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Review

Paleolithic nutrition revisited: A twelve-year retrospective on its nature and implications

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Introduction

The nutritional needs of today's humans arose through a multimillion year evolutionary process during nearly all of which genetic change reflected the life circumstances of our ancestral species (Eaton & Konner, 1985). But, since the appearance of agriculture 10 000 y ago and especially since the Industrial Revolution, genetic adaptation has been unable to keep pace with cultural progress (Cohen, 1989; Tooby & Cosimides, 1990). Natural selection has produced only minor alterations during the past 10 000 y, so we remain nearly identical to our late Paleolithic ancestors (Tooby & Cosimides, 1990) and, accordingly, their nutritional pattern has continuing relevance. The preagricultural diet might be considered a possible paradigm or standard for contemporary human nutrition. (O'Dea & Sinclair, 1983; Eaton & Konner, 1985; Burkitt & Eaton, 1989).

Nutrition science is rightly based on epidemiological, biochemical, and animal investigations; the ultimate arbiter in this field can only be experimental laboratory and clinical research. Still, these approaches might be complemented by insights from an evolutionary perspective. Twelve years ago, (Eaton & Konner, 1985) we proposed a model based on analyzing the nutritional properties of wild game and uncultivated vegetable foods, evaluating archeological remains, and studying the subsistence of recent foragers. (We use the terms foragers and hunter-gatherers interchangeably.) This approach (for method see appendix) allows estimation of an 'average' Paleolithic diet which is analogous to an 'average' American diet; the different patterns of Greenland Inuit and Australian Aborigines paralleling those of Americans from vegans to fast food addicts. This paper updates our prior effort in four ways: first, our database has been much expanded. The 1985 analyses were derived from a total of 69 game and wild vegetable items; now we have at least some data on 321. Secondly, the additional data permits assessment of consistency. Estimates presented in 1985 (Eaton & Konner, 1985) and subsequently amended (Eaton *et al*, 1988; Eaton, 1992) can be compared with those generated from the current data set (Table 1). Thirdly, the original paper presented estimates on only four micronutrients (sodium, potassium, calcium and ascorbic acid); now, we can formulate retrojections on 11 such dietary constituents. Fourthly, we now compare and contrast current dietary recommendations with our estimate of ancestral human nutrition. This exercise reveals both gratifying parallels and potentially instructive points of disagreement.

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Energy requirements

That Paleolithic humans were as tall as are members of current affluent societies has only recently been appreciated (Walker, 1993; Roberts *et al*, 1994), but the necessity for vigorous physical activity engendered by a nomadic hunting and gathering lifestyle has long been apparent. Skeletal remains show that our ancestors typically developed lean body mass considerably in excess of that common among us today (Ruff *et al*, 1993; Bridges, 1996). The physical demands of life during the agricultural period were also strenuous (Heini *et al*, 1995); it took the Industrial Revolution to dissociate productivity from human caloric expenditure. For example, the introduction of mechanized

Table 1 Paleolithic diet estimated macronutrient composition

	1985[a]	*1988*[b]	*1991*[c]	*1997*[d]
Data base				
Animals species, n	21	43	41	85
Plant components, n	44	153	153	236
Dietary makeup				
% Protein	34	33	32	37
% Carbohydrate	45	46	43	41
% Fat	21	21	25	22
P : S Ratio	1.41	1.41	1.45	1.40
Cholesterol (mg)	520	520	482	480

[a] Eaton & Konner, 1985.
[b] Eaton, Konner & Shostak, 1988.
[c] Eaton, 1992.
[d] Current Report.

farming in Japan reduced average daily work expenditure by over 50%, (Shimamoto *et al*, 1989), while, in Britain, proliferation of labor-saving devices between 1956 and 1990 reduced caloric expenditure (in excess of basal metabolic needs) by an astonishing 65% (Ministry of Agriculture, Fisheries and Foods, 1995).

The height, robusticity and unavoidable physicality of preagricultural humans mandated a caloric intake greater than that of most 20th century Westerners. Recently studied hunter-gatherers are nonetheless lean with skinfold thicknesses only half those of age-matched North Americans (Eaton *et al*, 1988). Therefore, our remote ancestors must have existed within a high energy throughput metabolic environment characterized by both greater caloric output and greater caloric intake than is now the rule. Furthermore, game and wild plant foods contain less fat, more protein, more roughage, and more micronutrients per unit weight than do foods typically selected from the supermarkets of today's industrialized nations (see below). As a result, the high caloric requirements of Paleolithic humans would have necessitated both nutrient and fiber intake considerably in excess of that common today.

Micronutrients and phytochemicals

Fruits, roots, legumes, nuts, and other non-cereals provided 65–70% of the average forager subsistence base (Eaton & Konner, 1985). They were generally consumed within hours of being gathered, typically with minimal or no processing (Schroeder, 1971) and often uncooked. Such foods and wild game are characterized by high average content of vitamins and minerals relative to their available energy (Table 2). Governmentally constituted bodies (for example, the Food & Nutrition Board, 1989) traditionally recommend levels of essential nutrient intake adequate to meet known metabolic needs (Food & Nutrition Board, 1989). However, assuming a 65:35 plant:animal subsistence pattern [that considered most likely by anthropologists (Lee, 1968)] and a 12558 kJ/d (3000 kcal/d) diet, it seems inescapable that our preagricultural ancestors would have had an intake of most vitamins and minerals much in excess of currently recommended dietary allowances, either in absolute terms (Table 3) or relative to energy intake (Table 4). For some nutrients (for example folic acid) the intake retrojected for Paleolithic humans would have reached theoretically beneficial levels now thought attainable only through use of supplements (Daly *et al*, 1995).

Paleoanthropological data can be used for triangulation with estimates of optimal intake derived from conventional approaches. For example, current recommendations for optimal vitamin C ingestion range from 6–750 mg/d (Levine *et al*, 1995). For a 12558 kJ (3000 kcal) diet, Paleolithic humans are likely to have averaged about 600 mg of vitamin C—within the spectrum of contemporary estimates, but toward the higher end. In addition, paleonutritional evidence may provide perspective when results of more conventional investigations conflict. Epidemiological studies on antioxidants currently seem at odds, (ATBD Study Group, 1994; Sies & Krinsky, 1995) but the evidence that ancestral humans consumed more tocopherol and carotene than do current humans appears straightforward Tables 3 and 4).

The content of non-nutrient phytochemicals in wild plant foods is unknown (but see Simopoulos *et al*, 1992); nevertheless it is plausible to suspect that their concentrations may be relatively high, like those of micronutrients. The physiological role of these substances, which are protease inhibitors, organic isothiocyanates, organosulfur compounds, plant phenols, and flavanoids, has not been established, but their possible function as biological response modifiers and/or chemopreventive compounds attracts continuing research attention (Watanabe *et al*, 1991; Zhang *et al*, 1992; Hertog *et al*, 1993; Flagg *et al*, 1994).

Table 2 Nutrient values of hunter-gatherer foods[a]

	Vegetable foods n = 236			*Animal foods n = 85*		
	n	*mean*	*range*[b]	*n*	*mean*	*s.d.*
Vitamins, mg/100 g						
Riboflavin	89	0.168	0.001–1.14	26	0.399	0.246
Folate	11	0.0180	0.0028–0.0618	3	0.00567	0.00170
Thiamin	101	0.115	0–0.94	28	0.215	0.197
Ascorbate	123	33.0	0–414	18	4.79[c]	5.43
Carotene	51	0.328	0–6.55	—	—	—
(retinol equivalents)	—	54.6	0–1090	—	—	—
Vitamin A	59	1.08	0–8.41	6	0.461	0.368
(retinol equivalents)	—	180	0–1400	—	76.8[d]	61.4
Vitamin E	24	1.93	0.007–9.08	—	—	—
Minerals, mg/100 g						
Iron	167	2.90	0.1–31	22	4.15	2.77
Zinc	91	1.12	0.1–9.5	11	2.67	0.860
Calcium	181	103	1–650	28	22.7[d]	30.9
Sodium	139	13.5	0–352	16	59	23.6
Potassium	112	448	5.1–1665	16	317	43.3
Fiber, g/100 g	132	6.15	0–44.9	—	—	—
Energy, kJ/100 g	184	456	16.7–2557	44	527	196
(*kcal/100 g*)	—	(109)	(4–563)	—	(126)	(46.8)

[a] Data from references listed in Appendix.
[b] Range necessary because weighting precludes s.d.; see Appendix.
[c] See values for seabirds in Mann *et al*. 1962.
[d] Vitamin A and calcium in animal foods from organ meat, skin, small bones, insects, shellfish and marrow.

