Nutritional ecology and the human demography of Neandertal extinction

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Abstract

Demographic trends in human populations are influenced by natural selection acting upon differential rates of fertility and mortality. In human societies, fertility is primarily influenced by individual decision-making, as well as socially accepted norms of behavior. Many factors influence mortality in human populations. Among the latter, nutrition in the form of diverse essential nutrient intake may greatly influence maternal and fetal-to-infant mortality. Nutritional ecology is the study of the relationship between essential nutrient intake and its effects on human demographic patterns. A demographic revolution occurred in Europe during OIS 3: all Neandertal populations were either subsumed within populations of Anatomically Modern *Homo sapiens* (AMHS) (genetic swamping) or they were eliminated altogether. Evidence from stable isotopes, faunal remains, and the paleopathology of human skeletons suggest that Neandertals consumed a low diversity diet centered on large and medium-sized terrestrial herbivores. In contrast, populations of early AMHS consumed a slightly more diversified diet. The effect of this dietary shift would have resulted in greater diversity of essential nutrient intake and lower maternal and fetal-to-infant mortality, which in turn would have sparked population increases during the early phases of occupation of the European continent by populations of AMHS. Greater diversity of essential nutrient intake by early populations of AMHS may have been one factor that led to the replacement of Neandertals in Europe during OIS 3.
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1. Introduction

Between ca. 250,000 and 40,000 BP, the only humans inhabiting the European continent were those collectively known as the Neandertals (Gamble and Roebroeks, 1999; Bar-Yosef, 2002). By ca. 28,000 BP, populations of Anatomically Modern *Homo sapiens* (AMHS) were present throughout Europe, and the Neandertals had entirely disappeared (Zilhão, 2000, 2001a). One answer to their disappearance may simply be that the transition represents a case of anagenesis; AMHS in Europe evolved directly from in situ Neandertal populations (Wolpoff et al., 2001). Mounting biological and archaeological evidence, however, suggest that AMHS evolved initially in Africa, and that

some of these founding populations later entered Europe via southwest Asia (Stringer, 1998; Templeton, 2002). As a result, some degree of interaction, indeed competition, probably ensued between the Neandertals and the incoming populations of AMHS (Zilhão, 2001b). If that is the case, then the causes underlying the extinction of European Neandertals during OIS 3 generally rest within the realms of human demography. As Ward and Weiss (1976, p. 2) noted some time ago: "The origin of new adaptive gene complexes due to natural selection arises through the processes of differential fertility and mortality. These factors need to be described in demographic terms before their impact can properly be appreciated in the evolutionary sense". It is possible that populations of AMHS outcompeted those of the Neandertals through behaviors that cumulatively led to lower mortality, higher fertility, or both.

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In some cases, however, populations of AMHS probably entered regions already abandoned by Neandertals, or entered regions in which Neandertals had previously become locally extinct. If these scenarios applied throughout Europe between 40,000 and 28,000 BP, then models accounting for the disappearance of Neandertals would not require the behavior of AMHS to be considered (Pettitt, 1999), since the Neandertals would have gone extinct with or without the presence of modern humans (Stewart, 2003). Transitional industries such as Châtelperronian and the relatively late dating of Neandertal skeletons after ca. 30,000 BP, however, suggest that at times direct and indirect contact and competition likely occurred between in situ Neandertal groups and incoming populations of AMHS (Zilhão, 2001a; Templeton, 2002; Shea, 2003) for 'living space'. In this case, the living space was the European continent. And while debates continue over whether the 'Middle-to-Upper Paleolithic Transition' should be viewed as a "revolution" (Bar-Yosef, 2002), there is no doubt that a demographic revolution occurred in Europe during OIS 3.

In this essay, we argue that explanations of Neandertal extinction would benefit from further discussions of the major factors that influence diachronic trends in human demography, or the primary factors influencing human fertility and mortality (e.g., Mellars, 1998; Eswaran, 2002). While this proposition may seem obvious, there are few studies of Neandertal extinction that take into account fundamental principles of human fertility and mortality (Wobst, 1976; Zubrow, 1989; Trinkaus, 1995; Pettitt, 2000). This essay explores the extinction of European Neandertals from a demographic perspective with a focus on how subsistence/ dietary choices affect human fertility and mortality. We suggest that both macronutrients (fats, carbohydrates, and proteins) and micronutrients (non-caloric vitamins and minerals) must be included in models that account for diachronic shifts in human populations within a selectionist framework because energy maximization alone may not lead to increased fitness levels in human populations, a fact that has not been completely ignored by anthropologists studying early human subsistence (e.g., Stini, 1981; Erlandson, 2001), and a fundamental principle of nutrition science that is gaining widespread support (Ashworth and Antipatis, 2001; Fall et al., 2003; Keen et al., 2003). These principles may assist in explaining the transition to AMHS across Europe near the end of OIS 3.

The most viable approach that explicitly relates total essential nutrient intake to differential rates of human fertility and mortality, as well as to average life expectancy, is nutritional ecology (Schwarcz and Schoeninger, 1991; Jenike, 2001; Hockett and Haws, 2003; Haws and Hockett, 2004). Below we explore in greater detail the extinction of European Neandertals through the lens of nutritional ecology. Before we describe the nutritional underpinnings of this approach in greater detail, we begin with a broader discussion of some of the factors that influence human fertility and mortality.

2. Principles of human demography: some factors that could have caused the extinction of European Neandertals

The two principal factors that influence long-term demographic trends in human populations are fertility and mortality (Ward and Weiss, 1976; Scott and Duncan, 2002). Livi-Bacci (1991) calls these factors 'choice' and 'constraint', respectively, because in human societies fertility rates are primarily influenced by individual decision-making and socially determined norms such as marriage rules and rules governing length of time of female abstinence from sexual contact following pregnancy. Mortality rates are primarily influenced by nutrition in the form of diverse essential nutrient intake, epidemics, warfare, and so forth. Of these, fertility is the most difficult for archaeologists to study, but in truth, both fertility and mortality are exceedingly difficult to delineate with any precision in contemporary and prehistoric foraging populations (Henneberg, 1976; Wood, 1998; Konigsberg and Frankenberg, 2002; Steckel and Rose, 2002; Stinson, 2002). However, that does not mean that archaeologists cannot study the factors that lead to differential fertility and mortality in prehistoric populations, and interpret their consequences.

