

Evolution, Diet and Health

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Introduction

The nutritional requirements of contemporary humans represent the end-result of dietary interactions between our ancestral species and their environments extending back to the origins of life on earth. Primates of modern aspect are thought to have emerged about 50 million years ago and appreciating the basic range of primate nutritional patterns over this

lengthy evolutionary period is critically important because only when the original simian baseline is characterized can subsequent dietary modifications within the hominid lineage be fully appraised. These nutritional changes have had significant evolutionary impact in the past and they now affect the health of contemporary human populations. The nature of

these interactions can best be understood when the dietary alterations are measured against a fundamental primate benchmark.

The Primate Baseline

With regard to diet what students of human evolution and advocates of evolutionary medicine need most from paleoprimatologists is an estimate of the nutritional pattern likely to have characterized the last common ancestor of apes and humans, a hypothetical species thought to have existed in Africa between seven and five million years ago.

If members of this elusive taxon were like current chimpanzees and bonobos, plant foods such as fruits, leaves, gums, and stalks probably comprised at least 95% of their dietary intake with insects, eggs, and small animals making up the remainder (Milton, 1993; Tutin & Fernandez, 1993). The general nutritional parameters of an eating pattern along these lines can be estimated with modest confidence, although certainly not with mathematical exactitude. Protein would have contributed a greater proportion of total energy than it does for most contemporary humans, but with much more from vegetable sources than from animal. (Popovich, 1997) Simple carbohydrate intake would have been strikingly below that now common, and, somewhat counterintuitively, such diets would have provided only moderate levels of starch and other complex carbohydrates so that the total carbohydrate contribution to dietary energy would have been less, not more, than is typical in contemporary affluent nations. Dietary fiber would have exceeded current levels by an order of magnitude: 200 grams vs. 20 grams a day (Milton, 1993): for some ancestral hominoids, colonic fiber fermentation may have provided over 50% of total dietary energy (Popovich, 1997). Daily intake of vitamins and minerals is likely to have been considerably greater than at present with the likely exception of iodine, consumption of which would have varied with geographic location according to oceanic

proximity, volcanic activity, prevailing winds and rainfall. As it is for all other free-living terrestrial mammals, sodium intake would have been only a fraction of that currently common and would have been substantially less than that of potassium. (Denton, 1995) Availability of phytochemicals, like that of vitamins and most minerals would, in all likelihood, have been substantially greater than for Americans and other Westerners.

Total fat intake, especially of serum-cholesterol-raising saturated and trans fatty acids, must have been greatly below current American and European levels; cholesterol intake would have been minimal. Within the polyunsaturated fatty acid [PUFA] category, partition between the omega 6 and omega 3 (w-6 and w-3) families would have been reasonably equal or skewed slightly towards the w-3s. Polyunsaturated fatty acids from plant sources are predominantly, if not exclusively, 18-carbon or less in chain length; linoleic acid (LA, C18:2, w-6) and α -linolenic acid (ALA, C18:3, w-3) are typical. Accordingly, dietary intake of the longer chain C20 and C22 PUFAs such as arachidonic acid (AA, C20:4, w-6) and docosahexaenoic acid (DHA, C22:6, w-3) would have been low (Eaton, 1998).

Scavenging, Hunting and Brain Expansion

Paleodental evidence suggests that after the divergence of early hominids from the hominoid ancestral line, a gradual increase in consumption of harder and/or more abrasive foods occurred - most likely nuts and seeds. This change probably increased intake of vegetable fat (mostly non-serum-cholesterol raising in nature) and would, perhaps, have facilitated overall access to food energy, but probably had little other nutritional effect. About 2.5 million years ago, however, there is evidence that animal foods began to occupy an increasingly prominent place in our ancestor's subsistence. Decreased molar size, less mandibular and cranial robusticity, and alterations in incisor shape all suggest greater emphasis on foods requiring less grinding and more tearing, such as meat.

