ISSUES

Nutritional Ecology and Diachronic Trends in Paleolithic Diet and Health

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Modern nutritional studies have found that diverse diets are linked to lower infant mortality rates and longer life expectancies in humans. This is primarily because humans require more than fifty essential nutrients for growth and cell maintenance and repair; most of these essential nutrients must come from outside food sources rather than being manufactured by the body itself; and a diversity of food types is required to consume the full suite of essential nutrients necessary for optimal human health. These principles and their related affects on human adaptations and demography are the hallmarks of a theoretical paradigm defined as nutritional ecology. This essay applies concepts derived from nutritional ecology to the study of human evolution. Principles of nutritional ecology are applied to the study of the Middle-to-Upper Paleolithic transition in order to broadly illustrate the interpretive ramifications of this approach. At any stage in human evolution, those hominid populations that chose to diversify their subsistence base may have had a selective advantage over competitors who restricted their diet principally to one food type, such as terrestrial mammals.

A fundamental principle of human health and nutrition is that diverse diets increase overall health patterns by lowering infant mortality rates[1] and increasing average life expectancy.[2] This principal is the core of the theoretical model of nutritional ecology.

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Jenike[3] recently defined nutritional ecology as "the interaction of diet, somatic maintenance, physical activity, and pathogenic agents as they relate to growth, body composition, development, and function in a constraining social, political, and natural environment" (p. 207). Here, however, we offer a modified definition of the concept: Nutritional ecology is the study of the relationship between essential nutrient intake and its effects on overall human health, including growth and maintenance in individuals and general demographic trends in populations. Our goals in this essay are to elaborate on the fundamental principals of nutritional ecology, which may help to clarify the consequences of dietary choices made by Paleolithic foragers at various stages of human evolution.

In order to comprehend fully long-term trends in Paleolithic diet from the perspective of nutritional ecology, it is important to understand the basic principles that underlie dietary diversity and human health patterns. With few exceptions,[4–6] previous studies of the diet of Paleolithic foragers have focused on the consumption of fat, protein, or calories[7–27] or on the net return of calorie extraction from the environment.[28–32] Although human populations have survived and reproduced by consuming a relatively non-diverse diet, maximizing essential nutrient intake through a diversified diet can lower infant mortality rates and increase average life expectancy,[1,2] thereby positively affecting demographic trends. The fact that modern humans require such a diverse suite of essential nutrients to achieve the maximum benefits of health and longevity suggests that this pattern evolved relatively early in hominid prehistory. Therefore, we view this pattern as analogous to a "primitive" condition or trait in cladistic analysis. Specialized diets (vegetarian or the near-exclusive consumption of animal products) may be viewed as derived dietary adaptations within the hominid lineage.

Diverse diets increase overall human health[1,2,4] because modern humans require dozens of essential nutrients to achieve optimal health conditions, and these are rarely found in one food item or one food group. Although the human body is capable of manufacturing some nutrients such as vitamin D, many of those that are essential must come from outside food sources. Thus, the more diverse the diet, the more diverse the intake of the essential nutrients necessary for optimal human health.

Essential nutrients are those that the human body must obtain from foods.[33] Humans require approximately fifty nutrients for growth and cell maintenance and repair. These nutrients are divided into six classes:

