

Back to Basics: Why Foods of Wild Primates Have Relevance for Modern Human Health

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Many current health problems are attributed to diet, and numerous views exist as to which types of foods contribute to such problems.^{1,2} This issue is not one of purely academic interest—rather, it has important ramifications for human health and well-being in the new millennium. It is difficult to comment on “the best diet” for humans because there have been and are so many different yet successful diets in our species. Humans can thrive on diets consisting almost exclusively of the raw fat and protein of marine mammals (Arctic Eskimo)³ and on diets composed largely of a few wild plant species (Australian aborigines of the Western Desert)⁴; and there is an almost infinite number of successful dietary permutations between these two extremes.

Because of the dietary diversity modern humans display, it is reasonable to conclude that human ancestors exhibited similar flexibility. Like extant wild primates, our ancestors were probably opportunistic foragers and took advantage of the most nutritious foods in their environment at any given time, so long as these could be secured without undue cost or hazard.

Present fossil evidence places the earliest human beings at approximately 2 million y ago.⁵ In contrast, evidence for agriculture has been dated to only some 12 000 y ago. This means for most of human existence, members of our genus (*Homo*) and species (*Homo sapiens*) have lived as hunter-gatherers, that is, people using only wild plants and animals as foods. Various attempts have been made to reconstruct the average daily macronutrient intake for paleolithic hunter-gatherers.^{6,7} The logic behind such attempts seems to be the belief that modern human biology is somehow adapted to paleolithic foodways and that, by following such a diet, we might be able to prevent many of the so-called diseases of civilization (e.g., cardiovascular disease, obesity, type II diabetes).

However, data from ethnographic studies of recent (largely 20th century) hunter-gatherers and evidence from historical accounts and archaeological sites indicate that past hunter-gatherer

societies enjoyed a rich variety of different diets, depending on locale and season of the year.^{8–10} Thus, nutrient estimates for “the average paleolithic diet” probably do not reflect actual daily intakes for many hunter-gatherers.⁶ In fact, we do not know much about the range of foods our paleolithic ancestors ate each day or season in almost any environment, although it seems likely that periods of relative food abundance may have alternated with periods of low food availability in many environments.

Regardless of what paleolithic hunter-gatherers were eating, there is little evidence to suggest that human nutrient needs or digestive physiology were significantly affected by such diets at any point in human evolution. To date, we know of few adaptations to diet in the human species that differentiate us from our closest living relatives, the great apes.^{11–13} Those identified are largely (although not exclusively) regulatory mutations such as lactase synthesis in adulthood, and unique selective pressures favoring such diet-associated mutations seem fairly well understood.¹¹

Food has played a major role in human evolution but in a somewhat different way than seems generally appreciated. Humans are not creations *sui generis*. Rather, they have an evolutionary history as anthropoid primates that stretches back more than 25 million y, a history that shaped human nutrient requirements and digestive physiology long before there were humans or even protohumans. Hunter-gatherers were not free to determine their diet—quite the opposite; it was their predetermined need for particular nutrients that constrained their evolution.

At the same time these dietary needs apparently allowed for natural selection to favor increased brain size in the human lineage and the concomitant development of technologic, social, and other abilities directed at securing these nutrients; in this sense, it can be said that diet influenced, indeed drove, human evolution. In turn, expansion of the human brain and increasing dependence on cultural behaviors to obtain and prepare foods buffered human biology from many selective pressures related to diet that other animal species must resolve largely through genetic adaptations.^{11,12} The difference in gut proportions between modern humans and great apes, for example, seems to reflect the fact that most foods humans consume are “predigested” by technology in one way or another before they ever reach the gut of the feeder.^{12,13} This “predigestion” minimizes dietary bulk relative to the diets of

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wild apes and generally enhances dietary quality.^{12,13} Comparative data suggest that human nutrient requirements and most features of human digestive morphology and physiology are conservative in nature and probably were little affected by the hunter-gatherer phase of human existence.^{12,13} For this reason, if humans deviate too far from these ancestral foodways and simultaneously consume foods at variance with their pattern of digestive kinetics, a pattern shared with the great apes and one predicated on a slow turnover of ingesta,^{12,13} they will likely suffer the consequences, some of which appear to be reflected in the diseases of civilization now affecting many individuals.

