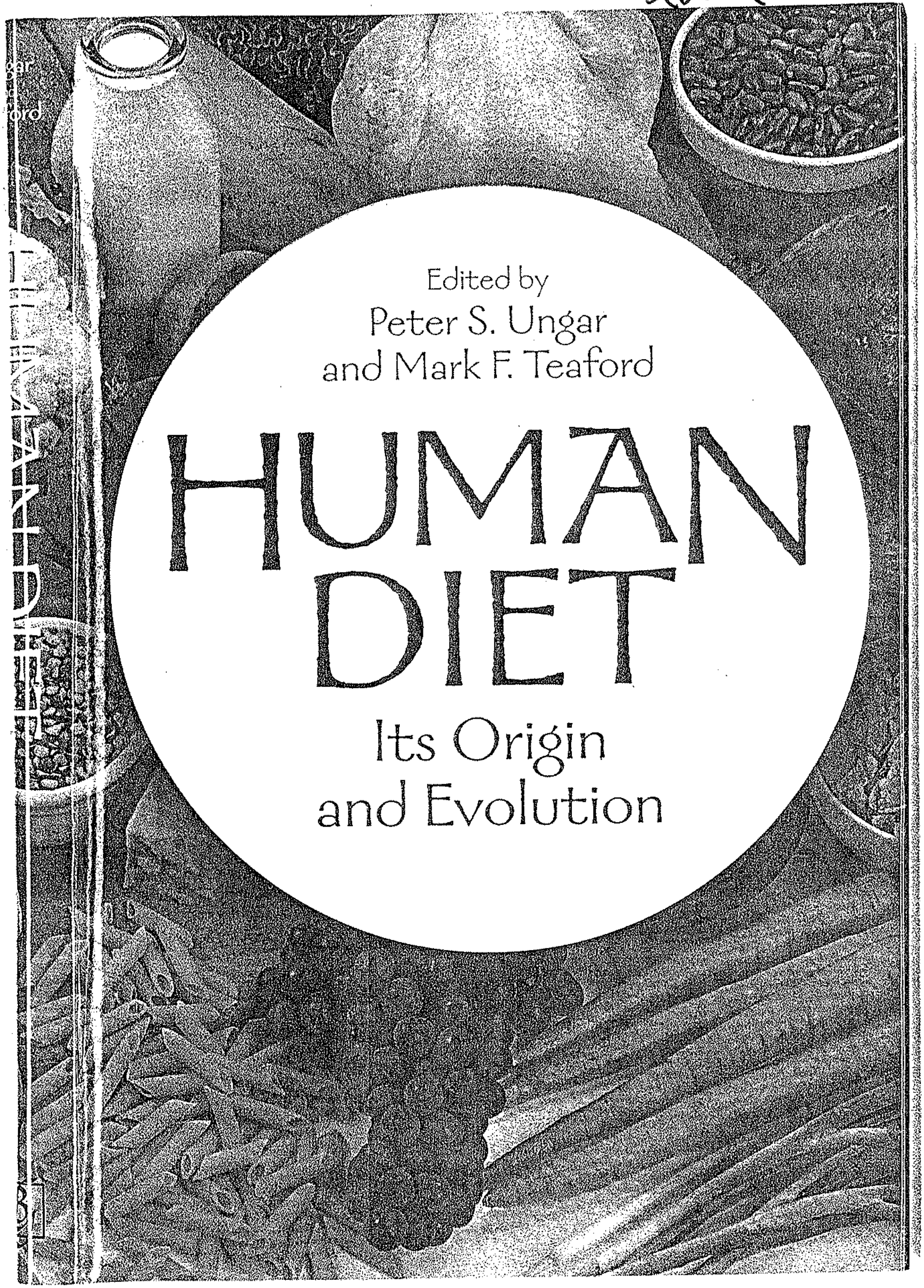
2002 Bergin & Garvey Press Westport Conn.