TABLE 1. COMPARISON OF CALORIC AND NONCALORIC ESSENTIAL NUTRIENTS OF 100 G OF FOODS OF VARIOUS CLASSES

Essential Nutrient	Terrestrial Mammals (muscle)[a]	Terrestrial Mammals (organs)[b]	Shellfish[c]	Birds[d]	Fish[e]	Plants[f]
Energy (kcal)	119	195	74	215	166	132
Fat (g)	2.8	10.0	.97	14.1	8.1	2.5
Protein (g)	22.0	20.0	12.8	21.7	21.7	8.3
Carbs (g)	0	4.0	2.6	0	0	14.8
Noncaloric						
C (mg)	.17	12.7	13.0	3.6	.17	32.5
Thiamin (mg)	.22	.16	.08	.19	.22	.13
Riboflavin (mg)	.26	2.4	.21	.20	.31	.19
Niacin (mg)	4.8	9.4	1.8	4.2	5.9	1.1
B-6 (mg)	.34	.50	.06	.53	.40	.07
B-12 (mg)	4.6	27.6	49.4	.65	6.6	0
A (IU)	0	9196[g]	300	118	322	138
Folate (mg)	7.4	105.0	16.0	21.0	16.7	2.4
D (mcg)	0	.75	4.0	—[h]	8.0	0
E (mg)	.20	1.2	1.0	.70	.25	2.2
Calcium (mg)	9.5	10.8	46.0	22.5	145.7	110
Iron (mg)	3.4	4.1	14.0	5.4	1.7	3.0
Potassium (mg)	338	313	314	288	416	387

[a] Based on average values of horse, bison, red deer, rabbit, wild boar, and reindeer.
[b] Based on average values of beef liver, brains, and kidneys.
[c] Based on the clam *Lamellibranchia*.
[d] Based on average values of grouse or partridge and duck.
[e] Based on average values of Atlantic salmon, sea trout, and sardines.
[f] Based on average values of over 200 edible plant foods found in the Mediterranean region.[4]
[g] 100 g of liver alone provides nearly 36,000 IU. A single daily serving of 35,000 to 50,000 IU may be lethal.[33]
[h] Egg yolks contain significant quantities of vitamin D; one egg yolk can supply a .60 mcg of vitamin D, almost as much as 100 g of beef liver.

proteins, lipids (fat), carbohydrates, vitamins, minerals, and water. These can be further divided into two groups, those that supply energy (calories) and those that do not supply energy. Proteins, fats, and carbohydrates supply energy, while vitamins, minerals, and water are noncaloric essential nutrients. Proteins, lipids, and carbohydrates provide both energy and the building blocks for tissue development and repair. Vitamins are organic molecules essential to human metabolism. Minerals are inorganic elements that play pivotal roles in cell structure and assist in metabolic processes. Water, which is essential to all life plays multifaceted, complex roles in metabolic reactions, transporting materials to cells and waste products away from cells.

The five primary food groups that supplied Paleolithic foragers with essential nutrients are terrestrial mammals, fish, shellfish, birds, and plants (Table 1). Subdividing animals by general taxonomic categories (such as terrestrial mammals, birds, shellfish, and fish) may be useful in discussions of long-term trends in human health during the Paleolithic. For example, terrestrial mammals may be lumped under a single category because most of them provide about the same proportions of essential nutrients per unit gram of flesh.[34] However, shellfish provide additional carbohydrates not generally available from terrestrial mammals; fish and shellfish are relatively rich sources of vitamins D and E; and birds are rich sources of lipids and provide nearly twice as many kilocalories per 100 g of flesh as do terrestrial mammals, shellfish, and some fish (Table 1). Thus, different types of animals provide different sources of essential nutrients. Paleolithic foragers could not have consumed a balanced intake of essential nutrients from a single animal group.

Plant foods provide several key nutrients that animal products either lack or generally provide in lower quantities (Table 1). These include various carotenoids, among them beta-carotene (a precursor to vitamin A), vitamin E, and vitamin C. Although terrestrial animal livers supply significant levels of vitamins A, C, and E, relying on liver for E and C may lead to dangerously toxic levels of vitamin A. Thus humans, particularly females during pregnancy, must moderate liver consumption.[33]

A diet consisting of a relatively equal combination of terrestrial mammals, birds, shellfish, fish, and plant foods would lead to healthier individuals than would a diet based solely or primarily on one type of animal food such as terrestrial mammals. This principle is heuristically illustrated in Figure 1.

