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A New Estimate for Neanderthal Energy Expenditure

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by

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Abstract

Past studies exploring Neanderthal total energy expenditure have done so using an additive approach. With this method, higher energy expenditure totals relative to modern day humans have been reported for Neanderthals, thus reinforcing long held beliefs about our closest ancestor's biology and behavior. Recently, however, explorations into a variety of disciplines within the field of anthropology have provided evidence that is changing some of these perceptions. Supported by energy expenditure and allocation studies suggesting a more complex relationship between total energy expenditure and physical activity than has previously been accounted for, this study presents a new estimate for Neanderthal total energy expenditure through the use of a constrained energy model. The new estimates for Neanderthal are then considered within the context of some recent analyses investigating Neanderthal life history traits, genetics, and the archaeological record. Together, the data supports the TEE estimates shown here and the likelihood that Neanderthals expended more moderate levels of energy similar to that seen in modern day hunter-gatherer groups such as the Hadza or the Yakut.

Introduction

Of all discoveries in the field of paleoanthropology, perhaps none has had more of a prolonged and circuitous route towards understanding than that of Neanderthal. When Irish geologist William King described the Düsseldorf type specimen in 1856, he could not have known what the consequences would be from concluding that the fossils represented an extinct human ancestor of "general 'simial' appearance…and relatively low levels of intelligence" (John, 2015, p. 6). This point of view would stymie research and arrest perceptions of these human ancestors as mindless hulks for more than a century. Recently, advancements in anthropological, archaeological, and genetic contexts have begun to redeem shortsighted and inaccurate interpretations of Neanderthal biology and behavior. In 2005, for example, the first complete Neanderthal skeleton was constructed; shedding light on their capacious thorax and laying the groundwork for new avenues of research into skeletal morphology and biomechanics while advanced methods applied to the examination of dental calculus and microwear patterns of teeth have recently permitted researchers to reconsider the variability of Neanderthal diets (Bastir et al., 2015; Ben-Dor, Gopher, & Barkai, 2016; Chapman et al., 2017; Estalrrich, Zaatari, & Rosas, 2017; Henry, Brooks, & Piperno 2011; Sawyer & Maley, 2005; Zaatari, Grine, Ungar, & Hublin, 2011). Additionally, some of the latest excavations have revealed the existence of underground constructions attributed to Neanderthals while innovative models have sought to elucidate the extent of hunting capabilities as well as predict the cause of their extinction (Jaubert et al., 2016; White, Pettit, & Schreve, 2016; Gilpin, Feldman, & Aoki 2016). Further, after partial success in 2006 and 2010, researchers at the Max Planck Institute successfully decoded the entire genome of a Neanderthal individual in 2014 (Green et al., 2006; Krause et al., 2010; Prüffer et al., 2014). These breakthroughs contributed to the revelation of human/Neanderthal introgression and led to investigations into the consequences of Neanderthal DNA in the modern human genome as well as the discovery of an unidentified hominin ancestor (Burgess 2016; Krause et al., 2010; Wang, Lachance, Tishkoff, Hey, & Xing, 2013; Wall et al., 2013). Burgeoning research has therefore been helpful in clarifying the nature of Neanderthal however many questions remain. The subject of their energy expenditure is chief among them.

The field of energetics has been of great interest to evolutionary biologists since the time of naturalist Charles Darwin and Scottish anthropologist Sir Arthur Keith. From early on, energetics was an area of focus as the relationship between living things and their environment was explored. Both men sought to clarify the role of trade-offs in biology, for example, and overall made pivotal contributions to the breakthroughs credited to many modern scientists more than one hundred years later (Pontzer, 2017). By the end of the 20th century, energetics was an established part of the evolutionary paradigm. Today, evolutionary biomechanics along with explorations into the energetic and metabolic costs of bipedalism have extended the reach of evolutionary research beyond what was conceivable through only the examination of fossils (Abitbol 1995; Carey & Crompton, 2005; Pontzer & Wrangham, 2004; Steudel-Numbers 2006; Wang, Crompton, Li, & Gunther, 2003; Watson, Payne, Chamberlain, Jones, & Sellers 2008). However, while insights garnered from the application of energetics in anthropology have been instructive and productive in moving the field forward, Neanderthals have languished. A general consensus on the topic of Neanderthal energy requirements has not been reached with each analysis producing different results. To that end, this study suggests a new method and estimate for Neanderthal energy expenditure and examines that estimate's validity in the context of the latest scientific data. Empirical insight into the energetics of Neanderthal is fundamental to understanding our closest relative and the story of human origins as a whole.

Additive and Constrained Energy Models

Traditionally, energy expenditure estimates for Neanderthal have been modeled using a factorial approach. Adapted in 1985, this method is used by the Food and Agriculture Organization, World Health Organization, and International Institute for Global Health (FAO/WHO/UNU) to estimate energetic requirements for humans ("Energy Requirements of Adults", n.d.). Also identified as an additive energy strategy, this technique determines an individual’s energetic requirements by multiplying regression derived BMR estimates based on measurements of body size, age, and sex, by a predicted level of average physical activity (Churchill, 2006; “Energy Requirements of Adults”, n.d.; Pontzer, 2015a; Snodgrass & Leonard, 2009). With its roots in public health—not anthropology or paleoanthropology, the application of the additive method in extinct hominin energetic studies is a departure from its traditional clinical use. Nevertheless, studies utilizing this strategy are numerous. For example, in an effort to understand Neanderthal bioenergetics and the thermoregulatory adaptation of large chests, Churchill (2006) determined BMR through surface area estimation and used physical activity levels (PAL) informed by Inuit hunter-gatherers. Total energy expenditure (TEE) for male Neanderthals was estimated at about 4,000-5,000 k/cal while females ranged between 3,500-4,500 k/cal (Churchill, 2006). In another study, Snodgrass and Leonard (2009) contributed a thorough investigation of Neanderthal energetics utilizing published sex specific body mass estimates for Neanderthal and a BMR regression formula based on a contemporary Siberian population. A PAL was established using published physical activity values of the same subsistence population (Snodgrass & Leonard, 2009). Results placed TEE for Neanderthal males between 4,000 and 7,000 calories per day—a value that the authors suggest was likely lower than what Neanderthals truly required (Snodgrass & Leonard, 2009). In a third analysis, Sorensen and Leonard (2001) investigated foraging efficiency and estimated Neanderthal male TEE to be between 4,000-6,000 kcal/day; relying upon BMR estimates derived from WHO regressions and an assumed high level of physical activity.

The use of a factorial or additive approach is thus a well-established technique for estimating Neanderthal energy expenditure. However, while pragmatic and meaningful in short interval analyses, an additive energy model is a poor method to estimate long-term TEE

(Pontzer, 2017). To begin, an additive approach assumes non-musculoskeletal activity is fixed despite changes in an organism's actual physical behavior (Pontzer, 2015a). Studies of birds, however, have linked the reduction of non-musculoskeletal activity, such as increased inter-birth intervals as well as slower somatic repair to increases in physical activity (Derenberg & Overkamp, 1999; Wiersma, 2005). Other experiments have shown delayed growth and ovulatory cycling in mice to be associated with prolonged high levels of exertion (Perrigo, 1987). In humans, mothers from a traditional farming community who had adapted to higher than average levels of physical activity were found to have decreased BMR and hormone levels (Heini et al., 1991). Males in similarly active populations have also shown reduced hormone levels compared to other men in more sedentary cultures (Ellison, 2002). Overall, by relying on BMR, TEE estimates from an additive approach fail to capture these kinds of "adaptive and dynamic changes in allocation" that take place throughout the life of an organism (Pontzer, 2015a; Pontzer, 2015b, p.179). What's more, there is evidence to suggest that the BMR estimates themselves are flawed. Henry (2005), who has contributed a review of commonly used BMR estimate formulas, points to weaknesses in the databases and methods used to develop regressions. In the FAO/WHO/UNU application of the factorial method, a BMR regression known as the Schofield equation is argued to significantly overestimate the value in most human populations (Henry, 2005). This overestimation of BMR is likewise a contributor of elevated TEE values in Neanderthal studies that rely on FAO/WHO/UNU guidelines (Henry, 2005).

The recent work of Pontzer and colleagues who focused on energy expenditure and evolved energy strategies in both human and nonhuman primates bolsters the case against additive energy models (Pontzer, 2015a; Pontzer, Raichlen Shumaker, Ocobock, & Wich 2010; Pontzer & Wrangham, 2004; Pontzer et al*.,* 2012; Pontzer et al*.,* 2015; Pontzer et al*.,* 2016).

Broadly, Pontzer's investigations have pointed to a far more complicated relationship between PA and energy expenditure (Pontzer et al*.,* 2016). Importantly, it is an association that additive models fail to capture (Pontzer et al., 2016). In an analysis from 2012, for example, Pontzer and his team looked at the daily energy expenditure of a hunter-gatherer group from Africa called the Hadza[1]. After predicting the very active Hadza would expend more energy than typical sedentary western populations, the researchers were surprised to see expenditure levels were virtually equivalent (Pontzer et al*.,* 2012). In another study using the doubly labeled water method, Pontzer and his team explored TEE in 332 adult human individuals of mixed sex taken from five populations across the world (Pontzer et al., 2016). Results confirmed what was seen in the earlier study but the data also revealed that anthropometric variables of the test subjects only accounted for little more than half of the variation in energy expenditure with fat free mass the most robust among them (Pontzer et al., 2016). What's more, the data showed a non-linear relationship between physical activity and TEE in the upper range of analysis with expenditure values eventually plateauing despite increases in PA (Pontzer et al., 2016).