Humans come from a fairly generalized line of higher primates, a lineage able to use a wide range of plant and animal foods. Data from various lines of evidence—atomic, physiologic, and paleontologic—support the view that the ancestral line (Hominoidea) giving rise to humans was strongly herbivorous (i.e., plant eating).^{11–15} The daily diet probably consisted largely of wild fruits, supplemented with young tree leaves and other high-quality plant parts in addition to some animal matter (insects, vertebrates) when this could be secured.^{13,15} It seems unlikely that the ancestral line leading to humans consumed a high foliage diet because of its low content of digestible energy and high content of indigestible bulk.¹³ Humans also lack the rapid passage rate of ingesta and specialized metabolic and other adaptations to flesh diets that characterize obligate carnivores.¹³

Given the dietary characteristics of the primate lineage leading to humans and the lack of evidence supporting any notable diet-related changes in human nutrient requirements, metabolism, or digestive physiology relative to those of great apes,¹³ a better understanding of the nutritional composition of plant foods in the daily diets of wild primates should enhance our understanding of human dietary requirements. Although the necessary nutrients for human beings have been fairly well established since the 1930s and 1940s, the quantities needed are constantly under revision as new facts become available,¹⁶ suggesting that there is more to learn in this area.

As most primates are arboreal, the plant foods they eat in the natural environment consist largely of the leaves, fruits, and flowers of tropical forest trees and vines.^{13–15} A number of analyses have been made of the nutritional and other chemical constituents of such plant foods from both the Old and New World tropics.^{17–19} When this information is compared with data on similar features in cultivated plant foods, some interesting differences emerge.

Most primates include considerable fruit in the diet. These wild fruits typically are more nutritious than cultivated fruits; they have a slightly higher protein content and a higher content of certain essential vitamins and minerals.¹⁵ Of interest is the fact that, as a rule, sugar in the pulp of wild fruits is dominated by hexose (considerable glucose and/or some fructose, and very little sucrose), whereas that of cultivated fruits is high in sucrose, a disaccharide.^{15,20} Cultivated fruits are therefore very tasty to humans because sucrose tastes sweeter than glucose. The sugar composition of cultivated fruits is one example of the way in which a strong sweet taste may be used to enhance the appeal and consumption of many foods humans now consume, foods that often consist largely of calories.

Because sucrose must be broken down into glucose and fructose before it can be absorbed, the difference in sugar content between wild and cultivated fruits may seem trivial. However, Western diets rich in sucrose have been suggested to relate to various health problems. The difference in sugar composition between wild and cultivated fruits could affect features of molecular transport and absorption and perhaps insulin production. Further, many wild fruits contain fibrous pulp and multiple seeds, which provide a high ratio of indigestible to digestible components and may slow sugar digestion and absorption.²¹

In terms of micronutrient levels, considerable comparative data indicate that wild plant foods, regardless of geographic locale, often show higher values and more interspecific variation in their

content of particular minerals than cultivated plant foods.¹⁵ Study of the vitamin-C content of wild plant foods consumed by primates in Panama has shown that most such foods, both leaves and fruits, contain notable vitamin C.¹⁵ Kuhnlein and Turner²² compared the nutrient composition of wild plant foods of Canadian indigenous peoples with that of commercial plant foods reported in the United States Department of Agriculture Handbook 8 Series and the National Canadian Nutrient Table. In particular, the list of commercial vegetable foods with a nutrient composition similar to that of wild vegetable foods was quite short (21 entries in total and many obscure species), suggesting that few commercial vegetables compared nutritionally to the wild species analyzed.