Table 3 Estimated daily paleolithic intake of selected nutrients compared to recommended and current levels

	Paleolithic intake[a]	*U.S. RDA*[b]	*Current U.S. intake*[b]
Vitamins, mg/d			
Riboflavin	6.49	1.3–1.7	1.34–2.08
Folate	0.357	0.18–0.2	0.149–0.205
Thiamin	3.91	1.1–1.5	1.08–1.75
Ascorbate	604	60	77–109
Carotene	5.56	—	2.05–2.57
(retinol equivalents)	(927)	(342–429)	—
Vitamin A	17.2	4.80–6.00	7.02–8.48
(retinol equivalents)	(2870)	(800–1000)	(1170–429)
Vitamin E	32.8	8–10	7–10
Minerals, mg/d			
Iron	87.4	10–15	10–11
Zinc	43.4	12–15	10–15
Calcium	1956	800–1200	750
Sodium	768	500–2400	4000
Potassium	10500	3500	2500
Fiber, g/d	104	20–30	10–20
Energy, kJ/d	12558	9209–12139	7326–10465
(*kcal/d*)	(3000)	(2200–2900)	(1750–2500)

[a] Based on 913 g meat and 1697 g vegetable food/d yielding 12558 kJ (3000 kcal). See Appendix for method.
[b] Food and Nutrition Board, 1989.

Table 4 Dietary micronutrient intake relative to energy intake. Estimated paleolithic and current levels

	mg/4189 kJ (1000 kcal)		*Ratio*
	Paleolithic[a]	*Current*[b]	*Paleolithic : Current*
Vitamins			
Riboflavin	2.16	0.6	3.60
Folate	0.119	0.08	1.49
Thiamin	1.30	0.51	2.55
Ascorbate	201	24	8.38
Carotene	1.85	1.09	1.70
(retinol equivalents)	(309)	(182)	—
Vitamin A	5.74	2.12	2.71
(retinol equivalents)	(957)	(353)	—
Vitamin E	10.9	3.5	3.11
Minerals			
Iron	28.5	4.9	5.82
Calcium	653	392	1.67
Zinc	14.5	5.3	2.74
Sodium	256	1882	0.136
Potassium	3500	1177	2.97

[a] From Table 2.
[b] Food and Nutrition Board, 1989.

Electrolytes

Typical adult Americans consume nearly 4000 mg of sodium each day (Food & Nutrition Board, 1989) of which fully 75% is added to food during processing (James *et al*, 1987); only about 10% is intrinsic to the basic food items. Potassium intake averages from 2500–3400 mg/d (Food & Nutrition Board, 1989) so Americans, like nearly all people living today, consume more sodium than potassium. Humans are the only free-living, non-marine mammals to do so. In the United States recommended dietary allowances for sodium are 500–2400 mg/d (although American food labels reflect only the 2400 mg figure) and for potassium 2000–3400 mg/d (Food & Nutrition Board, 1989). These recommendations are roughly intermediate between current and ancestral human experience.

Additional data on the sodium and potassium content of uncultivated plant foods and wild game (Table 2) allow earlier calculations (Eaton & Konner, 1985) to be updated. The refined estimate of Paleolithic intake parallels that of chimpanzees, the species phylogenetically closest to humans (Denton *et al*, 1995), and contrasts strikingly with our current pattern. Preagricultural humans are calculated to have consumed only 768 mg of sodium, but fully 10 500 mg of potassium each day. The potential implications of electrolyte intake at the Paleolithic level are apparent in data from the Intersalt Study (Intersalt Cooperative Research Group, 1988) whose subjects included Yanamamo and Xingo Amerindians and Asaro from New Guinea. These groups are rudimentary horticulturists, but they are relatively isolated, little acculturated and their food, like that of hunter-gatherers, is free of added salt. Their dietary sodium/potassium ratio (0.13) is similar to that retrodicted for preagricultural humans (0.07).

The Intersalt investigators found the Yanamamo, Xingo, and Asaro populations to have a ‘low’ average blood pressure (102/62), no blood pressure increase with age, and minimal (0.6%) prevalence of hypertension (Carvallo *et al*, 1989). These findings are consistent with those for multiple other previously studied forager and horticulturist groups (Eaton *et al*, 1988). In contrast, for 48 Intersalt study groups who did have access to salt, sodium intake averaged 3818 mg/d, but potassium only 2106 mg/d (Na/K = 1.81). Median blood pressure for these populations was 119/74 and tended to rise with age. Their prevalence of hypertension (BP > = 140/90) varied from 5.9–33.5% (Intersalt Cooperative Research Group, 1988).

The editorial which accompanied Intersalt's initial publication was subtitled 'Salt has only small importance in hypertension,' (Swales, 1988) but a follow-up article focusing on Intersalt's remote study groups concluded that '. . . a minimum intake of salt is required to produce a high frequency of hypertension in populations' (Carvallo *et al*, 1989). That minimum appears to exceed the level consumed during the Paleolithic.

Carbohydrate

The typical carbohydrate intake of ancestral humans was similar in magnitude, 45–50% of daily energy, to that in current affluent nations, but there was a marked qualitative difference. Under most circumstances during the late Paleolithic, the great majority of carbohydrate was derived from vegetables and fruit, very little from cereal grains and none from refined flours (Eaton & Konner, 1985). This practice extended the multimillion year experience of primates generally (Milton, 1993). Current recommendations, that individuals consume 55% or more of their energy as carbohydrate, are slightly high compared with our estimates of human evolutionary experience, but the different makeup of the carbohydrate involved probably has more important implications. Only 23% of American carbohydrate consumption is derived from fruit or vegetable sources (Committee on Diet and Health, 1989) while, for Europeans, the proportion is lower still (James *et al*, 1988). The corollary is that preagricultural humans consumed roughly three times the vegetables and fruit that typical Westerners do today. Their intake would have equaled or exceeded that of current vegans whose consumption of vegetables, roots, fruit, and berries is 2.6 times that of matched omnivores and whose antioxidant vitamin intake is 247–313% greater (Rauma *et al*, 1995).

Much current carbohydrate intake is in the form of sugars and sweeteners; in the mid-1980s, American per capita consumption in these categories exceeded 54.6 kg (120 lbs) annually (Committee on Diet and Health, 1989). Such products, together with foods made from highly refined grain flours provide 'empty calories' (that is food energy without essential amino acids, essential fatty acids, micronutrients, and perhaps phytochemicals). Energy sources of this type are much less available to hunter-gatherers; they are fond of wild honey, but as a seasonable delicacy and not always accessible even then. For recently studied foragers [Onge (Andaman Island) 1.2% (Bose, 1964); Anbarra (Australia) 0.4% (Meehan, 1982)] honey accounts for far less than the 18% (21% if lactose be added) contribution sugars/sweeteners now make to daily energy intake (Committee on Diet and Health, 1989). Not only are sugars and highly refined flour products devoid of intrinsic nutrients other than energy, they are also low in bulk so that they can be eaten quickly and occupy only a small proportion of gastric capacity. The bulky carbohydrate sources that fueled human evolution had to be eaten more slowly and usually produced more gastric distention for a given caloric load (Duncan *et al*, 1983).