Chapter 8

Hunter–Gatherer Diets: Wild Foods Signal Relief from Diseases of Affluence

Katharine Milton

There is general consensus that many chronic health problems, first noted in Western nations but increasingly prevalent worldwide, relate to diet (Trowell and Burkitt, 1981; Roe, 1979; Prasad et al., 1998; Bray and Popkin,1998; Lampe 1999). There is far less consensus, however, about the dietary factors implicated in such health problems. This lack of understanding has opened the door to a proliferation of different recommendations as to the best diet for modern humans. For clarification, let me note that all humans alive today are members of the same species, *Homo sapiens sapiens*, and as such, all are fully "modern" humans.

Increasingly, the average consumer has come to regard the American supermarket as a minefield of conflicting and potentially dangerous dietary decisions: low fat, high fat, no fat; no meat, high meat, less fatty meat; no eggs, one egg a week, unlimited eggs; less carbohydrate, more whole grains, no cereal products; more fruit, less sugar; and so on. Too much confusing information is available, too much attention is paid by the popular press and public to fad diets and preliminary dietary findings, and too little attention is paid to serious dietary recommendations advanced by entities such as the National Research Council and U.S. Department of Agriculture (USDA). Clearly, there is considerable room for improvement.

It is difficult to comment on "the best diet" for modern 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 (e.g., Arctic Eskimo; Ho et al., 1972) as well as diets composed largely of a few wild plant species (e.g., Australian aborigines of the Western Desert; Gould, 1980)—and there are an almost infinite number of successful dietary permutations between these two extremes. Yet in Western and more westernized nations today, it is also clear that some features of diet or some factors that interact with diet have somehow gotten out of step with modern human biology. It would seem that relatively recent changes in certain features of the modern human diet (e.g., cooking of most foods, heavy reliance on a single domesticated grain or root crop, selective cultivation to "improve" vegetables, fruits, or meat, the heavy consumption of highly processed foods, increased sugar and fat in the diet) may, in an evolutionary sense, have occurred so rapidly and so recently that human biology has not as yet had time to adapt to them (Kliks, 1978; Trowell and Burkitt, 1981; Eaton and Konner, 1985; Prasad et al., 1998).

WHAT DO WE KNOW ABOUT THE DIET OF EARLY HUMANS?

Present fossil evidence places the earliest humans at around 2.4 mya (Groves, 1999). Yet evidence for agriculture is dated at only some twelve thousand years ago. This means that 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 features of the average daily macro- and micro-nutrient intake for Paleolithic hunter–gatherers (Eaton and Konner, 1985; Eaton et al., 1998; Cordain et al., 1999). The logic behind such attempts seems to be the belief that over the approximately 2.4 million years of human existence, human biology has somehow become adapted to some type of "Paleolithic diet," and that by discovering and following such a diet today, we might be able to prevent many "diseases of affluence" (e.g., coronary heart disease, high blood pressure, atherosclerosis, type II diabetes, various cancers, obesity, eating disorders, and so on).

There are a number of problems with such an approach. One problem is that ancestral hunter–gatherers did not all eat the same diet. Data from ethnographic studies of nineteenth and twentieth century hunter–gatherers, as well as historical accounts and the archeological record, suggest that ancestral hunter–gatherers enjoyed a rich variety of different diets (Smyth, 1878; Ho et al., 1972; Lee, 1979; Gould, 1980; Hayden, 1981; Kuhnlein and Turner, 1991; Milton, 2000). Thus estimates of nutrient proportions for "the Paleolithic diet" are hypothetical, at best. In fact, we do not know much about the range of foods Paleolithic hunter–gatherers consumed in almost any environment at any time, though it seems likely that periods of relative food abundance alternated with seasonal periods of low food availability in most cases.

