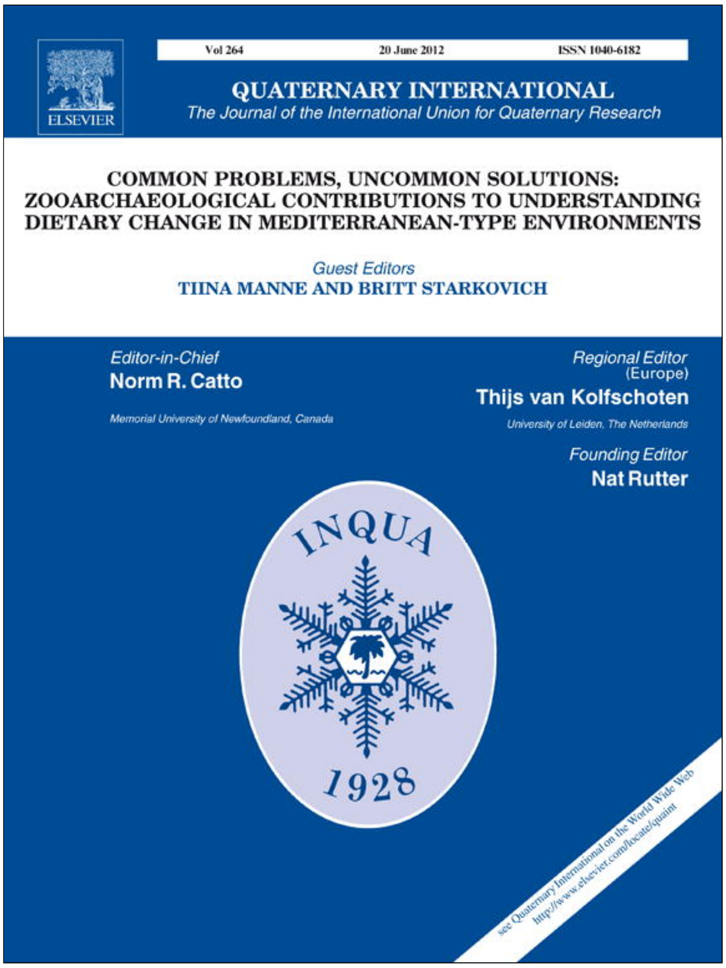
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The consequences of Middle Paleolithic diets on pregnant Neanderthal women

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ABSTRACT

Models of Neanderthal energetics and energy requirements suggest they required an average daily caloric intake well above the average for anatomically modern human foragers. The reasons stated for this include higher basic metabolic rates, less efficiency at thermoregulation, less efficiency at hunting, greater degrees of mobility, and reduced sexual division of labor in Neanderthal populations. These models suggest that Neanderthal Daily Energy Expenditure may have reached or exceeded 5500 calories per day. Given that most subsistence and isotope studies also suggest that Neanderthals focused their diet on large, terrestrial herbivores, this paper asks: what would be the nutritional consequences of such a diet on pregnant Neanderthal women? Applying a nutritional ecology perspective to the issue, a modeled diet consisting of 5500 calories per day derived exclusively from large, terrestrial herbivores indicates that such a diet would kill a pregnant Neanderthal woman and her developing fetus. This suggests that much remains to be learned about Neanderthal subsistence, mobility, and social relations, and that there is a long way to go before explaining the causes of Neanderthal extinction and modern human success in Europe and the Mediterranean region between 30,000 and 50,000 years ago.

1. Introduction

The fate of the Neanderthals is known. Migrations of modern humans into northern Europe commenced about 40,000 years ago. Approximately 10,000 years later, modern humans had spread throughout Europe, and the 250,000 year occupation by Neanderthals came to an end.

How the Neanderthals met this fate is a matter of debate. Differences in dietary intake and energy requirements between Neanderthals and modern humans are possible contributing factors (Cachel, 1997; Shea, 1998; Aiello and Key, 2002; Dufour and Sauther, 2002; Panter-Brick, 2002; Steegmann et al., 2002; Weaver and Steudel-Numbers, 2005; Adler et al., 2006; Kuhn and Stiner, 2006; Froehle, 2008; Froehle and Churchill, 2009; Snodgrass and Leonard, 2009; Sørensen, 2009; Weaver, 2009; Vallverdú et al., 2010). Dietary preferences and the availability of specific foods may lead to differences in essential nutrient intake, technological development, mobility patterns, and internal and external social relations amongst individual groups. One model that attempts to discover whether differences in total essential nutrient intake led to or accelerated Neanderthal extinction is nutritional ecology (Hockett and Haws, 2003, 2005). The core tenet of nutritional ecology is that both macronutrients (calories) and micronutrients (non-caloric vitamins and minerals) affect human mortality and fertility patterns, and thus human demographic trends through time.

