An Evolutionary Perspective Enhances Understanding of Human Nutritional Requirements

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Human nutritional requirements reflect evolutionary experience extending millions of years into the past, and for nearly all this period genetic and cultural changes occurred in parallel (Eaton and Konner 1985). However, agriculture and, especially, industrialization produced technical and behavioral change at rates exceeding the capacity of genetic adaptation to keep pace. Geneticists believe that the increased human number and mobility associated with civilization have produced more, not less, inertia in the gene pool and that when the humans of 3000–10,000 years ago (depending on locality) began to take up agriculture, they were, in essence, the same biological organisms as humans are today (Neel 1994). Accordingly, our ancestral dietary pattern has continuing relevance: an understanding of preagricultural nutrition may provide useful insight into the requirements of contemporary humans.

The science of nutrition must ultimately be based on animal, laboratory, clinical and epidemiological investigations, but the value of information derived from these approaches might be enhanced by correlation with evolutionary and paleoanthropological principles. We have previously (Eaton and Konner 1985) proposed a model based on analyzing the subsistence of recent foragers,[2] determining the nutrient properties of wild game and uncultivated vegetable foods and evaluating archeological remains. Of course the diets of Paleolithic humans must have varied with geographical location and season; there must have been periods of relative abundance and others of scarcity. There could have been no one universal subsistence pattern. However, after the appearance of *Homo erectus (H. erectus)*[3], nearly two million years ago (mya), when stature and body weight appear to have increased, probably as hunting and/or scavenging became important subsistence strategies (Walker 1993), human dietary requirements were perforce met by naturally occurring vegetative matter and by wild game. Given this starting point, central defining tendencies can be identified and an average Paleolithic diet, analogous to an average American diet (which factors in both vegans and fast-food addicts) can be extrapolated.

Since 1985 more nutrient analyses have been collected from the literature; there is now at least some information about a total of 329 different wild plant foods and game animals, whereas our earlier estimates were based on only 69 (Eaton and Konner, 1985). The new data allow assessment of consistency and also permit consideration of more micronutrients than could previously be appraised. In addition, we now compare and contrast current dietary recommendations with our updated estimate of ancestral human nutrition, an exercise that reveals both gratifying similarities and potentially heuristic differences.

Food energy

Contrary to popular misconception, human ancestors were taller than most current humans. Their average height would have placed them in the tallest 15% of the existing population from the time of early H. erectus, nearly 2 mya, until that of Magdalenian Cro·Magnons, 15,000 years ago (Roberts et al. 1994, Walker 1993). Their nomadic foraging lifestyle required vigorous physical exertion, and skeletal remains indicate

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[2] We use the terms foragers, hunter-gatherers and gatherer-hunters interchangeably.

[3] Abbreviations used: AA, arachidonic acid; ca., circa; DHA, docosahexaenoic acid; EPA, eicosapentaenoic acid; H., Homo; LA, linoleic acid; ALA, linolenic acid; mya, million years ago; PUFA, polyunsaturated fatty acid(s).

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TABLE 1

Nutrient concentrations of hunter-gatherer foods[1]

	Vegetable foods (*n* = 244)			Animal foods (*n* = 85)		
	n	Mean	SD	*n*	Mean	SD
Vitamins, *mg/100 g*						
Riboflavin	89	0.186	0.282	26	0.399	0.246
Folate	11	0.0241	0.0213	3	0.00567	0.00170
Thiamin	101	0.130	0.209	29	0.215	0.197
Ascorbate	123	32.5	54.4	18	4.79[2]	5.43
Carotene[3]	60	138	333	6	76.8[4]	61.4
Vitamin E[5]	24	2.24	4.44	—	—	—
Minerals, *mg/100 g*						
Iron	167	3.06	3.75	22	4.15	2.77
Zinc	91	1.23	1.55	11	2.67	0.860
Calcium	181	110	125	28	22.7[4]	30.9
Sodium	138	16.5	39.3	16	59.0	23.6
Potassium	112	387	303	16	317	43.3
Fiber, *g/100 g*	132	6.87	8.85	—	—	—
Energy, *kJ/100 g (kcal/100 g)*	185	553 (132)	557 (133)	44	527 (126)	196 (46.8)

