Paleolithic Nutrition : Twenty-Five Years Later

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Invited Review

Paleolithic Nutrition

Twenty-Five Years Later

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A quarter century has passed since the first publication of the evolutionary discordance hypothesis, according to which departures from the nutrition and activity patterns of our hunter-gatherer ancestors have contributed greatly and in specifically definable ways to the endemic chronic diseases of modern civilization. Refinements of the model have changed it in some respects, but anthropological evidence continues to indicate that ancestral human diets prevalent during our evolution were characterized by much lower levels of refined carbohydrates and sodium, much higher levels of fiber and protein, and comparable levels of fat (primarily unsaturated fat) and cholesterol. Physical activity levels were also much higher than current levels, resulting in higher energy throughput. We said at the outset that such evidence could only suggest testable hypotheses and that recommendations must ultimately rest on more conventional epidemiological, clinical, and laboratory studies. Such studies have multiplied and have supported many aspects of our model, to the extent that in some respects, official recommendations today have targets closer to those prevalent among hunter-gatherers than did comparable recommendations 25 years ago. Furthermore, doubts have been raised about the necessity for very low levels of protein, fat, and cholesterol intake common in official recommendations. Most impressively, randomized controlled trials have begun to confirm the value of hunter-gatherer diets in some high-risk groups, even as compared with routinely recommended diets. Much more research needs to be done, but the past quarter century has proven the interest and heuristic value, if not yet the ultimate validity, of the model. (*Nutr Clin Pract*. 2010;25:594-602)

Keywords: Paleolithic diet; hunter-gatherers; ancestral diet

Just over 25 years ago, an unusual article, "Paleolithic Nutrition: A Consideration of Its Nature and Current Implications," was published in a respected journal.[1] In it, we described a new paradigm for prevention based on very old human experience: nutrition during the course of human evolution. Drawing on modern studies of hunter-gatherers (HGs) and also on archeological and paleontological evidence, we argued for the discordance hypothesis, which in its simplest form states that our genome evolved to adapt to conditions that no longer exist (the environment of evolutionary adaptedness, or EEA), that the change has occurred too rapidly for adequate genetic adaptation, and that the resulting mismatch helps to cause some common chronic diseases.

Among these "diseases of civilization" are atherosclerotic cardiovascular disease (most coronary artery disease and cerebrovascular accidents), type 2 diabetes mellitus (T2DM), chronic obstructive pulmonary disease, lung and colon cancers, essential hypertension, obesity, diverticulosis, and dental caries. In another study, we to showed that serum cholesterol concentrations, aerobic fitness, and diabetes mellitus prevalence in nonindustrial, especially HG populations, revealed low risk of the diseases that most plague advanced societies.[2] Indeed, by the time of our first publication, it had been shown that former HGs in Australia who were suffering from T2DM showed marked improvement in their carbohydrate and lipid metabolism when they were experimentally returned to their former lifestyle.[3] Also by that time, archeologists working around the world had shown a decrease in body size and robusticity and an increase in markers of nutrition stress during the transition between hunting and gathering and agriculture,[4] suggesting that some aspects of the discordance began as long as 10,000 years ago.

The general criticism that the mismatch has been resolved by evolutionary adaptation since the HG era has not proved convincing. It is true that since modern humans left Africa between 100,000 and 50,000 years ago, genetic evolution during subsequent millennia has continued—for example, pigmentation changes (hair, eyes, skin), intestinal lactase retention beyond infancy, and adaptive defenses against microorganisms (such as hemoglobinopathies and immune system modifications). New analytic methods are revealing subtler genetic adaptations to

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dietary and other ecological niches, including different allele frequencies associated with dependence on cereal grains as opposed to roots and tubers.[5,6] However, the importance of these differences is not clear, but we know that core biochemical and physiological processes have been preserved.[7] Furthermore, it is now widely agreed that hundreds of thousands of preventable deaths in the United States alone are attributable to dietary and other lifestyle risk factors similar to those in which advanced countries differ from HGs.[8] No one proposes that genetic adaptations could have caught up with dietary and lifestyle changes over the past 2 centuries.