A preponderance of TEE studies drawing the same conclusions about adaptability and energy expenditure have led Pontzer and colleagues to advocate for an alternative to the common additive approach (Pontzer, 2015a). In learning about the physiological responses to increased levels of physical activity that have led to their model for TEE, these scientists have hypothesized that energy allocation across the body is reduced in the face of increased physical activity (Pontzer, 2015a). In an evolutionary context, this behavior is in accord with natural selection, allowing for reduced energy requirements during lean periods of resource availability

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[1] The Hadza are an unindustrialized people from Tanzania. They maintain small mobile groups and subsist with a traditional hunter-gatherer lifestyle thought to approximate that of our Paleolithic ancestors (Stephanie *et al* 2014).

(Pontzer 2015a). The dynamic focus of energy into organ systems accentuates the fitness of an organism by prioritizing expenditure in response to changes in conditions (Pontzer, 2015a). Thus the constrained energy model harmonizes opposing results from earlier TEE studies in a new context (Pontzer et al., 2010; Pontzer et al., 2016). The model addresses the body's ability and apparent need to maintain energy expenditure within a fixed range and draws attention to the physiology involved in diminishing the consequences of habitual physical activity. Importantly, the implementation of a constrained energy model involves the use of validated predictors of energy expenditure to estimate TEE rather than depending on a dose dependent methodology (Pontzer, 2015a; Pontzer, 2015b; Pontzer et al., 2016). Here, the constrained energy model will be used to determine Neanderthal TEE. As a new and novel approach to energy estimation it will be informative to see how a constrained energy model measures up to conventional additive methods.

Materials and Methods

In this study, Neanderthal metrics for sex, body mass, height, age, thermic effect of food, basal metabolic rate, resting metabolic rate, fat mass, fat free mass, and physical activity level were estimated for 13 male and 8 female Neanderthal fossil specimens from the middle to upper Paleolithic [Tables 1 & 2]. The male Neanderthal sample consisted of Kebara 2, La Chapelle-aux-Saints, Fon De Forét 1, La Farrassie 1, Neanderthal, Régourdou 1, Spy 2, Amud, Kiik Koba 1, and Shanidar 1-5. The female sample was comprised of La Quina 5, Spy 1, La Farrassie 2, Shanidar 6, Tabun C1, and Krapina 208, 209 and 214. Together this group represents a geographically broad set of Neanderthal individuals spanning sites found across Europe and the Near East.

Body mass and height estimates were taken from Churchill (2006) provided by Ruff, Trinkhaus, and Holliday (1997) and Feldesman, Kleckner, and Lundy (1990). Ruff's body mass estimates were achieved through three different methods depending on the completeness of each fossil assemblage. First, Neanderthal femoral head measurements were used in male and female body mass equations made from a diverse sample of modern humans (Ruff et al., 1997). Second, stature and bi-illiac breadth measurements of Neanderthal were used in male and female body mass equations derived from modern human data (Ruff et al, 1997). Last, a combined method when both femoral head and bi-illiac measurements were available was used to determine a mean body mass value (Ruff et al, 1997). Ruff computed Neanderthal height for Kebara 2, Kiik Koba 1, Régourdou 1, Shanidar 2 and 3, La Quina 5 and 18, Spy 1, and Tabun C1 (Ruff et al, 1997). The remaining Neanderthal stature estimates were established by Feldesman who developed a femur length to stature ratio based on a large sample (n=13,149) of modern humans from 51 populations and applied it to mid- and late-Pleistocene fossil hominids (Feldesman et al., 1990). Within this study, in three cases among the Neanderthal female group where height could not be estimated (Krapina 208, 209, 214), average height of the group was assigned to the individuals.

Neanderthal age was set at 24 years for both males and females based on a report by Trinkhaus (1995) because of the uncertainty involved in estimating individual age from the fossil record. Trinkhaus conducted a study on Neanderthal mortality compared to modern foraging populations based on dental development and osteological age indicators and concluded that 80% of Neanderthal adults died before the age of 40 (Trinkhaus, 1995). Fossil sampling biases aside, twenty-four years is thought to be a conservative estimate that captures Neanderthal at a metabolically prime stage of life. The thermic effect of food (TEF) was included in the final estimate as 10% of TEE and BMR for Neanderthal was estimated using the aforementioned Schofield database equation, as it is the preferred method of estimating BMR in WHO/FAO/UNU health studies as well as Neanderthal energetic analyses. Resting metabolic rate (RMR) for both low and high fat free mass was calculated using the Cunningham equation (Cunningham, 1980).

In this study, five separate human energy expenditure reports involving extant hunter-gatherer groups provided proxy measurements for Neanderthal body fat and physical activity and were also used to compare and contextualize anthropometric measurements and TEE values for Neanderthal. First, Pontzer and colleagues' 2015 Hadza study investigating the relationship between TEE and physical activity involving 15 males and 26 females (ages 18-80) provided measurements for age, mass, basal metabolic index (BMI), body fat percentage, fat free mass, and PAL, with TEE determined using the doubly labeled water method (Pontzer et al., 2015). Second, Snodgrass' analysis of the Yakut[2], a hunter-gatherer group from Siberia, involving 14 males (ages 19-47) and 14 females (ages 19-46) provided measurements for age, height, weight, body fat percentage, BMI, and PAL, with energy expenditure also determined using the doubly labeled water test (Snodgrass, Leonard, Tarskaia, & Schoeller, 2006). To model a stocky, cold adapted individual, Neanderthal was assigned a high body fat percentage ($\mu=25\%$) based on means from the same Yakut analysis while a fourth study, Pontzer's previously mentioned 2012 work on Hadza and Western population energetics, provided a mean low body fat ($\mu=13\%$/males and $\mu=20\%$/females) value to model a lean, temperate weather adapted Neanderthal (Pontzer et al., 2012; Snodgrass et al., 2006). Similarly, Neanderthal physical activity was based on the

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[2] The Yakut consist of approximately 380,000 nomadic-pastoral people from Siberia who have traditionally specialized in hunting, fishing and trapping. Today the Yakut rely on these subsistence activities supplemented with wages from the government as well as private industries. Their origins are from Mongolia and date back to 1200 AD (Snodgrass et al., 2006).

hunter-gatherer physical activity levels from these analyses. The mean PAL of all individuals was calculated for both the Hadza and Yakut hunter-gatherer groups to represent an average value of expenditure for foraging people of both low and high FFM [CPM/d=200, PAL=1.8, 2.0] (Pontzer et al., 2012; Snodgrass et al., 2006). A fifth study, Pontzer's large sample TEE study referenced above, observed a subject registering 650 CPM/d—the highest level of physical activity observed in the report, and was used here to address conventional thinking about elevated Neanderthal activity levels (Pontzer et al., 2016; Ruff, 1994; Weaver, 2009).

Variables for fat free mass, fat mass, height, age, sex, physical activity, and the thermic effect of food were inserted into an equation (see below) developed from the same constrained energy study by Pontzer, which uses standardized coefficients to estimate TEE (Pontzer et al., 2016 (see Pontzer Table 1, Model 3)). Strength of the equation in estimating energy expenditure comes from its variables, which are highly associated with TEE, especially fat free mass, which has been shown to account for 65-75% of TEE variation (Pontzer, 2015b). An estimate of TEE using an additive model, in which TEE was simply the product of BMR and PAL plus the thermic effect of food, was also used as a means to compare results between approaches.

$$\boxed{TEE = (-37.2+41.5FFM-0.9FM+1.4H+0.1A+60.2+1.1CPM+117.2)+TEF^{3}}$$

The Neanderthal energy expenditure studies mentioned in the outset and an additional analysis described below stand as a frame of reference within which the results from this work can be understood moving forward. Individual work by Churchill (2006) along with collaborative efforts from Snodgrass and Leonard as well as Sorensen and Leonard (2001) are thorough and thoughtful considerations of Neanderthal energy expenditure. All exercises, as it

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[3] FFM=fat free mass, FM=fat mass, H=height, A=age, CPM=physical activity level, TEF=thermic effect of food

has been written, reached conclusion through use of an additive energy model but each also make common assumptions. In answering the broader question of thermoregulation and the adaption of large chests, Churchill proposed Neanderthal surface area was similar to that of modern day Inuit and constructed his Neanderthal model accordingly (Churchill, 2006). Likewise, Snodgrass and Leonard based their BMR estimates on the idea that Neanderthal was closest in build to modern indigenous Siberian populations (Snodgrass & Leonard, 2009). Their study also presumed the thermic effect of food during winter months was as high as 20% and assumed elevated levels of BMR during this time to account for the effect of acute cold stress (Snodgrass & Leonard, 2009). Similarly, Sorensen and Leonard's analysis supposed a 10% upregulation of BMR to address the physiological effects of living in a glacial environment (Sorensen & Leonard, 2001). Churchill also supposed an upregulated BMR—reasoning that the effects of cold weather were diminished by calorically expensive physiological functions as opposed to physical barriers and buffers (Churchill, 2006). In another report exploring cold adaptation of Neanderthal, Steegman did not employ an additive approach but rather used expenditure values for circumpolar people by Shepard and Rode (1996) to extrapolate Neanderthal TEE (Steegman, Cerny, & Holliday, 2002). Critically, each of these examinations assumed a level of physical activity higher than the hunter-gatherer PAL averages used in this study. Sorensen and Leonard's model of TEE, for instance, proposed a very active Neanderthal with PAL values 1.5 times more active than averages recorded for Yakut in Snodgrass' study (Sorensen & Leonard 2001). The incorporation of both high and low fat mass estimates as well as high and moderate physical activity variables in this analysis goes a step further than past approaches by representing a variety of Neanderthal profiles.