Hunter-gatherers utilize many species of fruits and vegetables, often over 100 in each locality, to provide their yearly subsistence. In this respect, inhabitants of affluent industrialized nations, with ready access to an even wider variety of produce, are far better off than traditional agriculturists whose choices were often markedly constrained. Forager practice forestalled famine except under the most adverse climatic conditions and, in addition, provided a varied abundance of micronutrients and biologically active non-nutrient dietary constituents. Epidemiological investigations have demonstrated an exceptionally strong and consistent association between consumption of fruits/vegetables and cancer prevention (Steinmetz & Potter, 1991; Block *et al*, 1992; Ames *et al*, 1995). It is tempting to speculate that this association reflects their intrinsic micronutrient/phytochemical load. These are less prominent or negligible intrinsic components of sugars and highly refined flour products. It is potentially significant that a similar cancer preventive relationship has not yet been proven to exist for grain products (Block *et al*, 1992).

The glycemic index of wild plant foods is typically, though not invariably, lower than that of agricultural staples (such as potatoes, bread, spaghetti, rice, corn, etc.) (Thorburn *et al*, 1987; Brand *et al*, 1990) and current processing techniques, especially fine roller milling, accentuate this tendency. (Brand *et al*, 1985; Heaton *et al*, 1988) The net effect is that carbohydrate from current sources is more rapidly digested and absorbed than it was during ancestral experience, a factor of potential significance in the etiology of diabetes mellitus.

Fat

There is near unanimous current opinion that saturated fat should comprise less than 10% of each day's dietary energy, perhaps 7–8%. Similar consensus exists that high intakes of cholesterol (>500 mg/d) are to be avoided, an intake of 300 mg/d or less being widely advocated. Further, there is substantial agreement that high total fat diets (>40% of dietary energy) are unwise; however, there is dispute as to whether the target for fat consumption should be low (<20% of energy) or intermediate (in the 30–35% range) (Grundy, 1994).

Saturated fatty acids are calculated to have provided about 6% of the average total energy intake for Paleolithic humans (Eaton, 1992). Their cholesterol intake is estimated at 480 mg/d, unavoidable when game makes up a third of the nutrition base, and their overall fat intake is projected at 20–25% total energy Table 1), intermediate between the frequently lauded traditional (c. 1960) Japanese (11%) and Mediterranean (37%) patterns (Willett, 1994).

Cholesterol-raising fatty acids

Saturated fats, particularly C_{14} myristic and C_{16} palmitic acid (but not C_{18} stearic acid) are thought to be the most important dietary factors related to coronary heart disease (Grundy, 1994). At present, the chief sources of such fats in affluent nations are meat, dairy products, and tropical oils. Even though they are predominantly monounsaturated, trans fatty acids also raise serum cholesterol levels much like C_{14} myristic and C_{16} palmitic acids do. Each of these sources was much less or not at all a factor influencing lipid metabolism in the late Paleolithic.

Game has less fat overall than does modern commercial meat (4.2 g/100 g *vs* 20.0 g/100 g) (Eaton, 1992), while its proportion of C_{14} and C_{16} fatty acids is also lower (0.99 g/100 g *vs* 5.64 g /100 g fat). For these reasons, game has much less tendency to raise serum cholesterol levels than does meat from today's supermarkets (Sinclair *et al*, 1987; O'Dea *et al*, 1990). Because there were no domesticated animals during the Stone Age, adults and older children then had no dairy foods whatsoever. And while tropical plant species, including coconuts and palm nuts, were presumably important regional dietary resources, their entire edible portion was consumed, not just their oil. Unlike today, they were then available only seasonally and in areas to which they were indigenous.

Some trans fatty acids occur naturally in milk, but the great majority result from commercial hydrogenation. They effectively raise serum cholesterol levels, but, unlike C_{14} and C_{16} fatty acids, they reduce the HDL-cholesterol fraction (Judd *et al*, 1994). They would have made no contribution to adult Stone Age diets. After subtracting non cholesterol-raising C_{18} stearic acid and adding trans fatty acids, each about 3%, the overall contribution of cholesterol-raising fatty acids to the current American diet is about 13–14% of caloric consumption, far above both recommendations (7–8%) and Paleolithic experience (perhaps 5%).

Dietary cholesterol and serum cholesterol

Despite high dietary cholesterol intake, foragers studied in this century have manifested very 'low' serum cholesterol levels, averaging around 3.2 mmol/L (125 mg/dL) (Eaton *et al*, 1988), a figure within the range found for free-living non-human primates (90–135 mg/dL) (Eaton, 1992) and well below the American average of about 5.3 mmol/L (205 mg/dL) (Gore & Dalen, 1994). This similarity of serum cholesterol values may indicate existence of a natural primate pattern and thus counter contentions that 'low' serum cholesterol levels are irrelevant or even harmful to human health (Moore, 1989; Jacobs *et al*, 1992; Kritchevsky & Kritchevsky, 1992; Dalen & Dalton, 1996). Furthermore, the 'low' serum cholesterol of hunter-gatherers, despite their high intake, adds credence to observations that the effect of dietary cholesterol on serum levels is mitigated as the ratio between polyunsaturated and saturated fat (P:S) rises (Schonfeld *et al*, 1982). P:S for hunter-gatherers is 1.4, for Americans it is 0.4. It is estimated that an increase in dietary cholesterol of 200 mg/d should elevate serum cholesterol about 0.2 mmol/L (8 mg/dL) (Grundy, 1994). Forager intake, at 480 mg/d, is nearly 200 mg/d greater than the most common recommendation (<300 mg/d). Apparently, the high P:S ratio, low saturated fat content and low total fat intake of hunter-gatherer diets more than offsets the adverse effects of their 'high' cholesterol intake (Sinclair *et al*, 1987; O'Dea *et al*, 1990).

Polyunsaturated fatty acids (PUFA)

In affluent nations, *n*-6 PUFA intake is now roughly 11 times that of *n*-3 PUFA (Adam, 1989; Hunter, 1990), but the ratio in forager diets is more nearly equal, varying from 4:1 to 1:1 (Sinclair & O'Dea, 1993), a range encompassing the ratio for free-living primates [1.4:1 (Chamberlain *et al*,1993)]. Much research has focused on Greenland Inuit (Eskimos), for whom *n*-6:n-3 ratios of 1:40 have been calculated; however, their extensive exploitation of marine resources is at variance with the currently accepted paleoanthropological view of human savanna origins (but see Crawford *et al*, 1993). The terrestrial food chain provides both linoleic acid (LA 18:2, *n*-6) and alpha linolenic acid (ALA 18:3, *n*-3) from plant sources (Simopoulos, 1991) as well as their desaturation/elongation products, arachidonic acid (AA, an *n*-6 PUFA), eicosapentaenoic and docosahexaenoic acids (EPA and DHA, *n*-3 PUFAs) from animal tissue (Naughton *et al*, 1986). The prominence of game in typical hunter-gatherer diets produces high levels of AA, EPA and DHA in their plasma lipids relative to those found in Westerners (Sinclair & O'Dea, 1993).

Arachidonic acid is the metabolic precursor of powerful eicosanoids such as thromboxane (Tx A_2) and the four-series leukotrienes. The *n*-3 PUFA, especially EPA and DHA, apparently modulate eicosanoid biosynthesis from AA so that proaggregatory and vasoconstrictive eiconsanoid formation is reduced. For this effect, it appears that the ratio of *n*-6 to *n*-3 PUFA in the diet, rather than the absolute amount of *n*-3 PUFA, is the decisive factor (Boudreau *et al*, 1991) In addition, *n*-6 PUFA may act as promoters in carcinogenesis, a property seemingly absent for *n*-3 PUFA. Based on these considerations, some investigators have advocated a return to the dietary *n*-6:*n*-3 ratio of ancestral humans (Simopoulos, 1991; Sinclair & O'Dea, 1993).