Perhaps more to the point, however, is the fact that regardless of what Paleolithic hunter–gatherer societies were eating, there is little evidence to suggest that human nutritional requirements or human digestive physiology were significantly affected by such diets at *any* point in human evolution (Milton and Demment, 1988; Milton, 1999a,b, 2000). To date, we know of few adaptations to diet in the human species that would serve to differentiate humans from their closest living relatives, the great apes. Those identified are largely (though not exclusively) regulatory mutations such as lactase synthesis in adulthood, and the unique selective pressures favoring such diet-associated mutations in humans seem fairly well understood. Perhaps more significant, most or perhaps all such mutations appear to have arisen within the past twelve thousand years—that is, well *after* the advent of agriculture and animal domestication—and therefore are not associated with Paleolithic hunter–gatherers or their diets.

Food has played a major role in human evolution, but in a different way than seems generally appreciated. Humans have an evolutionary history as anthropoid primates that stretches back more than thirty million years, a history that shaped human nutrient requirements and features of human digestive physiology long before there were humans or even proto-humans. Because of these inherited traits, ancestral humans were not free to eat whatever they wanted—their pattern of gut morphology, passage kinetics, dentition, body size, and many other features set limitations on the types of foods they could successfully exploit. Elsewhere, I have argued that in the hominoid line, due to the influence of these inherited traits, dietary quality must be kept high for a physically active and highly social lifestyle (Milton, 1999a).

Evolving humans appear to have relied increasingly on brain power as the key element in their dietary strategy, utilizing technological and social innovations to secure and process foods before ingestion. Expansion of human brain size and an increasing dependence on cultural (asomatic) behaviors to secure and prepare foods, in turn, buffered humans from many selective pressures related to diet that other animals must resolve largely through genetic adaptation (Milton and Demment, 1988; Milton, 2000). It is important to understand here that it is the *behavioral* trajectory taken by humans to secure high-quality foods—rather than simply the foods themselves—that, in essence, has made humans human.

Comparative and experimental data show that modern humans, common chimpanzees, gorillas, and orangutans show close similarity in most features of gut anatomy as well as pattern of digestive kinetics (Milton, 1986, 1987; Milton and Demment, 1988; Caton, 1997; Milton, 1999a,b). Such striking similarities support the view that human nutritional requirements, gut anatomy, and physiology were little affected by the hunter–gatherer phase of human existence. For this reason, if modern humans deviate too strongly from ancestral foodways and simultaneously consume foods at variance with their pattern of digestive kinetics, a pattern predicated on a slow turnover of ingesta, they will likely suffer the consequences—some of which appear reflected in the "diseases of affluence" now affecting many modern humans (Milton, 2000).

COMPARATIVE ANALYSES OF PRIMATE DIETS

Given all of the above, it would seem that a better understanding of the nutritional composition of plant foods in the diets of extant wild primates could enhance our understanding of modern human dietary requirements. Though 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 (Lieberman, 1987), 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 (Milton, 1980; Milton, 1999b). Analyses have been carried out on a number of nutritional and other chemical constituents of wild plant foods consumed by anthropoids in both the Old and New World (Milton, 1979, 1999a; Dasilva, 1994; Heiduck, 1997; Conklin-Brittain and Wrangham, 2000). When this information is compared with data on similar features of cultivated plant foods consumed by modern humans, some interesting differences emerge.

Wild Fruits

Most monkeys and apes include considerable fruit in their diet. These wild fruits are more nutritious than cultivated fruits—they have a slightly higher protein content, as well as a higher content of certain vitamins and minerals (Milton, 1999a; Conklin-Brittain and Wrangham, 2000; Nelson et al., 2000). For example, in terms of protein, the average crude protein content dry weight of eighteen species of wild Panamanian fruits eaten by various monkey species was 6.5 ± 2.6%, while that of seventeen species of cultivated fruits of the type sold in American supermarkets was 5.2 ± 2.6% (Milton, 1999a). Average crude protein content dry weight of 50 species of wild fruits eaten by chimpanzees in Uganda was 10.7 ± 5.4% (Conklin-Brittain and Wrangham, 2000), while eight species of wild fruits eaten by lowland gorillas in Cameroon showed a crude protein dry weight of 6.3 ± 0.6% (Calvert, 1985a,b). For this reason, a wild fruit eater should net more protein than would be the case if it were eating the same amount of cultivated fruit.