1 Data compiled from: Anderson et al., 1989; Boyce and Swinburn 1993; Brand et al., 1983; Brand and Cherikoff 1985; Brand et al., 1985; Cherikoff et al., 1985; Crawford, 1968; Crawford et al., 1969; Crawford et al., 1970; Eaton, 1990; Fysch et al., 1960; Hoppner et al., 1978; Kuhnlein 1989; Kuhnlein 1990; Leger, 1968; Medcal Services Branch 1985; Morris et al., 1981; Naughton et al., 1986; Polacchi et al., 1982; Shostak n.d.; Simopoulos et al., 1992; Simopoulos and Salem, 1992; Sinclair et al., 1982; Tanaka 1976; Tanaka 1980; Wehmeyer, 1966; Wehmeyer et al., 1969; Wu Leung et al., 1968; Wu Leung et al., 1972.

2 Seabirds (e.g., eider duck, least auklet, sea pigeon, cormorant and white breasted puffin) were found to provide significant vitamin C by Mann et al. 1962, pp. 72–73.

3 Retinol equivalents.

4 The high content of vitamin A and calcium in animal foods reflects consumption of organ meat, skin, small bones, insects, shellfish and marrow.

5 α-Tocopherol equivalents.

that they were typically more muscular than we are today (Larsen 1981, Smith et al. 1984). Life during the agricultural period was also strenuous, but industrialization has progressively reduced obligatory physical exertion. In Japan, for example, the introduction of mechanized farming reduced average daily work expenditure by over 50% (Shimamoto et al. 1989).

Because our remote ancestors were tall, robustly built and led physically demanding lives, they presumably consumed more energy than most 20th century Westerners (Leonard and Robertson 1992). Recently studied gatherer-hunters are nonetheless lean; their skinfold thicknesses are half those of age-matched North Americans (Eaton et al. 1988). This suggests that hunter-gatherer, and, by extension, Paleolithic human, caloric intake and output were balanced over time, despite seasonal fluctuations in resource availability, in a pattern characterized by high energy throughput.

Micronutrients

Vitamins and minerals. The game and wild plant foods of Paleolithic humans generally contained higher levels of micronutrients relative to energy than do the foods most commonly consumed in the present (Eaton and Konner 1985) (**Table 1**). The fruits, nuts, legumes, roots and other noncereals that provided 65–70% of typical gatherer-hunter subsistence (Eaton and Konner 1985) were generally consumed within hours of being gathered, with little or no processing (Schroeder 1971) and often uncooked. For a 65:35 plant:animal subsistence base [the mean, median and modal ratio for 58 foraging groups studied in this century (Lee 1968) and a 10.46 MJ/d (2500 kcal/d) diet, (Leonard and Robertson 1992)] it seems inescapable that preagrarian humans would generally have had an intake of most vitamins and minerals that exceeded currently recommended dietary allowances (Food and Nutrition Board 1989), either absolutely (**Table 2**), or relative to energy intake (**Table 3**). But the levels available to our ancestors were only moderately higher, typically from 1.5 to 5 times those consumed at present; they were by no means megadoses.

Whether and to what degree wild plant foods contain nonnutrient phytochemicals has not yet been investigated, but it is likely that the concentration of such substances in naturally occurring edible fruits and vegetables may be relatively great, as is their content of micronutrients. The precise role played by phytochemicals—biological response modifiers such as flavonoids, plant phenols, protease inhibitors, organosulfur compounds and organic isothiocyanates—in disease prevention is not known with any certainty, but their possible function in this capacity is the subject of much speculation and current research effort. (Beecher 1994, Dragsted et al. 1993, Greenwald et al. 1995, Middleton and Kandaswami 1992).

Electrolytes

Adult Americans consume nearly 4000 mg of sodium in an average day (Food and Nutrition Board 1989), but only ~10% of this amount is intrinsic to the basic food items; the remainder is superfluous, added during processing, cooking or at table. Our mean potassium is lower, ~3000 mg/d (Food and Nutrition 1989), that is, Americans usually consume more sodium than potassium. This behavior is now typical for most people worldwide, but humans are the only free-living terrestrial mammals whose electrolyte intake exhibits this relationship. For all others potassium intake exceeds that of sodium, usually by a considerable amount. The recommended allowances for sodium 500–2400 mg/d and potassium 2000–3400 mg/d (Food and Nutrition Board 1989) invert our current intake pattern and, for sodium, are roughly intermediate between extant and preagricultural human experience.