On the basis of published data on the nutrient content of both meat and plant foods consumed by HGs around the world, together with anthropological data on the composition of HG diets, we put forward a model consisting of estimates of macro- and some micronutrients consumed by HGs and argued that this model was a reasonable approximation of the nutrient composition of the typical diet of our ancestors during the early history and evolution of our species. We then compared these estimates to published data on the average American diet in the mid-1980s as well as to then-current recommendations from relevant government institutions and other health authorities. It was also apparent that calorie output and throughput were much higher in hunter-gatherers than in the United States and similar societies and that levels of both aerobic and muscular fitness in HGs were maintained through most of life by their patterns of activity. Although beyond the scope of this article, our estimates of HG activity levels strongly suggested a need for large increases in all forms of exercise in modern populations.

Our papers and book[9] were greeted with a certain amount of media attention, including ridicule, some of it based on the short life span of hunter-gatherers. This point had of course not been lost on us; as we had shown in extensive reviews of the primary literature,[1,2] 30 to 35 years was roughly the average life expectancy at birth of preindustrial populations generally, due mainly not to the absence of older people but to extremely high infant and child mortality. Death in HGs was overwhelmingly due to infectious diseases we now control, and older HGs rarely got or died of coronary artery disease, diabetes mellitus, or chronic obstructive pulmonary disease, among other ailments common in societies like ours. We had not proposed that they were healthier in absolute terms, just that absent infection and osteoarthritis, they rarely had the chronic diseases we commonly have. Our review of various health measures in HG and other nonindustrial populations showed that average HG serum total cholesterol was always below 135 mg/dL, aerobic fitness of average men was in the athletic range for Western populations, and diabetes mellitus prevalence was very low.[2]

In the mid-1980s, the standard recommendations, based on clinical and experimental research, were urging Americans in most cases to change their diet in a direction consistent with the HG model. However, there were important differences. Intakes of saturated fat, salt, and refined carbohydrate levels were markedly lower in HGs than in the standard recommendations, whereas protein and fiber content were far higher. Cholesterol intake was also higher; both cholesterol and carbohydrate intake were roughly the same in HGs as in the average American diet, although the spectrum of carbohydrates was very different. We did not then and do not now propose that Americans adopt a particular diet and lifestyle on the basis of anthropological evidence alone; formal recommendations must rest on carefully executed laboratory, clinical, and epidemiological studies. Rather, we suggested that the standard recommendations of the time needed more research in light of the HG model. Here, we assess how that model has fared in relation to further analysis of HG diets, both in the archeological/paleontological record and in studies of recent living HG groups, as well as in comparison with the standard recommendations (then and now) in light of a quarter century of further research.

Hunter-Gatherer Diets: How Well Did We Characterize Them?

Some analyses in the past decade have suggested that we underestimated the proportion of meat in HG diets.[10-12] This is of substantial potential importance in estimating the intake of total fat, protein, carbohydrate, and fiber in those diets. However, this position has not gone unchallenged.[13] It is clear that ancestral human diets derive from higher primate diets that were overwhelmingly plant based,[14] supplemented by insects and (in some species) a small amount of animal flesh. Fossil evidence shows that this pattern continued to be true of early bipedal hominids (between 6 and 2 million years ago [mya]),[15] with a likely particular emphasis on underground storage organs (USOs; tubers)[16] and on large protected nuts and seeds.[17] Reliance on animal flesh increased substantially after 2 mya with the evolution of *Homo habilis* and especially *Homo erectus*, a species clearly capable of hunting large game, an ability shared by modern humans. However, much evidence points to continued significant (if not predominant) dependence on plant foods.

Consider the human gut. It is substantially smaller than the value predicted from the primate regression of gut on body weight (indeed, it is almost gram for gram reduced in proportion to excess human brain weight).[18] This is due in part to concentration of calories, both in plant foods (fruit and nuts as opposed to leaves and grass) and, later, meat, but it is clear that cooking played a key role beginning at least 0.23 mya and perhaps much earlier, reducing the need for human digestion of both plant foods and animal flesh.[19,20] However, the human gut retains

many structural and metabolic features of the herbivore/frugivore higher primate gut, departing in important ways from the typical gut of top carnivores.[13,21]

Furthermore, the archeological/paleontological record makes it clear that ancestral populations relevant to the origin of our species (anatomically modern *Homo sapiens*) relied on a variety of food sources in significantly varying environments; indeed, flexibility in adaptation may have been central to human evolution,[22] and we now speak of EEAs rather than a single EEA. This range undoubtedly included substantial reliance on plant foods in many times and places.[13,23,24] To support a very long human childhood, a unique human pattern of postweaning provisioning evolved,[25] including contributions of animal flesh from fathers[26] and of plant foods from mothers and grandmothers.[27,28] Fathers also contributed meat to their pregnant and nursing wives.[29] Children themselves foraged in many HG groups, collecting substantial amounts of plant foods, shellfish, and some small game such as lizards and birds,[30-33] although mastery of hunting was delayed well into adulthood.[34]