Unlike cultivated fruits, wild fruits frequently contain tiny insects and larvae that are consumed by feeding monkeys and apes. These tiny particles of animal matter probably are not useful protein sources per se, but they can serve as an important source of certain essential micronutrients such as B_{12} and perhaps also supplement particular amino acids, which tend to be low in fruits, both wild and cultivated (Milton, 1999a,b).

Another important difference between wild and cultivated fruits is that sugar in the pulp of wild fruits tends to be hexose-dominated (fructose and glucose), while that of cultivated fruits tends to be very high in sucrose, a disaccharide (Baker et al., 1998). As sucrose is broken down by sucrase into glucose and fructose before it can be absorbed, the difference in sugar composition between wild and cultivated fruits might seem trivial. However, Western diets high in sucrose have been suggested to relate to numerous health problems. The difference in sugar composition between wild and cultivated fruits could affect features of molecule transport and absorption (Vanderhoof, 1998) and perhaps insulin production. Humans clearly come from an evolutionary past in which hexose-dominated, not sucrose-dominated, fruits were consumed, and human digestive physiology should therefore be best adapted to a carbohydrate substrate similar to that of wild fruits.

Wild fruits also differ in another important respect from their cultivated counterparts, since they generally have a relatively high content of roughage—woody seeds, thick skins, fibrous strands, and, at times, considerable pectin (Milton, 1991 and personal observation). Wild fruits therefore provide a high ratio of indigestible (or slowly digesting) to digestible (or rapidly digesting) material, traits that might slow sugar digestion and absorption (Vanderhoof, 1998).

Micronutrients

Micronutrient (minerals and vitamins) intake is currently of strong medical and nutritional interest. Many problems formerly associated with malnutrition and child development in third world countries are now believed to involve, at least in part, an inadequate intake of particular vitamins and minerals (Calloway et al., 1992; Widdowson, 1992; Cunningham-Rundles and Ho, 1998). Micronutrient deficiencies are not confined to the third world. Many Americans take in suboptimal levels of particular minerals (or vitamins), and this lack may relate to various health problems (Pao and Mickle, 1981; Murphy et al., 1992; Block et al., 1992; Ames et al., 1995).

Comparative data indicate that wild plant foods, both fruits and leaves, often show higher values and more interspecific variation in their content of particular minerals than cultivated fruits and vegetables. For example, Nelson et al. (2000) looked at mineral concentrations for sixteen species of wild and four species of cultivated fruits in American Samoa. Four of the eight minerals examined (Cu, Fe, Na, and Ca) showed significantly higher values in wild fruits; wild fruits also showed more interspecific variation in mineral content relative to cultivated fruits (Nelson et al., 2000).

A small sample of wild Panamanian fruits eaten by several monkey species showed higher average values for Ca, P, K, and Fe than in cultivated fruits in the United States, while wild Panamanian leaves showed a higher Ca content than cultivated leafy vegetables from the American supermarket. Wild leafy vegetables consumed by the Kekchi people of Guatemala had generally higher nutrient values than cultivated vegetable foods grown in their gardens (Booth et al., 1992). These and other comparative data suggest that, as a class, wild plant foods, regardless of locale, often show higher values and more interspecific variation in their content of many important minerals than do cultivated plant foods.

Most wild primates eat a number of different plant foods each day and over the course of an annual cycle may take foods from 150 or more plant species (Milton, 1987). By taking foods from a variety of different plant species and eating plant parts of different types (e.g., leaves and fruit), monkeys and apes obtain a higher-quality diet than would generally be the case if feeding were focused on only one or two plant species per day (Nagy and Milton, 1979; Milton, 1987).