Data now available (Table 2) permit a refined estimate of Paleolithic electrolyte intake, one which contrasts strikingly with the existing pattern. Our preagricultural ancestors probably consumed ~600 mg of sodium but nearly 7000 mg of potassium each day. This retrodicted sodium-potassium intake ratio (0.09) is similar to that (0.13) observed for subjects from no-added-salt cultures who were included in the Intersalt Study (Intersalt Cooperative Research Group 1988). These peoples, Xingo and Yanamamo Amerindians and New Guinea Asaro, are rudimentary horticulturists, but they are relatively unacculturated and share with hunter-gatherers a lack of salt; all the salt they consume is intrinsic to their food.

Intersalt determined that these populations have blood pressure readings averaging 102/62 mm Hg, no blood pressure increase with age and only a minimal (0.6%) prevalence of hypertension (Carvallo et al. 1989), findings consistent with those for many other forager and horticultural peoples studied previously (Eaton et al. 1988). However, for the 48 Intersalt study populations who did have access to salt, mean sodium intake was 3818 mg/d, whereas that of potassium was only 2106 mg/d, a sodium-potassium intake ratio of 1.81. The median blood pressure for these populations was 119/74 and tended to rise with age. Hypertension (BP > 140/90 mm Hg) ranged from 5.9 to 33.5% (Intersalt Cooperative Research Group 1988).

The relationship between dietary sodium and blood pressure has been a contentious issue, but Intersalt's results suggest that for preagricultural humans, who consumed only sodium intrinsic to their food, essential hypertension would have been a vanishingly rare problem.

TABLE 2

Estimated daily Paleolithic intake of selected nutrients compared with current and recommended levels

	Paleolithic intake[1]	R.D.A.[2]	Current intake[2]
Vitamins, *mg/d*			
Riboflavin	5.01	1.3–1.7	1.34–2.08
Folate	0.340	0.18–0.2	0.149–0.205
Thiamin	3.07	1.1–1.5	1.08–1.75
Ascorbate	439	60	77–109
Vitamin A[3]	2,240	800–1,000	1,170–1,414
Vitamin E[4]	28.0	8–10	7–10
Minerals, *mg/d*			
Iron	62.4	10–15	10–11
Zinc	33.4	12–15	10–15
Calcium	1,520	800–1,200	750
Sodium	604	500–2,400	4,000
Potassium	6,970	3,500	2,500
Fiber, *g/d*	86.0	20–30	10–20
Energy, *kJ/d*	10,465	9,209–12,139	7,326–10,465
(kcal/d)	(2,500)	(2,200–2,900)	(1,750–2,500)

[1] Based on 673 g meat and 1250 g vegetable food/d yielding 10,465 kJ (2500 kcal). For method see Eaton and Konner 1985.
[2] Food and Nutrition Board 1989.
[3] Retinol equivalents.
[4] α-Tocopherol equivalents.

TABLE 3

Dietary micronutrients relative to energy intake Paleolithic and current experience

	Paleolithic[1]	Current[2]	Ratio Paleolithic: Current
	mg/4189 kJ (1000 kcal)		
Vitamins			
Riboflavin	2.00	0.6	3.33
Folate	0.136	0.08	1.70
Thiamin	1.23	0.51	2.41
Ascorbate	176	24	7.33
Vitamin A[3]	897	353	2.54
Vitamin E[4]	11.2	3.5	3.20
Minerals			
Iron	26.5	4.9	5.41
Calcium	610	392	1.56
Zinc	13.4	5.3	2.53
Sodium	242	1882	0.129
Potassium	2790	1177	2.37

[1] See Table 2.
[2] Food and Nutrition Board 1989.
[3] Retinol equivalents.
[4] α-Tocopherol equivalents.

