from dietary and/or activity changes, can have profound effects on the timing of conception and are important contributors to human birth seasonality (Ellison 2001, 2008; Ellison et al. 2005). Other primates, including common chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*), have been shown to have similar reproductive physiology in the response of fecundity to energy dynamics (Emery Thompson 2005; Emery Thompson et al. 2007; Emery Thompson and Wrangham 2008; Knott 2001).

The similarities in female reproductive function in response to energy fluctuations in living humans and extant hominoids argues for a similar response in other hominin species, including Neandertals. This strongly suggests that the extremely high metabolic rates reconstructed for Neandertals would limit energy available for reproduction and would have contributed to a pattern of relatively low overall fertility and pronounced birth seasonality. This hypothesis follows from several lines of evidence. First, extremely high energy costs associated with large body size, high physical activity levels, thermic effect of food, and high costs of thermoregulation coupled with a high-risk, energy-intensive subsistence strategy that would have had pronounced seasonal and periodic fluctuations in energy availability would have limited energy available for reproduction; this would have had profound effects on fecundity and likely would have shaped reproductive parameters such as interbirth interval (Ellison 2001, 2003, 2008; McNab 2002; Ricklefs 1973; Sorensen and Leonard 2001). A number of traditionally-living human populations from northern regions have been shown to experience pronounced birth seasonality (e.g., Condon 1991; Condon and Scaglion 1982), which recent research suggests is shaped by energy dynamics. A similar conclusion on seasonality was drawn by Mussi (2007) who argued that early hominin populations in Europe would have experienced pronounced birth seasonality with the peak of conceptions in the late summer and early fall in response to increasing energy available from the fat stores of terrestrial mammals. Second, Ne-

andertals do not appear to have had a pronounced sexual division of labor (see review in Kuhn and Stiner 2006); the participation of Neandertal females in energy-intensive hunting activities would have required high physical activity levels. This would have increased the energetic burden on females and may have contributed to lower fecundity, especially during certain times of the year. Third, relatively low fertility rates (along with high mortality rates), may have contributed to the relatively low population densities documented among Neandertals (Conard 2006; Hoffecker 2005; Kuhn and Stiner 2006; Mellars 1998).

Additional information on Neandertal demography comes from skeletal studies that document high rates of injury, high mortality risk (among both adults and subadults), and a relatively low life expectancy (Berger and Trinkaus 1995; Caspari and Lee 2004; Klein 1999; Trinkaus 1995). The harsh environment of glacial Europe would have exposed Neandertals not only to severe cold stress but also to dramatic fluctuations in resource availability within the context of a low energy terrestrial ecosystem. The relatively shorter life expectancy and high subadult mortality experienced by Neandertals would have also contributed to low fertility and small population size (Caspari and Lee 2004; Klein 1999; Pettitt 2000; Trinkaus 1986, 1987, 1989, 1995).

High resolution climatic data document rapidly deteriorating climatic conditions in Europe during the Late Pleistocene and into the Upper Pleniglacial, with maximum cold conditions during the Last Glacial Maximum (24,000–21,000 years ago) (Aiello and Wheeler 2003; Hoffecker 2005; Stringer 2008; Stringer et al. 2003). In particular, the increasingly severe climatic fluctuations that brought on a rapid and prolonged temperature drop at approximately 30,000 years ago would likely have strained Neandertal populations and contributed to major demographic shifts (Stringer 2008; Stringer et al. 2003). These effects may have come directly through increased cold injury and hypothermia, as well as indirectly through altered resource availability and increased energy costs. Neandertals were highly sensitive to environmental conditions, including temperature, and were unable to inhabit the colder, drier high-latitude arctic or subarctic zones where winter temperatures fell substantially below freezing; relatively minor changes in climate have been shown to have led to major distributional changes (Aiello and Wheeler 2003; Burke 2004; Conard 2006; Hoffecker 2005; Hoffecker and Elias 2003; Kuhn and Stiner 2006; Mellars 1998). The severity of the climatic deterioration can also be seen in the dramatic effects it had on modern human populations, which included population decreases and range contractions. These effects occurred even though modern humans had sophisticated technology for buffering from cold stress and a broader, more flexible dietary strategy than Neandertals (Hoffecker 2005; Hublin 1998). The availability of information provided by high-resolution climatic data has recently led a number of researchers to emphasize the role of climatic deterioration and environmental change in models of Neandertal extinction (Aiello and Wheeler 2003; Finlayson 2004; Finlayson and Giles-Pacheco 2000; O'Connell 2006; Stringer 2008;

Stringer et al. 2003).