Dietary impacts to human demographic trends are centered about the health and well-being of the mother and child (e.g., Ramakrishnan et al., 1999; Allen, 2005). This includes the health of women prior to pregnancy, during pregnancy, and post-partum (or during lactation). The "child" as defined here includes the developing fetus, neonate, and infant. Pregnant and lactating women require additional essential nutrients compared to other females (Dufour and Sauther, 2002). However, because humans produce large, precocial offspring by way of a long gestation period, relatively few additional calories are required during pregnancy. Further, human lactation also requires comparatively few additional calories because human postnatal growth is slow and prolonged, and because human breast milk is relatively dilute compared to that of other mammals of similar size. Human breast milk is low in fat and protein, but particularly rich in carbohydrates. Nevertheless, human lactation generally requires a greater increase in the percentage of daily energy intake than does pregnancy itself (Dufour and Sauther, 2002).

Importantly, the under-consumption of specific micronutrients, as well as the over-consumption (or toxicity) of others may negatively impact the percentage of successful pregnancies, child cognitive and physical growth and development, and maternal

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recovery following childbirth independent of the amount of calories consumed or the efficiency of caloric capture (e.g., Lockett et al., 2000; Fall et al., 2003). This is another way of stating that maintaining caloric levels above chronic energy deficiency does not guarantee adequate micronutrient intake, particularly during pregnancy and lactation, and therefore it is an inadequate proxy for measuring upward demographic trends that are related to essential nutrient intake.

This paper will explore the archaeological and biogeochemical interpretations of Middle Paleolithic diets on pregnant Neanderthal women using a model based on total essential nutrient intake (nutritional ecology). Similar modeling of the diets of early modern humans can be compared to these models in order to highlight differences in health patterns between the two human groups, which will assist in determining whether a lack in the diversity of essential nutrient intake contributed to Neanderthal extinction.

2. Modeling the health patterns of pregnant Neanderthal women

2.1. Concepts and theoretical underpinnings

This modeling exercise begins with establishing the amount of calories pregnant Neanderthal women consumed based on their Daily Energy Expenditure (or DEE), which is sometimes referred to as Total Energy Expenditure (or TEE) in kilocalories (kcals) per day. DEE is calculated by determining Basic Metabolic Rate (BMR), adding any additional calorie requirements such as a pregnancy (PR) or lactation (LC), and then multiplying that number by Physical Activity Level (PAL). This equation may be expressed simply:

$$(\mathrm{BMR} + [\mathrm{PR}] \text{ or } [\mathrm{LC}]) \times \mathrm{PAL} = \mathrm{DEE}$$

Several studies provide estimates of an average Neanderthal's BMR, most recently Snodgrass and Leonard (2009), which was published online along with a series of related papers on Neanderthal energetics by the Paleoanthropology Society. They started with an average BMR for modern subsistence foragers in Siberia. Taking into consideration factors such as differences in body proportions between Neanderthals and modern foragers, as well as hypothetical interpretations about possible differences in efficiency of body thermoregulation between the two human groups, they calculated that an average BMR for a Neanderthal woman was 1465 kcals (hereafter simply referred to as "calories") per day. Modern pregnant women require about 400 additional calories per day to sustain themselves and their developing fetus (PR = 400), so that figure is used as an approximation for pregnant Neanderthal women as well. PALs represent the amount of calories expended to maintain BMR plus all other physical activity performed during a daily routine. PALs are established as a factor of BMR, so that if a person could expend zero calories beyond BMR, then they would have a PAL of 1.0 (BMR = PAL). Modern women in the United States have an average PAL of about 1.72; modern women in subsistence populations have an average PAL of about 1.82 (Snodgrass and Leonard, 2009). Populations engaged in intensive agriculture have average PALs that range between 2.0 and 2.5. Snodgrass and Leonard (2009) argue that a Neanderthal's PAL would have matched or exceeded the high end of the physical activity spectrum of those engaged in intensive agriculture. They say 2.5 underestimates a Neanderthal's PAL and cite previous work using 3.0 as the high end.