Because primates tend to fill up each day largely on plant foods, they generally ingest much higher amounts of some vitamins and minerals on a body-weight basis than modern humans. These differences are not trivial. For example, a 7-kg wild howler monkey (*Alouatta palliata*) in Panama takes in some 600 mg of vitamin C per day and more than 6000 mg of potassium and some 38 mg of iron.¹⁵ Examination of the micronutrient intakes of captive primates fed commercial monkey chow has shown that these primates ingest markedly higher amounts of many micronutrients than are currently recommended for humans, on a body-weight basis.²³ The reason for including such high micronutrient levels in the commercial monkey chows was not known, even by the manufacturers.²³ Estimates for the level of certain micronutrients in the average paleolithic diet likewise are often higher than current recommended daily allowances,^{6,7} probably because, like wild primates, paleolithic hunter-gatherers were eating wild plant (and animal) foods.

Do non-human primates require much higher levels of certain micronutrients than humans on a body-weight basis or is their apparent high daily intake in the wild an unavoidable byproduct of their largely plant-based diet that actually serves no important physiologic functions? If these micronutrient levels do serve important functions, why don't humans likewise benefit from similar high levels of vitamins and minerals? Wild plant foods also contain a host of other biologically active compounds besides nutrients.¹ The physiologic effects of these other compounds in relation to plant nutrients are little studied or understood and could affect nutrient use and other functions. These topics seem of relevance for future research in terms of better understanding human nutritional physiology and nutrient requirements.

The diets of most wild primates contain saturated and unsaturated fats in fairly equal proportions (ratio of polyunsaturated to saturated fat in the howler monkey diet = 0.85) and close to the 1.0 ratio recommended for modern humans.²⁴ Fat intake is low. For example, dietary fat is estimated to contribute only around 17% of daily calories to the howler monkey diet,²⁴ and the largely plant-based diets of most other wild primates, including apes, are also estimated to be low in fat-derived calories.²⁵ The ratio of ω -3 to ω -6 in wild plant foods eaten by Panamanian howler monkeys averaged 0.7,²⁴ and similar ratios likely are typical of the diets of other wild primates. In contrast, the Western diet is often low in α -linolenic acid, high in calories from fat, and high in saturated fat.^{15,24}

In the wild, many primates take in more grams of vegetable protein per day than seem necessary based on body weight.¹⁵ This probably reflects the fact that vegetable protein, even high-quality protein, shows a lower digestibility than animal protein.²⁶ Assimilation studies have indicated that 20% or more of the total nitrogen concentration in wild plant parts is not available to the primate feeder.¹⁵ In contrast to wild primates, most Western humans obtain considerable daily protein from the meat (muscle) of domesticated livestock. This meat is marbled with fat, a condition not seen in the muscle tissue of wild prey, which is always lean, irrespective of the season, and does not marble.⁸ Because a high proportion of the fat of wild animals is structural fat, it is also relatively rich in long-chain polyunsaturated fatty acids.⁸

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small amounts of animal matter, most primates relish meat and will eagerly consume it when available in the wild or offered in captivity.^{12,13} The barrier to greater meat consumption by wild primates appears to be its patchy distribution and high cost of procurement in the natural environment rather than any physiologic or gustatory barrier to animal foods.^{11–13}

Archaeologic evidence indicates that even the earliest humans began to incorporate bone marrow, meat, and other animal products from vertebrates into the diet.^{27,28} Such animal foods may have been scavenged for a considerable period of time, but eventually social innovations such as cooperative hunting and technologic innovations permitted humans to capture wild prey.^{27,28} Using animal matter to satisfy daily requirements for protein, essential fatty acids, some energy, and many micronutrients would free up space in the gut for carbohydrate-rich plant foods (the principal energy source for most wild primates) and allow for their use as fuel (glucose) for the increasingly large human brain.¹¹