Finally, it has become clear since our initial publications that marine, lacustrine, and riverine species were important sources of animal flesh during the evolution of modern *Homo sapiens*[35] and may have played a role in the evolution of brain ontogeny.[36] In any case, shellfish and other aquatic animal species must be considered part of the spectrum of ancestral nutrition adaptations. Thus, there have been changes in the way we estimate the likely diets of ancestral HG populations, admitting more variability. However, the best current estimates restrict most of that variability to a range from 35% to 65% animal flesh, including substantial marine animal resources for at least 0.2 million years. As we will see, these new estimates do not affect the direction of the great majority of our recommendations.

The Discordance Model of Chronic Disease Prevention: How Well Has It Fared?

We now consider macro- and selected micronutrients, touching on our original estimates of levels in HG diets; changes and controversies about those estimates in the intervening years; current American intake levels; changes in standard guidelines for nutrition and health parameters in the United States; and accumulating evidence about the value for disease prevention of a return to or toward HG levels.

Fat and Saturated Fat

It was widely accepted by the late 1980s that saturated fat (SF) intake in the typical modern diet is far too high and that the C-14 and C-16 fatty acids are a major contributor to endemic atherosclerosis underlying most coronary artery disease and stroke, the first and third leading causes of death. Through energy load, total fat (TF) intake is an important contributor to endemic obesity and the growing epidemic of T2DM. Standard recommendations suggested that TF be reduced to no more than 30% of calories and that the ratio of SF to unsaturated fat be reduced markedly. At the time, we estimated that in the HG diet, TF contributed about 20% of calories, including about 6% SF, a level of restriction deemed by most authorities to be too difficult to achieve. On the basis of new analyses of HG diets, we have raised the estimated range of their likely TF intake to 20%-35%. Both low-fat (20%) and high-fat (40%) diets have been shown to aid in weight loss given appropriate caloric restriction and adherence,[37] but it has also been shown that very low TF may not only prevent or retard atherosclerosis but, combined with other lifestyle changes, partly reverse established atherosclerotic plaques.[38,39]

However, TF is only part of the story. Game animals have more mono- and polyunsaturated fatty acids (MUFA and PUFA) than supermarket meat.[10] It used to be recommended that SF intake be less than 10% of total energy, but according to the Institute of Medicine (IOM), any increase raises cardiac risk.[40] (However, recent evidence suggests that the C-14 and C-16 saturated fatty acids, and not C-18 stearic acid, are the chief serum cholesterol-raising components of animal fat.[41]) HG trans-fatty-acid intake was a small fraction of our 2% of total calories. Especially given their high estimated intake of marine animal flesh,[35,36] PUFA intake would have been nearly twice the present level of 15 g/d, due almost entirely to a greater proportion of cardioprotective ω-3 forms. The resulting ω-6:ω-3 ratio of about 2:1 contrasts with the current ratio of about 10:1, with 8:1 recommended.[40] We predict that future recommendations for this ratio will decline further.

Dietary Cholesterol

We reported that HG cholesterol intake was similar to or higher than that of modern Americans. Since muscle cell membranes have as much cholesterol as fat cell membranes, low-fat game meat and fish still had high cholesterol content. HG diets suggested that discordance did not apply to dietary cholesterol levels and that concern about them would lead to unnecessary restriction of low-fat meat and fish. It has since become clear that dietary cholesterol is not a major independent driver of serum cholesterol or its fractionation. The major dietary determinants are the cholesterol-raising fatty acids, with an additional contribution from dietary refined carbohydrates, suggesting that for most people, restriction of these 2 components of diet is sufficient to keep serum cholesterol and the low-density lipoprotein (LDL)/high-density lipoprotein (HDL) ratio very low.[42-45] HG cholesterol intake is estimated

at 480 mg/d, nearly 200 mg/d higher than recommendations. This level would be expected to elevate serum cholesterol about 0.2 mmol/L (8 mg/dL), but the impact is far outweighed by their lower intake of cholesterol-raising fatty acids. In addition, high-protein intake can be expected to have further mitigated the atherogenic effects of fat.