Protein

Retrodicted protein intake for Paleolithic humans, typically above 30% of daily energy (Table 1), is hard to reconcile with the 12% currently recommended for Americans. The RDA is actually a range, 0.8–1.6 g/kg/d, which contrasts with 2.5–3.5 g/kg/d for Stone Agers. Observed protein intake for other primates, such as chimpanzees, gorillas, baboons, and howler monkeys, is also higher than that advocated by human nutritionists and ranges from 1.6–5.9 g/kg/d in the wild (Casimir, 1975; Coelho *et al*, 1976; Hladik, 1977; Whiten *et al*, 1991). Furthermore, veterinary recommendations for higher primates in captivity also substantially exceed the RDA for Americans (Panel on nonhuman primate nutrition, 1978). It would be paradoxical if humans, who, during evolution, added hunting and scavenging skills to their higher primate heritage, should now somehow be harmed as a result of protein intake habitually tolerated or even required by their near relatives.

Protein and disease

Epidemiological studies have linked high protein intake with cancer, especially of the breast and colon, but such evidence is inconsistent, as is the effect of varying protein intake on spontaneous tumor incidence in animal experiments (Committee on Diet and Health, 1989). Intercountry correlation studies also show that diets high in meat have a strong positive correlation with atherosclerotic coronary artery disease, but such diets are presently linked with high intakes of total and saturated fat, which probably accounts for a large part of the association (Committee on Diet and Health, 1989). In addition, high meat diets in industrialized countries tend to have restricted levels of plant foods, especially fruits and vegetables, which may increase susceptibility to both cancer and atherosclerosis. Conversely, the high animal protein intake of preagricultural humans generally occurred within a nutritional context of low fat and high fruit/vegetable consumption. In such circumstances a high protein diet may actually elevate plasma HDL-cholesterol while lowering total cholesterol and triglyceride levels, thereby reducing cardiovascular risk (Wolfe, 1995).

High intake of purified, isolated protein increases urinary excretion of calcium, chiefly in experimental settings where phosphorus intake is held constant. But high protein natural diets have increased phosphorus as well and there is little evidence that such diets increase risk of osteoporosis (Committee on Diet and Health, 1989; Hunt *et al*, 1995; but see Abelow *et al*, 1992). Paleolithic humans developed high peak bone mass, probably reflecting their habitual levels of physical activity together with their ample calcium intake. While there are few older skeletons to evaluate, those available suggest Stone Agers experienced less bone loss with age than did subsequent low-protein-diet agriculturists (Eaton & Nelson, 1991).

High protein diets should worsen the course of chronic renal failure (Brenner *et al*, 1982). However, prominent underlying causes of renal disease such as diabetes and hypertension, are rare among foragers (Eaton *et al*, 1988) and health evaluations including autopsy studies have shown no increased frequency of renal disease among partially acculturated Alaskan and Greenland Inuit whose protein intake approximates that postulated for preagricultural humans (Mann *et al*, 1962; Arthaud, 1970; Kronmann & Green, 1980). Because of its largely vegetable nature, the high protein intake of non-human primates presumably has less anabolic effect than would a comparable level of animal protein for humans, but the resulting nitrogen load for the kidneys would be equivalent. While increased protein intake may not be actively harmful, the experiments of exercise physiologists make it hard to understand why humans might require dietary protein at the 2.5–3.5 g/kg/d level, at least in regard to nitrogen balance and lean body mass maintenance (Young, 1986). Perhaps protein intake at the levels which obtained during human evolutionary experience has physiological consequences apart from those inherent to nitrogen metabolism. The ratio of protein to carbohydrate in human diets affects the relative amounts of insulin and glucagon secreted after a meal (Westphal *et al*, 1990) and, by influencing desaturase activity, protein may modulate eicosanoid biosynthesis (Brenner, 1981; Sears, 1993). In any event, the protein nutrition experience of preagricultural humans was contrary to recent recommendations that protein intake not be increased to compensate for the calorie loss incumbent in dietary fat reduction for the American public (Committee on Diet and Health, 1989).

Fiber

Analysis of vegetable foods consumed by recently studied hunter-gatherers (Tables 2 and 3) and evaluation of archaic native American coprolith remains both suggest that preagricultural fiber intake exceeded 100 g/d (Table 3) (Eaton, 1990). Rural Chinese consume up to 77 g of fiber per day (Campbell & Chen, 1994) and estimates of from 60–120 g/d have been made for rural Africans (Burkitt, 1983). Chimpanzees and other higher primates obtain upwards of 200 g of fiber from each day's food (Milton, 1993). In contrast, fiber intake for adult Americans is generally less than 20 g/d and current recommendations range from 20–30 g/d (Butrum *et al*, 1988).

Because the fiber consumed by Paleolithic humans came primarily from fruits, roots, legumes, nuts and other noncereal vegetable sources, its content of phytic acid would have been less than that of the fiber consumed now in industrialized nations, which comes largely from grain (Eaton, 1990). For the same reason, the proportion of soluble, fermentable fiber relative to insoluble, non-fermentable fiber was likely to have been higher for preagricultural humans than for current citizens of affluent nations. Reservations about increasing the fiber content of Western diets revolve around potential adverse effects on micronutrient absorption, especially of minerals, due to binding by fiber. There is, however, little evidence that diets containing up to 50 g/d have a negative effect on absorption (Committee on Diet and Health, 1989), even when the fiber is predominantly wheat with its high phytic acid content. The bony remains of preagricultural humans suggest that they absorbed minerals adequately, even though their fiber intake exceeded that so far studied by nutritionists. The high proportion of soluble fiber in Stone Age diets should have favorably affected lipid metabolism (Kritchevsky, 1994; Rimm *et al*, 1996).

Discussion

In some respects, the nutritional experience of humans during evolution, that is, in 'the environment of evolutionary adaptedness,' (Tooby & Cosmides, 1990) parallels and supports existing dietary recommendations. For example, advice to decrease saturated fat intake below 10% of daily energy, which is interpreted to mean that cholesterol-raising fatty acids should comprise no more than 7–8% of each day's calories, nearly matches the 5% retrodicted for ancestral humanity. And with regard to energy balance, the American RDAs advocate increased energy expenditure through physical activity rather than voluntary reduction in energy intake as a preferred way of maintaining health and desirable body composition. This advice fits perfectly with our evolutionary past.

In other cases, the Paleolithic experience can serve as a reference standard when the recommendations of nutritionists are at variance. Many nutritional advisory bodies suggest that fat content not exceed 30% of caloric intake. Still, supporters of the 'Mediterranean' dietary paradigm (Grundy, 1994; Willett, 1994) debate with advocates of a traditional 'East Asian' (Japanese, Chinese) approach (Ornish *et al*, 1990; Campbell & Chen, 1994). The latter emphasizes very low fat intake, 10–15% of total energy, and increases carbohydrate up to 70% of caloric intake. In contrast, the former allows total fat in the 35–40% range, but stresses substitution of monounsaturated fat, for example olive oil, for saturated fat. Critics of the East Asian diet point out its tendency to lower HDL-cholesterol while raising triglyceride levels in the serum (Grundy, 1994)/ Furthermore, high carbohydrate diets may adversely affect control in diabetic patients (Garg *et al*, 1994). On the other hand, the Mediterranean diet has been faulted because its high fat content may promote obesity, because high fat diets may elevate serum insulin levels (Feskens *et al*, 1994), and because breast/colon cancer incidence consistently shows strong positive correlation with dietary fat in intercountry comparisons (Carroll, 1994). The retrojected preagricultural diet would have provided neither high carbohydrate nor high fat content. Intermediate between the Mediterranean and East Asian patterns, it might achieve the benefits of both while avoiding their drawbacks.