2.1. Fertility

Henneberg (1976) argued that relative fertility in a given age class remains more or less constant for a given level of social organization. If true, then this would imply that Neandertal and early AMHS populations had similar rates of fertility, as both were foragers relying exclusively on wild plant and animal foods. Henneberg (1976) referred to this pattern as an "archetype of fertility" and further suggested that differences in fertility rates among hunter–gatherer populations were primarily determined by variations in intervals between births. Frisch's (1973) "critical fatness hypothesis" showed that fertility had a nutritional component as well, as women who gained fat at an early age reached menarche sooner than those with leaner diets. However, early menarche does not guarantee greater rates of fertility because rules governing age at first pregnancy are largely determined by social factors. It has since been shown that birth-spacing also influences fetal-to-infant mortality, as well as maternal mortality, principally due to depleted stores of essential nutrients following each birth (Smits and Essed, 2001; King, 2003).

Wobst (1976) argued that Neandertals probably displayed very high fertility rates, just as did most small-scale hunter–gatherer societies in recent times. He showed that in modern glaciated areas, hunter–gatherers in the northern regions exploiting mainly large, terrestrial mammals and little to no fish displayed population densities ranging between .005 and .5 persons/km^2. Wobst (1976) further suggested that in the Pleistocene north, population densities for the Neandertals would have been toward the lower end of this scale. This in turn suggested that Neandertal mating networks probably ranged over large territories.

Livi-Bacci (1991) described how the flexible marriage patterns in 17th and 18th century England assisted in offsetting population crashes, while the relatively rigid marriage rules of France at this time did not produce a system to help offset impending population declines. Fertility rates, therefore, can vary between populations exhibiting similar economies and levels of social stratification. Differences in social norms guiding fertility rates could have favored populations of AMHS over those of the Neandertals. For example, early AMHS populations may have had more flexible marriage rules or relatively closed mating networks that acted to increase fertility rates.

These latter studies suggest that fertility rates can vary amongst hunter–gatherer populations, so there may have been differences in fertility rates between Neandertals and AMHS in Europe. Studies of Neandertal and AMHS fertility rates should continue and should remain vital to the quest of understanding Neandertal extinction. For example, it may one day be possible to delineate ancient kinship structures in human societies that affect rates of fertility, as recently discussed by Binford (2001, pp. 466–467). Even if it is determined that these structures cannot be known from the deep past, we should at least be aware that they may have been a factor contributing to paleodemographic trends, particularly if other demographic influences do not fully account for the patterns we see. Because rates of fertility are exceedingly difficult to model in prehistoric societies, however, the remainder of this essay focuses on possible differences in rates of mortality between Neandertal and early AMHS populations.

2.2. Mortality

Livi-Bacci (1991) sees the spread of epidemics such as small pox and the plague as the primary influence affecting mortality in historical European societies engaged in agricultural practices and market economies. The consensus among human demographers, nutritionists, and medical researchers is that nutritional factors play a key role in governing mortality among hunter–gatherer and agricultural societies alike (Zeitlin et al., 1982; Ramakrishnan et al., 1999; Solomons, 2000;

Ames, 2001; Bendich, 2001; Cintio et al., 2001; Neumann et al., 2002; Scott and Duncan, 2002). Certainly, the availability of large quantities of food and a relatively sedentary lifestyle resulted in demographic increases for horticultural and agricultural societies (e.g., Larsen, 2003). But once established, further demographic trends in agricultural communities were influenced by a host of interacting, complex processes, among them fertility, epidemics, health care, warfare, climate effects on arable land, and diversity of essential nutrient intake (Livi-Bacci, 1991; Palubeckaitė et al., 2002; Scott and Duncan, 2002).

Mortality rates among the small-scale hunter–gatherer societies that existed during the transition from Neandertals to AMHS in Europe probably were not greatly influenced by epidemics because low population densities would have isolated the spread of most of these types of fatal diseases. In addition, there is no evidence for the kinds of large-scale warfare that would have been necessary to significantly impact mortality amongst either the Neandertals or the early populations of AMHS. This leaves nutritional factors as one of the principle causes of any differences in mortality between the two groups.

Mortality in human populations has at least two primary effects on general demographic trends that are important for understanding Neandertal extinction. One effect is on the number of people added to the breeding population in succeeding generations. This effect is primarily influenced by the mortality rates of the mother, fetus, neonate, and infant (Ramakrishnan et al., 1999; Bendich, 2001; Cintio et al., 2001). The second effect is on average life expectancy after the transition from childhood to adulthood. In many human populations, this latter effect is of vital importance to provide elders who possess critical knowledge and skills that may influence the survival of mothers and infants alike in the succeeding generations.

Diversity in essential nutrient intake can greatly influence both pregnancy outcomes and average life expectancy (Ames, 2001; Ashworth and Antipatis, 2001; Bendich, 2001; Neumann et al., 2002; Fall et al., 2003). By the 1840s, medical researchers in Europe had concluded that nutrition in complex animals could be explained solely by their need for the energy producing essential nutrients (Harper, 1999). By 1881, however, experiments indicated that mice fed a relatively diverse diet lived twice as long as those fed a calorie sufficient but less diverse diet (Harper, 1999). Since the late 19th century, a wealth of evidence from medical researchers and nutritionists have shown that both macronutrients and micronutrients affect human mortality patterns in ways that can only be understood in a comprehensive framework that incorporates all essential nutrients (Zeitlin et al., 1982; Ramakrishnan et al., 1999; Solomons, 2000; Ames, 2001; Bendich, 2001; Cintio

et al., 2001; Neumann et al., 2002; Underwood, 2002; Viteri and Gonzalez, 2002; Neggers and Goldenberg, 2003).