Results

At 650 CPM/d within the constrained energy model, the male Neanderthals of low FFM expressed TEE within a range of 3,454-4,019 k/cal (μ=3,758 k/cal) [Table 3]. Females in this same group ranged 3,115-3,538 k/cal (μ=3,328 k/cal) [Table 4]. Alternatively, Neanderthal males of high FFM showed a slightly higher range of energy expenditure with values from 3,828-4,483 k/cal (μ=4,180 k/cal) [Table 5]. Females ranged from 3,258-3,710 k/cal (μ=3,487 k/cal) [Table 6].

Assigning a CPM/d of 200 (PAL~1.8, 2.0) produced expected results as both groups experiencing a reduction in physical activity saw average TEE values reduced by nearly 500 k/cal or about 13%. These results were the lowest of all TEE estimates produced in this study. Neanderthals males of low FFM under these conditions span a TEE range of 2,959-3,524 k/cal (μ=3,263 k/cal) [Table 7]. Females ranged from 2,620-3,043 k/cal (μ=2,833 k/cal) [Table 8]. Male Neanderthals with high FFM expressed a slightly higher range of TEE from 3,333-3,988 k/cal (μ=3,686 k/cal) while females with this profile ranged between 2,764-3,215 k/cal (μ=2,992) [Tables 9 & 10].

In the additive model iteration, PAL was again adjusted to represent vigorous levels of physical activity (650 CMP/d or PAL= ~2.2). TEE for Neanderthal males under these conditions ranged from 3,832-4,369 k/cal (μ=4,120) and 3,106-3,508 k/cal (μ=3,308) in females [Tables 11 & 12]. When PAL was adjusted to the modern hunter-gatherer mean (CPM/d=200 or PAL=1.86), male Neanderthal TEE values fell to between 3,311 and 3,859 k/cal (μ=3,606). Females ranged from 2,624 to 3,029 k/cal (μ=2,829 k/cal) [Tables 13 &14].

The new ranges of estimated energy expenditure, one of estimated low FFM, one of estimated high FFM, and each modeled at 650 CPM/d as well as 200 CPM/d provide a new and variable framework to think about Neanderthal TEE. Generally, both low and high FFM at 200 CPM/d the constrained model provides the some of the lowest estimates compared to the other Neanderthal TEE analyses so far, although there is slight overlay in the range of values provided by Steegman (2002), Churchill (2006), and Sorensen and Leonard (2001). When modeled using the high level of physical activity, 650 CPM/d, the Neanderthal TEE results were nested within the estimates provided by Steegman (2002), Churchill (2006) and Sorensen and Leonard (2001), but are generally lower and only slightly overlap the values predicted by Snodgrass and Leonard (2009). As expected, additive method estimates from both categories of physical activity were marginally higher compared to the values generated in their respective constrained model group Again, additive model TEE values assuming a PAL of 200 CPM/d overlap predictions of energy expenditure from Steegman (2002), Churchill (2006), and Sorensen and Leonard (2001) but are lower than reported numbers from Snodgrass and Leonard (2009). At 650 CPM/d, the additive approach from this study produces results most closely in line with those reported by Steegman (2002), Churchill (2006), Sorensen and Leonard (2001), and Snodgrass and Leonard (2009) [Table 15]. As discussed, these studies often factored in additional calorically expensive activities or behaviors that likely account for the difference in the values reported here. On its face, the TEE values from the additive model in this study and the constrained approach appear equivocal, as they bare only slight differences from one another. In short intervals, this would likely be the case but as has been mentioned, energy expenditure has been shown to be affected by long durations of physical activity—a physiological mechanism the constrained energy approach aims to account for in its reliance on fat free mass related variables. Additionally important to the comparison of the energy models used is the phenomenon—discussed earlier and elaborated on by Pontzer (2015a), of energy expenditure totals in a physically active individual to plateau before exceeding a set threshold, negating the effects of increased levels of PAL typically assumed in additive model studies. As new investigation unfold into this biological occurrence, they will have an important impact on the way Neanderthal energetics are considered.

The TEE values as a whole generally situate Neanderthal within the upper range of TEE observed in modern day hunter-gatherer populations, reorienting Neanderthals as energetically demanding but not significantly more so than their *Homo sapiens* counterparts [Figures 1-4]. Specifically, when modeled at 200 CPM/d, Neanderthals of both low and high FFM group the closest with the modern hunter-gatherers [Figure 3 & 4]. Under this level of physical activity, the average PAL of hunter-gatherers used in this study, Neanderthals most closely resemble the Yakut.

Discussion

The energy estimates in this analysis are the results of a more robust approach compared to those used in other Neanderthal TEE studies (Churchill 2006; Snodgrass & Leonard, 2009; Sorensen & Leonard, 2001). PAL values reflecting traditional views of a vigorous Neanderthal are represented in addition to the conservative PAL estimates that represent a more moderately active lifestyle. Likewise, both high and low FFM values offered here provide an opportunity to consider energy expenditure totals for Neanderthal of two body types. The combination of these variables in a constrained energy model return a broad spectrum of results and does so without making assumptions on the conjectural aspects of Neanderthal biology and behavior. What follows is a review of scientific literature to explore how these moderate TEE estimates comport with some of the new understandings of Neanderthal in three areas of study beginning first with a look at the relationship between TEE and life history traits. Second, an evaluation of the genetic breakthroughs and the contributions they have brought to the study of paleoanthropology. Lastly, an examination of some of the most recent archaeological findings and what they reveal about Neanderthal energetics. These areas of investigation can provide a balanced assessment of Neanderthal biology and behavior and help to substantiate or disprove the suggested expenditure values offered.

Neanderthal Life History

There is a direct relationship between an organism's life history and the energy it expends. All aspects that determine the evolutionary success of a life form, such as its rate of growth and reproduction, are components of a whole energy budget (Pontzer et al., 2014; Smith & Tompkins, 1995). With great variety in the life histories of organisms, studies have sought to quantify the differences. Research on mammals has narrowed focus of this subject to the role of metabolic adaptation and energy reallocation to explain the variability of energy use strategies. Studies of primates, which have fewer offspring, delayed sexual maturation, and longer inter birth intervals than members of other orders, have returned important and intriguing results on this matter (Fleagle, 1999; Jones, 2011; Pontzer et al., 2010; Pontzer et al., 2014; Robson & Wood, 2008). As a group, primates expend less energy than what would be predicted for other mammals of similar size and hominoids even more so (Pontzer et al., 2010). These metabolic changes could be viewed as adaptations to physiology and surrounding ecology (Pontzer et al., 2010). Orangutans, for example, live in an environment with volatile resource availability and have the lowest TEE levels for any primate when controlled for body size (Pontzer et al., 2010). Overall, what seems certain is that lower metabolic rates are a contributing component to slow life histories of primates (Pontzer et al., 2014). Analyses reporting evidence of life history characteristics of Neanderthal might thus provide a clue for how to think about their TEE. Robson and Wood's study of second order life history variables provides a good framework to discuss the information value of hominin life history studies (Robson & Wood, 2008). These variables: body mass, dental development and brain size will be discussed going forward.

Robson and Wood found body mass to be strongly correlated with first order life history variables in great apes and suggest there is strength in using body mass to determine those life history characteristics in fossil hominins (Robson & Wood, 2008). Increase in body mass can occur in response to nutrition and local selection pressures but also from selection in reduction of body mass sexual dimorphism (Plavcan, 2012; Robson & Wood, 2008). Working backwards, evidence of substantial reduction in sexual dimorphism and increased body mass in the fossil record implies long lives, a slow period of juvenility and delayed sexual maturity each of which are attributable to a pace of life-history equal or similar to that seen in modern humans. Robson and Wood suggest modern human-like sexual dimorphism was likely present from the time of *Homo heidelbergensis* onward—a span that includes Neanderthal (Robson & Wood, 2008). Thus, analyses comparing Neanderthal and modern human growth can reveal the degree to which Neanderthal and human life histories differed which may allow for important insights into their energy expenditure.