In terms of dietary efficiency, the nutritional ecology approach does not define this concept in terms of the net energy return of calories from the environment. Dietary efficiency is inextricably linked to consuming a diversity of foods in order to obtain the full suite of nutrients essential to optimal

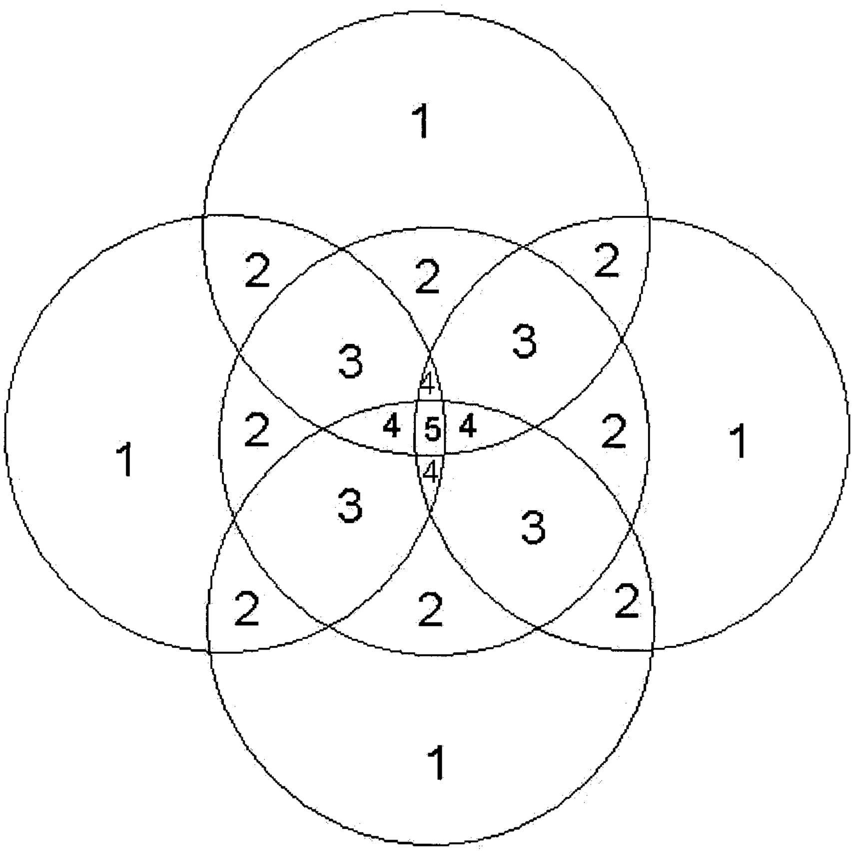

Figure 1. Geometric illustration of food diversity and overall human health. Each of the five circles represents one of the five food types defined in this essay: terrestrial mammals, shellfish, fish, birds, and plants. At the periphery, human foragers would consume only a single food type. As groups included more diversity and balance in their subsistence base, they would move closer to the center. All five circles intersect at the number "5," which represents groups foraging at the most nutritionally efficient level possible to maximize life expectancy rates and minimize infant mortality rates.

health. This is in part because the human body rarely uses single essential nutrients in the performance of single tasks. In other words, a human body functioning at optimal condition requires the full suite of essential nutrients to be present. As a result, a diverse diet is more efficient than one based on a limited number of food types, assuming that the daily requirement of calories (energy) is also met.

Without question, extracting enough calories from the environment to sustain human life is a critical factor in long-term survival, so energy intake affects human health patterns and demographic trends.[1,35] A person in a steady state of energy but at risk to health is defined as suffering from chronic energy deficiency.[36] From a nutrition perspective, some dietary models focus on chronic energy deficiency in prehistory because they are based on net caloric return rates rather than the intake of all essential nutrients. The nutritional ecology approach suggests that human populations can maintain levels above chronic energy deficiency but exhibit higher infant mortality rates and shorter life expectancies than others who may consume fewer calories but eat a more balanced diet of essential nutrients.