The most influential demographic consequences of a diverse dietary intake are reductions in maternal, fetal, neonatal, and infant mortality (Zeitlin et al., 1982; Widdowson, 1991; Ashworth and Antipatis, 2001; Fall et al., 2003; Keen et al., 2003). Thus, the nutritional influences on mortality trends in human populations are primarily centered on the health and well-being of the mother and child. Two primary factors that reduce maternal and fetal-to-infant mortality are diverse essential nutrient intake, as mentioned above, and health care (Bendich, 2001; Cohen and Mitchell-Weaver, 2001). Diversity in essential nutrient intake influences fetal-to-infant mortality in at least three ways: (1) improving maternal health before and during pregnancy; (2) proper cell development and, hence, proper development of the fetus; and (3) proper immune function in the fetus, neonate, and infant (Bendich, 2001; Cintio et al., 2001; Bergström, 2003). Health care refers to human foragers acquiring knowledge about the healing and body maintenance properties of specific wild plant resources (Johns, 1990; Lockett et al., 2000).

Humans who consume low-diversity diets (e.g., mainly shellfish or terrestrial mammals) suffer from the ill effects of the under-consumption of some essential nutrients and the over consumption of others. As a result, models that focus only on energy intake may not be particularly useful in explaining long-term mortality trends in human populations, particularly the reasons behind initial demographic pulses in foragers or the reproductive success of one population at the expense of another. This can be illustrated by examining the complex relationships that exist between essential nutrient intake, fetal development, and the body's defense against diseases. On one hand, children born to low birthweight mothers tend to be born underweight with increased susceptibility to sickness and disease (Ramakrishnan et al., 1999), so sufficient calorie intake is vital to maternal health and protecting neonates and infants from potentially deadly diseases (Scrimshaw and Young, 1989; Neumann et al., 2002). However comforting it may be to believe that birthweight in humans is controlled primarily by energy intake, the fact is that deficiencies in micronutrients play critical roles in neonates being born underweight (Cintio et al., 2001; Fall et al., 2003). Ironically, in a number of studies of populations experiencing relatively high rates of low birthweight babies, mothers fed high density proteins failed to give birth to adequate-weight babies; in addition, balanced energy and protein supplements have also produced marginal results (Fall et al., 2003). Fall et al. (2003, p. 1750S) stated: "Birth weight and other birth measurements were not associated with maternal energy, protein, or carbohydrate intakes. Higher fat

intakes at 18 wk were associated with longer neonatal length and larger skinfold thickness. The most striking finding was that mothers with high intakes of milk at 18 wk and of GLVs [Green Leafy Vegetables] and fruits at 28 wk had larger infants…. The trends were particularly strong for GLVs; women eating GLVs at least every alternate day had infants almost 200 g heavier than those who never ate them…." The densest concentrations of energy are often found in animal products; the densest concentrations of micronutrients are generally found in green leafy vegetables and fruits, although animal organs are dense in certain micronutrients as well. Thus, a combination of all types of resources leads to diverse essential nutrient intake and healthy human individuals.

In addition, the water-soluble vitamins are absolutely essential for energy metabolism. In principle, then, energy is almost useless to the human body without the micronutrients to metabolize and put that energy to use. It may also be noted that the human body simply has not evolved to maximize energy intake in relation to work effort; humans rather easily become fat and obese at a very young age when energy consumption outpaces work effort, increasing the rate of spontaneous abortions (Cintio et al., 2001) and shortening average life expectancies (Barnett, 2003). And in later years "…leanness is associated with tumor and infection resistance" (Yoshida et al., 1999, p. 738). It is becoming increasingly accepted that adults who consume the widest diversity of essential nutrients with the fewest calories may extend their life expectancy.

In sum, maternal, fetal, neonatal, and infant survival can be best enhanced by mother's who consume a diversity of macro- and micronutrients. The point is that the nutritional factors that most influence human mortality do not lie in energy intake alone; macronutrients and micronutrients affect mortality rates in complex ways that we are just now beginning to fully appreciate. There are many other factors that influence human demographic trends; diversity of essential nutrient intake is but one of them. These factors may be divided into three general categories, all of which may have played a role in giving the demographic edge to populations of AMHS over those of the Neandertals: physiological, social, and cognitive. Some of the specific factors that primarily fit under each of these categories are summarized in Table 1.

We suggest that the keys to understanding the demographic swamping of Neandertals by populations of AMHS can be found within the factors elaborated above and summarized in Table 1 and Fig. 1. Although it is possible that a single dietary factor such as iodine deficiency and its related affects on the thyroid may have been enough to sway the tide in favor of AMHS in some regions of Europe (Dobson, 1998; Arthur et al., 1999; Crockford, 2002; Foster, 2002), it is likely that several

Table 1
Primary factors that influence human demographic trends

| Physiological	Social	Cognitive
Fetal/neonate mortality; micronutrients play critical role	Fertility—flexible marriage rules and age at first pregnancy may increase population	Value placed on infants/children
Fecundity—nutrition impacts average age of menarche	Fecundity—flexible rules about average number of offspring females are likely to produce	Health care of neonates and children
Infectious diseases; macro- and micronutrients critical at neonate/infant stages		Recognition that diverse diets improve maternal and child survival
Low birthweight mothers; macronutrients help avoid failure-to-thrive infants; micronutrients critical to fetal development and proper neonate-infant weight		
Maternal recovery following birth; macro- and micronutrients critical		
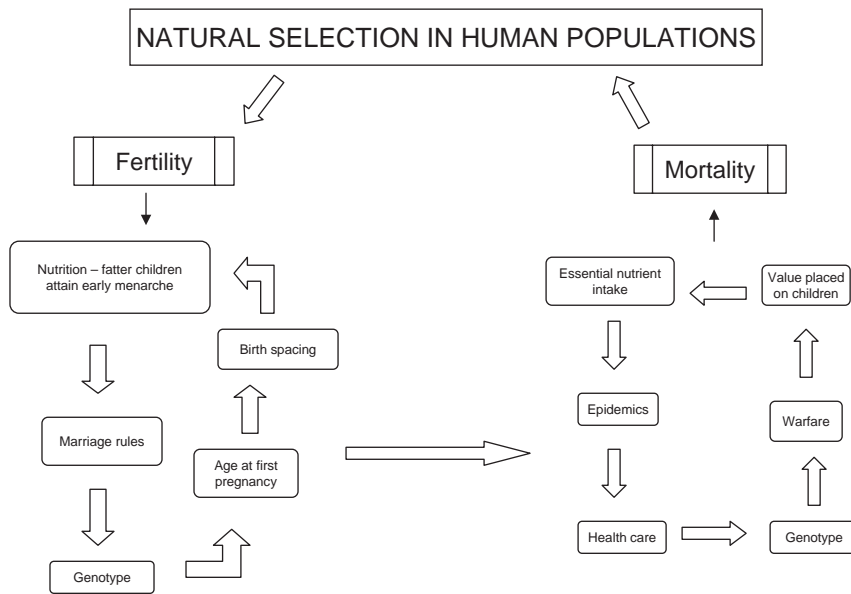
Fig. 1. Simplified flow chart illustrating some of the factors influencing natural selection in human populations.