The strongly plant-based diet of most higher primates tends to be high in dietary fiber. Approximately 44% of the daily dry-mass consumption of a 7-kg howler monkey, for example, is made up of fiber (some 88 g of fiber per day).²⁴ In contrast, a 70-kg American human probably takes in no more than 10–20 g of dietary fiber per day. Evidence from reconstituted human coprolites suggests that 10 000 y ago some human populations may have taken in as much as 130 g of fiber per day,²⁹ and even today some humans are reported to take in 70–90 g per day.³⁰ Fatty acids produced in fiber fermentation may provide more than 10% of the required daily energy for some human populations, and data suggest various important health benefits may be conferred by particular fermentation products.²¹

These comparative data indicate that the daily diets of monkeys and apes differ in a number of ways from the modern human diet. Higher primates eat a variety of fresh plant foods each day. Most of these foods come from dicotyledonous canopy tree species. In contrast, much of the plant food modern humans consume is cooked cereal grain from monocotyledonous grasses. Most cultivated cereals are nutritionally inferior to plant foods consumed by wild primates, and cereal grains, such as wheat, rye, and barley, contain highly insoluble fiber.²¹ Cultivated fruits and vegetables generally differ nutritionally from their wild counterparts. Furthermore, modern humans typically do not eat large quantities of fresh plant foods each day and thus take in lower amounts of many nutrients on a body-weight basis relative to wild primates and less dietary fiber and non-nutrient phytochemicals.

As noted above, there is considerable interest in better understanding causal factors related to "diseases of civilization." As appealing as the notion of the paleolithic diet is as a panacea for these health problems, data suggest that one does not have to be a paleolithic hunter-gatherer to escape them. Information on the diets and health of recent and contemporary traditional peoples, both hunter-gatherers and small-scale agriculturalists who also hunt and gather, show that all such societies are largely free of diseases of civilization whether the daily diet is made up primarily of wild animal foods, of wild plant foods, or of a single cultivated starchy carbohydrate supplemented with wild plant and animal foods.^{3,10,31–33} Thus, it is not some special paleolithic diet or macronutrient profile particular to hunter-gatherers that signals relief from diseases of civilization but rather shared features of the diets (and of lifestyle?) of many different traditional societies that spell the difference between their health and ours in this respect.¹¹

I suggest that it is the relatively low caloric density of most wild foods, both plant and animal, in combination with certain features of panhuman gut physiology that have played the critical role in the lack of diseases of civilization in hunter-gatherer societies, both past and present.¹¹ Similarly, indigenous hunter-gatherer agriculturalists of the Amazon Basin (e.g., Yanomamo, Parakana, Arawete), societies dependent for hundreds of years on a single staple cultivar to meet most caloric requirements, also appear constrained in daily caloric intake because such cultivars typically lack many essential nutrients, forcing the intake of other

foods, generally wild, and many staple cultivars also contain considerable fiber.

Because the human gut can hold only a limited amount of food at any one time and because transit time of food through the human gut is protracted (averaging 62 h with low-fiber diets and 40 h with high-fiber diets),³⁴ there is a clear upper threshold to the amount of such foods the human gut can process each day.^{11,12}

Recent technology has circumvented this natural caloric barrier by processing, condensing, refining, and otherwise altering both plant and animal foods such that many more calories can be ingested per unit of time than used to be possible. In addition, as many have noted, most Westerners lead sedentary lifestyles in comparison with more traditional peoples, who typically perform physical activities, often strenuous, for 8 h or more each day. Getting back to basics in terms of diet would appear to involve turning more to foods similar to those of wild primates and human ancestors, that is, unprocessed foods, in particular more fresh fruits and vegetables, grass-fed rather than grain-fed livestock, and developing a more physically active lifestyle.

A few cultivated cereal grains and domesticated livestock species cannot begin to compensate humanity for its loss of traditional foods or for the loss of genetic diversity of the myriad plant and animal species that have nourished humans and their ancestors for millions of years and that are rapidly being exterminated in the name of progress. As we enter a new millennium, we need to pause and reevaluate our dietary situation. Such reflection could lead to important changes in the types of foods we choose to eat and result in better human health.

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