Macronutrients

Carbohydrate. We believe preagricultural humans generally obtained from 45 to 50% of their daily energy intake from carbohydrate, a proportion similar to that for most contemporary affluent nations, but the sources differ greatly. For Paleolithic humans vegetables and fruit provided the bulk of dietary carbohydrate, cereal grains were used only in extraordinary circumstances and there was no refined flour or sugar at all (Eaton and Konner 1985). Preagrarian human experience mirrored that of primates generally (Milton 1993). Current recommendations, often suggesting that carbohydrate make up ~55% of individual energy intake, are reasonably close to our likely ancestral pattern, but the difference in sources has important implications. Less than a quarter of the carbohydrate consumed by Americans (Food and Nutrition Board 1989) or Europeans (James et al. 1988) is in the form of fruits and vegetables. The corollary is that preagricultural humans consumed roughly 3 times as much from these food categories as do Westerners today.

Current carbohydrate often takes the form of sugars and sweeteners; during the 1980s per capita American consumption exceeded 54.4 kg (120 lb) annually (Food and Nutrition Board 1989). Products of this sort, together with items made from highly refined grain flours constitute empty calories, energy devoid of accompanying essential amino and fatty acids, vitamins, minerals and possibly phytochemicals. Gatherer-hunters have many fewer foods of this type. Wild honey is analogous, but it is available seasonally, not year round, and is most often obtained with difficulty when it can be found. Because of their hardness, teeth are well-preserved at archeological sites, and the relative caries-free nature of those recovered from Paleolithic remains (Smith et al. 1988) suggests that preagricultural humans obtained much less honey than the 18% (or 21% if lactose is included) that sugars and sweeteners contribute to daily American energy intake (Food and Nutrition Board 1989).

Gatherer-hunters typically use many species of fruits and vegetables, often over 100 within the group's territorial range, to provide their yearly needs. This is an instance where inhabitants of affluent industrialized nations have a distinct nutritional advantage. The plant foods of foragers are often consumed in bulk, serially, as they come into season. At any one point in time only a small proportion of the annual total may be available, so current supermarket shoppers commonly have access to a wider variety of produce. But both foragers and members of contemporary affluent societies are far better off than are traditional agriculturists whose choices were often markedly constrained and for whom severe food shortages were (and are) relatively common. Hunter-gatherer practice forestalled famine except under the most adverse climatic conditions while providing a varied abundance of micronutrients and biologically active nonnutrient dietary constituents. Paleopathological changes that accompanied the transition from foraging to farming suggest a general superiority for preagrarian nutrition relative to that in the succeeding agricultural millennia (Cohen 1994).

Epidemiological investigations have demonstrated a strong, consistent inverse association between fruit and vegetable consumption and cancer incidence (Block et al. 1992). This relationship may reflect the micronutrients and phytochemicals that occur in vegetables and fruit. Such constituents are much less prominent intrinsic components of sugars and foods based on highly refined flours, which may explain why the same metaanalysis fails to document a similarly preventive role for cereal grain consumption. The inverse association between fruits and vegetables and cancer risk exhibits a stepwise pattern: the highest quartile had only half the risk of the lowest. This, in turn, invites speculation about overall cancer risk for our ancestors as their fruit and vegetable intake, we believe, was ordinarily about 3 times the current average.

Fat. Most nutritionists concur that saturated fat should provide no more than 10% of daily energy intake and, similarly, there is general consensus that excessive cholesterol intake, often construed as > 300 mg/d, should be avoided. In addition, high fat diets (fat > 40% total energy) are generally considered undesirable, but there is disagreement as to the appropriate target for fat consumption, some suggesting 10–20% and others 30–35% of energy intake (Grundy, 1994).

The Paleolithic nutritional model suggests that saturated fatty acids provided only ~6% of average total energy for preagricultural humans (Eaton 1992), but their cholesterol consumption was probably ~480 mg/d, a high intake being unavoidable because game made up one-third the substance base. Overall fat intake, in most localities, is likely to have contributed 20–25% of daily energy, a value intermediate between the traditional (ca. 1960) Japanese (11%) and Mediterranean (37%) paradigms (Willett 1994).

Serum cholesterol-raising fatty acids. Longer chain saturated fatty acids, particularly C14 myristic and C16 palmitic, but not C18 stearic acid,[4] elevate serum cholesterol levels (Grundy, 1994). The primary sources of these fats are commercial meat, dairy products and tropical oils. *Trans* fatty acids, which are chiefly monounsaturated, may also raise serum cholesterol levels, although the importance of this effect is disputed (Leveille 1995, Wahle and James 1993). Each of these sources was much less or hardly at all a factor influencing lipid metabolism for Paleolithic humans.