factors acted simultaneously to proliferate populations of AMHS across Europe after ca. 40,000 BP. We propose that nutritional ecology offers the best model to interpret whether or not nutritional influences impacted this demographic process because it incorporates both macro- and micronutrient intake by prehistoric populations within a framework that is testable against the archaeological record (Hockett and Haws, 2003).

3. Nutritional ecology

We recently defined nutritional ecology as "the study of the relationship between essential nutrient intake and its effect on overall human health, including growth and maintenance in individuals and general demographic trends in populations" (Hockett and Haws, 2003, p. 211). In that paper, we discussed nutritional ecology in its broadest sense, focusing on the fact that it is based on the premise that diverse diets lower maternal and fetus-to-infant mortality rates and increase average life expectancies in humans. As noted above, dietary diversity, and hence diversity of essential nutrient intake, is achieved by consuming a variety of food types (Southgate, 1991). Primary food types that were potentially available to European Paleolithic foragers include terrestrial mammals, fish, shellfish, birds, and plants (Hockett and Haws, 2003). In some areas, marine mammals, insects and reptiles could be added to this list. Specializing in any one of these food types would result in a lower diversity of essential nutrients consumed, thereby increasing maternal and

Diverse vs. Non-Diverse Diets

DIVERSE DIET
  – Red deer
  – Duck
  – Shellfish
  – Plant foods

NON-DIVERSE DIET
  - Red deer
  - Horse
  - Bison
  - Rabbit
  - Wild boar
  - Ibex
  - Mammoth

Fig. 2. Illustration of a diverse diet (left column) leading to healthier human populations compared to a non-diverse diet (right column) leading to higher fetal-to-infant mortality and shorter life expectancy.

fetus-to-infant mortality, as well as decreasing average life expectancy (Fig. 2). In contrast, regularly consuming foods from several food types, especially a combination of energy-rich animal foods and micronutrient-rich plant foods, should lead to healthier human populations and positively affect demographic trends. In retrospect, these principals are linked to our evolutionary past in which our ancestors adapted genetically to a diverse intake of essential nutrients, probably largely through a herbivorous diet supplemented by animal foods early on (Speth, 1989; Andrews and Martin, 1991; Broadhurst et al., 1998; Sponheimer and Lee-Thorp, 1999; Teaford and Ungar, 2000; Lee-Thorp et al., 2003), with generally increasing contributions from animal foods through time. It is within this general context that the demographic consequences of diverse essential nutrient intake can be understood.

With these principles in mind, the remainder of this essay explores general trends in the health of European Neandertal and early AMHS populations from a nutritional ecology perspective. We examine three types of proxy data that each provide information on general essential nutrient intake between roughly 50,000 and 25,000 BP: stable isotopes; faunal remains; and the paleopathology/biological anthropology of human skeletons. We compare and contrast these data in order to interpret whether principles derived from nutritional ecology might help explain the extinction of European Neandertals in space and time.

3.1. Stable isotopes

Stable isotope analysis is a direct method to infer past human diets (Richards et al., 2003). Briefly summarizing the recent literature on stable isotopes, the techniques currently measure the types of protein individuals consumed during the final decade of life (Richards et al., 2003). Analyzing ^{13}C and ^{15}N isotopes may determine whether the protein consumed was derived largely from plants or animals, and within the animal fraction, whether the protein derived mainly from terrestrial or marine sources (Schwarcz and Schoeninger, 1991; Bocherens et al., 1995; Schoeller, 1999; Richards et al., 2003).

The following data were compiled from stable isotopes extracted from a number of human and nonhuman bones recovered across Europe and the Asian steppe, most of which date between ca. 50,000 and 25,000 BP (Bocherens et al., 1995, 1999, 2001; Fizet et al., 1995; Ambrose, 1998; Katzenberg and Weber, 1999; Richards and Hedges, 1999; Iacumin et al., 2000; Richards et al., 2000a, b, 2003; Bocherens and Drucker, 2003). In general, European terrestrial herbivores return ^{13}C values that average about −20.0‰, while European carnivores that feed on terrestrial herbivores return ^{13}C values that average about −19.0‰. Thus, carnivorous diets focused on terrestrial herbivores tend to produce less negative ^{13}C values that typically range between 0.1‰ and 2.0‰ (Bocherens and Drucker, 2003). Comparing carbon isotope intake from marine and terrestrial sources, marine diets produce less depleted ^{13}C values that average about −12.0‰ rather than the −19.0‰ to −20.0‰ values of terrestrial diets.

^{15}N values generally rise about 2.0–4.0‰ per trophic level. On average, terrestrial C_3 plants in Europe exhibit ^{15}N values of about 3.0‰; terrestrial herbivores that feed on these C_3 plants exhibit ^{15}N values of about 4.0–6.0‰; and terrestrial carnivores that feed on these herbivores display ^{15}N values of about 9.0–10.0‰. ^{15}N enrichment generally ranges between 3.0‰ and 5.0‰ between predators and their average prey (Bocherens and Drucker, 2003). Comparing nitrogen isotope intake from marine and terrestrial sources, marine diets produce average ^{15}N values between 10.0‰ and 20.0‰ rather than the 4.0–10.0‰ of terrestrial diets.

