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Nutritional Characteristics of Wild Primate Foods: Do the Diets of Our Closest Living Relatives Have Lessons for Us?

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ABSTRACT

The widespread prevalence of diet-related health problems, particularly in highly industrialized nations, suggests that many humans are not eating in a manner compatible with their biology. Anthropoids, including all great apes, take most of their diet from plants, and there is general consensus that humans come from a strongly herbivorous ancestry. Though gut proportions differ, overall gut anatomy and the pattern of digestive kinetics of extant apes and humans are very similar. Analysis of tropical forest leaves and fruits routinely consumed by wild primates shows that many of these foods are good sources of hexoses, cellulose, hemicellulose, pectic substances, vitamin C, minerals, essential fatty acids, and protein. In general, relative to body weight, the average wild monkey or ape appears to take in far higher levels of many essential nutrients each day than the average American and such nutrients (as well as other substances) are being consumed together in their natural chemical matrix. The recommendation that Americans consume more fresh fruits and vegetables in greater variety appears well supported by data on the diets of free-ranging monkeys and apes. Such data also suggest that greater attention to features of the diet and digestive physiology of non-human primates could direct attention to important areas for future research on features of human diet and health. *Nutrition* 1999;15:488–498. ©Elsevier Science Inc. 1999

Key words: primates, humans, digestive physiology, wild plant foods, sugars, micronutrients, fatty acids

INTRODUCTION

There is broad consensus that many chronic diseases affecting humans in modern technologic societies relate to diet.[1–6] Increasingly throughout the world, as traditional diets alter and become more Westernized, many of these "Western" diseases rise in frequency. In addition, other health problems, particularly but not exclusively in developing nations, often appear due to dietary deficiencies of one type or another.[7–9]

These findings make clear that there is considerable room for improvement in terms of human dietary practices. It is difficult to comment on the types of foods best suited for human biology because there have been and are so many different yet successful dietary patterns in the human species.[10–12] As "cultural omnivores," humans clearly can flourish on an extremely broad range of food items and cuisines.[11,12] In spite of this dietary breadth, it also seems clear that most humans, regardless of their culture or geographic locale, require the same basic nutrients to remain in good health, though types and proportions can vary depending on the sex, age, activity patterns, and other features particular to a given individual or population.[9,13,14] Currently, for example, Americans are urged to eat more fresh fruits and vegetables and in great variety each day, and to lower their intake of sugar-rich foods and saturated animal fats.[15–18] However, there still remain many unresolved questions and conflicting opinions, even in specialist circles, about the best dietary practices for Americans.

DIETARY RECONSTRUCTION

To clarify what the best dietary practices for humans might be, one approach has been to attempt to "reconstruct" features of the diet of human ancestors.[19–25] The logic behind such attempts often rests on the assumption, probably valid, that relatively recent changes in certain features of the human diet (e.g., cooking of most foods, heavy reliance on a single domesticated grain or root crop, selective cultivation to "improve" vegetables and fruits,

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consumption of highly processed foods, increased sugar and saturated fats in the diet) may, in an evolutionary sense, have occurred so rapidly and so recently that the human gut and its attendant digestive physiology have not as yet had time to adapt to them.[1,2,4,5,23,26] Such "reconstructive" approaches often imply that Americans and others might benefit by emulating some features of the postulated dietary habits of their paleolithic ancestors.[23]

Modern humans are not creatures *sui generis*, but rather have a long evolutionary history. Human gut anatomy and dietary requirements, like those of any other animal species, are derived from an ancestral lineage that was associated with a particular dietary niche and array of foods. For this reason, another approach that might improve our understanding of the best dietary practices for modern humans is to focus attention not on the past but rather on the here and now; that is, on study of the foods eaten by the closest living relatives of modern humans—wild monkeys and apes—as well as their gut anatomy and patterns of digestive kinetics.[27–32] By comparing dietary features of humans and nonhuman primates, similarities and differences may be discerned that could improve our understanding of human dietary needs and digestive processes.

In advocating this comparative approach, I am not suggesting that Americans or other individuals should mimic the diets of wild primates, even if this were possible. As discussed below, certain features of modern human gut anatomy and physiology suggest that such dietary habits probably would not now be feasible. Nor am I advocating that animal foods be excluded from the human diet. Though it is possible today for humans to maintain good health without recourse to animal foods, data from the fossil and archaeologic record support the view that the routine consumption of animal protein and micronutrients played a key role in the emergence of our genus, *Homo*.[19,22,25,27,30] What I am suggesting is that a better understanding of the intake patterns and nutritional components of foods in the diets of wild monkeys and apes could improve our understanding of human dietary requirements as well as indicate promising areas for future research.

