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Evolutionary Aspects of Diet: Old Genes, New Fuels

Nutritional Changes Since Agriculture

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This paper contends that the nutritional patterns of current humans differ in important ways from those of our preagricultural human ancestors. The differences have serious implications for growth, development, and health, implications best appreciated in the light of three premises:

(1) Regarding susceptibility to chronic degenerative diseases, our current gene pool is hardly changed from that of Stone Age humans. The genetic constitution with which we are now endowed was selected through evolutionary experience for life circumstances which obtained in the past, not those which exist at present [1].

(2) Ancestral human nutrition was derived overwhelmingly from wild game and uncultivated plant foods. Depending on location, season and era, honey, fish and (in times of shortage) wild grains made varying contributions [2].

(3) Because they lacked motorized equipment, draft animals, and most simple machines, our ancestors' level of physical exertion greatly exceeded that at present; probably their caloric expenditure was about one-half more each day [3].

These premises lay the foundation for two propositions. First, we now eat substantially smaller amounts of the foods for which evolution has attuned our biochemistry and physiology. This is because we consume less energy overall, in line with our reduced physical exertion, and because we have developed and/or adopted a variety of new energy sources, foods which were not available (or at least little utilized) by human ancestors and which displace

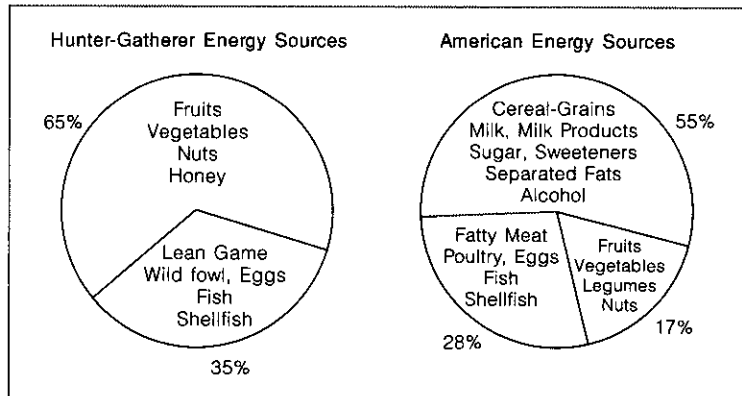


Fig. 1. Foods 'new' in evolutionary context have displaced/replaced a sizable fraction of the 'original' foods which fueled 99% of human evolution.

original, fundamental foods from our daily intake pattern (fig. 1). Second, the 'new' foods, which make up over half of what we now eat, include cereal grains, dairy products, prepared/processed foods, alcohol, separated fats, commercial meat, free salt, refined flours, and sweeteners. These collectively alter the mix of dietary constituents in ways detrimental to human health. That is, in addition to their passive effect of displacing much of the food which comprised nearly all Paleolithic human nutrition, the 'new' foods have an actively adverse influence resulting from constituents which have been shown to be harmful.

Nutrient Properties of Preagrarian Foods

Wild Vegetal Foods

The uncultivated fruits and vegetables consumed by hunters and gatherers generally contain high levels of micronutrients, except for sodium; potassium content greatly exceeds that of sodium in virtually all instances [2]. Some, such as nuts, beans, and seeds provide a substantial amount of fat, but this fat is predominantly unsaturated in nature and provides little of the C_{14}/C_{16} chain saturated fat which raises serum cholesterol levels [6]. Wild plants contain a considerable amount of dietary fiber, largely soluble in nature [7], which partly explains why their nutrient/food energy quotient is relatively great (table 1). The phytochemical content of wild plant foods is undetermined, but likely to be considerable, in line with their high average concentrations of vitamins and minerals [11].

Table 1. Energy and nutrients in vegetable foods

Food item(s) 100-gram portions	Energy kcal	Calcium, mg (mg/100 kcal)	Vitamin A, RE (RE/100 kcal)	Vitamin C, mg (mg/100 kcal)	Reference
Wheat, 5 varieties	331	39 (11.8)	0	0	8
Rice, brown	360	32 (8.9)	0	0	8
Granola	487	62 (12.7)	35 (7.2)	1 (0.2)	9
Pizza, cheese, no meat	245	155 (63.3)	132 (53.9)	5 (2.0)	10
French fries	275	15 (5.5)	tr.	22 (8.0)	10
236 uncultivated fruits/vegetables, mean	109	103 (94.5)	180 (165.1)	33 (30.3)	2

Wild Game

Game animals are typically lean, containing on average only one-fifth the fat and about half the energy provided by commercial meat. Game also has less cholesterol, but this difference is relatively slight. Fat from wild animals contains a high proportion (25–30%) of polyunsaturates, including the essential long chain constituents: arachidonic, eicosapentaenoic, and docosahexaenoic acids [6]. Because of its lower fat content, and hence lesser food energy, the nutrient/energy quotient of game, like that of wild plants, is high (table 2).