The Paleolithic diet was nutrient-rich; could it have provided dangerous amounts of vitamins and minerals? A recent review (Levine *et al*, 1995) advises against vitamin C intake in excess of 500 mg/d, about 100 mg less than the

Table 5 Paleolithic micronutrient intake and currently estimated minimum daily toxic doses

	Paleolithic intake[a]	*Minimum toxic dose*[b]
Vitamins, mg		
Riboflavin	6.49	1000
Folate	0.357	400
Thiamin	3.91	300
Ascorbate	604	1000–5000
Carotene	927	—
Vitamin A, IU	9570 IU	25,000–50,000 IU
Vitamin E	32.8	1200
Minerals, mg		
Iron	85.4	100
Zinc	43.4	500
Calcium	1960	12,000
Sodium	768	—
Potassium	10500	—

[a] From Table 2.
[b] Food and Nutrition Board, 1989, p 518.

estimate for Paleolithic humans, chiefly because of concern about producing oxalate stones. However, the relationship between ascorbate intake and formation of such stones is disputed (Diplock, 1995). Iron intake would have been high, but still below the minimum toxic dose (Table 5). Vitamin A consumption would have been well within traditionally accepted limits, but close to the 10 000 IU/d level above which teratogenic effects have recently been identified (Rothman *et al*, 1995). In each case the effects of high nutrient intake within a Paleolithic nutritional-developmental-experiential framework might differ from those of the same nutrient level within the typical affluent Western biobehavioral setting.

Two other features of reconstituted Paleolithic nutrition little in accord with contemporary nutritional theory are its content of fiber and protein, both much above current recommendations. Regarding these nutrients, it must be re-emphasized that Stone Agers subsisted almost exclusively on game and wild plant foods; there were no domesticated animals (for dairy foods) and significant use of cereal grains began only about 15 000 y ago—late in evolutionary terms. Given the nutritional properties of game (high in protein relative to energy) and uncultivated plants (high in fiber relative to energy), a preagricultural diet would necessarily have had high protein, high fiber, or both. If the average plant:animal subsistence ratio was 65:35, a 30% protein, 100 g fiber diet emerges. This near inescapable result seems strange to us today because we are used to diets containing large amounts of 'empty' calories, such as sugar, highly refined flour, and nonessential fat. It is actually diets of this sort which are novel, in evolutionary and comparative zoological terms.

Proponents of evolutionary (or Darwinian) medicine emphasize its heuristic potential and its capacity to suggest new avenues for conventional research. An example is the need for better nutritional analyses of wild game and vegetable foods; those presently available are non-standardized and frustratingly incomplete. For some, content of vitamin A and carotenoids is often comingled and there are no data (known to us) which would allow distinction of beta carotene from other carotenoids, even when total carotenoid content is provided. Similarly, information on omega-6/omega-3 partition is uncommon and data on PUFA other than LA and ALA is even less available. Any reconstruction of Paleolithic nutrition is utterly dependent on such data so a project to determine the nutritional makeup of foods available to foragers, especially in Africa, Europe and Asia (since the other continents were inhabited 'late'), would be extremely valuable. Even more urgent is the need to study the subsistence patterns of remaining and recently acculturated hunter-gatherers. Some acceptable data on this subject are already available, but populations able to directly verify and expand the data base are vanishing; this irreplaceable human resource needs to be utilized optimally while it still exists.

The numerous inconsistencies between current recommendations and retrodicted Paleolithic nutrition suggest obvious investigative possibilities. As advocated by Campbell (Campbell, 1994; Campbell & Chen, 1994), such research might best be conducted in a non-reductionist program, which also takes nutritional adaptation into account. For example, high fiber diets initiated by adults could be poorly tolerated, but when begun in childhood might be accommodated without difficulty, and perhaps demonstrate heretofore unappreciated plasticity in human gut development. A dietary protein level of 30% total energy may be harmful when the diet also includes excessive sodium and insufficient potassium, especially if operative nutritional and exercise patterns promote obesity. When the individuals involved are lean, normotensive and non-diabetic, abundant dietary protein may be beneficial. Similarly, an extremely high fiber intake may offset potentially adverse consequences of elevated dietary micronutrient levels, for example zinc and iron. The most meaningful research designed to reconcile current nutritional recommendations with the nutrition which shaped our metabolic needs during evolutionary experience will probably involve comprehensive integration of multiple dietary variables and exercise activities in studies which begin early in life and proceed through development into adulthood.

References

Abelow BJ, Holford TR & Insogna KL (1992): Cross-cultural association between dietary animal protein and hip fracture: a hypothesis. *Calcif. Tissue Int.* **50**, 14–18.

Adam O (1989). Linoleic and linolenic acid intake. In *Dietary w-3 and w-6 Fatty Acids. Biological Effects and Nutritional Essentiality* eds, C Galli & AP Simopoulos, pp. 33–42. New York: Plenum.

The Alpha-tocopherol, beta carotene prevention study group (1994): The effect of vitamin E and beta carotene on the incidence of lung cancer and other cancers in male smokers. *N. Engl. J. Med.* **330**, 1029–1035.

Ames BN, Gold LS & Willett WC (1995): The causes and prevention of cancer. *Proc. Natl. Acad. Sci.* **92**, 5258–5265.

Arthaud JB (1970): Cause of death in 339 Alaskan natives as determined by autopsy. *Arch. Path.* **90**, 433–438.

Block G, Patterson B & Subar A (1992): Fruit, vegetables, and cancer prevention: a review of the epidemiological evidence. *Nutr. Cancer* **18**, 1–29.

Boudreau MD, Charmugan PS, Hart SB, Lee SH & Hwang DJ (1991): Lack of dose response by dietary *n*-3 fatty acids at a constant ratio of *n*-3 to *n*-6 fatty acids in suppressing eicosanoid biosynthesis from arachidonic acid. *Am. J. Clin. Nutr.* **54**, 111–117.

Bose S (1964): Economy of the Onge of Little Andaman. *Man in India* **44**, 289–310.

Brand JC, Nicholson PL, Thorburn AW & Truswell AS (1985): Food processing and the glycemic index. *Am. J. Clin. Nutr.* **42**, 1192–1196.

Brand JC, Snow BJ, Nabhan GP & Truswell AS (1990): Plasma glucose and insulin responses to traditional Pima Indian meals. *Am. J. Clin. Nutr.* **51**, 416–420.

Brenner BM, Meyer TW & Hostetter TH (1982): Dietary protein intake and the progressive nature of kidney disease. *N. Eng. J. Med.* **307**, 652–659.

Brenner RR (1981): Nutritional and hormonal factors influencing desaturation of essential fatty acids. *Prog. Lipid Res.* **20**, 41–47.

Bridges PS (1996): Skeletal biology and behavior in ancient humans. *Evol. Anthropol.* **5**, 112–120.

Burkitt D (1983): *Don't Forget Fiber in Your Diet*, p 32. Singapore: Martin Dunitz.

Burkitt DP & Eaton SB (1989): Putting the wrong fuel in the tank. *Nutrition* **5**, 189–191.

Butrum RR, Clifford CK & Lanza E (1988): NCI dietary guidelines. *Am. J. Clin. Nutr.* **48**, 888–895.

Campbell TC & Chen J (1994): Diet and chronic degenerative diseases: perspectives from China. *Am. J. Clin. Nutr.* **59**, 1153S–1161S.

Campbell TC (1994): The dietary causes of degenerative diseases: nutrients vs. foods. In *Western Diseases. Their Dietary Prevention and Reversibility*, eds NJ Temple & DP Burkitt, pp 119–152. Totowa, NJ: Humana Press.

Carroll KK (1994): Lipids and cancer. In *Nutrition and Disease Update. Cancer*, eds KK Carroll & D Kritchevsky, pp 235–296. Champaign, III.: AOCS Press.

Carvallo JJM, Baruzzi RG, Howard PF, Poulter N, Alpers MP, Franco LJ, Marcopito LF, Spooner VJ, Dyer AR, Elliott P, Stamler J & Stamler R (1989): Blood pressure in four remote populations in the Intersalt Study. *Hypertension* **14**, 238–246.