COMPARATIVE GUT PROPORTIONS OF HUMANS AND APES

This comparative approach is particularly compelling because so much information is now available on the diets of wild primates as well as the evolutionary relationships between them. From these studies, we know that the extant great apes (chimpanzees, gorillas, and orangutans) are most closely related to modern humans, *Homo sapiens*.[33] The ancestral line leading to extant chimpanzees and modern humans may have diverged as recently as 4.5 million y ago.[33]

When the human gut is compared with guts of extant apes, both similarities and differences can be detected. All hominoids (apes and humans), in keeping with their descent from a common ancestor, show the same basic gut anatomy consisting of a simple acid stomach, a small intestine, a small cecum terminating in an appendix, and a markedly sacculated colon.[34] However, humans stand apart from extant apes in some features of gut proportions. In humans, more than half (>56%) of total gut volume is found in the small intestine, whereas all apes have by far the greatest total gut volume (>45%) in the colon (Fig. 1).[27–31] In addition, the size of the total human GI tract in relation to body size is small in comparison to those of apes.[31,35]

The dominance of the hindgut in apes suggests adaptation to a diet lower in quality than that consumed by modern humans, a diet containing considerable bulky plant material, such as plant fiber and woody seeds. In contrast, the proportions of the human gut, dominated as it is by the small intestine, suggest adaptation to a diet that is nutritionally dense and highly digestible relative to the diets of apes.[27–31] Currently, there is no way to determine when this difference in gut proportions between apes and humans may have originated; it could be relatively recent or quite ancient.[30]

In some small mammal and avian species, total gut size and the size of some gut sections are known to increase significantly within weeks in response to fluctuations in temperature or lowered dietary quality.[36–39] However, species showing such dramatic gut plasticity tend to be very small herbivores living in strongly fluctuating environments.[38,39] Though humans and some other primates are known to exhibit some degree of gut plasticity, the relative gut proportions shown in Figure 1 for extant apes and humans, respectively, are believed to be representative of all members of each of these two present-day lineages regardless of their diets or environmental conditions.

Experimental data show that Western humans, common chimpanzees, gorillas, and orangutans exhibit close similarity in their pattern of digestive kinetics.[31,40] In all species, the turnover time of ingesta is protracted [e.g., mean transit time of ingesta for human subjects on a refined western diet was 2.6 d; mean transit time for chimpanzees on a low fiber (14% neutral detergent fiber [NDF]) commercially prepared diet was 2.0 d].[31] Common chimpanzees and Western humans also show a similar kinetic response to different fiber levels in the diet (i.e., more rapid turnover of ingesta with increased fiber level) as well similarity in their respective abilities to degrade (via gut flora) the cellulose and hemicellulose of wheat bran.[31] These kinetic and digestive similarities are all the more striking because of the differences between humans and chimpanzees in some features of gut proportions (Fig. 1) and suggest that the pattern of gut kinetics in a particular lineage may be a conservative feature relative to some other traits, such as gut proportions.[31]

Though human gut proportions and some characteristics of the human diet may have altered over time, humans should still require the same basic nutrients as apes. If humans deviate too strongly from these common nutrient requirements and, at the same time, consume foods that are at variance with their pattern of digestive kinetics, one predicated on a fairly slow turnover of ingesta, they will likely suffer the consequences—some of which appear to be reflected in various of the diet-related health problems now affecting many Americans and other individuals in Western nations.

FOODS OF WILD PRIMATES

Primates are believed to have evolved in tropical forests and even today this is where most primate species are found.[29] Indeed, the most recent paleontologic evidence suggests that the earliest known hominid (*Ardipithecus ramidus*—a taxon estimated to be some 4.4 million y old) lived in a closed wooded rather than more open savanna environment.[41,42] As forest dwellers, primates have found the foods available for most of their evolutionary history have been the leaves, fruits, and flowers of tropical forest trees and vines.[27–30]

Almost without exception, extant apes and monkeys take the greatest proportion of their daily diet from plant foods—new leaves, ripe fruits, seeds, exudates, nectars, flowers, pith—eating only moderate to trace amounts of animal matter, generally invertebrates.[27,43,44] All great apes are markedly herbivorous. Gorillas and orangutans are estimated to take most of their annual diet from plant foods, eating only small amounts of animal matter, largely invertebrates.[27–32,43,45,46] Though common chimpanzees "fish" for termites and "dip" for ants as well as hunt and eat vertebrate prey (often monkeys), such foods tend to make up only a small percentage (4–6%) of the chimpanzee annual diet, which is composed in large part of ripe fruits.[47–50]

Using data from various lines of evidence—anatomic, paleontologic, and physiologic—there seems general agreement that the ancestral line leading to apes and humans was markedly herbiv-