Nutrient Properties of Foods Introduced Since Agriculture

Cereal Grains

Wheat, rice, millet, corn and other grains made possible dramatic population growth as they became major dietary resources: they increased the total food energy which could be extracted from a given land area. But paleopathological findings at the origins of agriculture may in part reflect the nutrient/energy quotient of cereal grains which is lower than that of pre-agricultural foods (table 1). While whole grains are good fiber sources, especially for insoluble fiber, finely-milled flours contain hardly any fiber at all [7]. Cereals contain little fat of any type and especially little saturated fat; however polyunsaturated fat from certain commercially-important grains, including corn, is preponderantly omega-6 in nature [6]. Metaanalytic findings that grains have little cancer-preventive effect, relative to fruits/vegetables, suggest that their phytochemical content is lower and/or less effective.

Table 2. Energy and nutrients in animal foods

Food item(s) 100-gram portions	Energy kcal	Iron, mg (mg/100 kcal)	Thiamin, mg (mg/100 kcal)	Riboflavin, mg (mg/100 kcal)	Reference
T-bone Steak					
Total edible	397	2.2 (0.55)	0.06 (0.02)	0.13 (0.03)	8
Separable lean	164	3.2 (1.95)	0.09 (0.06)	0.19 (0.12)	8
Hamburger					
Regular	268	2.7 (1.01)	0.08 (0.03)	0.18 (0.07)	8
Lean	179	3.1 (1.70)	0.09 (0.06)	0.16 (0.09)	8
Frankfurters	309	1.9 (0.62)	0.16 (0.05)	0.20 (0.07)	8
Pork sausage	498	1.4 (0.28)	0.43 (0.09)	0.17 (0.03)	8
85 game species, mean	126	4.2 (3.33)	0.22 (0.18)	0.40 (0.32)	2

Dairy Foods

About half the energy in whole cow's milk is derived from fat, most of which is saturated. Furthermore, fat from dairy sources contains a substantial level of the C₁₄/C₁₆ saturated fatty acids which raise serum cholesterol levels. Milk carbohydrate is all lactose, a simple sugar tolerated poorly by many humans. Cow's milk used for bottle feeding displaces the cellular macrophages and protein antibody immune factors previously supplied to infants from mothers' milk. Allergy to cow's milk proteins is a problem for a minority of the population and there is gradually increasing evidence that exposure to cow's milk protein during infancy and early childhood may promote development of type I diabetes mellitus in susceptible individuals [12].

Commercial Meat

During the late 19th and most of the 20th century, animals intended to provide meat were bred and raised to maximize their fat content; the much prized marbling effect and the price structure for prime, choice, and good beef, which vary stepwise in their fat content, are manifestations of this practice [6]. Thus, commercial meat animals have had, and still have to a lesser extent, a disproportionately high level of storage fat which is predominately saturated in nature and which contains a considerable amount of the C₁₄/C₁₆ serum cholesterol-raising fatty acids. Compared with forage-fed animals, the polyunsaturated fat from grain-fed beef is skewed towards a high n-6:n-3 ratio [13].

Separated Fats

If they were like recently studied foragers, human ancestors eagerly sought fat, a desire reflecting its general scarcity in their diets coupled with the

requirement for essential long-chain polyunsaturated fatty acids (PUFA). But preagricultural humans had no source of separated fat. Those now available vary in their nutritional effects, but all, including olive oil, make it possible to add gratuitous food energy to otherwise lower-fat containing foodstuffs, and frying emerged as a popular cooking technique only when separated fats became generally available [6]. Lard and dairy fats are sources of cholesterol-raising C_{14}/C_{16} saturated fatty acids while most vegetable oils provide a proportion of n-6 PUFA much higher than that of the fat typically available to ancestral humans [14].