The nutritional ecology perspective has important ramifications for the causal and chronological relationships among subsistence and demographics during the Paleolithic. For example, nutritional ecology interprets the consumption of an eclectic diet consisting of large and small terrestrial game, plant foods, fish, and shellfish as increased efficiency in essential nutrient intake that would increase overall human health and positively affect demographic trends. As a result, nutritional ecology suggests that increases in human population densities may be a result of changes in human diet rather than demographic pressure instigating dietary changes. Positive changes in Paleolithic demography may have been the result of foragers diversifying their diet at specific places during specific time periods.[37]

OPERATIONALIZING THE MODEL

Is the nutritional ecology model testable against the archeological record? Yes, it is. Due to an incomplete archeological record and taphonomic concerns, any model that purports to explain Paleolithic subsistence patterns will run into problems with respect to equifinality and agreements among researchers on what constitutes adequate testing procedures.[38,39] Nevertheless, the nutritional ecology model is testable through a variety of methods. One method is simply to show diachronic trends in the relative proportions of the five food types emphasized here through standard zooarcheological statistical techniques such as NISP, MNE, MNI, MAU and Indices of Diversity.

The faunal remains of four of the food groups emphasized here are relatively sturdy and often are well preserved in archeological contexts, particularly caves and rockshelters. It has long been acknowledged that a preservation bias exists with respect to the recovery of plant remains. However, modern excavation techniques are beginning to show success in retrieving evidence of plant use during the Paleolithic in some environments.[40–42] Because both plants and animals often have seasonally restricted availability, seasonality determinations must be made, especially in areas where caves and rockshelters provide the only subsistence evidence. This is a critical problem because these sites were often used during cold months for shelter or for special tasks throughout the year. The conclusion that their faunal remains represent the entire dietary repertoire may be erroneous.

Stable isotope analysis of skeletal remains used to interpret hominid dietary adaptations and diversity are showing promising results.[43–57] These proxy data may illuminate trends in dietary diversity during the Paleolithic, including general trends in essential nutrient intake. For example, a tendency in the archeological record away from the consumption of primarily terrestrial mammals toward the consumption of more equal proportions of terrestrial mammals, shellfish, fish, birds, and plants would indicate healthier populations and positively affect demography trend. These interpretations based on faunal and floral analyses, could then be further tested through isotope analysis of human skeletal remains, as well as the paleopathology of those remains.[58–61] Thus, the assumptions of nutritional ecology can be satisfactorily investigated through a series of methods that act to cross-check interpretations.

NUTRITIONAL ECOLOGY AND HUMAN EVOLUTION

The issues and questions concerning the evolution of modern humans that nutritional ecology may assist in researching are vast in number, and certainly cannot be fully addressed here. Nevertheless, the Middle Paleolithic-Upper Paleolithic transition in Europe can be used as an example of an issue that may be examined through nutritional ecology. We make no assumption that nutritional ecology can explain all facets of human evolution in all environments and during all time periods. Any model that made such a claim would do a serious injustice to the vast array of environmental and social circumstances that Paleolithic peoples adapted to over the last three million years.

Studies of later Paleolithic subsistence suggest that a trend toward diversified diets may have occurred between the Middle Paleolithic and Upper Paleolithic in parts of Europe[62] and the Near East.[28,63] By at least a quarter of a million years ago, and probably much earlier, hominids in Europe had become efficient big-game hunters.[63] Recent zooarcheological and stable isotope studies suggest that northern populations of Neandertals focused their subsistence strategies on the procurement of large game animals,[27,28,62,64] but that Neandertal diets were probably more diverse in the southern portions of their range.[65,66] Upper Paleolithic technologies tend to be associated with an even greater increase in food diversity.[28,62,63,67] From a nutritional perspective, these changes did not represent reduced foraging efficiency and subsistence stress across the transition from the Middle to Upper Paleolithic, but rather marked increasingly diversified and more nutritionally balanced diets that probably led to increased population fitness levels, longer life expectancy, and, ultimately, increased population densities for Upper Paleolithic foragers.