In terms of vitamins, vitamin C is of particular interest because, unlike most mammals that can synthesize their own ascorbate internally, all anthropoids, including humans, lack the enzyme L-gulonolactone oxidase (GLO, EC 1.1.3.8), which catalyzes the final step in ascorbate synthesis from glucose (Milton and Jenness, 1987). For this reason, monkeys, apes, and humans must have a dietary source of vitamin C.

Wild plant foods consumed by Panamanian primates contain notable amounts of vitamin C (Milton and Jenness, 1987). For example, eating a typical leaf-and-fruit diet, a 7-kg wild howler monkey (*Alouatta palliata*) is estimated to take in some 600 mg of vitamin C per day. The great apes—and here we are speaking of animals as large or larger than many modern humans—are eating diets estimated to contain from 2 to as much as 6 or more *grams* of vitamin C per day (Milton and Jenness, 1987). In contrast, the recommended vitamin C allowance for the average adult American is 60–70 mg per day.

Vitamin C is widely regarded as a potent antioxidant (Ames, 1998; Prasad et al., 1998; Bengmark, 1998). The physiological processes of wild primates appear to be carried out with generous amounts of fresh vitamin C continuously present in the body. Other than vitamin C, information is scarce on the vitamin content of wild plant foods monkeys and apes eat, but they likely are rich in vitamin E and provitamin-A—like vitamin C, regarded as potent antioxidants—as well as vitamin K and folic acid (Potter and Hotchkiss, 1995; Booth and Suttie, 1998).

As anthropoids tend to fill up each day largely on plant foods, they generally ingest much higher amounts of many vitamins and minerals on a body-weight basis than most modern humans. Do nonhuman primates require much higher levels of certain micronutrients than modern humans, or is their high daily intake in the wild an unavoidable byproduct of their largely plant-based diet that actually serves no important physiological functions? If these micronutrient levels do serve important functions, why do humans not likewise benefit from similar high levels of vitamins and minerals? Wild plant foods also contain a host of other biologically active compounds besides nutrients (Prasad et al., 1998). The physiological effects of these other compounds in relation to plant nutrients are little known, but could affect nutrient utilization or other functions. These topics seem of relevance for future research in terms of improving our understanding of human nutritional requirements.

Fatty Acids

Diets of most monkeys and apes tend to be low in fat. For example, dietary fat is estimated to contribute only around 17% of daily energy to the diet of wild howler monkeys (Chamberlain et al., 1993), and the largely vegetarian diets of many other wild primates are also estimated to be low in fat-derived energy. It is recommended that dietary fats not exceed 30% of daily energy intake in the U.S. diet, though most Americans take in more energy from fat each day than recommended (i.e., >36% of calories) (Eaton and Shostak, 1986; Horrobin, 1989; Murphy et al., 1992). The diet of wild Panamanian howler monkeys contains saturated (S) and unsaturated (P) fats in fairly equal proportions (P/S ratio = 0.85), a ratio close to the 1.0 P/S ratio recommended for modern humans (Chamberlain et al., 1993). In contrast to wild howler monkeys, Americans have P/S ratios of around 0.4.

Panamanian plant parts—basically an opportunistic selection of wild plant foods monkeys routinely eat—also contain notable amounts of alpha-linolenic acid (ALA, 18:3, n-3), as well as linoleic acid (LA, 18:2, n-6). Linoleic and alpha-linolenic acids are 18-carbon chain polyunsaturated fatty acids. These two fatty acids cannot be synthesized internally and require a dietary source. Once ingested, LA and ALA can be modified into various long-chain polyunsaturated fatty acids regarded as absolutely essential for many critical body functions (Adam, 1989; Horrobin, 1989). The ALA/LA ratio of most of the wild samples ranged from between 0.26 to 0.40, but occasionally this ratio was much higher (i.e., 5.65, 6.47) (Chamberlain et al., 1993). The routine inclusion of notable amounts of ALA as well as LA differentiates the diets of wild monkeys and apes from those of most Americans. Much of the fat Americans eat is either saturated animal fat or oil from monocot seeds. Most seed oils are high in LA, but low in ALA ; the few seed oils high in ALA (e.g., soy, canola) tend to be low in LA (Adam, 1989; Horrobin, 1989).