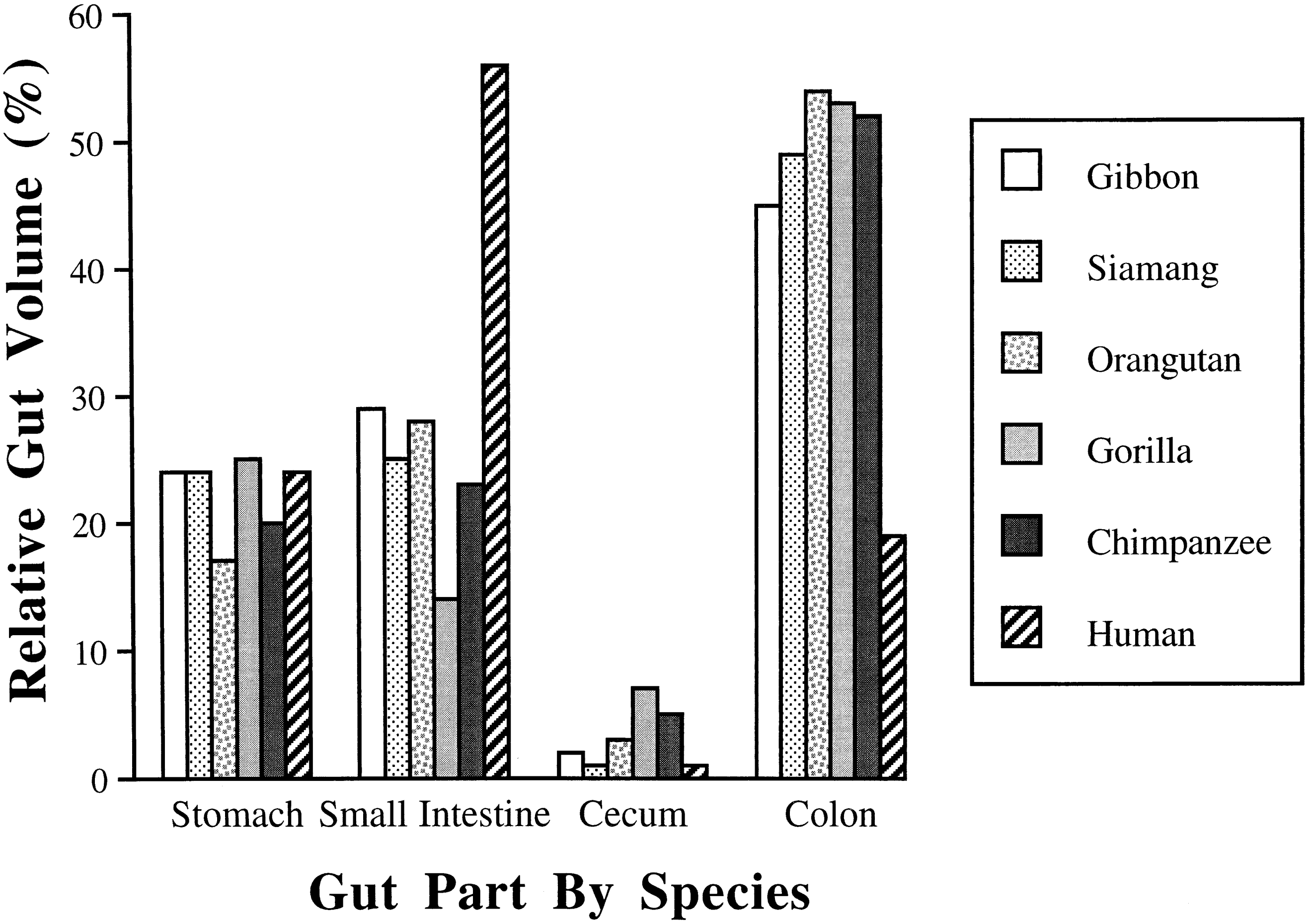

FIG. 1. Relative gut volume proportions for some hominoid primate species (percentage of total volume): gibbon (*Hylobates pileatus*); siamang (*Hylobates syndactylus*); chimpanzee (*Pan troglodytes*); gorilla (*Gorilla gorilla*); orangutan (*Pongo pygmaeus*); human (*Homo sapiens*). See Milton[27] for sources of raw data. All calculations of relative volume by K. Milton.

orous.[27,30,34,51,52] It would appear that both human nutritional requirements and the human pattern of digestive kinetics reflect a ancestral past in which dicotyledenous plant parts (leaves, flowers, and fruits from angiosperm tree and vine species) formed the basis of the daily diet, with perhaps minor input from animal matter, largely invertebrates.[27–29,51]

As wild plant parts compose most of the diet of extant primates and appear to have contributed strongly to the diet of human ancestors, it would be of interest to compare information about the nutritional characteristics of wild plant foods with similar features of foods found in the current American diet. Below such information is summarized and compared with similar data on cultivated plant foods eaten by Americans. No attempt is made to draw any health conclusions from these data; rather, they are presented for consideration.

Most wild plant foods analyzed come from mature trees found in the lowland tropical forest on Barro Colorado Island, a 1500 hectare nature preserve in the Republic of Panama. Analytic protocols are described in the relevant publications. From one to four different monkey species in the Barro Colorado forest eat these wild foods. Other free-ranging primates in forests of Central and South America, Africa, and Southeast Asia have likewise been observed to eat foods from many of the same plant families, genera, and, occasionally, even the same species as these Panamanian monkeys.[53–55] For this reason, results of Panamanian plant analyses are believed to be characteristic of wild plant foods eaten by primates on a pantropical basis.

WILD VERSUS CULTIVATED FRUITS

Domesticated fleshy fruits such as those purchased in American supermarkets typically have an attractive appearance, considerable succulent pulp, and few or no seeds. These fruits have been selectively bred for such characteristics and for a very sweet taste. They appear highly superior to their wild counterparts in the tropical forest, which tend to have a high seed-to-pulp ratio, a less pronounced sweet taste and, often an unappealing appearance (unpublished observations). However, most non-human primates, including the line giving rise to humans, evolved eating wild fruits similar or identical to those primates eat today, not the cultivated fruits humans now eat.

One important difference between wild and cultivated fruits is that sugar in the pulp of wild fruits tends to be hexose-dominated (some fructose and considerable glucose; Table I) while that of cultivated fruits tends to be highest in sucrose, a disaccharide.[56–60] For example, the major sugars in Haden mangos, a cultivated fruit variety, were 20.6% fructose, 5.3% D-glucose and 74.1% sucrose.[58] Juices from the cultivated Valencia orange and Darcy tangerine showed the same sugar pattern as Haden mangos—

TABLE I.