Protein

In the 1980s, most dietary advice called for a reduction in protein intake, especially in the form of meat. This was not consistent with the HG model, and we reasoned that the ill effects of meat were mainly due to its almost inevitable association in our culture with high cholesterol-raising fat intake. Another concern raised by some authorities was that nitrogen load might become excessive with high meat consumption. Subsequent analyses have substantially increased the estimate of HG protein intake,[10-12] but there is no evidence as yet that lean meat (similar to wild game) intake corresponding to the levels in the average HG diet has adverse health consequences. It has, in fact, been shown that although diets rich in lean beef raise arachidonic acid concentrations (a negative), their long-chain ω-3 PUFA content, plus the intrinsic hypocholesterolemic effect of protein, results in a serum lipid profile thought to be protective against atherosclerosis.[46] To the extent that HG diets included aquatic species,[35] this effect would have been further enhanced.

Carbohydrates

Americans obtain about half their daily energy from carbohydrate (CHO), including 15% from added sugars. HG CHO consumption ranged widely, from about 35%-65%,[10,13,47] with perhaps 2%-3% from honey. Cereal grains (85% refined) are our largest single CHO source, with dairy products another significant contributor. HGs had little of either, so nearly all CHO came from fruits and vegetables (adding up to less than a fourth of current CHO), which generally yield more desirable glycemic responses. The IOM recommends a CHO range from 45%-65% of total energy, with no more than 25% from added sugars.[40] This recommendation would approximate HG total CHO intake, but qualitative equivalence would require that nearly all CHO come from fruits and vegetables, with a minimum from cereal grains, none refined. It is of particular interest that a randomized controlled trial of the Mediterranean diet compared with a simulated HG diet found the latter to be more effective in improving insulin resistance and cardiovascular risk factors in T2DM (see below for further discussion).[48,49]

Fiber

Uncultivated vegetables and fruits are markedly more fibrous (13.3 g fiber/100 g) than commercial ones (4.2 g/100 g).[50] Our 1985 estimate was limited to crude fiber, but soon thereafter data on total fiber content became available and suggested that total fiber intake (TFI) would have averaged 150 g/d. With lower estimates of total HG CHO intake, the estimate could be as low as 70 g/d but not lower. The IOM suggested 25 g/d for women and 38 g/d for men, a bit more than twice the current median intake, but found insufficient evidence to set a tolerable maximum.[40] High fiber intake may adversely affect mineral bioavailability, especially in the presence of phytic acid, a prominent constituent of many cereal grains but minimal in uncultivated fruits and vegetables.[50] Fruit and vegetable fiber is also more completely fermented than cereal fiber, enhancing its advantages. Finally, the HG ratio of insoluble to soluble fiber was much higher than at present, approximately 1:1.

Sodium and the sodium/potassium ratio

Both sodium (Na^+) intake (768 mg/d) and the sodium/potassium (Na^+/K^+) ratio were found to be extremely low in HG diets. Although it is widely agreed that secondary prevention of hypertension (HTN) should include lowering a very high salt intake, debate has continued over the importance of these measures in primary prevention. The INTERSALT study demonstrated a relationship between dietary Na^+ and blood pressure (BP). With a 100 mmol/d lower urinary Na^+, population systolic pressure would rise 9 mm Hg less from age 25 to 55 years, corresponding at age 55 to a risk reduction of 16% for coronary death and 23% for stroke death.[51,52] Subsequent analysis showed that the same difference in Na^+ excretion would correspond to a systolic/diastolic BP difference of 10-11/6 mm Hg.[53,54] Critics noted that 4 of the 52 centers in the study accounted for most of the observed relationship.[55]

However, only in these 4 (Kenya, Papua New Guinea, and 2 Native American groups in Brazil) was Na^+ intake near the range we found for HG populations, which show little or no rise in BP with age. The Yanomamo, for example, had a very low urinary sodium excretion (0.9 mmol/24 h), mean systolic/diastolic BP of 95.4/61.4 mm Hg, and no cases of HTN. Their BP did not rise with age, and within the population, urinary Na^+ was positively and urinary K^+ negatively related to systolic BP, after controlling for age and body mass index (BMI).[56] Epidemiological research rarely includes a group with low enough Na^+ intake and Na^+/K^+ ratio to be in the HG range; this limitation might help to explain why clinical studies did not initially show a strong relationship between these electrolytes and HTN.