Thompson and Nelson (2001) took a broad look at maturation rates in the fossil record and determined full maturation of dental, cranial, and postcranial elements of Neanderthal was achieved by periods of growth and delay dissimilar to *H. sapiens*. However, when difference in adult body size between the species was accounted for, the growth rates appeared more similar (Thompson & Nelson, 2001). More recently, Rosas and workers (2017) reconstructed the development of Neanderthal using a juvenile specimen from El Sidrón, Spain. The specimen, estimated to be about 7 years old at the time of death, consisted of cranial, dental, and postcranial material giving researchers an opportunity to appreciate body mass and growth from analysis of a single individual (Rosas et al., 2017). Dental development of the individual fell within the range of modern tooth type and in general, growth of the postcranial skeleton followed similar rates as well (Rosas et al., 2017). Brain development in the specimen from El Sidrón was 87.5% of mean brain size of adult Neanderthals compared to 95% observed in modern humans indicating brain mass continued to grow beyond the seventh year (Rosas et al., 2017). Rosas and colleagues concluded the specimen was consistent with the markers of human ontogeny and suggested a slow pace of life would have facilitated fluctuations in brain growth (Plavcan, 2012; Rosas et al., 2017).

The type of big picture analysis provided by the El Sidrón specimen is important because it allows researchers to assess the growth of a variety of aspects in context with one another. Many isolated tooth analyses, for example, lack this kind of association leaving their utility as a life-history indicator less clear. Studies engaged in analysis of tooth growth as a marker for life-history traits have included analysis of perikymata packing patterns on anterior dentition as well as tooth enamel formation and tooth eruption (Dean et al., 2001; Macho, 2001). Robson and Wood state the latter is considered the best predictor of life history in extant primates although its application in the fossil record has proven difficult (Robson & Wood, 2008). Broadly, there is great variation among all aspects of tooth development in great ape species and the correspondence between these measures and life history traits is not all that strong (Robson & Wood, 2008). As such, studies investigating Neanderthal tooth development have returned contradictory results that cast doubt on reliability of the approach. Machiarelli et al. (2006), for example, looked at internal microstructure of a single Neanderthal molar to determine enamel and root formation times compared to modern humans and reported results that all but confirm the likeness between Neanderthal and human life history variables. Smith and colleagues' however, used a similar method applied to a juvenile Neanderthal mandibular specimen from Belgium and drew different conclusions (Smith, Toussaint, Reid, Olejniczak, & Hublin, 2007). Results from their study asserted the slow paced life exhibited by *H. sapiens* was unique to them (Smith et al., 2007).

As with tooth development, Robson and Wood raised concerns about assumed differences between chimpanzee and human brain development and their applicability in making inferences about hominins (Robson & Wood, 2008). From a cross-sectional data set of humans and chimpanzees, they found humans achieve 90% of their adult brain size far earlier than expected considering long subadulthood and long life-history and do so only one year later than chimpanzees (Robson & Wood, 2008). Additionally, Robson and Wood claimed at time of birth, chimpanzee and human brain size is relatively much more similar than previously assumed and also found similar relative growth trajectories in chimpanzees and humans complicating the idea that modern human adult brain size is the result of a longer duration of post-natal brain growth (Robson & Wood, 2008). Generally, their work upends notions that brain growth and development determine the rate of life history as brain growth in their study was poorly correlated to length of adulthood in humans and chimpanzees (Robson & Wood, 2008). Instead, a key distinction made by the authors places emphasis on pace of growth, which is likely set by mortality rates determined by environmental risks while features of ontogeny conform to life-history parameters (Robson & Wood, 2008). This important point in the brain-growth-life-history-relationship was also made wtih León and colleagues' (2008) reconstruction of three

Neanderthal neonates from Russia and Syria. There, Neanderthal brain growth at the time of birth was the same as that seen in modern humans but the authors went on to claim that compared to modern humans, Neanderthals had a higher pace of brain growth following birth that allowed for their large brains and a life-history that was as slow or perhaps lagged in comparison to H. sapiens (Léon et al., 2008). These results were later corroborated by a different study from Gunz and collegues (Gunz, Neubauer, Maureille, & Hublin, 2010). A more recent follow up by León and associates (2016) from an analysis of an expanded Neanderthal sample reiterates original conclusions that Neanderthal endocranial development was similar to the growth observed in modern humans, a finding which challenges concepts of biologic uniqueness in our species (León, Bienvenu, Akazawa, & Zollikofer, 2016). Until more data and analysis emerge that further demystify brain growth velocity and life history traits in great apes and humans, adult brain size has been shown to correlate strongly with many life-history variables (Robson & Wood, 2008). In their investigation of this connection, Robson and Wood plotted endocranial volume of Neanderthals with other hominin taxa and found the group to be indistinguishable from *H. Sapiens* (Robson & Wood, 2008).

For now, while analyses of body mass, dental growth, and brain development return mixed results as they pertain to hominin life history, the studies provide an important framework future investigations can build on. A deeper understanding of life history markers along with the biological and physiological responses associated with them should further propel forthcoming studies of human Neanderthal TEE. If prospective exploration into these areas of Neanderthal life-history confirms some of the conclusions discussed here—those that determine the timing and rate of Neanderthal life history variables were the equivalent to that seen in modern humans, it would align Neanderthals closer with modern humans and lend further support to more moderate estimates of TEE like the ones presented in this study.

Neanderthal Genetics

Genetic analysis as it pertains to Neanderthal dates back to 1997 when mitochondrial DNA (mtDNA) was successfully extracted and duplicated from the humerus of the type specimen from Dusseldorf (Krings et al., 1997). Results from the study placed Neanderthal mtDNA outside that of modern humans and showed the Neanderthal mtDNA sequence diverged before mtDNA divergence in human lineages (Krings et al., 1997). Research from 2006 of one million base pairs of Neanderthal DNA proposed this time of separation at approximately 500,000 years and overall demonstrated the feasibility of massive sequencing of the Neanderthal genome (Green et al., 2006; Meyer et al., 2012). A 2014 study that successfully mapped the Neanderthal genome, along with works from 2012 and 2016 that partially explicated the extent of Neanderthal-modern human gene flow, have made the last twenty years a truly new and productive era of Neanderthal research (Green et al., 2006; Martin et al., 2016; Prüfer et al., 2014; Sankararaman, Patterson, Li, Pääbo, & Reich, 2012).

With genetic studies of Neanderthal in the opening stage, answers to many specific questions remain elusive while the breakthroughs and assertions one day are sometimes called into question the next. In 2007, for instance, the derived version of a gene involved in affecting development of human language, known as FOXP2, was found in the genome of Neanderthals from Spain and suggested to be present in the common ancestor of Neanderthals with humans (Krause et al., 2007). The implications were immediately apparent and the consideration that Neanderthal was capable of sophisticated verbal communication became a real possibility. In

2008, however, Coop and colleagues challenged the timing of the FOXP2 selective sweep, or when the allele became fixed within the human genome, with an analysis of their own and claimed the proposed date of fixation (300,000 years ago) was actually much more recent (Coop, Bullaughey, Luca, &Przeworski, 2008). Their work led the researchers to offer that the gene observed in the Neanderthal genome could have introgressed from humans but also raised concerns about human contamination in the Neanderthal DNA sample (Coop et al., 2008). In 2013, Maricic et al. reported on the cause of the FOXP2 selective sweep in humans and proposed that a substitution at a transcription factor binding site affecting regulation of the gene was likely responsible.

Collectively these studies exemplify the promise genetics bring to paleoanthropology in delivering new lines of inquiry. Still, they serve as a reminder that the work is ongoing and often raises more questions than answers. Indeed, investigations into FOXP2 continue and considerable debate persists around the question of Neanderthal language. Ultimately, should the evidence support complex verbal communication amongst Neanderthal, the implications would follow a trend in upsetting long-held notions about Neanderthal general intelligence. A Neanderthal's ability for language would affect ideas about their capacity for symbolism and problem solving and restructure concepts about their social networks and interactions. Significances would extend into the realm of energetic studies affecting concepts of Neanderthal hunting and foraging efficiency and thus diet, the latter of which will be discussed at further length in the next section.

Setting language aside, genetic analysis has sought to address another aspect of Neanderthal biology—one with more direct consequences for their TEE. Brown adipose tissue has been proposed as a feature of Neanderthal physiology to insulate against the elements. This idea draws support from a variety of studies in human and non-human primates that indicate brown adipose tissue in some humans is present in greater quantities and performs a larger role than suspected (Beall, Jablonski, & Steegman, 2012; Chafee et al., 1975; Hims-Hagen, 1984; Lean, 1989; Nedergaard, Bengtsson, & Cannon, 2007; van Marken Lichtenbelt, et al., 2009). In Steegman's study on Neanderthal cold adaptation, he writes at length of non-shivering thermogenesis facilitated by brown adipose tissue (Steegman et al., 2002). Functionally, thermogenesis occurs as a sympathetic response to cold stress and results in the release of energy (heat) within cell mitochondria (Sazzini et al., 2014). Working in concert with active and passive methods of thermoregulation such as reduced perception of pain related to cold, localized control over vasoconstriction and vasodilation, and increased muscle mass and subcutaneous fat, brown adipose tissue would theoretically mitigate the effects of cold on Neanderthal bodies by elevating an individual's BMR in response to drops in ambient temperature (Sørensen, 2009; Steegman et al., 2002). Studies that utilize an additive method for energy estimation, of which BMR is a main component, would thus return higher TEE estimates to account for this thermoregulatory feature. Churchill's research used within this study as a comparative TEE analysis adopts Steegman's view that this kind of body fat was present in Neanderthal. In Churchill's work, the metabolism of brown adipose tissue is presented as support to assume elevated levels of TEE (Churchill 2006; Steegman et al., 2002). Likewise, adipose tissue as a thermoregulator is a partial component to the premise devised by Snodgrass and Leonard in establishing pronounced levels of BMR and, by extension, elevated TEE (Snodgrass & Leonard, 2009).