Before displaying the number of calories that pregnant Neanderthal women must have consumed in order to reach these PAL estimates, it is important to point out that hypotheses developed by modern researchers influence the final calculations of Neanderthal DEE's. For examples, using measurements of the efficiency of modern foragers as a baseline, a researcher may choose three hypothetical interpretations that effect estimates of Neanderthal BMR: (1) Neanderthals were less efficient at thermoregulation compared to modern foragers, therefore Neanderthal BMRs were higher than early modern humans; or (2) Neanderthals were more efficient at thermoregulation compared to modern foragers, therefore Neanderthal BMRs were lower than early modern humans; or (3) Neanderthals were equally efficient at thermoregulation compared to modern foragers, therefore Neanderthal BMRs were similar to early modern humans. Similarly, a researcher may decide that: (1) Neanderthals were less efficient at hunting compared to modern foragers, therefore Neanderthal PALs were higher than early modern humans; or (2) Neanderthals were more efficient at hunting compared to modern foragers, therefore Neanderthal PALs were lower than early modern humans; or (3) Neanderthals were equally efficient at hunting compared to modern foragers, therefore Neanderthal PALs were similar to early modern humans. Two additional behaviors that effect estimated calculations of Neanderthal DEE's are mobility patterns and degree of sexual division of labor, both of which increase a PAL and DEE in models that argue that Neanderthals had a greater degree of mobility and a lesser degree of sexual division of labor compared to the average modern forager. As a result, those who suggest that Neanderthals had significantly higher DEE's than early modern humans usually suggest that Neanderthals were less efficient at thermoregulation, less efficient at hunting large game, displayed a greater degree of mobility, had limited sexual division of labor, and perhaps that Neanderthal women engaged in close-encounter hunting episodes with dangerous, large herbivores as did their male companions.

2.2. Caloric requirements and essential nutrient consequences

Using the PAL figures discussed above, DEEs for pregnant Neanderthal women can be estimated. A BMR of 1465 calories and a PAL of 3.0 for a pregnant woman equates to a daily caloric intake of 5500 calories (Table 1). PALs of 2.5 and 2.0 equate to daily caloric intakes of 4650 and 4250 calories, respectively. Portraying a DEE of 5500 calories per day from the perspective of a modern fast food diet, a pregnant Neanderthal woman would need to eat 10 large cheese burgers per day (or three in the morning, three at mid-day, and four in the evening), or 17 orders of chicken nuggets per day (or five orders in the morning, six at mid-day, and another six in the evening). This perspective assists in understanding the amount of food that these models are suggesting pregnant Neanderthal women consumed on a daily basis, although it certainly does not negate that possibility.

Pregnant Neanderthal women, of course, did not have the luxury of a modern fast food diet so readily available. What did Neanderthals eat? Although there is variability in the archaeological record, most zooarchaeological and isotopic studies suggest that the average Neanderthal diet consisted primarily of large, terrestrial herbivores (e.g., Patou-Mathis, 2000; see also Hockett and Haws, 2005 for a review). Therefore, it is both useful and

Table 1
Pregnant Neanderthal women DEE's, based on BMR figures supplied in Snodgrass and Leonard (2009).

(BMR + PR) × PAL = DEE				PAL equivalent to:
1465	400	3.0	5500	High end of intensive agriculturalist
1465	400	2.5	4660	Average of intensive agriculturalist
1465	400	2.0	3780	High end of forager
1465	400	1.8	3357	Average of modern Siberian forager

Table 2
The modeled daily diet of a pregnant Neanderthal woman based strictly on the consumption of terrestrial herbivores.

Food	3.0 PAL	2.5 PAL	2.0 PAL
Bison (cups)[a]	9	6	5
Deer ribs (oz.)[b]	16	16	14
Brains (oz.)	2	1	1
Liver (oz.)	2	1	1
Tongue (oz.)	2	2	2
Stomach	4	2	2
Oxtails (oz.)	16	14	12
Snowshoe hare	1	1	1
Lard (cup)[c]	½	½	½
Approx. kcal	5500	4600	3800
Meat (lbs.)[d]	5.7	4.5	4.0
%Fat	39	41	47
Cholesterol (mg)	4815	3275	3080

[a] 1 cup bison meat equals approximately 300 g.
[b] 1 oz. equals approximately 30 g.
[c] 1 cup lard equals approximately 125 g.
[d] 1 lb. equals 0.454 kg.

necessary to model Neanderthal diets based primarily or exclusively on large, terrestrial herbivores using large game body parts and portion sizes that equal the estimated DEE's for these humans. The adequacy of these diets for pregnant Neanderthal women can then be interpreted based on a comparison of their total essential nutrient intake with modern Recommended Daily Allowance (RDA) standards, as well as with lower and upper limit nutrient values that result in moderate to catastrophic health problems as a baseline. While RDA standards are partially politically motivated, they still can serve as modeled approximations for daily essential nutrient requirements in humans; importantly, the lower and higher end of essential nutrient intake values that result in health and pregnancy problems are based on research unmotivated by political concerns.