Refined Flours and Sweeteners

Perhaps reflecting the multi-million-year phase during which our remote primate ancestors were chiefly frugivorous, humans today like sweets. Hunter-gatherers enjoy honey to the point that in some localities and at favorable times of year it can provide 20% of total energy intake [15]. However, the relatively caries-free nature of most dental remains from the Paleolithic suggests that, in general, honey was much less available to our ancestors than are equivalent sweeteners today [16]. Both sweeteners and highly refined flours allow preparation of foods with artificially high energy content while they add few or no nutrients. Even refined flours fortified with vitamins and minerals lack the phytochemicals which appear to be constituents of fruits and vegetables.

Salt

Preagricultural humans, like a few isolated remaining current horticulturists, had no access to sodium except for that intrinsic to their basic foods. Nowadays, use of salt as a preservative, for food preparation, and as a seasoning has resulted in vastly increased human consumption: only 10% of the sodium consumed at present is intrinsic to our foods themselves [5]. This increased availability of sodium has inverted the sodium:potassium relationship which characterized human evolutionary experience. For human ancestors, as for other free-living terrestrial mammals, potassium intake greatly exceeded that of sodium; now this intake pattern is reversed [2].

Prepared and Processed Foods

Postagricultural humans are the only free-living mammals to consume foods whose natural origin is unrecognizable. Bread, cheese, sausage and similar items have been staples for millennia, but artificially fabricated foods have undergone an explosive increase in popularity during the past century. Food manufacturers were quick to recognize that salt, fat, and sugar were ingredients which enhanced acceptance of their products so a substantial

proportion of the items in this general category provide empty calories, excessive fat, and often more sodium in a single serving than human ancestors obtained during a whole day [2].

Alcohol

Alcohol has been estimated to provide about 4.5% of average adult American energy intake [5]. Since most alcoholic beverages afford few if any nutrients, the energy derived from alcohol is another source of empty calories akin to sweeteners and highly refined flours. However, alcohol has pharmacological properties, some beneficial and some harmful, which distinguish it from other sources of food energy. Increasing evidence indicates that alcohol mitigates the development and/or consequences of coronary atherosclerosis [17], but it is associated with fetal alcohol syndrome, cirrhosis, accidents, violence, increased cancer risk, and chronic alcoholism [5]. No foragers studied in the past century have been able to make alcoholic beverages, so paleoanthropologists assume it was generally unavailable to preagricultural humans [18].

Old Foods vs. New Foods: Nutrient Implications

Energy

Until the late 19th century the circumstances of human existence appear to have demanded daily adult physical exertion which roughly equaled resting metabolic needs; that is, if resting metabolic rate (RMR) was 1,500 kcal/day, then total daily caloric expenditure was generally around 3,000 kcal [3]. This relationship seems to have characterized both Paleolithic and agricultural populations. However, in the late 20th century, the requirement for physical exertion, over RMR, has decreased by a staggering 60% or more [19]. For persons with an RMR of 1,500 kcal/day, typical total daily caloric expenditure is now 2,000 kcal or even less [3].

At the same time, the energy/nutrient quotient of our foods has increased. Commercial meat, separated fats, sweeteners, and many popular prepared/processed foods exhibit this property (tables 1, 2). In consequence, it is now possible to achieve (and often exceed) our energy needs, while our intake of nutrients other than energy is substantially lower than that which would be provided by 'natural' foods (i.e. ones consumed prior to agriculture). Nutrient intake is lower still in comparison to levels which would have been typical when activity patterns mandated greater energy intake. The latter point is not trivial: demand for essential nutrients increases with physical activity far less than the elevation in energy output would seem to warrant [20]. Thus, in the Paleolithic, when humans expended more energy through physical activity,

the resulting increase in nutrient intake would have provided a reserve, or extra quota, above currently established requirements. This consideration may relate to contention regarding optimal and minimal nutrient levels [21].

Micronutrients

The immediately preceding discussion affects comparison of vitamin and mineral intake for Paleolithic and current humans. For such assessment it is most appropriate to contrast Stone Agers consuming 3,000 kcal/day with affluent Americans or Europeans eating only 2,000 kcal/day. If, for example, folate intake for an individual living 15,000 years ago was 0.136 mg/1,000 kcal and for a typical American 0.08 mg, then actual daily intake was likely to have been around 0.408 mg for the former and to be 0.16 mg for the latter. This makes the actual intake ratio 2.55 whereas simply comparing nutrients on the basis of dietary folate/1,000 kcal would suggest a deceptively lower ratio of 1.7 [2].