PRINCIPAL SUGARS IN FIVE SPECIES OF WILD PANAMANIAN FRUIT

Wild fruit species from Panama	Sugar	Proportion by weight	Ratio (sucrose/glucose + fructose)
Ficus insipida	sucrose	.037	.040
	glucose	.613	
	fructose	.335	
Ficus costaricana	sucrose	.049	.052
	glucose	.616	
	fructose	.300	
Ficus trigonata	sucrose	.048	.050
	glucose	.643	
	fructose	.309	
Spondias mombin	sucrose	.027	.029
	glucose	.524	
	fructose	.421	
Gustavia superba	sucrose	.085	.100
	glucose	.522	
	fructose	.331	

All data from unpublished work carried out by I. Baker and H. Baker on fruits from tree species in Panama eaten by wild primates. Methodology used for individual sugar determinations described in Baker and Baker.[56] Though the above is a small sample, the extensive work carried out by Baker and Baker on the nectars and fruit sugars of a very large sample of tropical forest plant species confirm that it is a representative sample.

highest by far in sucrose, followed by fructose, and lowest in glucose.[59] Ripe papaya, another cultivated fruit, is also highest in sucrose (i.e., 48.3% sucrose, 29.8% glucose, and 21.9% fructose).[60] Cultivated fruits, therefore, show a different pattern of sugars than is generally found in wild fruits eaten by free-ranging monkeys and apes (Table I).

In terms of sweetness to humans, fructose is ranked 115–170, sucrose 100, and glucose 70.[61] Cultivated fruits are, therefore, very taste appealing to humans, as they have been artificially selected so that they offer sucrose (and fructose) rather than glucose as their principal sugar reward. Refined sugar, for example, is almost 100% sucrose.

Humans clearly come from an evolutionary past in which hexose- rather than sucrose-dominated fruits were consumed, and human digestive physiology should, therefore, be best adapted to a carbohydrate substrate similar to that of wild fruits. But, in addition, wild fruits differ in other respects from their cultivated counterparts. These include a high content of roughage—woody seeds, fibrous strands—as well as higher average protein levels, higher levels of many essential micronutrients (discussed in following sections) and, at times, considerable pectin.

Though pectin is generally thought of in connection with fruits, data show that as a class wild tropical tree leaves average a higher content of pectic substances than wild fruits.[62] However, some species of wild fruits consumed in quantity by many primates are rich in pectic substances.[62] Most or perhaps all mammals, including humans, possess microorganisms in the lower tract that rapidly and efficiently ferment pectic substances.[63–67] Volatile fatty acids produced in fermentation can provide energetic benefits to the feeder.[63–67] Some volatile fatty acids (i.e., butyric) produced in fermentation[65] exhibit strong anticancer properties against a variety of tumors both in vitro and in vivo.[5]

As a class, succulent (fleshy) wild fruits are not high in protein (average crude protein content dry weight of 7 species of wild Venezuelan fruits eaten by red howler monkeys = 7.0 ± 1.1%;[44] average crude protein content dry weight of 23 species of wild fruits eaten by chimpanzees in Uganda = 7.7%;[49] average crude protein content dry weight of 8 species of wild fruits eaten by lowland gorillas in Cameroon = 6.3 ± 0.6.[67] The average crude protein content dry weight of 18 species of wild Panamanian fruits eaten by several monkey species was 6.5 ± 2.6% (KM, unpublished data, Kjeldahl technique and 6.25 conversion factor). All of these wild fruit samples show a somewhat higher average crude protein content dry weight than cultivated fruits in the US (average crude protein content dry weight of 17 species of cultivated fruits = 5.2 ± 2.6%; mean calculated by KM from protein values given for each species in Nutritive Value of Foods).[68] Wild fruits also frequently contain tiny insects and larvae which are inadvertently consumed by feeding monkeys and apes along with fruit pulp. These particles of animal matter are probably not useful as a protein source[69] but they can serve as an important source of essential micronutrients such as vitamin B_{12}. Many wild fruits also contain considerable vitamin C. Though cultivated fruits look appealing and taste sweet, data suggest they may be less nutritious overall than wild fruits, and, perhaps, more demanding of some features of human physiology.

MINERALS

Micronutrients—minerals and vitamins—are rapidly moving into a prominent position in medical and nutritional circles. Many problems associated with malnutrition and child development in developing countries are now believed to involve an inadequate intake of energy or particular vitamins and minerals.[7,9,70] Until recently, it was widely believed that protein or amino acid deficiency was responsible for the symptomology of chronic malnutrition in many developing nations.[7] Careful analysis of diet in several areas of symptomatic chronic malnutrition, namely Mexico, Egypt and Kenya, appears to have effectively eliminated the possibility that protein or amino acids are the culprit here.[7] Interest has now shifted to the likelihood of energy, vitamin, and mineral deficiencies as primary factors.[7,9] Micronutrient deficiencies are not confined to the developing nations. Many Americans take in suboptimal levels of particular minerals or vitamins and this lack may relate to various health problems.[16,17,72,73]