A genetic study of 10 indigenous Siberian populations including the Yakut identified several genes positively selected for cold adaptation (Cardona et al., 2014). These genes code for the secretion of a hormone that activates non-shivering thermogenesis as well as for mechanisms regulating systolic blood pressure, andrenarche, vasoconstriction, vasodilation, and general smooth muscle function all of which are relevant to cold adaptation (Cardona et al., 2014). The analysis highlights the non-uniform way in which cold adaptation physiology has spread among different populations but also underscores how harsh weather acclimatization in humans is accomplished through a concert of genes that produce a multitude of physiologic responses (Cardona et al., 2014). Largely, the study presents important research that point to alternative methods of thermoregulation if quantities of brown adipose tissue were only partial or completely absent in Neanderthal (Cardona et al., 2014). A different study by Racimo and colleagues (2016) conducted on the genome of Inuit from Greenland suggests this might have been the case. In it, two genes for cold adaptation influencing the development of adipose tissue and distribution of body fat were traced to their source (Gburcik, Cawthorn, Nedergaard, Timmons, & Cannon, 2012; Heid et al., 2011; Liu et al., 2013, Liu et al., 2014; Racimo et al., 2016; Shungin et al., 2015). The research showed the haplotype for the associated genes was introduced into modern populations via introgression with an archaic ancestor more closely related to a different hominin species known as the Denisovans[4] instead of Neanderthal, suggesting the sequence could be missing from the genomes of Neanderthals entirely (Racimo et al., 2016). Another study from 2014 seems to support this possibility. Scientists examined a panel of 28 genes involved in the pathway to metabolism or regulation of brown adipose tissue in

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[4] In 2010 mitochondrial DNA was extracted from the distal fifth phalanx of a hominin individual recovered from the Denisova cave site in Altai, Russia. The original analysis revealed the mtDNA sample was neither human nor Neanderthal and it contained nearly twice the number of differences modern human mtDNA has to Neanderthal (Krause et al., 2010). One recently proposed estimate for the divergence of Neanderthals and Denisovans is 445,000-473,000. years ago while a purported date of separation of modern humans from Neanderthals and Denisovans is 550,000 to 765,000 years ago (Racimo et al, 2016).

populations from Africa, East Asia, and Europe as well as samples of Neanderthal and Denisovans (Sazzini et al., 2014). The objective was to identify patterns of variation in the genes to help better understand the evolution of thermogenesis and thermoregulation in humans and our ancestors (Sazzini et al., 2014). Crucially, introgression of these alleles from Neanderthals and Denisovans to humans was limited, leading researchers to speculate that archaic humans may have independently evolved entirely different biologic mechanisms along different functional pathways to assuage the effects of cold weather (Sazzini et al., 2014).

The areas of interest touched on above will continue to allow for a more focused and nuanced perspective of Neanderthal especially as the field of genetics proceeds to develop and innovate. For instance, the discipline of epigenetics is a new area of research and has already produced intriguing results for paleoanthropology by exploring gene regulation through non-genetic influence (Schneider, El Hajj, & Haaf, 2014). In the interim, the advancements made thus far should caution the use of some traditional assumptions. Estimating differences in Neanderthal and modern human thermoregulation, for example, is a complicated task requiring inherently speculative methods to predict Neanderthal BMR, insulation provided by muscle and fat or body hair, as well as surface area of head, hands and feet to calculate loss of body heat (Wales, 2012). Research of the last twenty years has shown that Neanderthal shares 99.5% DNA with *Homo sapiens*, and perhaps biologically should not be expected to behave radically different from humans (Noonan et al., 2006). Where genetic analysis has highlighted distinctions between the species, it would be prudent to consider them in future TEE analyses.

Neanderthal and the Archaeological Record

Archaeological investigations into Neanderthal have, for some time, gone beyond excavations of stone and bone. Ecology, specifically diet, along with cognition are two such areas of inquiry that factor into Neanderthal TEE in direct and incidental ways. Historically, the Neanderthal diet has been defined by protein (Fairzy, David, & Jaubert, 1994; Jaubert et al., 1990; Mellars, 1996; Stiner, 1994). Bolstered by the ubiquity of faunal remains discovered in association with paleolithic fossil sites, this characteristic of Neanderthal has long been central to their reputation as habitual predators (Churchill, 2006; Estalrrich et al., 2017; Richards et al., 2000; Steegman et al., 2002). Indeed, a comprehensive review by Patou-Mathis (2000) of faunal assemblages from 323 Neanderthal fossil sites throughout Europe depicted Neanderthal as a voracious and widespread hunter. Chemical analyses have also supported this idea (Bocherens, Drucker, Billiou, Patou-Mathis, & Vandermeersch, 2005; Henry et al., 2011; Hovers, 2006; Richards & Trinkhaus, 2009). A study by Richards and colleagues (2000) analyzed stable isotopes of bone collagen from two Neanderthal fossils from Croatia and confirmed large quantities of meat made up the Neanderthal diet. However, more recent works have questioned such a conclusion and suggest a shift in thinking might be needed. A study from 2008, for example, looked into the diet of coastal Neanderthals from sites at Gibralter and determined consumption of marine life was not uncommon, effectively broadening Neanderthal's subsistence repertoire (Stringer et al., 2008). A different investigation exploring exploitation of megafauna by Neanderthal in Western Europe supported the notion of a meat-oriented diet but cautioned the use of isotope analyses in drawing the conclusion that nutrition came from large terrestrial mammals (Smith, 2015). Instead, the authors suggest megafauna hunting was "opportunistic" and Neanderthal meat more likely came from medium-sized ungulates (Smith, 2015). In 2012, Hockett explored the repercussions of a high protein diet on a pregnant Neanderthal. Using Snodgrass and Leonard's (2009) BMR estimates for a female Neanderthal and assuming a high level of physical activity, pregnant Neanderthals were estimated to require 5,500 calories per day (Hockett, 2012). Reconstruction of the diet needed to achieve this sum of calories, consisting strictly of terrestrial herbivores, was shown to kill the expectant Neanderthal and her fetus due to vitamin and nutrient poisoning (Hockett, 2012). A reduction of the daily caloric requirements did little to resolve the macro and micronutrient related issues (Hockett, 2012). Still, the strongest evidence to support the idea that Neanderthal diets were more varied and supplemented by plant-based resources comes from a multitude of dental, and more recently, dental calculus analyses (Fiorenza et al., 2015; Hardy et al., 2012; Henry et al., 2011; Henry, Brooks, & Piperno, 2014; Sistiaga, Mallol, Galván, & Simmons, 2014; Zaatari et al., 2011). Henry and colleagues (2011) looked at the dental calculus from the teeth of three Neanderthal individuals from Iraq and Belgium and observed a variety of starch grains and phytolith microfossils present on the samples. The plants consumed by the individuals consisted of grasses, legumes, and dates, some of which showed evidence of being cooked (Henry et al., 2011). In a follow up study, Henry (2014) examined 209 Neanderthal and middle-upper Paleolithic modern human samples from 30 sites in the Near East, Europe, and Africa. The material allowed the researchers to make comparisons between Neanderthal and human plant usage but also facilitated exploration of the geographic breadth of plant consumption (Henry et al., 2014). Results of the analysis indicated widespread exploitation of plants as food amongst Neanderthal and modern humans leading the scientists to surmise there was little difference in plant use between species (Henry et al., 2014). Moreover, the conclusions went further to suggest that Neanderthal's varied and habitual recruitment of plants as food were indicative of an investment in technology and likely a division of labor (Henry et al., 2014). Power and colleagues (2018) recent work supports these ideas. Presenting an environmentally diverse analysis of Neanderthal dental calculus, they concluded plant consumption was widespread and an entrenched method of subsistence (Power et al., 2018).

As is the case with diet, Neanderthal cognition is a topic of interest not without competing perspectives. Researchers have long debated the degree to which Neanderthal brainpower differed from modern humans, with advocacy for each perspective drawn distinctly. However, as is also the case with the study of Neanderthal diet, new perspectives are emerging due to advanced investigative methods as well as reinvigorated interest in old discoveries. Together with DNA analyses, which have explained the common legacy and shared genetics of Neanderthal and modern humans, archaeology is strengthening the argument that Neanderthal cognition was comparable to *Homo sapiens* (Martin et al., 2016; Sankararaman et al., 2012). For example, archaeologists at a site in Northern Italy found an abundance of faunal remains including 660 bones of 22 avian species of which several birds of prey were found apparently harvested for decorative feathers (Peresani, Fiore, Gala, Romandini, & Tagliacozzo, 2011). In a different study from 2017, a raven bone uncovered in Crimea was found decorated with notches attributed to Neanderthal, and presented as some of the latest evidence in support of symbolic thought (Ana et al., 2017). Recently, pieces of cave art from three walls within the Monte Castillo cave complex in Spain were dated to a minimum of 64,800 years, predating the appearance of modern humans in Europe by 20,000 years and thus implicating the artists were Neanderthals (Hoffman et al., 2018). The images drawn in red pigment are perceived by scientists as symbolic depictions of a series of dots, lines, and hand stencils that were intentionally displayed on specific regions of rock surface (Hoffman et al., 2018). Further, the cave art is argued to have likely been an established behavior by Neanderthals from the dated time period and is assumed to be present in other cave systems throughout Europe (Hoffman et al., 2018).