Modern commercial meat contains more fat than does meat from wild game (20.0 g/100 g vs. 4.2 g/100 g) (Eaton 1992), and its proportion of C14 and C16 fatty acids is also greater (5.64 g/100 g fat vs. 0.99 g/100 g fat). Accordingly, meat from contemporary supermarkets has more tendency to raise serum cholesterol levels than does game meat (O'Dea et al. 1990, Sinclair et al. 1987). Domesticated animals (including goats and

[4] All three are apparently thrombogenic (Ulbricht and Southgate 1991).

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cattle) appear in the archeological record no earlier than 10,000 years ago (Smith 1995), so during the Paleolithic period, adults and older children could have had no dairy foods at all. And while tropical plant species, including coconuts and palm nuts, were probably important dietary items in their native geographical areas, their entire edible portion was consumed then, not merely their separated oil. Some *trans* fatty acids occur naturally in milk and in the fat of ruminant animals, but the great majority result from commercial hydrogenation. These substances can raise serum cholesterol, but unlike the longer chain saturated fatty acids, they tend to reduce HDL-cholesterol levels (Judd et al. 1994). Their contribution to preagricultural diets would have been minimal.

Cholesterol-raising fatty acids—myristic, palmitic and the *trans* fatty acids—together account for ~13–14% of American energy consumption, much above both recommendations, perhaps 7–8%, and Paleolithic experience, estimated at ~5%.

Serum cholesterol and dietary cholesterol. Gatherer-hunters studied in this century have had serum cholesterol levels averaging ~3.2 mmol/L (125 mg/dL) (Eaton et al. 1988), a value subsumed within the range observed for free-living nonhuman primates [2.3–3.5 mmol/L (90–135 mg/dL)] (Eaton 1992). Such similar serum levels throughout the primate order imply that this range is physiologically appropriate for primates generally and, by extension, tend to rebut arguments that serum cholesterol levels much below 5.2 mmol/L (200 mg/dL) are irrelevant or even injurious to human health (Jacobs et al. 1992, Moore 1989).

Foragers maintain their low serum cholesterol levels despite high dietary intake, estimated at 480 mg/d, nearly 200 mg/d greater than the most common recommendation, ≤ 300 mg/d. Other factors being equal, an increase in dietary cholesterol of 200 mg/d should elevate serum cholesterol ~0.2 mmol/L (8 mg/dL) (Grundy 1994). Apparently, the discrepancy in other factors [a high ratio of polyunsaturated to saturated fat (P:S), 1.4 for hunter-gatherers, 0.4 for Americans; low saturated fat content; and low total fat intake] more than offsets the modest adverse influence of dietary cholesterol for foragers.

Polyunsaturated fatty acids (PUFA). For hunter-gatherers the ratio of dietary (n-6) to (n-3) PUFA has been estimated at from 1:1 to 4:1 (Sinclair and O'Dea 1993), a marked contrast to that observed in affluent Western nations, 11:1 (Adam 1989, Hunter 1990). Terrestrial plant foods provide both linoleic acid [LA, 18:2(n-6)] and alpha linolenic acid [ALA, 18:3(n-3)], whereas arachidonic acid [AA, 20:4(n-6)], an (n-6) PUFA, together with eicosapentaenoic and docosahexanenoic acids [EPA, 20:5(n-3)] and [DHA, 22:6(n-3)], (n-3) PUFA are found in animal tissues. The high proportion of game meat in typical hunter-gatherer diets produces high levels of AA, EPA and DHA in their plasma lipids compared with those of Americans and Europeans (Sinclair and O'Dea 1993).

Arachidonic acid is metabolized to form potent eicosanoids such as thromboxane and the four-series leukotrienes. The (n-3) PUFA, particularly EPA and DHA, appear to inhibit eicosanoid biosynthesis from AA so that formation of vasoconstrictive and proaggregatory eicosanoids is reduced. This effect seems to depend on the dietary ratio of (n-6) to (n-3) PUFA, not on the absolute amount of (n-3) PUFA (Boudreau et al. 1991). In addition, (n-6) PUFA may have a cancer-promoting effect, a function not observed for (n-3) PUFA. On the basis of these considerations, some investigators have recommended altering current (n-6) and (n-3) PUFA consumption in the direction of our ancestral pattern (Simopoulos 1991, Sinclair and O'Dea 1993).