Table II presents comparative data on mineral levels in wild fruit and leaf species eaten by free-ranging monkeys and other mammals and cultivated fruits and vegetables eaten by Americans. Nelson et al. (unpublished observations) looked at mineral concentrations for Fe, Na, Ca, Cu, K, Mn, Zn, and Mg in 16 species of wild and 4 species of cultivated fruits in American Samoa (Table II). Four of the eight minerals examined (Cu, Fe, Na, Ca) showed significantly higher values in wild fruits; wild fruits also showed more interspecific variation in mineral content relative to cultivated fruits (unpublished observations). A small sample of wild Panamanian fruits eaten by monkeys showed higher average values for Ca, P, K, and Fe relative to cultivated fruits; wild Panamanian leaves averaged higher Ca than leafy vegetables eaten in the United States (Table II). Booth et al.[74] noted that wild leafy vegetables consumed by the Kekchi people of Alta Verapaz, Guatemala, had generally higher nutrient values than domesticated green vegetables grown in Kekchi gardens, and stressed the high iron content of wild leafy foods. Kuhnlein[75] showed that the average mineral content (Ca, Ma, Mg, Fe, Zn) of traditional Hopi cereals was higher than values for comparable USDA commodities. These and other comparative data suggest that, as a class, wild plant foods, regardless of geographic locale, may often show higher values and more interspecific variation in their content of some important minerals than cultivated plant foods.[74,75]

TABLE II.

MINERAL CONTENT OF WILD AND CULTIVATED PLANT FOODS (MEAN ± SD, EXCEPT WHEN <4 SPECIES)

	Ca	P	K	Na	Mg	Fe	Mn	Cu
	mg/g dry weight					μg/g dry weight		
Wild Panama*								
Leaves, young (6 species)	14.9 ± 15.5	2.2 ± 1.2	21.1 ± 5.8	2.3 ± 3.9	4.6 ± 2.6	84.4 ± 25.5	74 ± 81	19.6 ± 17.0
Fruits, ripe	12.7	1.5	24.1	0.5	2.5	52	54	5
(2 species)	13.6	1.2	26.1	0.5	3.1	53	39	3.5
Fruits, immature (1 species)	13.3	2.5	23.3	0.6	6.2	183	79	15.1
Flowers (1 species)	3.0	2.7	39.6	2.7	4.3	59.0	4.0	22.7
Wild Samoa†								
Fruits (16 species)	5.1 ± 3.7	—	20.0 ± 9.0	1.5 ± 0.9	3.3 ± 1.3	86.9 ± 63.3	10.6 ± 6.4	9.0 ± 3.6
Cultivated US‡								
Foliar cultivars (11 species)	11.2 ± 7.8	4.9 ± 1.8	34.9 ± 17.6	—	—	188.3 ± 124.9	—	—
Other cultivars (10 species)	3.3 ± 2.8	5.9 ± 2.6	22.5 ± 2.6	—	—	81.0 ± 32.6	—	—
Root cultivars (3 species)	1.3 ± 1.0	2.5 ± 0.8	14.2 ± 5.9	—	—	33.0 ± 12.3	—	—
Cultivated fruits (20 species)	1.3 ± 0.8	1.1 ± 0.3	13.0 ± 4.6	—	—	34.8 ± 14.6	—	—
Cultivated Samoa†								
Cultivated fruits (4 species)	1.2 ± 0.9	—	20.8 ± 2.9	0.2 ± 0.1	2.5 ± 0.6	8.3 ± 6.3	8.5 ± 2.9	5.0 ± 2.1

* Nagy and Milton.[76]

† Nelson et al. (unpublished observations).

‡ USDA, Nutritive Value of Foods.[68]

Ca, calcium; Cu, copper; Fe, iron; K, potassium; Mg, magnesium; Mn, manganese; Na, sodium; P, phosphorous.

— indicates no information available.

Nagy and Milton[76] estimated the daily intake of certain minerals in the natural diet of wild Panamanian howler monkeys (Table III). Relative to body weight, these monkeys, and by analogy other wild monkeys and apes, take in high amounts of many important minerals each day relative to recommendations suggested for the average adult American (Table III).[15,77] The mineral requirements and efficiency of assimilation of most minerals for monkeys and apes is not known, though there seems little doubt that they require most if not all nutrients, including minerals, known to be required by humans.[44]

VITAMIN C

Vitamin C is of particular interest in terms of human nutrition because, unlike most mammals that synthesize their own ascorbate internally, all anthropoids tested to date, including humans, lack the enzyme L-gulonolactone oxidase (GLO, EC 1.1.3.8), which catalyzes the final step in ascorbate synthesis from glucose.[78] For this reason, monkeys, apes, and humans must ingest adequate vitamin C in the diet. The inability to synthesize vitamin C appears to be the derived condition since most extant mammals can synthesize their own supply. Its lack in present-day anthropoids suggests that the common ancestor of all anthropoids could not synthesize vitamin C and, therefore, that the diet of this ancestor was rich in vitamin C. It is presumably not a coincidence that the few other mammalian groups unable to synthesize their own vitamin C (for example, the guinea pig, some lagomorphs, and some bats) are all, like anthropoids, strongly herbivorous.[78]

Analysis of some common wild plant foods consumed by free-ranging primates in Panama shows that many of these foods contain notable amounts of vitamin C (Table IV).[78] One species of wild fig, *Ficus yoponensis*, showed a vitamin C content in both its very young leaves and unripe fruits that appears to be among the highest ever reported.[78] Our closest living relatives, the great apes (and bear in mind that we are speaking of animals that can be as large or larger than many adult Americans), are eating diets that, depending on species and sex, may contain from 2 to as much as 6 or more g of vitamin C per d (Table V). In contrast, the recommended vitamin C allowance for the average adult American is 60 mg per d.[15]

Vitamin C is widely regarded as a potent antioxidant.[5,6,79,80] The physiologic processes of wild primates appear to be carried out with generous amounts of fresh vitamin C continuously present in the body. Though these wild plant foods have not, as yet, been analyzed for other vitamins, it is likely that the young leaves and fruits wild monkeys and apes eat are also rich in vitamin E and provitamin-A, like vitamin C regarded as antioxidants,[5,6,79,80] as well as vitamin K and folic acid.[77,81,82]

FATTY ACIDS

There is strong interest in the types and amounts of fatty acids best suited for human health, and the percentage of daily calories

TABLE III.