The nutritional ecology approach suggests that, on average, individual Neandertals in the southern latitudes were healthier and lived longer than their counterparts in the northern latitudes. This may help explain why it took Upper Paleolithic foragers 10,000 years to subsume, drive out, or replace the southern populations of Neandertals, . . .

The potential implications of the nutritional ecology approach to the Middle Paleolithic-Upper Paleolithic transition are complex. Quite possibly, southern Neandertals incorporated greater amounts of essential nutrients into their diet than did the northern Neandertals. The nutritional ecology approach suggests that, on average, individual Neandertals in the southern latitudes were healthier and lived longer than their counterparts in the northern latitudes. This may help explain why it took Upper Paleolithic foragers 10,000 years to subsume, drive out, or replace the southern populations of Neandertals, thereby partially explaining the existence of the "Ebro Frontier."[68] However, we must also note Zilhão's[69,70] suggestion that this delay could have been caused by other paleoenvironmental and social factors. If healthier Neandertal populations to the south contributed to this delay, then it is currently unclear why the Vindija population of Croatia occurred so late. Nevertheless, relatively late Neandertal skeletons are being recovered from southern Iberia,[69–71] a place with more diverse and dense edible foods than were available in central and northern Europe.[72] We hope that those specimens will yield enough collagen to allow the measurement of stable isotopes and trace elements.

In contrast to the northern Neandertals, anatomically modern human specimens from mid-Upper Paleolithic (Gravettian) sites in central and eastern Europe show a broader dietary source of protein based on $\delta^{13}C$ and $\delta^{15}N$ values. Richards and coworkers[46,47] have argued that less depleted $\delta^{13}C$ values in the modern humans were due to an increase in freshwater fish and waterfowl in the diet, possibly as high as 50% in the $\delta^{15}N$ values for the Kostenki sample. There seems little doubt that the Gravettian (ca. 27,000–21,000 BP) in Europe witnessed the expansion of Paleolithic peoples into regions that previously were unoccupied or had low population densities.[73,74] This may represent the first real "paying-off" period in terms of lowered infant mortality rates and longer life expectancies resulting from diversified early Upper Paleolithic diets. The subtle shift toward greater dietary diversity may have been sufficient to enable anatomically modern humans finally to out-compete the Neandertals in certain regions. Zubrow's[75,76] computer simulations, for example, showed that a mere 2% difference in mortality rates could lead to replacement. Whether this replacement was at the grade or species level is irrelevant to the nutritional ecology model. That model can accommodate invasionist replacement, diffusionist gene flow, or in-situ mosaic evolutionary models. It only predicts health consequences based on diet choices made by hominids given particular circumstances in time and space; it makes no assumptions concerning directional trends in human evolution.

Diverse diets seem to have been a trademark of humans in lower and mid-latitudes during the Late Pleistocene. It is ironic that dietary diversity should be detected in the mid-Upper Paleolithic of central Europe. This was not a period of depressed large game populations; on the contrary it was the "Golden Age."[77] Binford[78] and Flannery[79] assumed that the terminal Pleistocene broadening of the diet was the result of constant population growth based on Upper Paleolithic hunting success, which ultimately led to the over-harvesting of large game. This supposedly led to technological innovations such as grinding stones, nets, and weirs, which lowered handling costs, thus making plants, small game, and fish more economical.[80] However, it is becoming increasingly apparent that grinding stones should not be considered a requisite to the exploitation of nuts and seeds as food.[40–42,81–83] Fine-grained recovery techniques, taphonomic studies, and biochemical analyses have shown that plants, small game, and fish were regularly exploited much earlier. Increasingly, archeologists are pushing the concept of a broad-spectrum adaptation further back in time.[46,84]

It is our hope that nutritional ecology will assist in synthesizing research projects aimed at linking diet and Paleolithic adaptations into a more cohesive framework for understanding the importance of all essential nutrients to long-term human health patterns and their demographic consequences. From an evolutionary perspective, specific dietary changes may have allowed certain groups to out-compete rival foragers and perhaps nonhuman predators. This may have set in motion processes that would have profound affects on human history during the Holocene.

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