Taken together, the ^{13}C and ^{15}N isotope values derived from a skeletal sample may indicate whether that individual ate primarily an herbivorous, carnivorous, or omnivorous diet, and whether the protein consumed derived primarily from terrestrial, marine, or a combination of terrestrial/marine sources. It is important to note, however, that these average values and ranges are based on a wide range of studies across Europe; in practice, interpretations must always be based on a case-by-case basis depending on the geographic setting, climate, and time period that faunal specimens derive (e.g., Bocherens et al., 1999; Bocherens and Drucker, 2003). In addition, variations in stable isotope values due to metabolic differences among individuals may hinder our ability to make broad generalizations about diets at the population level. Current and future research will help clarify these issues.

With these cautions in mind, carbon and nitrogen isotopes have been extracted from a number of Neandertal and Gravettian-aged AMHS skeletons in central and northern Europe (Fizet et al., 1995; Ambrose, 1998; Bocherens et al., 1999, 2001; Richards et al., 2000a, b), as well as a wide variety of large herbivores, small mammals, and carnivores (Bocherens et al., 1995, 1999, 2001; Fizet et al., 1995; Ambrose,
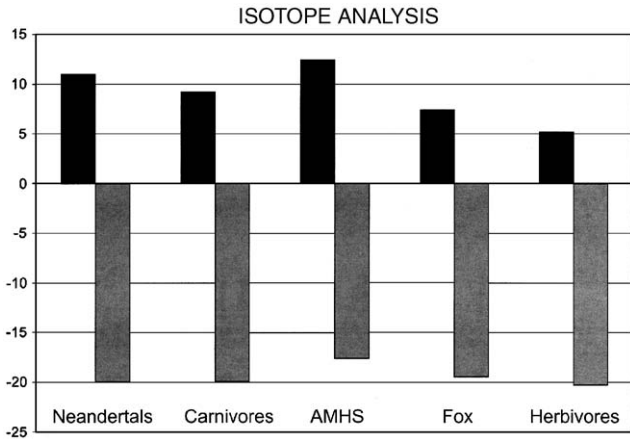
Fig. 3. Average ^{13}C (bottom row) and ^{15}N (top row) values for carnivores, omnivores, herbivores, Neandertals, and early AMHS in Europe.

AVERAGE ISOTOPE VALUES

Diet	^{15}N	^{13}C
Terrestrial Herbivores	4 to 6‰	-20 to -21‰
Terrestrial Carnivores	9 to 10‰ [10.5‰]	-19 to -20‰ [-19‰]
Marine (fish, shellfish)	10 to 20‰ {12.5‰}	-12 to -13‰ {-17.5‰}

[ ] = Neanderthal   { } = AMHS

Fig. 4. Average ^{13}C and ^{15}N values of carnivorous, herbivorous, and omnivorous diets in Europe.

1998; Katzenberg and Weber, 1999; Richards and Hedges, 1999; Iacumin et al., 2000; Richards et al., 2000a, b; Bocherens and Drucker, 2003; Richards et al., 2003). Thus far, the data are consistent: the ^{13}C and ^{15}N ranges of central and northern European Neandertals suggest they were top-level carnivores, subsisting primarily on a highly specialized diet of large and medium-sized terrestrial herbivores (Figs. 3 and 4). The carbon and nitrogen isotope values of these Neandertals average about −19.0‰ and 10.5‰, respectively, which closely match the average and range values obtained from specimens of wolf and lion from the same regions and time periods (Figs. 2 and 3).

In contrast, the carbon and nitrogen isotope values of the early-to-mid AMHS specimens thus far analyzed average about −17.5‰ and 12.5‰, respectively, which not only suggests an omnivorous diet, but a diet that incorporated significant quantities of fish and/or shellfish (Richards et al., 2001; Pettitt et al., 2003). These latter figures are all the more interesting when one considers that the Gravettian was not a time of depressed populations of large, terrestrial herbivores in central and northern Europe (Roebroeks et al., 2000).

The stable isotope data cannot be used alone as a proxy for Neandertal and early AMHS diets throughout their respective ranges. There are currently no published records of stable isotopes retrieved from southern or south-coastal ranging Neandertals. As outlined below, zooarchaeological studies suggest that some of the southern populations of Neandertals were consuming a more diversified diet. This may have lowered fetal-to-infant mortality rates amongst these Neandertals compared to their northern brethren.

3.2. Faunal remains

Patou-Mathis (2000) and Conard and Prindiville (2000) recently summarized Neandertal subsistence and settlement patterns for much of central and northern Europe based on the study of nonhuman faunal remains; Boyle (2000) has done so for southern France; Aura Tortosa et al. (2002) completed a summary for east-central Spain; and Straus and Clark (1986) and Hockett and Haws (2002) have contributed similar overviews for other parts of Iberia, mainly northern Spain and central Portugal. Additional studies that we rely on here include Blasco (1997), Bosinski (2000), Djindjian (2000), Gaudzinski (2000), Hahn (2000), Nývltová-Fišáková (2000), Perlès (2000), and Valensi (2000). The locations of some of the major Neandertal sites used here are shown in Fig. 5; some of the early Upper Paleolithic sites are shown in Fig. 6. Together with the stable isotope analyses briefly outlined above, a clearer picture of Neandertal subsistence in Europe is emerging.