ESTIMATED MINERAL INTAKES OF WILD MONKEYS AND HUMANS

Mineral	Estimated intake–wild monkey, kg/d*	Total daily intake–7 kg adult monkey*	Total daily RDA, adult human male
Calcium, mg	653	4571	800
Phosphorus, mg	104	728	800
Potassium, mg	917	6419	1600–2000
Sodium, mg	26	182	500
Chloride, mg	254	1778	750
Magnesium, mg	189	1323	350
Iron, mg	5.5	38.5	10.0
Manganese, mg	2.6	18.2	2.0–5.0
Copper, mg	0.4	2.8	1.5–3.0

* Modified from material in Nagy and Milton.[76] Intakes derived from feeding trials and observations of wild howler monkeys eating a typical leaf and fruit diet. See Nagy and Milton[76] for details of feeding trials and analytical protocols. RDAs for humans taken from RDA 10th ed.[15]

TABLE V.

ESTIMATED DAILY ASCORBIC ACID INTAKE (MG/KG BODY WEIGHT/D)$^{-1}$

Wild howler monkey	88 mg/kg or ∼600 mg ascorbate per d for a 7-kg monkey
Wild spider monkey	106 mg/kg or ∼744 mg ascorbate per d for an 8-kg monkey
Wild mountain gorilla	20–30 mg/kg or 2–4 g (or more) ascorbate per d for a 100–160 kg gorilla
Recommended daily intake, average adult American male >25 y of age*	60 mg per d

* Human value from RDA, 10th ed.[15]
Modified from Milton and Jenness.[78]

that should come from dietary fat.[4,6,7,72] Analysis of the fatty acid composition of wild plant foods eaten by Panamanian monkeys showed the predominate fatty acids to be palmitic (30%), linoleic (23%), alpha linolenic (16%), and oleic (15%).[83] Fatty acids with less than 16 and more than 18 carbon chains were uncommon (range 0–7%).[83]

Wild plant foods tended to show a fairly equal balance between saturated (average = 45%) and unsaturated (average = 54%) fat.[83] The P/S ratio of wild howler monkeys eating their natural fruit-and-leaf diet is estimated at 0.85 which is very close to the 1.0 ratio recommended for humans.[83,84] In contrast, Americans have P/S ratios of around 0.4.[83] It is recommended that dietary fats not exceed 30% of daily caloric intake in the US diet, though most Americans take in more fat each day than recommended (>36% of calories).[72,84–86] Dietary fats are estimated to contribute only some 17% of daily caloric intake for howler monkeys.[83]

All wild foods analyzed for fatty acids—basically an opportunistic selection of wild plant foods monkeys routinely eat—contained notable amounts of alpha linolenic (ALA, 18:3, ω-3) as well as linoleic acid (18:2, ω-6). The routine intake of notable amounts of ALA as well as linoleic acid 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 oils from monocot seeds. Most seed oils are high in linoleic but low in ALA.[84,86] The few seed oils high in ALA (e.g., soy, canola)[84,86] tend to be low in linoleic acid.

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).[84] But most Americans do not consume large quantities of these plant foods either fresh or cooked; cooking of these foods also tends to destroy ALA.[84] The diet of human ancestors (like the diets of extant monkeys and apes) was likely rich in both linoleic acid and ALA from fresh plant tissues and for this reason the fatty acid composition of such plant foods is likely to be most compatible with human biology.

TABLE IV.

COMPARISON OF THE ASCORBIC ACID (MG/G DRY WEIGHT) CONTENT OF WILD AND CULTIVATED FOODS

	No. species	No. specimens	Ascorbic acid Mean	Ascorbic acid SD
Panamanian wild foods				
Fruits	10	14	2.7	3.2
Fruits*	10	13	2.0	1.8
Leaves	16	40	2.8	3.5
Leaves†	16	39	2.2	1.1
Flowers	3	4	1.7	5.2
Cultivated Foods, US				
Fruits	20	—	1.6	1.7
Vegetables	18		5.4	4.4
Vegetables‡	17	—	4.7	3.2
Root cultivars	3	—	0.8	0.1

* With unripe fruits of *Ficus yoponensis* excluded.
† With very young leaves of *F. yoponensis* excluded.
‡ With sweet pepper excluded.
Source of Panamanian data: Milton and Jenness.[78]
Source of cultivated foods, US: calculated by K. Milton from information in USDA, Nutritive Value of Foods.[68]

PROTEIN AND AMINO ACIDS

Carpenter[87,88] has discussed the many misconceptions regarding protein requirements of humans, particularly misconceptions regarding the need for, or benefits of, large quantities of animal protein in the human diet. We now know that the average adult American appears to require somewhat less than 1 g of high quality protein per kg of body weight per day (0.75 g/kg average daily requirement for reference protein)[15] to meet protein requirements.[77,81] When thinking of protein sources, tree leaves and fruits do not generally come to mind. However, if one examines the diet of a wild primate such as a howler monkey, it is clear that leaves and fruits generally satisfy its daily protein as well as energy requirements.[89,90] As noted, even very large primates such as gorillas, orangutans, and chimpanzees thrive on diets composed largely of plant foods, both leaves and fruits, though on occasion, small amounts of animal matter may also be ingested.[45–50,67,91]

Because larger-bodied anthropoids tend to satisfy most (and at times all) protein requirements from the ingestion of plant matter,

TABLE VI.