The substantial amount of evidence indicating Neanderthals possessed the requisite capacity for personal adornment and symbolic thought bolsters material support for their use of clothing and fire. It would not be sensible to allow for Neanderthal creative ability in one sense and deny it in another. The routine incorporation of either combustion or dressings to manage life on a daily basis has obvious consequences for Neanderthal energy expenditure as recruitment of fire or clothing for warmth would address the problem of heat loss during spells of extreme cold in an energetically inexpensive way. Evidence of use of fire by Neanderthals is well documented and known from European sites as well as the Near East (Berna & Goldberg, 2007; Meignen, Goldberg, & Bar-Yosef, 2007; Sørensen 2009; Vaquero, Vallverdo, Rosell, Pastó, & Allué, 2001). Excavations at the Middle Paleolithic level at Kebara cave in Israel have uncovered an abundant amount of features indicating combustion events including hearths in a variety of modalities (Meignan et al., 2007). Albert and collegues (2012) contributed an extensive analysis of plant use at fire sites in Kebara through micromorphologic analysis of phytoliths, or silica left over from the original plant sources, that were present in the cave sediment. Their work identified tree bark and a variety of grasses which overall allowed them to conclude that plant use for fire was common in the caves (Albert, Berna, & Goldberg, 2012). In Europe, work investigating fire at a two sites in France, Peche de l'Asé IV and Roc de Marsal revealed an assortment of locations as well as a diversity of techniques and morphology involved in the hearth construction (Goldberg et al., 2012). Comparative analyses between the sites highlight these differences however it should be pointed out the specific utility of the hearths and the fire they once contained remains unknown (Goldberg et al*.,* 2012).

Compared to the evidence in support for use of fire, substantiation of Neanderthal clothing is far more limited (Wales, 2012). This is due in large part to the decay of organic materials over several thousand years in addition to the uncertainty surrounding lithic artifacts that may or may not have been involved in the preparation and production of clothing (Keeley, 1980; Wales, 2012). Additionally, in comparison to sites recognized as belonging to early anatomically modern human, Neanderthal sites are remarkably lacking in clothing-specific tools that would indicate activities such as weaving or sewing (Soffer, 2004). This paucity of proof has led a number of researchers like Gilligan and Churchill to simply conclude that Neanderthals did not wear clothing at all (Gilligan, 2007; Churchill, 2006; Wales, 2012). This point of view advocates for methods of thermoregulation like the ones outlined above but as Wales (2012) points out, it is a deduction made without the benefit of any research attempting a detailed reconstruction of Neanderthal garments. To supplement the incomplete data on Neanderthal clothing, Wales used Binford's geographically broad database of descriptions and photographic data of 595 individuals from 245 modern hunter-gatherer groups as well a wind chill temperature index compiled by the National Oceanic and Atmospheric Administration to develop a predictive model to estimate types of Neanderthal clothing as well as what body parts would have needed to been covered (Wales, 2012). The research concluded that clothing would have been essential for Neanderthals however the type and degree of coverage would have been dependent on location and season (Wales, 2012). Collard and colleagues (2016) also used ethnographic evidence to approach the question of Neanderthal clothing. Looking at this data along with faunal remains uncovered in Neanderthal associated strata, their work demonstrated differences in early modern human and Neanderthal clothing, and determined clothing would have been an imperative for Neanderthals (Collard et al., 2016). Different from the conclusions drawn by Wales, Collard suggests Neanderthals would have employed pliable, form-fitting cape-like garments compared to the dedicated cold weather clothing of their early modern human counterparts (Collard et al., 2016).

Together these studies have an impact on Neanderthal TEE. In the case of Neanderthal plant use, the effects are twofold. First, steady supplementation of typically low calorie plant foods would indicate the required caloric threshold for Neanderthal was low. Second, if Neanderthal TEE constraints were conservative, they were likely being met with minimal effort, requiring levels of physical activity like those observed in modern hunter-gatherer groups, not the exorbitant values of PAL suggested in other TEE studies. The consequences of Neanderthal use of fire and clothing are similarly straightforward. Both strategies of cold weather buffering would diminish the affects of cold weather on Neanderthals. From the perspective of modeling TEE, a Neanderthal's reliance on the strategies of fire and clothing would lessen the need for substantially inflated levels of BMR or thermoregulatory techniques, which add to the total energy budget.

Conclusion

As recent investigations into human energetics have shown energy expenditure to be more complex than ever suspected, the time has come to rethink strategies and concepts for comprehending Neanderthal TEE. The TEE estimates reported here are a step towards that goal; they have been attained through the use of a constrained energy approach and are generally more modest than the values described in past Neanderthal studies that have employed an additive model. The values are supported by a growing number of life-history, genetic, and archaeological studies that continue to upend longstanding notions and blur the line distinguishing Neanderthal and modern human biology. While more work needs to be done, these areas of focus support the estimates provided within this report, as they suggest Neanderthal was similar to modern hunter-gatherers in terms of total energy expenditure.

There are inherent challenges associated with modeling Neanderthal TEE. For example, there is great uncertainty involved in the estimation of Neanderthal body mass and average levels of physical activity—two important variables in TEE estimation. These impediments, however, should not deter future investigations into Neanderthal TEE as this study has shown there is resolve that can be found in the interplay between energetic and paleoanthropologic studies.

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Tables and Figures

*Table 1. Male Neanderthal body metrics**

ID	Age	Height	Mass (kg)	BMR (kcal/d)	HFFM RMR (kcal/d)	LFFM RMR (kcal/d)	HFFM (kg)	LFFM (kg)
Kebara 2	24	166	75.6	1834	1939	1744	65.4	56.5
La Chapelle	24	162	75.8	1860	1971	1772	65.6	56.7
Fon De Foret 1	24	160	83.9	1961	2097	1881	72.6	62.8
La Farrassie 1	24	172	85	1978	2118	1899	73.5	63.6
Neanderthal	24	166	78.9	1885	2001	1798	68.3	*59*
Regourdou 1	24	164	72.1	1781	1872	1686	62.3	53.9
Spy	24	161	83.6	1957	2091	1876	72.3	62.5
Amud	24	179	75.3	1830	1933	1739	65.1	56.3
Kiik Koba 1	24	164	78.1	1873	1986	1785	67.6	58.4
Shanidar 1	24	172	80.5	1909	2032	1825	69.6	60.2
Shanidar 2	24	160	75.2	1828	1931	1737	65	56.2
Shanidar 3	24	166	79.9	1900	2021	1815	69.1	59.8
Shanidar 4	24	161	72	1779	1870	1685	62.3	53.9
Shanidar 5	24	168	68.5	1726	1804	1627	59.3	51.2

*Table 2. Female Neanderthal body metrics**

ID	Age	Height	Mass (kg)	BMR (kcal/d)	HFFM RMR (kcal/d)	LFFM RMR (kcal/d)	HFFM (kg)	LFFM (kg)
Krapina 208	24	156	68.4	1502	1704	1626	59.2	51.2
Krapina 209	24	156	63.7	1433	1621	1548	55.1	47.7
Krapina 214	24	156	62.2	1411	1595	1524	53.8	46.5
La Quina 5	24	163	71.2	1543	1753	1672	61.6	53.3
Spy 1	24	161	67.5	1489	1688	1611	58.4	50.5
La Farrassie 2	24	155	67	1481	1680	1603	58	50.1
Shanidar 6	24	148	59.4	1370	1545	1478	51.4	44.4
Tabun C1	24	156	63.2	1425	1612	1540	54.7	47.3

*BMR=basal metabolic rate, HFFM=high fat free mass, LFFM=low fat free mass, RMR=resting metabolic rate

Table 3. Constrained Energy Model Total Energy Expenditure for Male Neanderthals of Low Fat Free Mass (650 CPM)

ID	LFFM (kg)	TEE LFFM (k/cal)
Kebara 2	56.5	3691
La Chapelle	56.7	3743
Fon De Foret 1	62.8	3963
La Farrassie 1	63.6	4020
Neanderthal	59	3803
Regourdou 1	53.9	3570
Spy	62.5	3955
Amud	56.3	3701
Kiik Koba 1	58.4	3773
Shanidar 1	60.2	3867
Shanidar 2	56.2	3669
Shanidar 3	59.8	3837
Shanidar 4	53.9	3562
Shanidar 5	51.2	3454

Table 4. Constrained Energy Model Total Energy Expenditure for Female Neanderthals of Low Fat Free Mass (650 CPM)

ID	LFFM (kg)	TEE LFFM (k/cal)
Krapina 208	51.2	3432
Krapina 209	47.6	3273
Krapina 214	46.5	3222
La Quina 5	53.3	3538
Spy 1	50.5	3409
La Farrassie 2	50.1	3383
Shanidar 6	44.4	3115
Tabun C1	47.3	3256

Table 5. Constrained Energy Model Total Energy Expenditure for Male Neanderthals of High Fat Free Mass (650 CPM)