In central and northern Europe, faunal analyses suggest that Neandertals targeted large, gregarious herbivores that occupied open environments (Patou-Mathis, 2000). Small game hunting is unknown to any large degree, and the incorporation of a diverse suite of animal types such as birds, fish, and shellfish is relatively rare. The pattern is one of high residential mobility, with populations and regions of occupation shifting through time as open-environment species such as horse, bison, and reindeer shifted their populations (Patou-Mathis, 2000). Neandertals in central and northern Europe may have largely eschewed temperate environments especially between 250,000 and 300,000 BP to 127,000 BP (OIS 8-7), focusing instead on the hunting of large, open-environment adapted herbivores (Patou-Mathis, 2000). Patou-Mathis (2000) called this the "Old Phase" of the Middle Paleolithic in terms of faunal exploitation. After OIS 7, large gregarious herbivores such as horse and reindeer continue to dominate many faunal assemblages except during the very warm OIS 5e, which saw greater numbers of medium-sized herbivores incorporated into Neandertal diets (Patou-Mathis, 2000). Throughout the reign of the Neandertals in central and northern Europe, their diets were notable
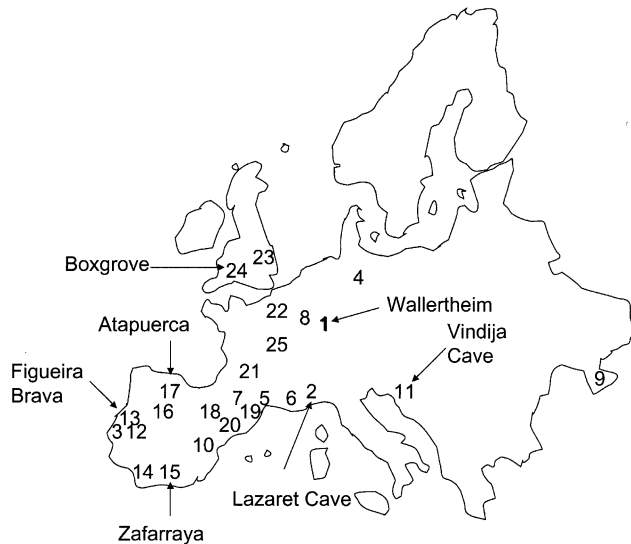
Fig. 5. Location of major Neandertal sites used in this review producing faunal remains suggesting a diet based primarily on large, terrestrial herbivores: (1) Wallertheim, Germany; (2) Lazaret Cave, France; (3) Galeria Pesada, Pego do Diabo, Portugal; (4) Salzgitter Lebenstedt, Germany; (5) Tournal, Hortus, Les Canalettes, France; (6) Adaouste, Cèdres, France; (7) Mauran, France; (8) Spy, Engis, Sclayn (Scladina Cave), Belgium; (9) Prolom II Cave, Ukraine; (10) Cova Negra, Cova Beneito, Spain; (11) Vindija Cave, Croatia; (12) Foz do Enxarrique, Portugal; (13) Figueira Brava, Furninha, Portugal; (14) Devil's Tower, Gorham, Spain; (15) Zafarraya, Spain; (16) Arriaga, Spain; (17) Atapuerca, Spain; (18) Gabasa, Spain; (19) Cueva de l'Arbreda, Spain; (20) Abric Romaní, Italy; (21) Pech de l'Azé, Combre Grenal, France; (22) Cagny, France; (23) Hoxne, England; (24) Boxgrove, England; (25) Arcy-sur-Cure, Grotte du Renne, France.
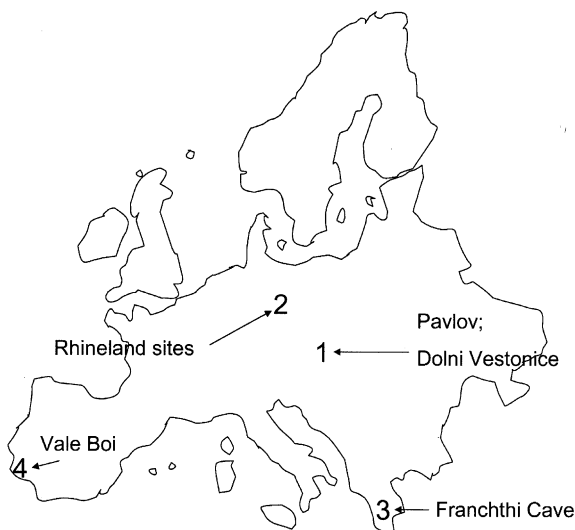

Fig. 6. Location of major early Upper Paleolithic sites used in this review producing faunal remains suggesting a more diversified diet compared to the typical Neandertal diet.

for their lack of diversity and their focus on large to medium-sized terrestrial herbivores.

In the middle latitudes such as southwestern France and northern Spain, Neandertal diets overall lacked

diversity as well: the focus was on terrestrial mammals for subsistence (Boyle, 2000). The main difference in subsistence between the middle latitudes and those to the north was the incorporation of larger quantities of medium-sized herbivores such as red deer, ibex, roe deer, wild boar, tahr, and chamois in the middle latitude sites together with larger game such as bison, horse, rhino, and elephant (Boyle, 2000). Thus, Neandertals in these regions actively exploited woodland habitats along with open environments. Typically absent in the middle latitude Neandertal sites, including those from temperate climatic periods producing open woodlands, were grinding stones and bones of birds and fish, although exceptions are known.

In the Mediterranean Region, Neandertals may have consumed primarily large and medium-sized terrestrial herbivores as well (Aura Tortosa et al., 2002). However, at sites located close to fossil coastlines, there is evidence that some Neandertal populations consumed a more diversified diet than their counterparts in the central and northern regions. In Gorham's and Vanguard caves in Gibraltar, charred pine nut shells and shellfish have been recovered from Neandertal occupations (Finlayson et al., 2001). In addition, there is some evidence that Neandertals in central Portugal consumed shellfish, and may have also consumed birds and marine mammals at sites such as Figueira Brava (Antunes, 2000). For this reason, we have recently suggested that the southern populations of Neandertals may have had lower infant mortality rates and higher average life expectancies than populations to the north, which in turn may help to explain the presence of Neandertals in the southern latitudes until ca. 28,000 BP (Hockett and Haws, 2003).