INDIVIDUAL AMINO ACID CONTENT OF TROPICAL PLANT PARTS—ESSENTIAL AMINO ACIDS FOR HUMANS*
(G AMINO ACID/100 G DRY SAMPLE)

	His	Iso	Leu	Lys	Met	Val	Phe	Thr
Tachigalia paniculata, very young leaves	0.71	1.06	1.79	1.48	0.30	1.37	1.39	1.03
Ceiba pentandra, very young leaves	0.42	1.02	1.82	1.65	0.39	1.27	1.07	0.90
Zanthoxylum panamensis, flower buds	0.30	0.86	1.32	1.12	0.24	1.05	0.99	0.80
Ficus insipida, rolled very young leaves	0.21	0.77	1.28	0.96	0.17	1.02	0.89	0.76
Ficus inspida, mature leaves	0.00	0.76	1.41	0.83	0.28	1.05	0.99	0.75
Ficus inspida, leaves of moderate age	0.29	0.69	1.15	0.83	0.31	0.90	0.94	0.70
Tababuia guyacan, flowers	0.29	0.65	1.09	0.63	0.42	0.85	0.82	0.60
Ceiba pentandra, mature leaves	0.23	0.65	1.08	0.80	0.22	0.86	0.79	0.54
Tetragastris panamensis, mature leaves	0.19	0.52	0.98	0.75	0.22	0.73	0.73	0.52
Ficus nymphaefolia, mature leaves	0.14	0.42	0.71	0.48	0.15	0.57	0.40	0.39
Protium panamensis, mature leaves	0.10	0.40	0.79	0.52	0.18	0.52	0.54	0.39
Dioclea reflexa, flowers	0.18	0.40	0.64	0.49	0.12	0.53	0.44	0.36
Ficus insipida, ripe fruit	0.00	0.36	0.60	0.35	0.18	0.51	0.46	0.36

* Wardlaw and Insell.[93] No analysis done for tryptophan. Leaf proteins typically contain from 1.6–2.1% tryptophan.[44]

Modified from Milton and Dintzis.[92] Data from duplicate samples using a standard 24-h hydrolysis.

His, histidine; Iso, isoleucine; Leu, leucine; Lys, lysine; Met, methionine; Phe, phenylalanine; Thr, threonine; Val, valine.

it is useful to examine some characteristics of plant protein. Young leaves routinely consumed by wild monkeys in Panama show an average crude protein content dry weight of 12.4 ± 4.2%;[89] flowers too are often high in protein (range 9–10% to 20–25% crude protein dry weight).[90] Though not particularly high in protein relative to young leaves, as discussed above, wild fruits usually average a higher protein content than their cultivated counterparts.

Protein estimates for plant samples from Panama were derived by obtaining the total nitrogen content of each sample using the Kjeldahl method and then multiplying the result by the standard 6.25 conversion factor, a factor originally derived from studies of animal protein. Data suggest that a more accurate protein conversion factor for wild plant parts is 4.4.[92] Use of this conversion factor would lower the protein estimates given above (as well as alter similarly derived protein values in the literature for cultivated plant parts). However, regardless of whether the 6.25 or 4.4 conversion factor is used, it is clear that many wild primates are able to fulfill most or all of their estimated daily protein requirements largely or entirely from plant foods.

Though some grains, nuts, and seeds are low in 1 or more of the essential amino acids humans require,[93] amino acid profiles for the 10 major amino acids of leaf protein and animal protein are very similar.[94] Perhaps in response to the often considerable inter- and intraspecific variation in the percentage of a particular amino acid in wild plant parts (Table VI), we find that free-ranging monkeys and apes typically eat leaves and fruits from a variety of different trees, vines, and other plant species each day.[27,47,49,91] For example, howler monkeys take foods from an average of 8 different plant species per d (and occasionally from as many as 24 or more species),[90] while spider monkeys take foods from an average of 9 plant species per d;[95] both monkey species, like most wild primates, typically take foods from well over 125 different plant species per y.[27,90] By mixing plant parts from a variety of different tree and vine species each day, these monkeys are able to upgrade overall dietary quality in terms of complementary amino acids as well as other nutrients.[76,96] Humans can achieve the same result by mixing together two vegetable foods such as corn and beans.