A number of cultivated leafy vegetables Americans eat are rich (>50% of total fatty acid content) in ALA (e.g., chinese cabbage, white and red cabbage, kale, brussel sprouts, parsley) (Adam, 1989). But most Americans do not eat large quantities of these foods either fresh or cooked, and cooking tends to destroy ALA (Adam, 1989). The diet of human ancestors, like the diets of extant monkeys and apes, likely contained notable amounts of both ALA and LA. For this reason, a similar intake of both essential fatty acids is likely to be most compatible with human biology. In keeping with this suggestion, the addition of ALA as well LA to infant formula has recently been recommended, though the ratio of ALA/LA and types of oils best suited for this purpose are still a matter of debate (Lien, 1994; Crozier, 1994).

Dietary Fiber

The strongly plant-based diets of most higher primates tend 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/d) (Chamberlain et al., 1993). Currently, evidence suggests an average dietary fiber intake in the range of 20 to 40 g/d in the majority of human populations studied throughout the world (Jenkins, 1988). However, some present-day rural African populations are estimated to consume 70–90 g of dietary fiber per day (Jenkins, 1988). Fatty acids produced in fiber fermentation may provide >10% of required daily energy for some individuals, and recent data suggest that important health benefits may be conferred by particular fermentation products such as buteric acid (Vanderhoof, 1998).

Data from rehydrated human coprolites estimated to be some ten thousand years old show that these individuals, who were consuming what appeared to be coarse, high-residue diets, appear to have taken in ≥130 g of plant fiber per day (Kliks, 1978). There is little reason to assume that the digestive abilities of humans ten thousand years ago differed to any significant degree from those of present-day humans—all are anatomically modern *Homo sapiens sapiens*. But a diet containing hundreds of grams of dietary fiber seems unsuited to modern human gut anatomy and physiology (Milton, 1986; Milton and Demment, 1988).

Protein

Carpenter (1994) has discussed many past misconceptions regarding human protein requirements, particularly those concerning the need for or benefits of large quantities of animal protein in the human diet. The average adult American appears to require less than one gram of high-quality protein per kilogram of body weight per day (0.75 g/kg average daily requirement for reference protein; National Research Council, 1989) to meet protein requirements (Potter and Hotchkiss, 1995).

When one thinks of protein, wild leaves and fruits do not generally come to mind. If one examines the diets of the larger anthropoids, however, it is clear that leaves and fruits appear to satisfy most or perhaps all their daily protein requirements. Young leaves consumed by wild monkeys in Panama show an average crude protein content dry weight of 12.4% ± 4.2; flowers too are often high in protein (9%–10% to 20%–25% crude protein dry weight) (Milton, 1979, 1980). Though not particularly high in protein, wild fruits average 6.5% ± 2.6 protein; n = 18 wild Panamanian fruit species).

Though many cultivated grains as well as some nuts and seeds are low in one or more essential amino acids humans require (Wardlaw and Insel, 1995), amino acid profiles for the ten major amino acids of young leaf protein and animal protein are very similar (Moir, 1994). Regardless of protein quality, however, plant protein generally is digested with lower efficiency than animal protein, a fact that could reflect the influence of secondary compounds on protein digestion. Assimilation studies indicate that 20% or more of the total N in wild plant parts is not available to the primate feeder (Milton et al., 1980). Perhaps for this reason, many primates take in more grams of plant protein each day than seem necessary based on body weight (Milton et al., 1980).

In contrast to wild primates, Americans obtain considerable daily protein from the meat (muscle tissue) of domesticated livestock. This meat typically is marbled with fat—often heavily. This is a condition not seen in the muscle tissue of wild animals, which is always lean, irrespective of the season, and does not marble (O'Dea, 1991). Because a high proportion of wild animal fat is structural, it is also relatively rich in long-chain polyunsaturated fatty acids, rather than saturated fat (Naughton et al., 1986; O'Dea, 1991).