A PAL of 3.0 can be used to model the essential nutrient intake of a pregnant Neanderthal woman who consumes 5500 calories of exclusively terrestrial mammal parts per day. In order to model an average Neanderthal daily diet consisting solely of terrestrial mammals, bison (*Bison bison*) was used as a representative bovid, deer (*Odocoileus* spp.) as a representative cervid, and hare (*Lepus americanus*). A combination of muscle meats and internal organs was used, with the assumption that every edible portion of carcasses would be eaten. Shattered long bone fragments found at many Middle Paleolithic sites suggest that Neanderthals were consuming bone marrow as well, so ½-cup (~125 g) of pure fat (lard) was included into each daily diet analysis (Table 2).

The results are quite revealing, and they suggest that a pregnant Neanderthal woman (along with her developing fetus) could not survive on such a diet given the DEEs predicted in the literature (Table 3). The major problem with this diet for a pregnant Neanderthal woman in terms of macronutrients is the potential toxic levels of protein intake. The modeled diet consists of 55–60% protein, with a daily intake of nearly 800 g. The RDA for a modern pregnant woman is between 10 and 35% daily protein intake, which equates to 71–245 g. The absolute protein ceiling for a modern pregnant woman and her fetus is unknown, but consuming 2.5 times the modern RDA may well have been deadly for both Neanderthal mother and child.

Importantly, the modeled Neanderthal diet included fatty cuts of both meat and internal organs, including ribs as the representative cervid meat portion, oxtails in the bovid meat portion, and tongue and brains in the internal organ portion. In addition, the modeled diet included ½-cup of pure fat or marrow per day. This diet resulted in the pregnant Neanderthal woman with a 3.0 PAL consuming nearly 40% of her diet from fat, a relatively generous percentage obtained from wild terrestrial game. However, this diet probably would have killed a pregnant Neanderthal woman and her fetus.

If protein poisoning did not kill this pregnant Neanderthal woman, the toxic levels of vitamin A, niacin, iron, zinc, and selenium, as well as the severe under-consumption of carbohydrates and vitamin C, probably would have done so (Table 3). Further, the pregnant Neanderthal woman would have had a chronic under-consumption of calcium, and combined with the fact that extremely high intake of protein blocks calcium absorption translates into major micronutrient-based health problems for mother and child.

All of the macronutrient and micronutrient problems associated with the 3.0 PAL pregnant Neanderthal woman are also seen in the 2.5 PAL woman except for reduced toxic levels of vitamin A, which results from reducing the intake of liver from 2 ounces (60 g) to 1 ounce (30 g) per day (Table 3). The 2.0 PAL pregnant Neanderthal woman also possesses nearly all of the essential nutrient problems as the 3.0 and 2.5 women, although the degrees of over-consumption or under-consumption of essential nutrients are lessened. This is true for all nutrients except folate, a critical micronutrient in the development of a healthy fetus. Interestingly, problems associated with the under-consumption of folate emerge in the 2.5 PAL and 2.0 PAL women because a diet based solely on terrestrial animal products requires great quantities of calories in order to consume adequate amounts of this pregnancy-vital micronutrient.

Arguing that this modeled diet is too speculative and untestable is an empty suggestion. This is so because no matter how one changes the distribution and portion sizes of muscle and internal organs to reach a hypothetical DEE, the end result is the same: dead Neanderthals. Dead Neanderthals result from this diet because of two main reasons: (1) Neanderthals could not have consumed such large quantities of calories per day without consuming very large quantities of terrestrial animal muscle and internal organs,

Table 3
Essential nutrient intake for various DEEs and PALs for a pregnant Neanderthal woman strictly consuming terrestrial herbivores. The body mass of the average Neanderthal woman was set at 66 kg (145 lb.).