Protein. Protein intake for Paleolithic humans naturally varied with locality and season but is likely to have averaged 30% of daily energy intake, say 2.0–3.0 $g \cdot kg^{-1} \cdot d^{-1}$. In contrast, current recommendations center on 12–15% daily energy or 0.8–1.6 $g \cdot kg^{-1} \cdot d^{-1}$. Although their protein intake is chiefly from plant sources, free-living nonhuman primates (e.g., chimpanzees, gorillas, baboons and howler monkeys) consume 1.6–5.9 $g \cdot kg^{-1} \cdot d^{-1}$ (Casimir 1975, Coelho et al. 1976, Hladik 1977, Whiten et al.1991), so the forager intake pattern is in line with, while conventional nutritional recommendations deviate from, general primate experience. Furthermore, veterinary recommendations for higher primates in captivity substantially exceed existing recommendations for human protein intake (Panel on Nonhuman Primate Nutrition 1978).

Protein and disease. Epidemiological evidence on the relationship between high protein intake and cancer incidence is inconsistent as are the results of animal experiments on dietary protein and spontaneous carcinogenesis (Food and Nutrition Board 1989). High meat diets are positively correlated with coronary heart disease, but such diets, nowadays, also provide copious amounts of total and saturated fat, which probably accounts for much of the association (Food and Nutrition Board 1989). Furthermore, high meat diets in most industrialized countries commonly provide relatively small amounts of fruits and vegetables, which may increase susceptibility to both cancer and atherosclerosis. In contrast, the animal protein intake of Paleolithic humans was not associated with excessive intake of saturated fat, and their usual consumption of fruit and vegetables was exceptionally high by contemporary standards. Low fat, high protein diets have been associated with serum cholesterol lowering in human experiments (Sinclair et al. 1987, Wolf and Giovannetti 1991) while both anthropologists (Stefansson 1960) and epidemiologists (Hildes and Schaefer 1984) have observed little cancer among Eskimos whose protein intake is very high.

A high intake of purified, isolated protein increases urinary calcium excretion in experimental settings, but

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high meat-protein natural diets have little such effect (Food and Nutrition Board 1989, Hunt et al. 1995). Preagrarian humans developed high peak bone mass, probably reflecting synergy between their obligatory physical exertion and abundant calcium intake. Although there are relatively few skeletal remains of older Stone Agers, those which have survived suggest that our Paleolithic ancestors experienced age-related bone loss at a slower rate than did their successors—agriculturists who ate less protein (Eaton and Nelson 1991).

In patients with chronic renal disease, high protein diets accelerate deterioration (Brenner et al. 1982), but two primary causes of renal failure, hypertension and diabetes, are rare in hunter-gatherers (Eaton et al. 1988). Health evaluations and autopsy studies conducted on partially acculturated Eskimos, whose protein intake equals or exceeds that postulated for Stone Agers, show no evidence of excessive kidney disease (Arthaud 1970, Kronman and Green 1980, Mann et al. 1962).

Protein-endocrine-eiconsanoid relationships. The evidence that a high protein, low fat diet can be tolerated by humans fails to explain why protein intake substantially above recommended levels might have beneficial effects, at least with regard to nitrogen balance and maintenance of lean body mass (Hoerr et al. 1982). However, the principles of evolutionary adaptation suggest that if a dietary pattern is maintained within a lineage for nearly two million years, it must be optimal. The relative proportions of dietary carbohydrate and protein influence secretion of insulin and glucagon after a meal (Westphal et al. 1990). The ratio of these two hormones in turn affects lipid metabolism (especially storage vs. utilization) and, by influencing desaturase activity, modulates eicosanoid biosynthesis (Brenner 1981, Sears 1993). Possibly these or presently unknown protein-endocrine-eicosanoid interrelationships may explain why high protein intake has apparently been integral to human nutrition since the appearance of H. erectus (Aiello and Wheeler 1995, Leonard and Robertson 1992).