Archeological evidence indicates that even the earliest humans began to incorporate bone marrow, meat, and other animal products from wild vertebrates into the diet (Blumenschine, 1992; Marean and Assafa, 1999). Using wild animal matter to satisfy daily requirements for protein, essential fatty acids, some energy, and many micronutrients would have freed 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 (Milton, 1999b).

OVERVIEW

The daily diets of monkeys and apes differ in a number of respects from those of most modern humans. Most wild primates eat a variety of fresh plant foods each day, and larger anthropoids typically consume little animal matter. Most plant foods consumed by monkeys and apes come from dicotyledonous canopy tree species. In contrast, many modern human populations derive almost all of their daily energy from a single cooked cereal grain from a monocotyledonous grass (Calloway et al., 1992; Widdowson, 1992). Most cultivated cereals as well as root cultivars are nutritionally inferior to the plant foods consumed by wild primates (Sakai, 1983; Coursey, 1983; Widdowson, 1992; Wardlaw and Insel, 1995), and cereal grains, such as wheat, rye, and barley, contain highly insoluble fiber as well (Vanderhoof, 1998). Cultivated fresh fruits and vegetables also differ nutritionally from their wild counterparts. Furthermore, modern humans typically do not eat large quantities or many varieties of fresh uncooked plant foods each day and take in lower amounts of many micronutrients, as well as less dietary fiber and non-nutrient phytochemicals, on a body-weight basis than most wild primates.

As noted above, there is considerable interest in better understanding dietary factors that may relate to "diseases of affluence." As appealing as the notion of "the Paleolithic diet" is as a panacea for such 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 eat wild foods, show that *all* such societies are largely free of diseases of affluence whether the daily diet is made up primarily of wild animal foods, wild plant foods, or a single cultivated starchy carbohydrate supplemented with wild plant and animal foods (Lee, 1968; Ho et al., 1972; Truswell, 1977; Neel, 1977; Walker, 2000). Thus, it is not some special Paleolithic diet or macronutrient profile particular to (ancestral) hunter–gatherers that signals relief from diseases of affluence, but rather shared features of the diets (and lifestyles) of many different traditional societies that spell the difference between their health and ours in this respect (Milton, 2000).

I suggest that it is the relatively low digestible energy density of most wild foods, both plant and animal, *in combination* with certain pan-human features of gut physiology that have played the critical role in the lack of diseases of affluence in hunter–gatherer and other traditional societies, both past and present (Milton, 2000). As the human gut can hold only a limited amount of food at any one time and as transit time of food through the human gut is protracted (averaging sixty-two hours with low fiber diets and forty hours with high-fiber diets; Wrick et al., 1983), there is a clear upper threshold to the amount of most wild foods the human gut can process per day (Milton and Demment, 1988; Milton, 2000).

Recent technology has circumvented this natural barrier to excess energy intake in humans by processing, condensing, refining, and otherwise altering both plant and animal foods such that much more energy can be ingested per day than was possible eating wild foods. In addition, as is often stressed, most westerners lead sedentary lives in comparison with more traditional peoples, who typically carry out physical activities, often strenuous, for eight or more hours per day (Milton, 1984). Lowering the incidence of diseases of affluence would appear to involve turning more to foods similar in composition to foods of wild primates, hunter–gatherers, and more traditional rural societies; that is, natural, unprocessed foods, particularly more fresh fruits and vegetables, as well as grass-fed rather than grain-fed livestock—and a more physically active lifestyle.

ACKNOWLEDGMENTS

The paper presented at the 1998 Williamburg symposium on Origins and Evolution of the Human Diet was published in 1999 in *Nutrition* (Milton, 1999b). I have drawn on this paper, as well as a shorter summary, also published in *Nutrition*, to prepare this chapter. Readers wishing more information on specifics of nutrient analyses mentioned in this chapter are referred to the 1999 paper.