An increasing proportion of meat in the diet would obviously have provided more animal protein, a factor perhaps related to the stature increase which appears to have accompanied the transition from Australopithecines through *Homo habilis* to *H. erectus*, (McHenry, 1992) but greater availability of animal fat was probably a more important dietary alteration. Even crude Oldowan stone tools would have allowed early humans access to brain and marrow from a broad range of animals obtained by scavenging or hunting - including some species larger than those from which chimpanzee hunters preferentially extract brain tissue and marrow fat. These and other carcass fats were probably prized by the early hominids as they are by recently-observed modern human hunter-gatherers. (Steffanson, 1960) More animal fat in the diet meant not only additional energy, but also a source of ready-formed long chain PUFAs, including AA, DTA (docosatetraenoic acid (DTA, C22:4, w-3), and DHA. These three fatty acids together make up over 90% of the long chain PUFA (i.e. the structurally significant and biochemically active fat) found in the brain gray matter of all mammalian species (Sinclair, 1975).

A cardinal feature of human evolution has been development of increasing brain size: *Homo sapiens*' cranial capacity is thrice that of *Australopithecus afarensis*. A prime selective force driving this increase was almost certainly the complex nature of social interactions among early hominids. There is, however, no a priori reason to assume that such interactions, at first, differed much from those of chimpanzee and gorilla ancestors. Social complexity was thus a necessary, but insufficient, selective pressure acting to increase brain size. Another necessary factor was probably adequate dietary substrate to allow formation of brain tissue. (Crawford, 1992) The limiting raw materials, AA, DTA and DHA, could have been provided by animal tissues as hunting and/or scavenging activities assumed greater importance in human subsistence. (Eaton, 1998) Increasing complexity of interpersonal and social interactions together with availability of animal tissues – to provide the necessary structural lipid - constituted a unique psychonutritional nexus which may explain human brain expansion.

Dramatic nutritional, anatomic, and behavioral changes accompanied hunting and scavenging: division of labor by sexes, increased day range, reduced sexual dimorphism, decreased gut size, greater stature and increasing brain size. (Leonard & Robertson, 1994; Aiello & Wheeler, 1995) However, it is important to recognize that these changes were gradual. *H. habilis* evolved into *H. erectus* over the course of several hundred thousand years and this rate of cultural change, in all likelihood, allowed for concomitant genetic modification. The behavior, subsistence and biological characteristics of anatomically modern Late Paleolithic humans differed strikingly from those of *H. habilis*, but these changes developed over a 2.5 million year period. In contrast, subsequent comparably dramatic changes in both behavior and subsistence have occurred with far greater rapidity, almost certainly overmatching the capacity of genetic evolution to keep pace.

The Neolithic

Adoption of agriculture and animal husbandry, while perhaps not explosive enough to justify being termed a "revolution", nevertheless generally required only a few thousand years and, in some cases, only a few hundred. Genetic evolutionary responses must have been evoked by the altered circumstances, but given the time frame, only high order selective pressures (e.g. newly appearing epidemic infectious diseases capable of killing young people before the age of reproduction) have had sufficient time to significantly impact the human genome.

The chief dietary innovation which accompanied agriculture involved cereal grains. Earlier humans recognized that grains could be consumed in times of shortage; however, with primitive technology, the work involved in milling grains to render them digestible was sufficient to discourage their routine use. But when population density reached the point that nomadic exploitation of game and wild plant foods became difficult or impossible and Mesolithic humans adopted a more settled way of living, utilization of cereals became attractive. Actual crop cultivation followed and, in most areas, cereals became staples. This nutritional departure was unparalleled; no other free-living primates routinely consume cereal grains. (Milton, 1993)

Increasing dependence on cereal grains as an energy source decreased dietary breadth and necessarily reduced consumption of fruits and vegetables which had been prime foodstuffs throughout primate and hominid evolution. Paleolithic humans commonly obtained 65% of their food energy from fruits and vegetables (often from 50 to 100 individual species over a year's time), but becoming dependent on grains may have reduced intake of fruits and vegetables to 20% or less of total energy intake. Accordingly access to micronutrients (vitamins, minerals and phytochemicals) previously supplied by fruits and vegetables was substantially decreased. Of course, cereal grains also provide micronutrients, but not necessarily those to which human biology became accustomed throughout a multimillion year evolutionary experience during which fruits and vegetables were the overwhelmingly dominant plant foods.