However, recent work helps resolve the uncertainty in favor of the discordance model, even without including very low salt intake populations. A meta-analysis of prospective observational studies conducted from 1966 to 2008 (19 independent samples from 13 studies including 177,000 participants) concluded that reducing salt intake

from the estimated adult average of 10 g/d to the World Health Organization (WHO) recommendation of 5 g/d would be associated with a 23% difference in the rate of stroke and a 17% difference in the overall rate of cardiovascular disease (CVD), preventing more than 4 million deaths worldwide annually.[57] Two randomized controlled trials in which dietary interventions reduced Na^+ intake by 25%-35% achieved small but significant reductions in BP over a 1.5- to 4-year period, but follow-up 10-15 years later showed a reduced risk of cardiovascular (CV) events of 25%.[58] Most recently, a well-validated computer simulation projected the effect on U.S. mortality from CHD and stroke of linearly reducing salt intake by 0-3 g/d from current estimates of 10.4 and 7.3 g/d for adult males and females, respectively; the estimated reduction of the number of deaths per year was 44,000 to 92,000.[59] An accompanying editorial called the evidence "compelling" and the potential benefits "huge."[60] This is a long way from the seemingly equivocal evidence relating salt intake to illness that was available when we first pointed out an order of magnitude difference between HGs and ourselves in this dietary risk factor.

Electrolyte and Acid Base Balances

Due in part to the changes in the K^+/Na^+ ratio, acid base balances have also changed markedly. In addition to the roughly 10-fold difference between estimated HG Na^+ intake and ours, their K^+/Na^+ ratio was probably at least 5:1; now Na^+ exceeds K^+, due to added Na^+ and low consumption of K^+-rich fruits and vegetables.[61] The latter would also have driven systemic pH toward alkalinity, whereas cereal grains and most dairy products are net acid yielding.[62] Over decades, the corrective metabolic measures needed to offset acid-yielding diets cause urinary calcium loss, accelerated skeletal calcium depletion, calcific urolithiasis, age-related muscle wasting, and deteriorating renal function.[62] A recent effort to model the net endogenous acid-producing potential of the diets of 229 HG groups suggests that the majority had a net positive acid load,[63] but many of these had adaptations that could not have been ancestral ones (eg, equestrian hunting and circumpolar residence). Those HG diets that were predominantly plant based (such as those of ancestral East African populations) would have had a more favorable net negative acid load, so that an earlier estimate, which suggested an overall alkaline net load for HG diets, remains pertinent to the model.[62]

Experimental Clinical Studies

As noted above, an early study returning sedentary Australian former HGs with T2DM to their traditional diet and lifestyle for a period of 7 weeks lowered fasting and postprandial glucose, increased insulin response, and markedly lowered fasting plasma triglycerides.[3] We have considered such studies to be of the greatest importance and urged further clinical experiments, especially with people living in modern industrial states, to test the discordance model. Fortunately, this work is now under way.

In 1 noncontrolled challenge study, 9 nonobese, sedentary, healthy volunteers consumed their usual diets for 3 days, then 3 "ramp-up" diets with increasing fiber and K^+ intake for 7 days, and finally an HG-type diet of lean meat, fruits, vegetables, and nuts for 10 days, omitting cereal grains, dairy products, and legumes.[64] Participants were monitored to ensure absence of weight loss. They experienced modest but significant reductions in BP with improved arterial distension; decreased insulin secretion (area under curve, AUC) in a 2-hour oral glucose tolerance test (OGTT), with a marked reduction in insulin/glucose ratio; and 16% and 22% reductions in total serum and LDL cholesterol, respectively.[64] These outcomes seem remarkable for such a short-term intervention.

More interesting still are results from randomized controlled trials (RCTs). In the most persuasive study to date, 29 patients with ischemic heart disease and either glucose intolerance or T2DM were randomized to 12 weeks of a "Paleolithic" diet (n = 14) based on lean meat, fish, fruit, vegetables, root vegetables, eggs, and nuts or a Mediterranean-like "Consensus" diet (n = 15) based on whole grains, low-fat dairy products, vegetables, fruits, fish, oils, and margarines.[49] In OGTTs, the Paleolithic group showed a 26% reduction in AUC glucose compared to a 7% reduction in the Consensus group. There was a greater decrease in waist circumference in the Paleolithic group (–5.6 cm) than in the Consensus group (–2.9 cm), but the glucose reduction was independent of that measure.