ID	HFFM (kg)	TEE HFFM (k/cal)
Kebara 2	65.4	4104
La Chapelle	65.6	4165
Fon De Foret 1	72.6	4421
La Farrassie 1	73.5	4483
Neanderthal	68.2	4234
Regourdou 1	62.4	3963
Spy	72.3	4411
Amud	65.1	4112
Kiik Koba 1	67.6	4199
Shanidar 1	69.6	4305
Shanidar 2	65	4079
Shanidar 3	69.1	4273
Shanidar 4	62.3	3955
Shanidar 5	59.3	3828

Table 6. Constrained Energy Model Total Energy Expenditure for Female Neanderthals of High Fat Free Mass (650 CPM)

ID	HFFM (kg)	TEE HFFM (k/cal)
Krapina 208	59.2	3598
Krapina 209	55.1	3427
Krapina 214	53.8	3373
La Quina 5	61.6	3710
Spy 1	58.4	3573
La Farrassie 2	58	3545
Shanidar 6	51.4	3259
Tabun C1	54.7	3409

Table 7. Constrained Energy Model Total Energy Expenditure for Male Neanderthals of Low Fat Free Mass (200 CPM)

ID	LFFM (kg)	TEE LFFM (k/cal)
Kebara 2	56.5	3196
La Chapelle	56.7	3248
Fon De Foret 1	62.8	3468
La Farrassie 1	63.6	3524
Neanderthal	59.0	3308
Regourdou 1	53.9	3075
Spy	62.5	3460
Amud	56.3	3206
Kiik Koba 1	58.4	3278
Shanidar 1	60.2	3372
Shanidar 2	56.2	3174
Shanidar 3	59.8	3342
Shanidar 4	53.9	3067
Shanidar 5	51.2	2959

Table 8. Constrained Energy Model Total Energy Expenditure for Female Neanderthals of Low Fat Free Mass (200 CPM)

ID	LFFM (kg)	TEE LFFM (k/cal)
Krapina 208	51.2	2937
Krapina 209	47.6	2778
Krapina 214	46.5	2727
La Quina 5	53.3	3043
Spy 1	50.5	2914
La Farrassie 2	50.1	2888
Shanidar 6	44.4	2620
Tabun C1	47.3	2761

Table 9. Constrained Energy Model Total Energy Expenditure for Male Neanderthals of High Fat Free Mass (200 CPM)

ID	HFFM (kg)	TEE HFFM (k/cal)
Kebara 2	65.4	3609
La Chapelle	65.6	3670
Fon De Foret 1	72.6	3926
La Farrassie 1	73.5	3988
Neanderthal	68.3	3739
Regourdou 1	62.4	3468
Spy	72.3	3916
Amud	65.1	3617
Kiik Koba 1	67.6	3704
Shanidar 1	69.6	3811
Shanidar 2	65	3584
Shanidar 3	69.1	3778
Shanidar 4	62.3	3459
Shanidar 5	59.3	3333

Table 10. Constrained Energy Model of Total Energy Expenditure for Female Neanderthals of High Fat Free Mass (200 CPM)

ID	HFFM (kg)	TEE HFFM (k/cal)
Krapina 208	59.2	3103
Krapina 209	55.1	2932
Krapina 214	53.8	2878
La Quina 5	61.6	3215
Spy 1	58.4	3078
La Farrassie 2	58	3050
Shanidar 6	51.4	2764
Tabun C1	54.7	2914

Table 11. Additive Energy Model: Total Energy Expenditure for Male Neanderthals (650 CPM)

ID	BMR (kcal/d)	TEE (kcal/d)
Kebara 2	1834	4057
La Chapelle	1860	4105
Fon De Foret 1	1961	4314
La Farrassie	1978	4369
Neanderthal	1885	4163
Regourdou	1781	3941
Spy 2	1957	4306
Amud	1830	4068
Kiik Koba 1	1873	4134
Shanidar 1	1909	4224
Shanidar 2	1828	4034
Shanidar 3	1900	4195
Shanidar 4	1779	3933
Shanidar 5	1726	3832

Table 12. Additive Energy Model: Total Energy Expenditure for Female Neanderthals (650 CPM)

ID	BMR (kcal/d)	TEE (kcal/d)
Krapina 208	1502	3408
Krapina 209	1433	3257
Krapina 214	1411	3209
La Quina 5	1543	3509
Spy 1	1489	3387
La Farrassie 2	1481	3362
Shanidar 6	1370	3106
Tabun C1	1426	3241

Table 13. Additve Energy Model: Total Energy Expenditure for Male Neanderthals (200 CPM)

ID	BMR (kcal/d)	TEE (kcal/d)
Kebara 2	1834	3542
La Chapelle	1860	3591
Fon De Foret 1	1961	3805
La Farrassie 1	1978	3860
Neanderthal	1885	3650
Regourdou 1	1781	3423
Spy	1957	3796
Amud	1830	3553
Kiik Koba 1	1873	3621
Shanidar 1	1909	3712
Shanidar 2	1828	3519
Shanidar 3	1900	3683
Shanidar 4	1779	3415
Shanidar 5	1726	3311

Table 14. Additive Energy Model: Total Energy Expenditure for Female Neanderthals (200 CPM)

ID	BMR (kcal/d)	TEE (kcal/d)
Krapina 208	1502	2928
Krapina 209	1439	2776
Krapina 214	1411	2727
La Quina 5	1543	3029
Spy 1	1489	2906
La Farrassie 2	1481	2881
Shanidar 6	1370	2624
Tabun C1	1426	2759

Table 15. Comparative range of TEE (kcal/day) averages from Neanderthal TEE studies

Study	Male	Female
This Study	200 CPM/d: 3262-3685* 650 CPM/d: 3758-4180* 200 CPM/d: 3311-3860** 650 CPM/d: 3832-4369**	200 CPM/d: 2833-2992* 650 CPM/d: 3328-3487* 200CPM/d: 2721-3029** 650 CPM/d: 3106-3509**
Steegman 2002	3360-4480	---
Churchill 2006	3682-5523	2870-4305
Sorensen/Leonard 2001	~3600-5500	~2900-4300
Snodgrass/Leonard 2009	4085-6754	2933-5274

* Constrained energy model values represent averages of low and high fat free mass
** Additive energy model values

Figure 1.

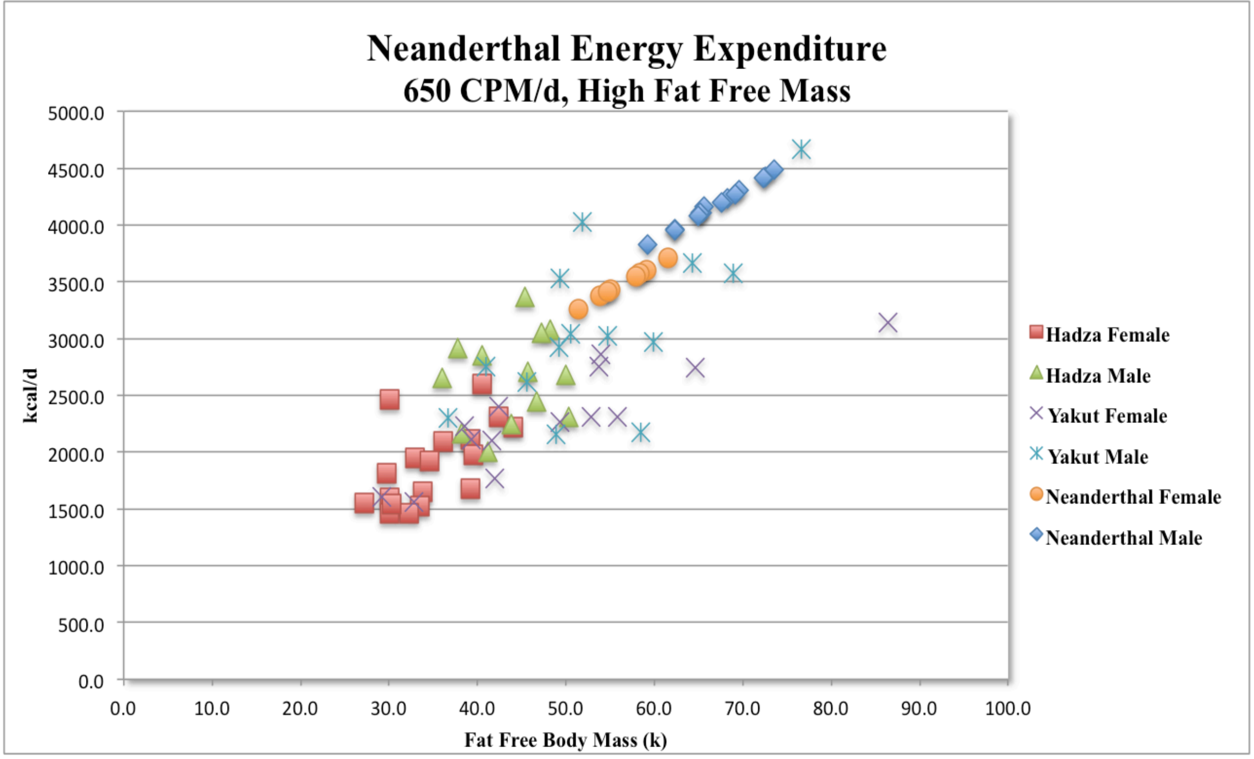


Figure 2.