For pastoralists, consumption of animal protein probably continued at approximately Paleolithic levels, but for most agriculturalists, meat was less available than it had been for Stone Agers. This change may have been a factor in the stature decrease which accompanied transition from foraging to agriculture. (Cohen, 1989) Less meat together with cereal grain preponderance increased the w-6 : w-3 PUFA ratio and also reduced intake of preformed longer-chain PUFAs, including AA, DTA and DHA.

The fiber available from rice and wheat is predominantly insoluble while that from fruits and vegetables is mainly soluble, hence while total fiber intake probably changed little, in the old world agriculture generally increased the insoluble:soluble dietary fiber ratio. (Eaton, 1990)

Further dietary changes which occurred during the agricultural millennia included development of alcoholic beverages, commercial salt production, and the gradual spread of sugar cane cultivation. Each was new in primate/hominid experience and each has had profound consequences for human health.

Industry and Diet

The industrial era and agribusiness have further distanced nutrition from its primate and Paleolithic antecedents. Roller-milling has reduced the fiber content of cereal grain-based foods so that total fiber intake has plummeted to levels much below those obtaining for agriculturalists, hunter-gatherers, or primates. (Eaton, 1990) Cold-pressing has facilitated extraction of vegetable oils (e.g. corn, sunflower, safflower) rich in w-6 PUFA and thereby exacerbated the w-6 : w-3 imbalance existing in the diets of affluent nations. (Simopoulos, 1991) The pricing structure for beef and other commercial meat has, until recently, rewarded breeding and feeding practices which maximize carcass fat deposition. This fat is deposited as an energy reserve, not for structural purposes, so its content of saturated, serum cholesterol-raising fatty acids is high. And not only do commercial meat animals have more depot fat than do their wild relatives; because they are now fed grain instead of forage, the w-6 : w-3 partition of their lipid is highly unnatural, with a marked w-6 excess (Marmer, 1984).

Foods popular in late 20th century affluent nations include a profusion of commercially-prepared items. Humans are the only free-living species to consume such foods, whose natural origin is obscure, and the entities created by the food industry commonly provide inapparent salt, refined flour, sugar or corn sweeteners, and trans fatty acids in extraordinary concentration.

Another characteristic feature of contemporary nutrition is the unprecedented availability of food energy. If there were some way to judge the human effort necessary to obtain a given amount of food energy, citizens of existing Western nations would almost certainly "enjoy" the highest calorie-to-effort return ratio yet experienced by humans and their hominid, hominoid, or primate ancestors. We have "optimized foraging" to an unprecedented degree and while an advantage in some respects, this relationship has adverse health implications as well. Because energy expenditure and energy intake have been largely uncoupled in contemporary affluent nations, growth and development are unnaturally accelerated while abnormal body composition (hyperadiposity and musculoskeletal deficiency) have become unprecedentedly common. The consequences range from insulin resistance and diabetes to age-related fractures. (Eaton & Eaton, 1998)

Dietary Discordance and Chronic Diseases

The altered nutritional parameters which differentiate contemporary diets from Paleolithic and primate patterns impact health in many ways, some beneficially (e.g. greater life expectancy), but many adversely. Five examples of deleterious effects include:

1) Electrolytes and blood pressure - Humans are the only free-living terrestrial mammals who ordinarily consume more sodium than potassium, the only species to commonly experience rising average blood pressure with increasing age, and the only mammals to commonly develop hypertension. Stone Age humans consumed only one fourth the sodium average Westerners now do (Eaton, 1997). About 90% of current sodium intake results from food processing, preparation and flavoring: only 10% is intrinsic to the foods themselves. Many groups of hunter-gatherers, pastoralists and rudimentary horticulturalists who lack commercially available salt have been studied in this century: these ancestral human surrogates experience neither rising blood pressure with age nor clinical hypertension. (Eaton, 1988)

2) Cereal grains and cancer - No primates other than humans ordinarily consume cereal grains, but from the introduction of agriculture onwards grains have been the single most important contributor to human food energy, providing from 40 to 90% of human caloric requirements. In doing so they have displaced fruits and vegetables which, until the Neolithic, had been the dominant energy source for Stone Agers, earlier hominids and our antecedent primate ancestors for 50 million years. A recent comprehensive analysis (150 scientists reviewed 4500 research studies) puts this phenomenon into perspective (World Cancer Research Fund & American Institute for Cancer Research, 1997). The influence of dietary variables on 18 different cancers was assessed. Vegetables were found to exert a convincing preventive effect for five cancers, a probable preventive effect for four others, and a possible preventive effect for another seven. For fruits the

analysis revealed four convincing, four probable and four possible preventive relationships. But for cereal grains there were no convincing or probable preventive relationships, only one possible preventive effect and, for one cancer (of the esophagus) grains may possibly have increased risk.