In contrast to the typical Neandertal diet of large to medium-sized herbivores, faunal remains recovered from early Gravettian-aged sites in central Europe confirm the interpretations derived from isotope analyses of similar-aged AMHS skeletons: diets became more diversified at this time. At Pavlov I, birds make up nearly 10% of the faunal remains recovered (Musil, 1994; Svoboda et al., 2000). At Dolni Vestonice II and Kostenki IV, grinding stones probably suggest the incorporation of significant quantities of plant foods (Svoboda et al., 2000). In Germany, Upper Paleolithic sites such as Geissenklösterle Cave contain fish remains by 35,000 BP; other early Upper Paleolithic sites in Germany tell a similar tale: numerous fish remains recovered from Hohle Fels, and abundant waterfowl at sites such as Brillenhöhle. Grinding stones are also found at several early Upper Paleolithic sites in the Rhineland (Bosinski, 2000; Hahn, 2000).

Many early Upper Paleolithic sites created by AMHS in the middle latitudes were subjected to post-depositional erosion, so preservation becomes a problem (Djindjian, 2000). However, at sites such as La Riera in northern Spain, the earliest Upper Paleolithic faunal

remains are similar to those seen in the Middle Paleolithic: horse and red deer dominate, with little to no evidence for the use of aquatic resources or birds (Straus and Clark, 1986). During the Solutrean, this situation changes to medium-sized herbivores such as ibex and red deer, but also significant quantities of aquatic resources such as shellfish and salmon were incorporated in the diet for the first time. This shift to a broader number of food types may have been caused by an influx of populations migrating southward during LGM (Straus and Winegardner, 2000; Straus et al., 2000).

In the southern regions, AMHS diets continued to be diversified, with the incorporation of fish, shellfish, and plants. For example, in southern Greece, data from Franchthi Cave suggest that shellfish, fish, plants, and perhaps birds were all consumed in greater frequencies during the early Upper Paleolithic than during the Middle Paleolithic (Perlès, 2000). In the Gravettian levels of Vale Boi in southern Portugal, the earliest Upper Paleolithic occupation shows dietary diversity in the exploitation of terrestrial mammals, a few birds, and especially shellfish (Bicho et al., 2003; Stiner, 2003).

3.3. Paleopathology/biological anthropology

In 1995, Eric Trinkaus interpreted the paleopathological patterns of 206 European and Near Eastern Neandertal skeletons ranging in age from 100,000 to 35,000 BP. Among Trinkaus' (1995) findings were the following salient points: (1) few Neandertals survived beyond their prime reproductive years, as 70–80% of individuals died before the age of 40; (2) Neandertal life expectancy rates suggest that they may have been at extremely low levels of population density in many parts of their range, and they may have experienced frequent periods of local extinctions and recolonizations; and (3) these data, combined with increasing degrees of dental hypoplasias through time, "imply that periods of poor nutritional quality and/or famine must have been relatively common among these late archaic humans, in both Europe and the Near East" (Trinkaus, 1995, p. 138).

A more recent summary by Pettitt (2000) concludes that Neandertals seem to have had high infant mortality, high mortality among children and young adults, and short life expectancies. The combination of high infant and young adult mortality, in particular, would suggest that Neandertals maintained very low population densities. The number of early AMHS skeletal samples is not large, but Soffer (1994) suggested that juvenile mortality was lower among populations of early AMHS in northern Eurasia compared to those of the Neandertals.

Based on dental wear patterns, Skinner (1997) concluded that Upper Paleolithic infants were weaned on average at about 2 years of age. Upper Paleolithic infants tend to show greater degrees of dental attrition than Neandertal infants (Skinner and Newell, 2000), which may suggest that Neandertal mothers breast-fed their babies longer than AMHS mothers. If that was the case, then "(t)his difference may signal longer average birth spacing among Neandertals than modern humans" (Pettitt, 2000, pp. 354–355), which may in turn have lowered Neandertal fertility relative to AMHS. However, rather than relating directly to differences in fertility, Skinner (1996) and Skinner and Newell (2000) concluded that the higher incidence of dental attrition in AMHS infants was more likely due to suboptimal vitamin-A absorption due to low fat intake.

Additional studies of dental wear, striation, and trauma patterns suggest that many Neandertal populations consumed a highly carnivorous diet (Lalueza et al., 1996; Tattersall and Schwartz, 2000).

4. Nutritional ecology of Neandertal extinction

We recently outlined the nutritional ecology approach in broad terms and briefly discussed its potential for understanding Neandertal extinction (Hockett and Haws, 2003). Here, we link nutritional ecology within the broader context of natural selection and the processes that lead to differential fertility and mortality in human populations (Fig. 1). In humans, fertility is primarily influenced by social rather than biological factors, although there are links between nutrition and fertility. If we accept that mortality was primarily influenced by biological factors at the Middle-to-Upper Paleolithic transition, then nutrition should form an intrical part of any model that attempts to explain that transition. Nutritional effects on human mortality patterns are not influenced primarily by net energy return in relation to work effort; rather, they are primarily influenced by diverse essential nutrient intake of the mother, fetus, neonate, and infant. To model the nutritional impacts on human mortality patterns, our focus must be on complete essential nutrient intake.

There are at least three proxy data that may inform on essential nutrient intake in prehistoric foragers: stable isotopes, faunal remains, and paleopathology of human skeletons. These proxy data can be interpreted through the broader lens of the nutritional ecology model to form a more coherent picture of Neandertal and early AMHS health patterns and demography. These interpretations, in turn, may assist in explaining Neandertal extinction in specific places and times, though we make no claim that the model represents a panacea that explains the nature and timing of the extinction of every population of Neandertal across Europe. The emerging picture is as follows:

PLEISTOCENE PREDATORS

	MIDDLE PALEOLITHIC	UPPER PALEOLITHIC
Top-level carnivores	Neanderthal, wolf, hyena, lion	wolf, lynx, wildcat etc.
Omnivores	fox	AMHS, fox
Herbivores	cave bear	n/a

Fig. 7. Generalized niches of Neandertals and early Upper Paleolithic foragers in Europe.