In a second randomized crossover pilot study, the starting point was 13 patients (3 women) with T2DM who were placed on a Paleolithic diet based on lean meat, fish, fruit, vegetables, root vegetables, eggs, and nuts, and a Diabetes diet according to the American Diabetes Association guidelines[65] (evenly distributed meals with increased vegetables, root vegetables, fiber, whole-grain bread and other cereal products, fruits, and berries, but decreased TF, especially cholesterol-raising SF).[48] Participants were on each diet for 3 months. Compared to the Diabetes diet, the Paleolithic diet produced lower mean levels of hemoglobin A1c, triacylglycerol, diastolic BP, weight, BMI, and waist circumference, and higher mean HDL.

Although these are small studies, it is very gratifying that the era of explicit experimental study of the discordance model has begun and that initial results are consistent with our original predictions. It is especially noteworthy that 2 of the studies were randomized trials that compared the HG diet to other recommended model diets rather than to a baseline or typical Western diet. We hope and trust that this work will continue.

Table 1. Widely Agreed-on Qualitative Differences Between Average Ancestral (Hunter-Gatherer) Diets and Contemporary Western Diets

	Ancestral (Hunter-Gatherer)	Contemporary Western
Total energy intake	More	Less
Caloric density	Very low	High
Dietary bulk	More	Less
Total carbohydrate intake	Less	More
Added sugars/refined carbohydrates	Very little	Much more
Glycemic load	Relatively low	High
Fruits and vegetables	Twice as much	Half as much
Antioxidant capacity	Higher	Lower
Fiber	More	Less
Soluble:insoluble	Roughly 1:1	<1 insoluble
Protein intake	More	Less
Total fat intake	Roughly equal	
Serum cholesterol-raising fat	Less	More
Total polyunsaturated fat	More	Less
ω-6:ω-3	Roughly equal	Far more ω-6
Long-chain essential fatty acids	More	Less
Cholesterol intake	Equal or more	Equal or less
Micronutrient intake	More	Less
Sodium:potassium	<1	>1
Acid base impact	Alkaline or acidic	Acidic
Milk products	Mother's milk only	High, lifelong
Cereal grains	Minimal	Substantial
Free water intake	More	Less

Discussion

Although not an across-the-board vindication of the HG model, and despite some changes from our macronutrient estimates as originally presented, research in the past quarter century has vindicated the clinical and epidemiological relevance of the model. Without supplying numbers, some of which might be controversial, we can confidently estimate the direction and magnitude of the modern diet's deviation from the HG diet in the range of EEAs (Table 1). More notably, research has suggested that where the model departed from standard 1985 recommendations, a shift toward the model would contribute further to primary prevention of several important diseases. Indeed, in some instances, the standard recommendations have already shifted in that direction (Table 2). This is the case for total serum cholesterol; it is now considered highly desirable to be under 180 mg/dL, whereas in 1985, the threshold was 200. We predict that the threshold will be lowered further in future recommendations.

The HG model and the discordance hypothesis suggest that meat and fish consumption can safely be higher than in current recommendations. Recent dietary fads, based on unproven theories of metabolism, claim that very low carbohydrate intake combined with high protein and fat consumption can safely produce weight loss. That this kind of diet can produce at least temporary weight loss has been demonstrated,[66,67] and several studies now show that levels of lean meat and fish intake higher than those in many officially recommended diets are as safe or safer for some groups of patients. We continue to believe that the risk associated with the consumption of meat is almost entirely explained by the high proportions of TF and especially SF in commercial meats. Neither the protein content of meat nor the cholesterol content of cell membranes has been shown to adversely affect health at the (fairly high) level characteristic of HG diets.