In short, the best available evidence suggests that vegetables and fruits have far more cancer-preventing potential than do grains. This probably reflects the phytochemical content of fruits and vegetables, phytochemicals to which current human biology became adapted through many million years of evolutionary interrelationships. The phytochemicals of grains have interacted with the human genome for only 10,000 years, hence substitution of grains for vegetables and fruits in human diets might readily diminish our resistance to development of neoplastic disease.

3) Energy intake:output uncoupling and insulin resistance - For primates and other mammals in natural settings food procurement is inextricably linked to energy expenditure, a relationship which establishes a range of body composition appropriate for any given species. The ratio of fat to muscle generally varies with season, but typically within fairly narrow limits; hyperadiposity, as it exists for many contemporary humans, is rare or nonexistent for other primates. The necessity for physical exertion, unavoidable for most humans until the industrial era and, especially, the 20th Century, ensured substantial muscularity, in the proportionate range existing for current free-living nonhuman primates. In the present, however, obtaining food energy is no longer dependent on muscular exertion: from childhood on, calories are available at the lowest cost in human experience without reciprocal energy expenditure. The result is relative sarcopenia - deficiency of skeletal muscle. For many individuals in affluent nations the proportions of adipose tissue and skeletal muscle are grossly out of line with what obtained during prior evolutionary experience.

Both fat and muscle take up glucose from the blood in response to insulin stimulation, but the capacity of muscle in this regard far exceeds that of adipose tissue per unit weight (DeFronzo, 1997). Existing control mechanisms for carbohydrate homeostasis were established over evolutionary time during which ancestral body composition almost never approached the extremes of hyperadiposity and sarcopenia manifested by many contemporary humans. For such individuals a given insulin secretory pulse, in response to a carbohydrate-containing meal, now produces less reduction in blood glucose levels than would have been achieved for prior humans with evolutionarily "appropriate" body composition. Additional, "extra" pancreatic insulin secretion is required to produce glucose homeostasis. This constitutes functional insulin resistance, a pathophysiological state exacerbated by low muscular metabolic activity (another result of exercise deficit). (Eaton & Eaton, 1998) In genetically susceptible individuals the process can proceed to glucose intolerance and overt diabetes. Prevalence of type 2 diabetes (that related to insulin resistance and, by far, the most common form) has multiplied 10-fold in the United States since the 1930's (American Diabetes Association, 1996) as the increasing disconnect between caloric accessibility and energy expenditure has produced an ever-larger number of obese, sarcopenic Americans.

4) Dietary fat and coronary heart disease (CHD) - While many other dietary, behavioral

and genetic factors influence the inception and progression of coronary heart disease, hypercholesterolemia is a paramount factor. Recently-studied hunter-gatherers have serum total cholesterol levels averaging 125 mg/dl (Eaton, 1988), a value within the range for free-living non-human primates (Eaton, 1992). Human societies with similar average serum total cholesterol levels have vanishingly low prevalences of CHD. Americans and other affluent Westerners, conversely, have average total serum cholesterol values exceeding 200 mg/dl - well outside the "natural" primate range - and, for these populations, CHD is the single leading cause of mortality.

Evidence linking dietary fat to serum total cholesterol concentrations is incontrovertible: the prime agents are saturated and trans fatty acids. For ancestral humans the cholesterol-raising saturated fatty acids constituted about 5% of total energy intake and trans fatty acid intake was almost negligible. For Americans, cholesterol-raising saturated fatty acids approach 15% of dietary energy while hydrogenated vegetable fats and oils provide an unprecedented quantity of trans fats (Eaton, 1997).

The w-6 : w-3 imbalance in current Western diets also affects coronary disease. Excessive w-6 AA relative to w-3 DHA and eicosapentaenoic acid (EPA, C20:5, w-3) adversely affects platelets and arterial walls so as to promote development of coronary atherosclerosis. (Riemersma, 1992) The more balanced w-6 : w-3 dietary PUFA intake of Paleolithic humans would have negated this effect.