Casimir MJ (1975): Feeding ecology and nutrition of an eastern gorilla group in the Mt. Kahuzi region (Republique du Zaire). *Folia. Primatol.* **24**, 84–136.

Chamberlain J, Nelson G & Milton K (1993): Fatty acid profiles of major food sources of howler monkeys (Alouatta palliata) in the neotropics. *Experientia* **49**, 820–824.

Coelho AM, Bramblett CA, Quick LB & Bramblett SS (1976): Resource availability and population density in primates: a socio-bioenergetic analysis of the energy budgets of Guatemalan howler and spider monkeys. *Primates* **17**, 63–80.

Cohen MN (1989): *Health and the Rise of Civilization*. New Haven: Yale Univ. Press.

Committee on Diet and Health, National Research Council (1989): *Diet and Health*. Washington, D.C.: National Academy Press, pp 15, 58, 59, 263–265.

Crawford MA, Cunnane S & Harbige L (1993): A new theory of evolution: quantum theory. In *Essential Fatty Acids and Eicosanoids*, eds A Sinclair & R Gibson, pp 87–95. Champaign, Illinois: AOCS.

Dalen JE & Dalton WS (1996): Does lowering cholesterol cause cancer? *JAMA* **275**, 67–69.

Daly LE, Kirke PN, Molloy A, Weir DG & Scott JM (1995): Folate levels and neural tube defects. Implications for prevention. *JAMA* **274**, 1698–1702.

Denton D, Weisinger R, Mundy NI, Wickens EJ, Dixson A, Moisson P, Pingand AM, Shade R, Carey D, Ardaillou R, Paillard F, Chapman J, Thillet J & Michel JB (1995): The effect of increased salt intake on blood pressure of chimpanzees. *Nature Med.* **1**, 1009–1016.

Diplock AT (1995): Safety of antioxidant vitamins and carotene. *Am. J. Clin. Nutr.* **62** (suppl), 1510S–1516S.

Duncan KH, Bacon JA & Weinsier RL (1983): The effects of high and low energy density diets on satiety, energy intake, and eating time of obese and non-obese subjects. *Am. J. Clin. Nutr.* **37**, 763–767.

Eaton SB, Konner M & Shostak M (1988): Stone agers in the fast lane: chronic degenerative diseases in evolutionary perspective. *Am. J. Med.* **84**, 739–749.

Eaton SB & Konner M (1985): Paleolithic nutrition. A consideration of its nature and current implications. *N. Engl. J. Med.* **312**, 283–289.

Eaton SB & Nelson DA (1991): Calcium in evolutionary perspective. *Am. J. Clin. Nutr.* **54**, 281S–287S.

Eaton SB (1990). Fibre intake in prehistoric times. In *Dietary Fibre Perspectives. Reviews and Bibliography 2*, ed. AR Leeds, pp 27–40. London: John Libbey.

Eaton SB (1992): Humans, lipids and evolution. *Lipids* **27**, 814–820.

Feskens EJM, Loeber JG & Kromhout D (1994): Diet and physical activity as determinants of hyperinsulinemia: the Zutphen elderly study. *Am. J. Epidemiol.* **140**, 350–360.

Flagg EW, Coates RJ, Jones DP, Byers TE, Greenberg RS, Gridley G, McLaughlin JK, Blot WJ, Haber M, Preston-Martin S, Schoenberg JB, Austen DF & Fraumeni JF (1994): Dietary glutathione intake and the risk of oral and pharyngeal cancer. *Amer. J. Epidemiol.* **139**, 453–465.

Food and Nutrition Board, National Research Council (1989): *Recommended Dietary Allowances*, 10th edn. Washington, D.C.: National Academy Press.

Garg A, Bantle JP, Henry RR, Coulston AM, Griver KA, Raatz SK, Brinkley L, Chen Y-DI, Grundy SM, Huet BA & Reaven GM (1994): Effects of varying carbohydrate content of diet in patients with non-insulin dependent diabetes mellitus. *JAMA* **271**, 1421–1428.

Gore JM & Dalen JE (1994): Cardiovascular disease. *JAMA* **271**, 1600–1601.

Greenwald P, Kelloff G, Burch-Whitman C & Kramer BS (1995): Chemoprevention. *Ca. Cancer J. Clin.* **45**, 31–49.

Grundy SM (1994): Lipids and cardiovascular disease. In *Nutrition and Disease Update. Heart Disease*, eds D Kritchevsky & KK Carroll, pp 211–279. Champaign III.: AOCS Press.

Heaton KW, Marcus SN, Emmett PM & Bolton CH (1988): Particle size of wheat, maize, and oat test meals: effects on plasma glucose and insulin responses and on the rate of starch digestion in vitro. *Am. J. Clin. Nutr.* **47**, 675–682.

Heini AF, Minghelli G, Diaz E, Prentice AM & Schutz Y (1995): Free-living energy expenditure assessed by two different methods in lean rural Gambian farmers. *Am. J. Clin. Nutr.* **61**, 893 (abstract).

Hertog MGL, Feskens EJM, Hollman PCH, Katan MD & Kromhout D (1993): Dietary antioxidant flavonoids and risk of coronary heart disease: the Zutphen elderly study. *Lancet* **342**, 1007–1011.

Hladik CM (1977): Chimpanzees of Gabon and chimpanzees of Gombe: some comparative data on the diet. In *Primate Ecology: Studies of Feeding and Ranging Behavior in Lemurs, Monkeys and Apes*, ed. TH Clutton-Brock, pp 481–501. London: Academic Press.

Hunt JR, Gallagher SK, Johnson LK & Lykken GI (1995): High- versus low-meat diets: effects on zinc absorption, iron status, and calcium, copper, iron, magnesium, manganese, nitrogen, phosphorus, and zinc balance in post menopausal women. *Am. J. Clin. Nutr.* **62**, 621–632.

Hunter JE (1990): *n*-3 fatty acids in vegetable oils. *Am. J. Clin. Nutr.* **51**, 809–814.

Intersalt Cooperative Research Group (1988): Intersalt: an international study of electrolyte excretion and blood pressure. *Brit. Med. J.* **297**, 319–328.

Jacobs D, Blackburn H, Higgins M, Reed D, Iso H, McMillan G, Neaton J, Nelson J, Potter J, Rifkind B, Rossouw J, Shekelle R & Yusuf S (1992): Report of the conference on low blood cholesterol: mortality associations. *Circulation* **86**, 1046–1060.

James WPT, Ferro-Luzzi A, Isaksson B & Szostak WB (1988): *Healthy Nutrition. Preventing Nutrition-Related Diseases in Europe*. Denmark: WHO.

James WPT, Ralph A & Sanchez-Castillo CP (1987): The dominance of salt in manufactured food in the sodium intake of affluent societies. *Lancet* **I** 426–429.

Judd JT, Clevidence BA, Muesing RA, Wittes J, Sunkin ME & Podczasy JJ (1994): Dietary trans fatty acids: effects on plasma lipids and lipoproteins of healthy men and women. *Am. J. Clin. Nutr.* **59**, 861–886.

Kritchevsky D (1994): Dietary fiber and cardiovascular disease. In *Nutrition and Disease Update. Heart Disease*, eds D Kritchevsky & KK Carroll, pp 189–210. Champaign, III.: AOCS Press.

Kritchevsky FB & Kritchevsky D (1992): Serum cholesterol and cancer risks: An epidemiologic perspective. *Ann. Rev. Nutr.* **12**, 391–416.

Kronmann N & Green A (1980): Epidemiological studies in the Upernavik district, Greenland. Incidence of some chronic diseases 1950–74. *Acta. Med. Scand.* **208**, 401–406.

Lee RB (1968): What hunters do for a living, or, how to make out on scarce resources. In *Man the Hunter*, eds RB Lee & I DeVore, pp 30–48. Chicago: Aldine.