Neandertals were effective hunters of large, gregarious, open-environment herbivores, as well as medium-sized herbivores, perhaps as early as a quarter-of-a-million years ago (Fig. 7). Throughout much of their range, they were top-level carnivores, occupying that spot with other large carnivores such as wolves and lions (Fig. 6). By restricting their diet to large terrestrial game, many Neandertal populations would have consumed inadequate quantities of some micronutrients and over-consumed others. They probably enjoyed adequate calorie and protein intake. The lack of adequate and consistent intake of some micronutrients such as vitamins A, C, and E, however, meant that many Neandertal women probably had high incidences of abortions, miscarriages, and stillbirths resulting in high fetal-to-infant mortality. Their high rate of young adult mortality may have had as much to do with their lifestyle of constantly pursuing large game animals than nutritional factors (Trinkaus and Zimmerman, 1982; Berger and Trinkaus, 1995; Pettitt, 2000).

This subsistence specialization may have doomed the Neandertals facing increasing environmental warming and competition with AMHS populations without a rather drastic change in diet, particularly if early AMHS were consuming a more diversified diet. A restricted diet of large mammal meat and organs, regardless of the calories provided, would not have allowed Neandertal populations to compete with AMHS if the latter were consuming a more diversified diet. The low-diversity Neandertal diet may have been the best subsistence strategy possible given the Pleistocene environments of central and northern Europe that were conducive to the propagation of large, gregarious herds of herbivores, and during time periods when their competition consisted of nonhuman predators such as wolves, lions, and hyenas. In fact, energy maximization may be more important to relatively cold-adapted, northern foragers because higher energy intakes are often necessary for thermoregulation of the body (Stini, 1981). In short, the Neandertals may have been doing the best they could given the environments of Pleistocene Europe before ca. 40,000–30,000 BP. This possibility is especially important considering these ecosystems have no modern analogues for us to stand in judgment.

The subsistence strategy of the Neandertals, however, would have been inferior to competition from other human populations consuming a diverse range of food types (Stini, 1981, p. 61) because the latter decreases maternal and fetal-to-infant mortality, as well as increases average life expectancy. Both of these latter demographic parameters would result in upward population curves through time; increasing average life expectancies would be especially important in the social transmission of information needed to schedule the exploitation of diverse food types.

In head-to-head competition, Neandertal populations consuming a lower diversity of essential nutrients would not have been able to maintain their genetic uniqueness in the face of healthier and longer-living AMHS populations—in short, the Neandertals would have been demographically swamped by the more reproductively successful AMHS populations. Faced with the changing ecological dynamics between 40,000 and 30,000 BP and incoming populations of AMHS, Neandertal populations either did not or could not instigate behavioral modifications quickly enough to avoid becoming genetically swamped by human populations engaged in economic strategies that resulted in the consumption of a diverse suite of essential nutrients. This would be the case even if the AMHS populations did not possess so-called superior technologies or mental faculties.

Eswaran (2002) recently provided a model that describes mathematically how this genetic swamping could have occurred. What that model lacks are the precise factors that provided the advantages to AMHS populations when their gene pools collided with those of the Neandertals. We think Eswaran was on the right track when he sought factors that would lead to different infant mortality rates between the two human groups. However, Eswaran (2002) suggested that it may have been an anatomical trait, namely differences in the birth canal widths between Neandertal and AMHS populations, that led to greater infant mortality rates in Neandertals. Although this suggestion was criticized (e.g., Rosenberg, 2002; Trinkaus, 2002; Wolpoff, 2002), we agree with Eswaran's suggestion that infant mortality may have been higher in Neandertals compared to many populations of AMHS. However, these differences probably were at least partially related to differences in essential nutrient intake, and, as Eswaran (2002) showed, a decrease in infant mortality rates of only one-half of one percent may have been enough for the AMHS gene pool to swamp that of the Neandertals.

Targeting large, gregarious herds of herbivores served Neandertals well for at least one-quarter of a million years, but ultimately proved unsuccessful in competition with human groups having more diversified diets, and perhaps other as yet unidentified genetic advantages. In terms of testing these interpretations against the

archaeological record, faunal and human skeletal data from the transition period of roughly 40,000–30,000 BP is incomplete and spotty. We have much more information on the succeeding Gravettian after ca. 28,000–25,000 BP. By this time, the faunal and skeletal records suggest that diets were more diversified than the 'typical' Neandertal diet, and the beginnings of a noticeable population expansion is seen throughout Europe as previously unoccupied environments begin to be filled with human foragers (e.g., Mussi, 2000). This population explosion correlates with diverse dietary intake, particularly the increasing consumption of small non-mammalian animals and plant foods. Following the Gravettian, the Solutrean witnessed a return to relatively harsh climatic conditions in many regions of Europe. A drop in dietary diversity in these areas coupled with a reliance on primarily terrestrial mammals similar to the Neandertal pattern would have resulted in increased fetal-to-infant and maternal mortality at this time for these populations of AMHS. Other regions of Europe, however, such as the coastal and near-coastal subregions of the southern Iberian Peninsula, did not experience shifts in vegetation and faunal communities as dramatic as further north during the Solutrean, and thus local shifts in human demographics there may have more to do with migration than with nutritional affects on mortality patterns (e.g., Straus et al., 2000).

The "Broad Spectrum Revolution" (Flannery, 1969) near the transition to agriculture at the end of the Pleistocene was in fact not a subsistence revolution in Europe in terms of diverse dietary intake, rather it represented a return to large-scale dietary diversity following LGM conditions. The initial broad-spectrum diet was probably practiced by several species of early hominids, including those on the direct line to AMHS. Much later, diverse diets re-occurred across many regions of Europe by at least the Gravettian, with the demographic consequences of lower maternal and fetal-to-infant mortality seen in the population expansion of this time. In fact, diverse diets in the form of energy-rich animal foods and micronutrient-rich plant foods may also help explain the early success of hominids hundreds of thousands of years before the early Upper Paleolithic. Whether the 'neo-revolution' in essential nutrient intake began at the earliest stages of the occupation of Europe by populations of AMHS, thereby accelerating Neandertal extinction, awaits further testing and confirmation.

Acknowledgments

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