Any appraisal of preagricultural phytochemical intake must be purely speculative since, to the authors' knowledge, almost no determinations of such constituents have been made for uncultivated fruits and vegetables [but see ref. 11]. However, it seems likely that the phytochemical load for wild plants would have paralleled their high content of established micronutrients. Fruits and vegetables contributed a higher proportion of total energy for Stone Agers, typically about two-thirds of their intake as compared with roughly one-fifth to one-fourth for Europeans and Americans [2]. The foods we consume at present are often fortified with known vitamins and minerals, otherwise the discrepancy between Paleolithic and current micronutrient intake would be even greater than it is. However, phytochemical fortification is not practicable at present; therefore, the degree to which Paleolithic intake of such constituents exceeded our own was probably much more striking than the discrepancy in vitamin/mineral intake.

Electrolytes

Recently studied groups lacking free salt have electrolyte intake patterns reasonably similar to those retrojected for Paleolithic humans. Both populations consume(d) less than a gram of sodium and over five grams of potassium each day. In contrast, societies for whom salt is abundant commonly consume nearly 4 g of sodium, but only about 2,500 mg of potassium. All societies lacking salt have been found by anthropologists and/or epidemiologists to have low average blood pressures and virtually no hypertension [2, 18]; accordingly it is tempting to hypothesize that the control mechanisms regulating human blood pressure were selected during evolutionary adaptation to operate within a low-sodium, high-potassium nutritional context.

Fats

The relatively high fat content of dairy foods and commercial meat together with the availability of separated fat and the development of often high-fat prepared foods explain why fat intake in Western nations exceeds that for recently studied hunter-gatherers and, presumably, for preagricultural humans as well. Higher dietary fat content necessitates a greater overall energy/bulk ratio and thus, of itself, affects rates of obesity. However, changes in the nature of dietary fat are probably more important than is its increased contribution to total energy intake.

The fat available to contemporary humans is more highly saturated than that consumed by Stone Agers. The average content of C14 and C16 fatty acids in wild game is less than a fifth that found in commercial meat [6]. Highly saturated dairy fats were wholly unavailable to Paleolithic adults and, while coconuts, palm nuts and the like were locally available in certain geographical regions, their separated oils were not. Furthermore, commercially hydrogenated fats, which also raise serum cholesterol levels, are a recent innovation. These factors largely explain why foragers studied in this century, and who serve as inexact surrogates for Paleolithic humans, have serum cholesterol levels averaging around 125 mg/dl – despite dietary cholesterol intake well above 400 mg/day [6].

The ratio of n-6 to n-3 PUFA is estimated to have been far lower for preagricultural humans than for Americans [6, 14]. Game animals have considerably more n-3 PUFA relative to their n-6 PUFA content than do grain-fed commercial meat animals [13]. Because preagrarian humans ate so much wild game, their intake of n-3 PUFA from this source would have been considerable. In contrast, the vegetable oils currently used in the United States in prepared foods, for cooking, and as spreads afford far more n-6 than n-3 PUFA [14]. The ratio of dietary n-6 and n-3 essential fatty acids is thought to affect eicosanoid biosynthesis and thereby activity of n-6 and n-3 family eicosanoids [14, 22] so the higher level of n-6 PUFA relative to n-3 PUFA in current diets may have important physiological consequences.

Protein

The prominence of game in preagricultural economies insured that protein contributed a relatively greater proportion of overall energy intake for Stone Agers than at present. There must have been considerable variation depending chiefly on geographical location, but most paleoanthropologists believe that, on average, hunted and/or scavenged meat has provided about one-third of overall subsistence during the last 1.5 million years of human evolutionary experience [23]. This, in turn, suggests that protein (from both animal and vegetable sources) would have comprised 30–35% of daily energy for typical

Paleolithic humans. Even though their access to animal foods is far less, protein is estimated to provide from 1.6 to 5.9 g/kg/day for nonhuman primates. This compares with an estimated 2.5–3.5 g/kg/day for Stone Agers and contrasts with current recommendations of 0.8–1.6 g/kg/day [2].

Such high levels of dietary protein fit poorly with conventional nutrition theory. There is dispute as to whether high dietary protein adversely affects calcium balance, but its tendency to accelerate deterioration in renal failure is almost uncontested [24]. Regarding the latter, there is little evidence that high protein intake can, by itself, induce renal dysfunction and, since diabetes and hypertension were likely to have been rare, instances of kidney failure were presumably uncommon in the remote past.