5) DHA deficiency and the brain - While human cranial capacity tripled over the 2.5 million years after *H. habilis* first appeared, this trend has recently reversed. Since peaking among Cro Magnons and other humans living during the Late Paleolithic, cranial capacity has fallen off about 11%. (Ruff, 1997) This diminution has paralleled a decrease in consumption of animal foods and, consequently, a diminished dietary intake of preformed long chain PUFA, the building blocks necessary for formation of brain tissue. These PUFA can be synthesized by humans from their 18 carbon precursors, LA and ALA, but the process appears too slow to supply the amounts of AA, DTA and DHA needed for optimal brain growth during fetal development and infancy. (Woods, 1996; Salem, 1996) DHA deficiency is especially important, first because its concentration in brain tissue exceeds those of AA and DTA and second, because our current w-6 excess tends to promote formation of long chain w-6 AA and DTA while inhibiting synthesis of w-3 DHA. Association is not necessarily causation, but the fluctuations which have occurred in brain size over evolutionary time, both increases and decreases, correlate well with dietary intake of the preformed long chain PUFA necessary for formation of brain tissue so it is tempting to speculate on a causal relationship.

Current w-6 : w-3 imbalance together with absolute dietary DHA intake quite low in human evolutionary perspective may be relevant to the frequency of unipolar depression, a debilitating neuropsychiatric disorder which accounts for more "disability adjusted lost years" in the total world population than heart attacks, lung cancer or AIDS. (Murray & Lopez, 1996) Prevalence of depression has increased substantially during the 20th Century (Klerman & Weisman, 1989; Weisman, 1996) while dietary intake of w-6 PUFA has soared relative to that of w-3 PUFA, primarily because of increased vegetable oil

consumption and corn-feeding of commercial meat animals. Fish are good sources of w-3 PUFA (including DHA) and national fish consumption is inversely correlated with national rates of depression (Hibbeln, 1997). Furthermore, studies of plasma w-6 : w-3 ratios in patients with depression reveal a direct association: higher ratios of w-6 to w-3 PUFA are correlated with more frequent and severe depressive episodes. (Adams, 1996; Hibbeln, 1997) Early therapeutic trials with w-3 PUFA have shown symptomatic improvement. (Hibbeln & Salem, 1995) These findings are preliminary and, as yet, only suggestive, but their implication is that an w-6 : w-3 dietary ratio (and perhaps magnitude) similar to that which obtained throughout human evolutionary experience may be an integral component of mental health.

Conclusion

Deviations from the postulated ancestral primate nutritional baseline have had important evolutionary impact and they appear to influence human health in the present. Because of these significant relationships, better understanding of primate nutritional patterns would be desirable. The diets of Miocene and Pliocene apes are particularly relevant and the goal would be to estimate as accurately as possible the nutrition of the last common ancestor of existing pongids and humans.

Toward this end establishing relationships between dentition and nutrient intake would be extremely valuable. While folivorous primates presumably exhibit interspecific nutritional variation, there may be generalizations about such diets which are valid across broad subsistence categories.

Bioarchaeology, assessing lifetime experience from archaeological sites and skeletal-dental remains, may aid in assessing primate diets through evolutionary time. Craniofacial adaptations as well as isotopic and elemental dietary "signatures" may provide important clues.

Another area of necessary research involves proximate analyses of the foods consumed by primates generally and by pongids especially. In order that these can be conveniently related to current and past human nutrition, the analyses should provide wet weight data. Both macro- and micronutrient compositional values will be helpful, including analyses (e.g. individual lipid species) not commonly performed. Once a sufficient body of proximate analyses for the plant foods, insects, and small mammals consumed by primates has been assembled, and the proportions of such foods making up differing primate diets determined, modeling representative average nutritional intake for primates with varying subsistence patterns should become possible. And, in turn, this information will permit estimation of the last common ancestral diet.

The above research "wish list" is a tall order, but the potential for expanding understanding of primate, hominoid, hominid, and human evolution together with the benefit for health promotion based on evolutionary medical principles should provide more than sufficient incentive for the investigational effort.

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