Essential Nutrients																
Energy					Vitamins							Minerals				
PAL	kcal	Pro. (%CAL)	Fat	Carb	A	C	E	Thia.	Nia.	Fol	B6	Ca	Fe	Zn	K	Se
3.0	5500	784 (57%)	237	3	3740	11	11	2.3	126	395	9.8	275	102	143	8440	738
2.5	4600	634 (55%)	210	2	1870	6	9	1.8	104	262	7.7	224	83	122	6691	540
2.0	3800	569 (60%)	200	2	1870	6	8	1.5	95	244	6.9	206	75	110	5981	476
RDA	2400	46	~100	130	700	75	15	1.1	14	400	1.3	1000	18	8	4700	55
Toxic@		>35%		!!!	3000	!!!			35	!!!	100	!!!	45	***	***	400

!!! = severe under-consumption of micronutrients; *** = moderate to severe over-consumption of micronutrients that currently do not have toxic levels established but are known to be potentially damaging to internal organs (e.g., heart, liver, kidney) at high levels; Carb. = carbohydrates, Thia. = Thiamin; Nia. = Niacin; Fol. = Folate.

culminating with the end result of rather severe over- and under-consumption of essential nutrients; and (2) within the "terrestrial mammal" component of a diverse diet based on animal types (e.g., terrestrial mammals, birds, shellfish, insects, fruits, nuts, green leafy vegetables), there is little diversity in essential nutrient composition; this is another way of saying that it does not matter much whether Neanderthals ate multiple species of terrestrial herbivores (e.g., bison, deer, rabbit, wild goat) – the only way for them to have consumed a greater diversity of essential nutrients was to consume a greater diversity of food types, not a greater number of species of the same animal type. There is, however, a tendency for a greater diversity of essential nutrients to be found within the "green leafy vegetable" food type group compared to the "terrestrial animal" food type group.

3. Lessons learned

There are a large number of potential lessons to be learned here. Principle among them is that researchers should consider the possibility that previous models have, to one degree or another:

1) Under-appreciated the Neanderthals' abilities to regulate body temperature;
2) Under-appreciated the Neanderthals' abilities to efficiently hunt terrestrial animals;
3) Under-appreciated the degree of sexual division of labor within Neanderthal groups generally, and for pregnant and lactating women, specifically;
4) Under-appreciated the amount of non-mammal foods eaten by Neanderthals, such as fish, shellfish, insects, birds and eggs;
5) Under-appreciated the amount of plant foods eaten by Neanderthals;
6) Under-appreciated the differences in metabolic processing of essential nutrients such as protein between Neanderthals and modern humans;
7) Under-appreciated the role of micronutrient deficiencies to Neanderthal extinction;
8) Exaggerated the degree of mobility in the average Neanderthal group compared to modern hunting-gathering societies; and
9) Exaggerated the degree of close-encounter, dangerous hunting techniques that Neanderthal women participated in.

The number and extent with which these nine propositions are true effect the interpretations of the causes of Neanderthal extinction. Incorporating these errors into models of Neanderthal extinction contributes to interpretations of Neanderthal DEEs and average diet that are equally erroneous. This point has been recently brought into focus by studies indicating that Neanderthals consumed greater amounts of plant foods than previously envisioned through zooarchaeological, macrobotanical, and isotopic studies, as well as through energy-based economic modeling (e.g., Revedin et al., 2010; Henry et al., 2011). As the modeling exercise presented here makes vividly clear, Neanderthals must have consumed greater amounts of non-terrestrial mammal foods than the archaeological record suggests.

Nevertheless, while some news media outlets immediately interpreted these discoveries as suggesting that Neanderthals and early AMHS ate a similar 'balanced diet', researchers are in fact a long way from making such a proclamation. As noted, the nutritional ecology model can illustrate what many suspected all along: Neanderthals could not have survived on terrestrial animal products alone. It is also a fact, however, that a diversity of consumption of animal types (e.g., fish, birds, shellfish) can act as a substitute for certain micronutrients that are found in relatively large quantities in specific plant foods. As an example, fish eyes and viscera may supply rich sources of vitamin A (Roos et al., 2002). Long-term survival rates for individual foragers can hinge as much on knowledge of how to survive periods of food shortages or famine as on the daily intake of a diversity of essential nutrients (e.g., Lockett et al., 2000).

Learning more about the actual consumption of the variety of foodstuffs typically consumed by Neanderthals and early AMHS will allow better judgments of whether both human groups did or did not consume a near-identical variety of essential nutrients. Whether or not an understanding of possible differences in strategies to survive food shortages between Neanderthals and AMHS can be achieved is unknown. These answers are a long way off. In the interim, however, the nutritional ecology approach points out just how poor our knowledge of ancient diets must be. Future research can also continue to compare Neanderthal and AMHS diets nutritionally as the data emerge through discovery, and see where the answers to specific events such as Neanderthal extinction may be found.

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