Reduction of carbohydrates to extremely low levels is not consistent with the HG model, but neither is a very high CHO, "meat as a condiment"–type diet; furthermore, CHO sources are important. HG CHO came from fruit, vegetables, and nuts, not from grains. Refined, concentrated CHOs such as sucrose played virtually no role, and the consumption of plant CHO necessarily resulted in high fiber intake. If we were to rebuild the food pyramid along HG lines, the base would not be grains but fruits and vegetables, which could be chosen to provide adequate fiber content. The second tier would be meat, fish, and low-fat dairy products, all very lean. Whole grains might come next (although even these were very unusual for HGs), whereas fats, oils, and refined carbohydrates would occupy the same very small place at the top, essentially functioning as condiments in a healthy diet. These guidelines would not exactly replicate the HG diet in terms

Table 2. Changing Recommendations for Diet and Biological Markers, as Compared With Current Estimates for Hunter-Gatherers in the Range of Environments of Evolutionary Adaptedness

	Recommendations		
	Pre-1990	Current	Estimated Ancestral
Nutrients			
Carbohydrate, % daily energy	55-60	45-65	35-40
Added sugar, % daily energy	15	<10	2
Fiber, g/d	—	38 male; 25 female	>70
Protein, % daily energy	10-15	10-35	25-30
Fat, % daily energy	30	20-35	20-35
Saturated fat, % daily energy	<10	<10	7.5-12
Cholesterol, mg/d	<300	<300	500+
Eicosapentaenoic acid and docosahexaenoic acid, g/d	—	0.65	0.7-6.0
Vitamin C, mg/d	60	90 male; 75 female	500
Vitamin D, IU/d	400	1000	4000 (sunlight)
Calcium, mg/d	800	1000	1000-1500
Sodium mg/d	2400	1500	<1000
Potassium mg/d	2500	4700	7000
Biomarkers			
Blood pressure, mm Hg	<140/90	115/75	110/70
Serum cholesterol, mg/dL	200-240	115-165	125
Body composition, %lean:%fat			
Females	—	<31% fat	35-40:20-25
Males	—	<26% fat	45-50:10-15
Physical activity, kcal/d	—	150-490	>1000

of food categories, but it would do so roughly in terms of macronutrients.

Na^+ and the Na^+/K^+ ratio no longer provide a challenge for the HG model since large prospective epidemiological studies and randomized clinical trials have recently shown a clear correlation between dietary sodium and the risk of CV disease, even for differences within a range much higher than HG intake. However, since sodium intake levels in those studies have rarely reached down into the HG range, it remains possible that much greater gains could be achieved than those suggested by current studies.

As for other aspects of lifestyle, tobacco products, rare in HG environments, have been the targets of increasingly strong societal restriction, and we know that the frequency and duration of exercise, including walking and other less intense exercise, should be much higher than it is and should include resistance and flexibility as well as cardiovascular components. Interestingly, we had been skeptical of the notion, common in the 1980s, that walking was not an adequate exercise because half of our HG ancestors—the women—exercised in this manner and did very little running. The subsequent finding that walking and other moderate exercise also reduce the risk of cardiopulmonary disease was consistent with the HG model.

Further research on HG populations themselves in the past quarter century has confirmed most of our earlier generalizations about them.[68,69] Unfortunately, Westernization worsens their diet and their health indicators, for example among the Australian Aborigines.[70,71]

Not every prediction of the HG model will result in the best recommendation. The case of ethanol consumption, extremely low before the invention of agriculture, departs from the model. A number of studies show that mild to moderate ethanol intake reduces cardiovascular risk, at least against the background of a modern diet. The ease with which ethanol intake progresses to levels that pose a wide range of other health risks suggests that we were not set up by our evolution to handle this compound without difficulty, but the positive value of small amounts shows that the HG model cannot answer all questions.

Still, a review of research since our original publication largely vindicates the model we presented 25 years ago. Common arguments against the approach have been effectively answered.[72] Ridicule notwithstanding, the HG paradigm offers a good provisional alternative to the sometimes confused, occasionally conflicting, and often inadequately prioritized stream of research findings.[72] It is almost certainly superior to the vast majority of diet fads, the scientific basis of which is almost always dubious, and which have failed to halt what has been called an obesity pandemic[73] and an ominous rise in T2DM,[74] even in children and adolescents.[75]

Unfortunately, a great many Americans have yet to accept the basic facts and theory of evolution, an obvious obstacle to offering everyone the paradigm we advocate. However, most people respond to the notion of a "natural" diet and lifestyle, and the HG model is the first and only scientific approach to that notion. Certainly most physicians and medical scientists can accept it as one organizing principle for past and future research. Although an anthropological model cannot be accepted at face value—only the best clinical, experimental, and epidemiological research can finally justify recommendations—we can be increasingly guided in this research by such a model. Meanwhile, we can keep an open mind about what we may learn from our remote ancestors.

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