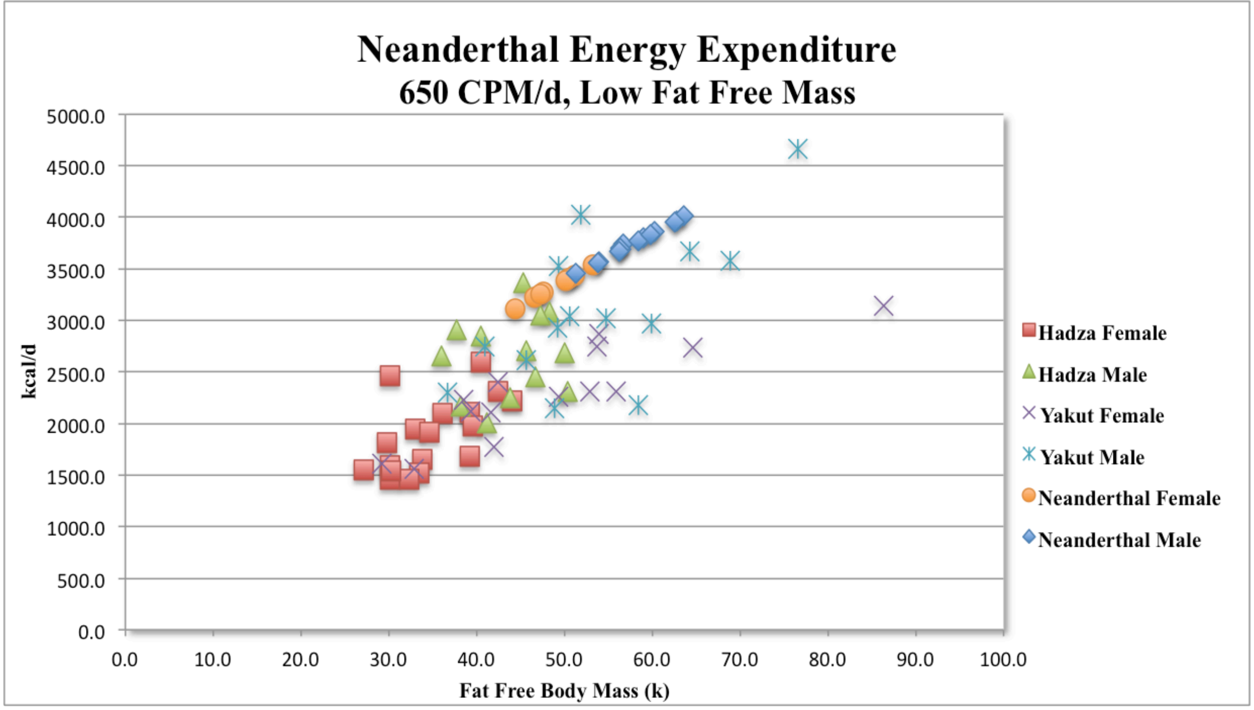


Figure 3.

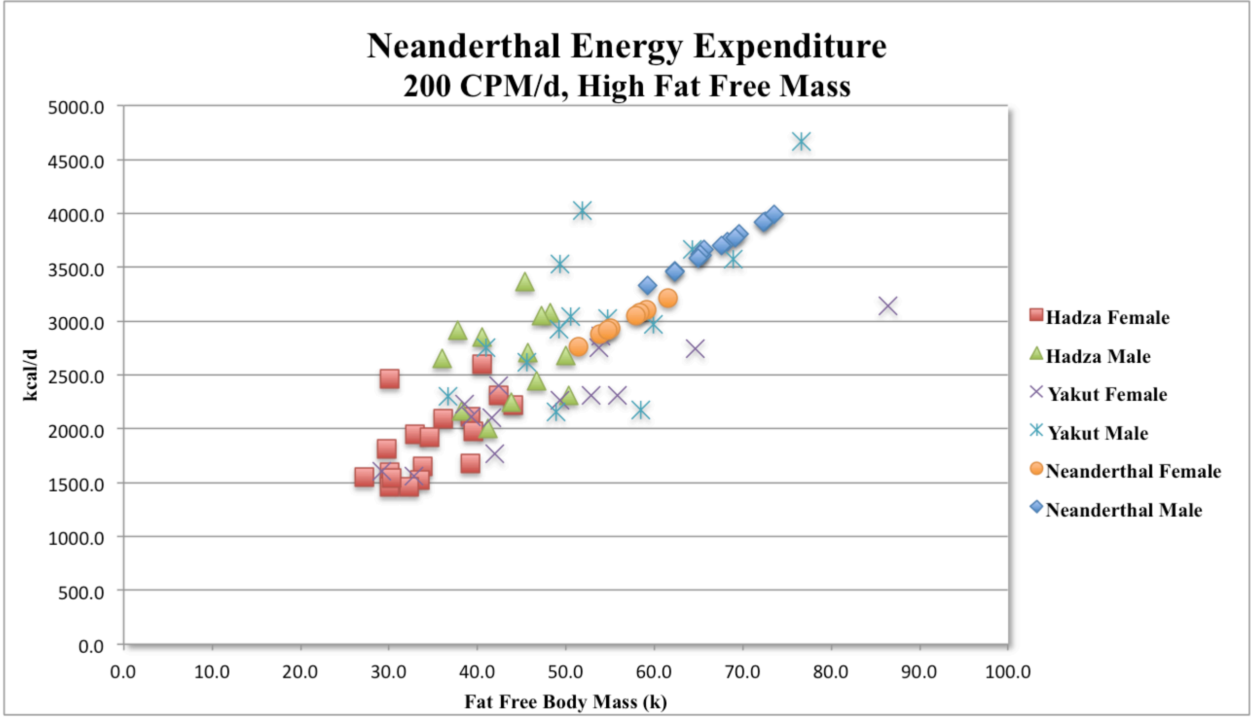
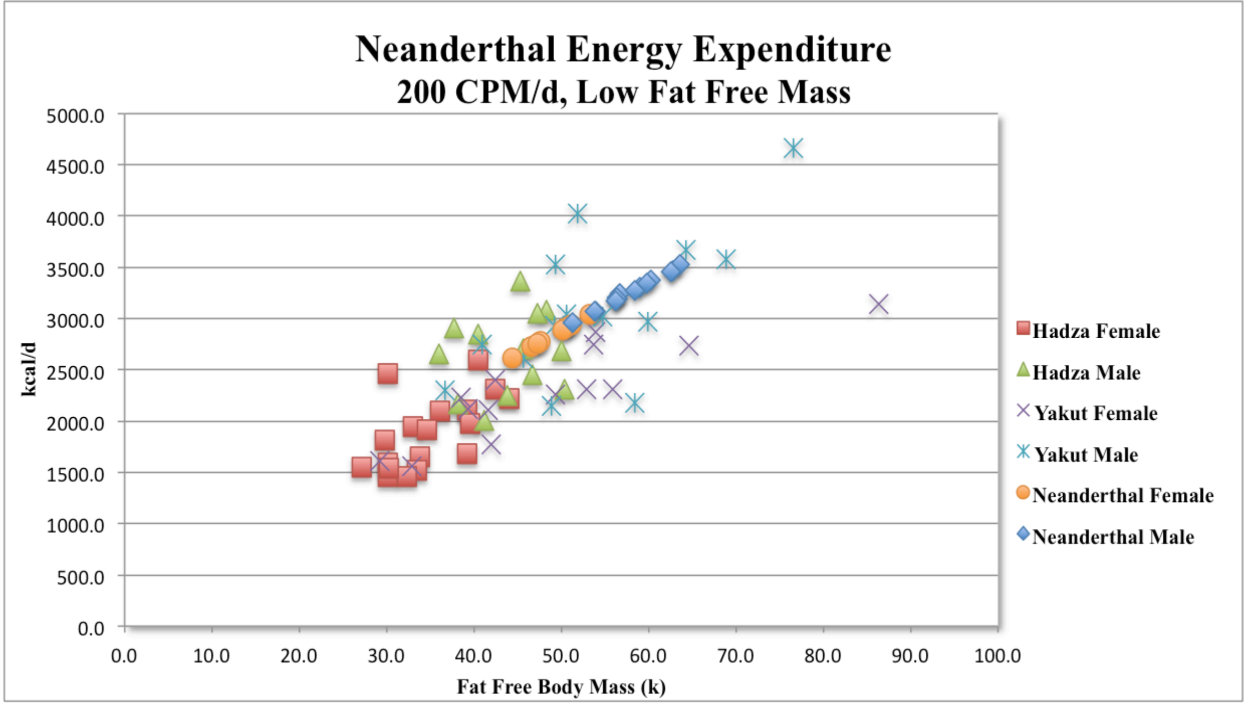


Figure 4.


Neanderthal Energy Expenditure
200 CPM/d, Low Fat Free Mass
kcal/d
5000.0
4500.0
4000.0
3500.0
3000.0
2500.0
2000.0
1500.0
1000.0
500.0
0.0
0.0
10.0
20.0
30.0
40.0
50.0
60.0
70.0
80.0
90.0
100.0
Fat Free Body Mass (k)
Hadza Female
Hadza Male
Yakut Female
Yakut Male
Neanderthal Female
Neanderthal Male

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