Given this evidence that climatic change would have had a major effect on Neandertal populations, this raises questions about whether modern humans played a supporting role in the extinction of Neandertals. In order to address this issue, we must consider two questions. First, did competition with modern humans lead to a reduction in resources available to Neandertals? And second, did this resource reduction contribute to Neandertal extinction? The answer to the first question hinges on evidence for interspecific contact, as well as the reconstruction of hominin population parameters and details of environmental carrying capacity. As discussed above, there clearly was temporal and geographic overlap between modern humans and Neandertals in Europe and the Near East, with several lines of evidence strongly suggesting interactions between the species. The extensive overlap in resource use, with both species primarily dependent on the hunting of medium- and large-bodied terrestrial herbivores, is one of the strongest pieces of evidence that there would have been extensive resource competition (Adler et al. 2006; Bocherens and Drucker 2006; Conard 2006; Drucker and Bocherens 2004; O'Connell 2006; Roebroeks et al. 1992; Shea 2003). There does appear to have been regional variation in the nature of interaction and the severity of competition between species (Conard 2006). Regions with limited plants and aquatic resources, such as parts of Eastern Europe and Russia, appear to have experienced more rapid replacement of Neandertals by modern humans; this may reflect a more intense competition between the species for similar terrestrial mammal prey (Hoffecker 2005). Southern areas, with their broader resource base, appear to have experienced reduced competition; this probably resulted from an increased dietary breadth of modern humans in these regions that included more intense use of fish, small-bodied birds and mammals, and plant foods (Burke 2004; Hoffecker 2005; Klein 2003; Munzell and Conard 2004; Richards 2007; Richards et al. 2001; Stewart 2004; Stiner 2001, 2002; Stiner et al. 2000). The broadening of the modern human diet in the Upper Paleolithic, which included lower ranked prey that required greater investment in capture and processing, may indicate a depletion of higher ranked resources, such as medium- to large-bodied terrestrial herbivores (O'Connell 2006). In sum, there is solid evidence for contact and resource competition between the species, with some indication of reduced resources available to Neandertals.

To answer the second question, we can use an energetics perspective to evaluate key behavioral and biological differences between modern humans and Neandertals that may have affected fertility and demography. We focus here on four key differences. First, the body sizes of Upper Paleolithic humans were significantly smaller than Neandertals (Ruff et al. 1997), which would have translated into absolutely lower BMRs and reduced total energy costs. Even relatively small differences in body weight (~5–10 kg) could have substantially reduced metabolic costs.

Second, cultural and technological changes that increased cold weather protection would have dramatically

reduced the costs associated with thermoregulation in modern humans. Archaeological evidence strongly suggests major differences between Neandertals and modern humans in cold-related technology, with the latter showing a greater investment in shelter construction, more efficient hearths, and more complex (i.e., tailored) clothing (Goebel 1999; Hoffecker 2002, 2005; Klein 1999; Soffer 1985; Soffer et al. 2000; Trinkaus 2005). In addition to lowering energy costs associated with thermoregulation, cold protection technology in modern humans likely enhanced their ability to perform subsistence tasks in cold conditions.

Third, differences in technology and social organization in modern humans may have reduced physical activity and lowered total energy costs. Technological changes that began in the Upper Paleolithic, such as refinements in tools that increased hunting efficiency through increased capture and processing ability, may have contributed to lower activity costs in modern humans (Bar-Yosef 2007; Conard 2006; Conard et al. 2006; Klein 1999; Marean 2007). Support for this idea comes from studies of the introduction of labor-saving technology in traditionally living contemporary human populations, which have been shown to lead to changes in reproduction and an overall increase in fertility (Kramer and McMillan 2006). The appearance of population-level, sex-based division of labor in modern humans, postulated by several authors (Kuhn and Stiner 2006; Soffer 1994), may have reduced female energetic costs by transferring more of the energetic burden to males. Some support for sex-based energetic differences comes from activity data from three hunter-gatherer groups (!Kung, Ache, and Inuit) and several other subsistence populations (e.g., Evenki reindeer herders and Gambian agriculturalists); these data show that men on average are moderately more physically active than women (Panter-Brick 2002; Leonard 2008), although the differences are small and should be interpreted with caution. The emergence of a sex-based division of labor also may have increased resource extraction ability and increased environmental buffering through use of a broader diet (Kuhn and Stiner 2006).

Finally, dietary patterns and resource utilization in modern humans may have contributed to more favorable energy dynamics compared to Neandertals. Although Upper Paleolithic humans appear to have relied upon many of the same resources as Neandertals, including medium- and large-bodied terrestrial mammals, they did this within a broader, more flexible diet that included a greater range of resources, including fish, small-bodied prey, and plant foods (Hoffecker 2005; Munzell and Conard 2004; Richards 2007; Richards et al. 2001; Stewart 2004; Stiner 2001, 2002; Stiner et al. 2000). These dietary differences and improved efficiency in resource acquisition were likely accomplished through technological developments that allowed more efficient hunting, including more efficient predation on very large mammals (e.g., mammoths), as well as the use of snares, nets, and traps to capture small prey (Hoffecker 2005). The increased ability to extract energy and nutrients from foods through processing and food storage would also have contributed to differences in energy avail-

ability (Conard 2006; Conard et al. 2006; Hoffecker 2005; O'Connell 2006). Further, the expansion of social ties and long-distance exchange networks may have served to buffer against resource shortages and to have minimized risk (Adler et al. 2006; Gamble 1996, 1999; Horan et al. 2005; McBrearty and Brooks 2000). These key differences in diet, most likely including overall increase in energy availability as a result of increased fat and carbohydrate consumption, may have contributed to more favorable energy dynamics and increased reproductive success.

In conclusion, Neandertals occupied an ecologically precarious position in the Late Pleistocene that was highly sensitive to environmental change. The high-risk, energy-intensive subsistence strategy of Neandertals likely had consequences for both mortality and fertility. The deteriorating climate in the terminal Late Pleistocene would have presented severe challenges for the survival of the species, even without competition from modern humans. However, given evidence for resource competition and the potential for competitive exclusion, especially within the context of climatic deterioration, we cannot discount a role for modern humans. If the two species were in direct competition, several behavioral and biological features of modern humans would have led to more favorable energetic profiles and may have contributed to higher fertility and served as a competitive advantage. Even small differences in mortality or fertility, as demonstrated by Zubrow (1989), could lead to fairly rapid (<1000 years) extinction of Neandertals and replacement by modern humans.

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