Levine M, Dhariwal KD, Welch RW, Wang Y & Park JB (1995): Determination of optimal vitamin C requirements in humans. *Am. J. Clin. Nutr.* **62** (suppl), 1347S–1356S.

Mann GV, Scott EM, Hursh LM, Heller CA, Youmans JB, Consolazio CF, Bridgforth EB, Russell AL & Silverman M (1962): The health and nutritional status of Alaskan Eskimos. *Am. J. Clin. Nutr.* **11**, 31–76.

Meehan B (1982): *Shell Bed to Shell Midden*, pp 152–155. Canberra: Aust. Inst. Aboriginal Studies.

Middleton E & Kandaswami C (1992): Effects of flavonoids on immune and inflammatory cell functions. *Biochem. Pharmacol.* **43**, 1167–1179.

Milton K (1993): Diet and primate evolution. *Sci. Amer.* **269** (Aug), 86–93.

Ministry of Agriculture, Fisheries and Foods (1995): *Household Food Consumption and Expenditure, 1990. With a Study of Trends Over the Period 1940–1990*. London: HMSO.

Moore TJ (1989): The cholesterol myth. *Atlantic Monthly* **264** (Sept), 37–70.

Naughton JM, O'Dea K & Sinclair AJ (1986): Animal foods in traditional Australian Aboriginal diets: polyunsaturated and low in fat. *Lipids* **21**, 684–690.

O'Dea K & Sinclair A (1983): The modern western diet—the exception in man's evolution. In *Agriculture and Human Evolution*, eds KA Boundy & GH Smith, pp 56–61. Melbourne: Australian Institute Agricultural Science.

O'Dea K, Traianedes K, Chisholm K, Leyden H & Sinclair AJ (1990): Cholesterol-lowering effect of a low-fat diet containing lean beef is reversed by the addition of beef fat. *Am. J. Clin. Nutr.* **52**, 491–494.

Ornish D, Brown SE, Scherwitz LW, Billings JH, Armstrong WT, Ports TA, McLanahan SM, (1990): Can lifestyle changes reverse coronary heart disease? The lifestyle heart trial. *Lancet* **336**, 129–133.

Panel on nonhuman primate nutrition (1978): *Nutrient Requirements of Nonhuman Primates*, pp 36–41. Washington, D.C.: National Acad Sci.
Rauma AL, Torronen R, Hanninen O, Verhagen H & Mykkanen H (1995): Antioxidant status in long term adherents to a strict uncooked vegan diet. *Am. J. Clin. Nutr.* **62**, 1221–1227.
Rimm EB, Ascherio A, Giovannucci E, Spiegelman D, Stampfer MJ & Willett WC (1996): Vegetable, fruit, and cereal fiber intake and risk of coronary heart disease among men. *JAMA* **275**, 447–451.
Rothman KJ, Moore LL, Singer MR, Nguyen U-SDT, Manning S & Milunsky A (1995): Teratogenicity of high vitamin A intake. *N. Engl. J. Med.* **333**, 1369–1373.
Roberts MB, Stringer CB & Parfitt SA (1994): A hominid tibia from middle pleistocene sediments at Boxgrove, UK. *Nature* **369**, 311–313.
Ruff CB, Trinkhaus E, Walker A & Larsen CS (1993): Postcranial robusticity in Homo. 1: Temporal trends and mechanical interpretation. *Am. J. Physical Anthropol.* **91**, 21–53.
Schonfeld G, Patsch W, Rudel LL, Nelson C, Epstein M & Olson RD (1982): Effects of dietary cholesterol and fatty acids on plasma lipoproteins. *J. Clin. Invest.* **69**, 1072–1080.
Schroeder HA (1971): Losses of vitamins and trace minerals resulting from processing and preservation of foods. *Am. J. Clin. Nutr.* **24**, 562–573.
Sears B (1993): Essential fatty acids and dietary endocrinology: a hypothesis for cardiovascular treatment. *J. Adv. Med.* **6**, 211–224.
Shimamoto T, Komachi Y, Inada H, Doi M, Iso H, Sato S, Kitamura A, Iida M, Konishi M, Nakanishi N, Terao A, Naito Y & Kojima S (1989): Trends for coronary heart disease and stroke and their risk factors in Japan. *Circulation* **79**, 503–515.
Sies H & Krinski NI (1995): The present status of antioxidant vitamins and carotene. *Am. J. Clin. Nutr.* **62**, 1299S–1300S.
Simopoulos AP (1991): Omega-3 fatty acids in health and disease and in growth and development. *Am. J. Clin. Nutr.* **54**, 438–463.
Simopoulos AP, Norman HA, Gillaspy JE & Duke JA (1992): Common purslane: A source of omega-3 fatty acids and antioxidants. *J. Am. Coll. Nutr.* **11**, 374–382.
Sinclair A & O'Dea K (1993): The significance of arachidonic acid in hunter-gatherer diets: implications for the contemporary Western diet. *J. Food Lipids* **1**, 143–157.
Sinclair AJ, O'Dea K, Dunstan G, Ireland PD & Niall M (1987): Effects on plasma lipids and fatty acid composition of very low fat diet enriched with fish or kangaroo meat. *Lipids* **22**, 523–529.
Steinmetz KA & Potter JD (1991): Vegetables, fruit and cancer. I. Epidemiology. *Cancer Causes Control* **2**, 325–357.
Swales JD (1988): Salt saga continued. Salt has only small importance in hypertension. *Brit. Med. J.* **297**, 307–308.
Thorburn AW, Brand JC & Truswell AS (1987): Slowly digested and absorbed carbohydrate in traditional bushfoods: a protective factor against diabetes. *Am. J. Clin. Nutr.* **45**, 98–106.
Tooby J & Cosimides L (1990): The past explains the present. Emotional adaptations and the structure of ancestral environments. *Ethology and Sociobiology* **11**, 375–424.
Walker W (1993): Perspectives on the Nariokotome discovery. In *The Nariokotome Homo Erectus Skeleton*, eds A Walker & R Leakey, pp 411–430. Cambridge, Mass.: Harvard Univ Press.
Watanabe T, Kondo K & Oshi M (1991): Induction of in vivo differentiation of mouse erythroleukemia cells by genistein, an inhibitor of tyrosine protein kinases. *Cancer Res.* **51**, 764–768.
Westphal SA, Gannon MC & Nuttall FQ (1990): Metabolic response to glucose ingested with various amounts of protein. *Am. J. Clin. Nutr.* **52**, 267–272.
Whiten A, Byrne RW, Barton RA, Waterman PG & Henzi SP (1991): Dietary and foraging strategies of baboons. *Phil. Trans. Roy. Soc. (Lond.) Series B* **334**, 187–197.
Willett WC (1994): Diet and health: what should we eat? *Science* **264**, 532–537.
Wolfe BM (1995): Potential role of raising dietary protein intake for reducing risk of atherosclerosis. *Can. J. Cardiol.* **11** (Suppl G), 127G–131G.
Young VR (1986): Protein and amino acid metabolism in relation to physical exercise. In *Nutrition and Exercise*, ed. M Winick, pp 9–29. New York: John Wiley.
Zhang Y, Talalay P, Cho CG & Posner GH (1992): A major inducer of anticarcinogenic protective enzymes from broccoli: isolation and elucidation of structure. *Proc. Natl. Acad. Sci.* **89**, 2399–2403.

Appendix

Method

We have collected from the literature nutrient analyses of wild plant and animal foods which have been utilized by recent gatherer-hunters and which were presumably consumed by preagricultural humans as well. Essentially none of these foods (236 plants, 85 animals) have had all their relevant nutrients analyzed: for some only one or two data points are available. In certain cases different investigators have evaluated the same species with results which vary to a greater or lesser degree; for these we have simply averaged the available figures (Table 6).