There is, however, little reason to believe that such a high protein diet is 'necessary', at least with regard to nitrogen balance and maintenance of lean body mass, even in vigorously active individuals. For this reason possible protein-endocrine-eicosanoid relationships are intriguing [23]. The relative proportions of dietary protein and carbohydrate affect secretion of insulin and glucagon following a meal [25] and thereby influence both lipid metabolism and eicosanoid formation [26]. Integrated over the day, a higher proportion of protein to carbohydrate would act to increase the glucagon/insulin secretory ratio, thus reducing fat storage and inhibiting n-6 eicosanoid synthesis.

Fiber

Uncultivated vegetables and fruits tend to be highly fibrous so diets obtaining two-thirds of their energy from such sources necessarily provided a great deal of fiber, probably in excess of 100 g/day [7]. Both analysis of wild vegetal foods and evaluation of archaic native American coproliths support this estimate which is intermediate between nonhuman primate experience (for example, chimpanzees consume more than 200 g/day [2]) and dietary levels typical in affluent Western nations, which are generally below 20 g/day.

Like the high protein intake believed to characterize ancestral diets, daily fiber intake of 100 g or more fits ill with current concepts of optimal nutrition. Since the fiber consumed before agriculture was derived from fruits and vegetables rather than from grains, it provided little phytate, the factor of most significance relative to concerns about fiber's potentially adverse effect on mineral absorption. Furthermore, fruits and vegetables afford a higher proportion of soluble, fermentable fiber than do cereals, especially wheat and rice, whose fiber is preponderantly insoluble [7].

Formal, well-controlled evaluations of high-fiber diets in humans have focused on adults; however, the impact of such diets initiated after the conclusion of growth and development might differ from the effects of a similar

diet consumed from childhood on. The latter, of course, more closely resembles the nutritional situation believed to have existed for preagricultural humans.

Discussion

Denis P. Burkitt wrote ‘... modern Western man has, in a very short period of time by evolutionary standards, deviated greatly from the biological environment to which his body has been adapted. This is the best explanation for ... the high frequency of Western diseases within the communities that have deviated most from the lifestyle of their ancestors ...’ [27]. Similarly, James V. Neel believes ‘... there is now little room for argument with the proposal that health ... would be substantially improved by a diet and exercise schedule more like that under which we humans evolved’ [1].

The endorsement of such respected figures is, of course, welcomed by proponents of paleonutrition, but well-designed, comprehensive research efforts directed towards testing its effects in current circumstances would be more desirable still. The core project would evaluate an experimental group consuming shellfish, lean meat, fish, vegetables and fruit – prepared and served without use of salt, separated fat, or oil. Dairy products and foods based on or containing cereal grains would also be excluded as would alcohol and sweeteners other than honey. In some studies individuals could self-select from the sanctioned food groups; others might employ a more structured dietary regimen, aiming to approximate the 30% protein, 45–50% carbohydrate, 20–25% fat pattern thought to be most representative of preagricultural experience. Because fruits, vegetables and lean meats available in affluent, industrialized nations differ nutritionally from their wild counterparts, the effects of supplementation to duplicate retrojected Paleolithic micronutrient levels and an n-6:n-3 ratio of 5 or less might be investigated as well. Further projects could explore the physiological and biochemical effects of paleonutrition in conjunction with typical Western sedentarism and compare the same nutritional protocol’s influence on individuals exercising at or near Paleolithic levels. The program’s effects on differing age groups might vary: older children, young adults, and aging individuals might benefit, or be harmed, to differing degrees.

Paleonutrition is an intellectually appealing, but unproved, dietary paradigm. Its theoretical basis is arguably more logical than vegetarianism and the Mediterranean or East Asian nutritional models. However, the latter have been formally investigated; each has benefits and drawbacks, while for paleonutrition similar advantages and flaws have not been determined. It is possible that life circumstances prevailing in affluent industrialized nations, including

longer life expectancy, may interact adversely with the dietary (and physical exertion) patterns which prevailed while our gene pool was being selected. Alternatively, the insights of Neel and Burkitt may be correct. In either case, the ancestral human pattern, in force during nearly all the two million year experience of humanity, deserves serious investigation by current nutrition scientists.

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