Fiber. Analysis of vegetable foods consumed by foragers in this century (Table 1) and evaluation of archaic native American coproliths suggest that ancestral human fiber intake exceeded 100 g/d (Eaton 1990). Rural Chinese consume up to 77 g/d (Campbell and Chen 1994), rural Africans up to 120 g/d (Burkitt 1983) and chimpanzee consumption may exceed 200 g/d (Milton 1993). In contrast, typical adult American intake is $<$ 20 g/d, whereas current recommendations are in the 20–30 g/d range (Butrum et al. 1988).

The fiber in preagricultural diets came almost exclusively from fruits, roots, legumes, nuts and other naturally occurring noncereal plant sources, so it was less associated with phytic acid than is fiber from cereal grains (Eaton 1990). And, because they ate noncereals, the proportion of soluble, fermentable fiber was probably higher for preagrarian people than for most people in contemporary affluent nations. The former consideration should mitigate concerns about the putative adverse effects of high fiber diets on mineral absorption, although, even when wheat is the primary fiber source, diets containing up to 50 g/d have had little negative impact on micronutrient absorption (Food and Nutrition Board 1989). The skeletal remains of preagricultural humans provide little evidence for mineral malabsorption (Eaton and Nelson 1991). The higher proportion of soluble fiber in Stone Age diets should have favorably affected lipid metabolism (Kritchevsky 1994), perhaps contributing to the low serum cholesterol levels that have been found in recently studied hunter-gatherers (Eaton et al. 1988).

DISCUSSION

Near unanimity regarding reduction of saturated fat intake contrasts with the variety of means proposed to achieve this result. The American Heart Association dietary plan, the traditional Mediterranean and East Asian paradigms and vegetarianism each has its advocates and supporting literature. As far as we can evaluate its nature, the average Paleolithic diet was similar to all these currently recommended regimens in providing only a very small proportion of its energy as saturated, cholesterol-raising fat. Those foragers who have been studied have extremely low serum cholesterol levels, averaging ~3.2 mmol/L (125 mg/dL), and although autopsy and sophisticated medical evaluations of hunter-gatherers have not been performed, electrocardiographic studies have revealed no manifestations of myocardial ischemia (Eaton et al. 1988). For these reasons, opposition to the ancestral human diet because of coronary artery disease-related considerations should be minimal.

The more nearly equal contributions of (n-6) and (n-3) fatty acids that, we believe, characterized Paleolithic diets anticipated contemporary recommendations that appear with increasing frequency, but only further investigations will establish the ultimate importance of this factor.

Because they rarely used cereal grains, Stone Agers would have consumed more fruits and vegetables than do any agricultural or industrial societies at present, probably 3 times the amount most common in the United States. There is growing appreciation that increased consumption of fruits and vegetables is desirable, so this aspect of ancestral nutrition is intriguing, in part because it implies an increased intake of phytochemicals, vitamins and minerals. Our best estimates suggest that Paleolithic intake of micronutrients exceeded those now recommended, both in absolute terms and relative to energy intake, but, although higher, their levels were of moderate magnitude, not equivalent to the megadoses sometimes recommended by vitamin enthusiasts. The obvious exception was sodium because the amounts that occur naturally in plant and animal foods provide far less than is now added artificially during processing, cooking and at table.

Although the attributes of Paleolithic nutrition discussed above seem relatively unobjectionable, the likely contributions of fiber and, especially, protein to preagricultural diets raise serious theoretical and practical questions regarding mineral (especially calcium) metabolism and renal physiology. Relative to energy content naturally occurring edible vegetation contains much fiber, whereas game has a high protein-energy ratio, so preagrarian, noncereal-consuming human ancestors would necessarily have eaten a great deal of fiber, of protein or both, no matter what their specific subsistence pattern. It seems inescapable, therefore, that ancestral human diets differed from those common at present in containing far more protein and/or fiber.

This apparent reality should elicit neither premature endorsement nor reactionary rejection but should provide intellectual stimulation and impetus for research regarding the effects of such diets. It may be that the circumstances of life in affluent, industrial nations, including our longer average life expectancy, are somehow incompatible with the dietary practices that fueled human evolution for the past million years or more. On the other hand, reinstitution of an ancestral nutritional pattern, in conjunction with other essential features of that lifestyle, might reduce the burden of chronic degenerative disease which encumbers aging Americans and produces most mortality in the United States and similar nations. In either event, the type of nutrition upon which humans evolved over so long a period merits the best investigational efforts of today's nutrition scientists.

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