For wild game, nutrient analyses from all species have been pooled and averaged. For plant foods we used a weighted average based on forager plant utilization in eastern and southern Africa (Peters & O'Brien, 1981). This method does focus on the likely ancestral human homeland, but fails to include items such as gums and fungi which are commonly consumed by foragers living elsewhere. For both game and plant foods we have disregarded egregious outlier values—for example Australian green plum (3150 mg vitamin C/100 g), mongongo nut (96 α-tocopherol equivalents/100 gm).

Table 6 Representative uncultivated vegetal foods and wild game

	g/100 g			*mg/100 g*			*Energy*	
	Fiber	*Protein*	*Fat*	*Sodium*	*Calcium*	*Vitamin C*	*kJ*	*kcal*
Plants								
Brachychiton gregorii (desert kurrajung)	7.6	0.5	1.0	2	175	—	177	42
Capporis lasiantha (native orange)	10.2	10.1	4.9	3	58	6	343	82
Carissa lanceolata (conkerberry)	9.3	2.5	2.35	5	65	4	597	143
Dioscorea bulbifera (cheeky yam)	14.8	1.6	0.2	—	7	233	127	30
Sclerocarya caffra (marula fruit)	0.5	0.5	0.1	1	6	68	—	—
Bauhinia esculenta (tsi bean)	3.8	1.5	0.3	15	24	4	193	46
Allium porrum (leek flower)	1.1	5.5	0.5	—	23	40	230	55
Brassica juncea (Indian mustard stem)	0.6	1.3	0.1	—	22	16	67	16
Portulaca goadrifida (purslane leaves)	0.2	1.6	0.8	—	150	—	159	38
Chenopodium album (lambsquarters)	1.5	3.3	0.6	1	246	70	142	34
Animals								
Agrotis infusa (bugong moth)	1.5	26.8	19.8	22	219	—	1260	301
Varanus sp. (sand goanna)	1.8	29.2	5.7	9	119	—	736	176
Castor canadensis (beaver)	—	24.1	4.8	51	15	—	611	146
Rangifer tarandus (caribou)	—	22.6	3.36	57	17	—	531	127
Antilocapra americana (pronghorn antelope)	—	22.4	2.03	51	3	—	477	114

Given mean energy values for game and wild plant foods, a simple model allows calculation of average daily intake in grams:

$$A(C^{a}X) + B(C^{p}X) = \text{Daily Energy Intake}$$

A and B are mean energy content [kJ/g (kcal/g)] of animal and vegetable foods, respectively, C^a and C^p are the proportions of animal and plant foods, respectively 0.35 and 0.65, and X is the total number of grams required to provide any given amount of food energy. For this paper we have used 0.35 and 0.65 as proportions of animal and vegetable foods, respectively, because they are believed by anthropologists to be most typical (Lee, 1968); however, the model can accommodate other estimates (See Eaton & Konner, 1985).

When both the gross amounts (913 g meat and 1697 g vegetable food in this case) and the mean nutrient concentrations have been estimated, the amounts of individual nutrients, as amount/d or as amount/4186 kJ (amount/1000 kcal), can be calculated readily by multiplying the amount of meat or vegetable food per day times the nutrient concentration, for example (9.1×100 g meat/d) $\times$ (4.15 mg iron/100 g meat) = 37.8 mg iron/d from meat.

References for Appendix

Anderson BA, Clements ML, Dickey LE, Exler J & Hoke IM (1989): *Composition of Foods: Lamb, Veal, and Game Products. (Agriculture Handbook no. 8–17)*. Washington, D.C.: United States Department of Agriculture.

Boyce VL & Swinburn BA (1993): The traditional Pima Indian diet. Composition and adaptation for use in a dietary intervention study. *Diabetes Care* **16**, 369–371.

Brand JC, Cherikoff V, & Truswell AS (1985): The nutritional composition of Australian Aboriginal bush foods. 3. Seeds and Nuts. *Food Tech. Austral.* **37**, 275–279.

Brand JC & Cherikoff V (1985): The nutritional composition of Australian Aboriginal food plants of the desert regions. In *Plants for Arid Lands*, eds GE Wickens, JR Goodin, DV Field & G Allen, pp 88–104. London: Royal Botanic Gardens.

Brand JC, Rae C, McDonnell J, Lee A, Cherikoff V & Truswell AS (1983): The nutritional composition of Australian Aboriginal bush foods. 1. *Food Tech. Austral.* **35**, 294–298.

Cherikoff V, Brand JC & Truswell AS (1985): The nutritional composition of Australian Aboriginal bush foods. 2. Animal foods. *Food Tech. Austral.* **37**, 208–211.

Fysch CF, Hodges KJ & Siggins LY (1960): Analysis of naturally occurring foodstuffs of Arnhem Land. In *Records of the American-Australian Scientific Expedition in Arnhem Land vol. 2*, ed. CP Mountford, pp 136–139. Melbourne: Melbourne University Press.

Hoppner K, McLaughlan JM, Shah BG, Thompson JN, Beare-Rogers J, Ellestad-Sayad J & Schaefer O (1978): Nutrient levels of some foods of Eskimos from Arctic Bay, N.W.T., Canada. *J. Am. Diet Assn.* **73**, 257–261.

Kuhnlein HV (1989): Nutrient values in indigenous wild berries used by the Nuxalk people of Bella Coola, British Columbia. *J. Food Comp. Analysis* **2**, 28–36.

Kuhnlein HV (1990): Nutrient values in indigenous wild plant greens and roots used by the Nuxalk people of Bella Coola, British Columbia. *J. Food Comp. Analysis* **3**, 38–46.

Lee RB (1968): What hunters do for a living, or, how to make out on scarce resources. In *Man the Hunter*, eds. RB Lee & I DeVore, pp 30–48. Chicago: Aldine.

Mann GV, Scott EM, Hursh LM, Heller CA, Youmans JB, Consolazio CF, Bridgforth EB, Russell AL & Silverman M (1962): The health and nutritional status of Alaskan Eskimos. *Am. J. Clin. Nutr.* **11**, 31–76.

Medical Services Branch (1985): *Native Foods and Nutrition*, pp 86–94. Canada: Ministry of National Health and Welfare.

Morris EA, Witkind WM, Dix RL & Jacobson J (1981): Nutritional content of selected aboriginal foods in northeastern Colorado: buffalo (Bison bison) and wild onions (Allium spp.). *J. Ethnobiol.* **1**, 213–220.

Murphy SP, Subar AF & Block G (1990): Vitamin E intakes and sources in the United States. *Am. J. Clin. Nutr.* **52**, 361–367.

Peters CR & O'Brien EM (1981): The early hominid plant-food niche: insights from an analysis of plant exploitation by Homo, Pan, and Papio in Eastern and Southern Africa. *Current Anthropol.* **22**, 127–140.

Polacchi W, JC McHargue & BP Perloff, eds. (1982): *Food Composition Tables for the Near East*. Rome: F.A.O.

Shostak M. Unpublished data on Vitamin E content in 24 !Kung San vegetal foods.

Tanaka J (1976): Subsistence ecology of the central Kalahari San. In *Kalahari Hunter-Gatherers*, eds. RB Lee & I DeVore, pp 100–116. Cambridge, Mass.: Harvard University Press.

Tanaka J (1980): *The San, Hunter-Gatherers of the Kalahari: a Study in Ecological Anthropology*, pp 71, 73. New York: Columbia University Press.

Wehmeyer AS, Lee RB & Whiting M (1969): The nutrient composition and dietary importance of some vegetable foods eaten by the !Kung Bushmen. *S. Afric. Med. J.* **43**, 1529–1530.

Weymeyer AS (1966): The nutrient composition of some edible wild fruits found in the Transvaal. *S. Afric. Med. J.* **40**, 1102–1104.

Woodburn J. Unpublished data on 21 Hadza vegetal food items.

Wu Leung W-T, Busson F, Jardin C (1968): *Food Composition Table for Use in Africa*. Rome: F.A.O.

Wu Leung W-T, Butrum RR & Chang FH (1972): *Food Composition Table for Use in East Asia*. Rome: F.A.O.