For various reasons, it is generally the case that plant protein has a lower biological value and a lower digestibility than protein from whole animal foods.[88] Meat protein, which is essentially identical in its protein composition to human protein, can "be deposited with virtually no modification" and is generally 95–100% digestible (average digestibility = 98%).[88] In contrast, vegetable foods such as legumes and oilseed flours show a protein digestibility in humans of some 84–97% (average digestibility = 90%).[88]

One reason for the lower digestibility of plant protein could be that plant parts generally contain secondary compounds (e.g., tannins, phenolics, alkaloids, terpenoids, and the like).[90,97–99] Some compounds, such as condensed tannins, can bind with protein in the gut, rendering it largely unavailable to the feeder.[99,100] Perhaps in response to the tannin content of many wild plant foods, humans and probably most primates possess proline-rich proteins (PRPs) in saliva.[101] These proteins have a high affinity for tannins and have been demonstrated to reverse the detrimental effects of tannins in the diets of rats and mice.[101] About 70% of the proteins in human salivary secretions consist of PRPs.[101]

Because of the many secondary compounds in their foods, wild primates may need to consume more grams of protein per day than would be predicted by body weight.[102] Assimilation studies suggest that, on average, some 20% or more of the total N in wild plant parts is unavailable to the primate feeder.[102] Thus, for example, a 7–9 kg wild howler monkey might have to take in some 20 or more g of protein each d in its wild foods to net the 12 or so g of protein it is estimated to require.[102]

Monkeys and apes can digest both meat and vegetable protein[43,103] and many anthropoid species that have not been noted to eat vertebrate prey in the wild seem willing to eat meat in captivity if it is offered. However, studies of the feeding behavior of primates in the natural environment show that, in general, wild monkeys and apes do not typically eat large quantities of animal matter each day and many larger anthropoids rarely ingest animal matter. Though animal protein may generally be of higher quality and more digestible, plant protein appears to suffice for many monkey and ape species.

Because wild leaves, even young leaves, typically have a high percentage of indigestible cell wall material (average cell wall content dry weight [NDF] of Panamanian young leaves = 35%)[89] as well as a wide range of secondary compounds,[44,89–91,97–100] it is difficult to speculate on just how useful such foilage could have been as a protein source for human ancestors, because the synergistic effect of all these unknown characteristics must be factored in. Though there is no reason to assume that, in terms of basic nutritional requirements, modern humans are any different than their ancestors or extant apes, the gut proportions and overall gut size which characterize anatomically modern humans could pose problems in terms of the efficient digestion of large quantities of uncooked vegetable matter.

Southgate has estimated that the average adult human would have to consume more than 10 kg fresh weight of leafy plant foods to meet daily protein and energy demands.[104] If these leafy foods had an average water content of 80% and an NDF content similar to wild Panamanian leaves (i.e., 35%), this implies a daily intake of some 700 g of dietary fiber—a considerable amount. Currently, for humans, evidence suggests an average dietary fiber intake in the range of 20–40 g/d in the majority of populations studied throughout the world.[105] However, some present-day rural African populations are estimated to consume 70–90 g of dietary fiber per d.[105] Data from rehydrated human coprolites estimated to be some 10 000 y old show that these individuals appear to have taken in at least 130 g of plant fiber per d and were consuming what appeared to be coarse, high-residue diets.[26] There is little reason to assume that the digestive abilities of humans 10 000 y ago differed to any significant degree from those of present-day humans—all are anatomically modern *Homo sapiens*. But a diet containing hundreds of grams of dietary fiber per day seems unsuited to present-day human gut anatomy and physiology and likely would also prove excessively timely to gather and consume.[104]

DIETARY FIBER

Cellulose and hemicellulose (along with pectin) are the major constituents of dietary fiber.[63,64,106] Until recently, it was commonly believed that humans could not utilize the constituents of dietary fiber and for this reason there was no need to include them in the diet.[106] No mammal, including humans, is known to produce enzymes that can degrade cellulose and hemicellulose. What many mammals including humans do have, however, are anaerobic bacteria and other gut flora in various sections of the digestive tract that can carry out this function.[64–67,90] These microorganisms break down the cellulose and hemicellulose of plants in the process known as fermentation, releasing energy-rich volatile fatty acids which can often be absorbed in significant amounts by the host and may make an important contribution to the host's energy budget.[63–66] It is estimated that some present-day human populations with a high intake of dietary fiber may derive 10% or more of their required daily energy from volatile fatty acids produced in fermentation.[64,107]

Experimental work on human fiber digestion shows that human microflora are very sensitive to different dietary fiber sources.[63,64] Humans are very efficient at degrading the relatively unlignified hemicelluloses and cellulose of dicot vegetable fibers such as cabbage or carrots, but are less efficient on monocot cereal fibers such as wheat bran, or monocot plant fibers such as alfalfa, which show a high cellulose-to-hemicellulose ratio and considerable lignification.[63,64] The traditional foods of anthropoids come from dicot, not monocot, plants[27] and, as noted above, available data suggest that the human pattern of digestive kinetics as well as human fermentation efficiencies on different fiber substrates are similar to those of extant chimpanzees.[31]

CONCLUSIONS AND SUMMARY

Paleontologic, phylogenetic, and morphologic evidence indicate that modern humans come from an ancestral lineage in which the ripe fruits and young leaves of tropical trees and vines are likely to have played a key dietary role. Analytical data suggest that many of the wild plant foods monkeys and apes currently consume differ in some respects from many cultivated fruits and vegetables eaten by humans. In contrast to humans, wild primates also take a high percentage of the daily diet from fresh, uncooked plant foods.

Though most present-day human populations likewise take a high percentage of their daily diet from plant foods, in the human case this plant food is often a single cooked monocot grain or a root product rather than a diverse array of fresh plant parts.[7,14,70] Roots in particular, but also many grains, tend to be low in many essential nutrients humans require.[7,70,93,108,109] Most wild primates do not feed on grasses, grass seeds, or underground storage organs and, as noted, wild monkeys and apes tend to eat a mix of different fresh plant foods each day—a feeding pattern that can result in a higher intake of essential nutrients than would be the case if that primate focused on food from only one or two plant sources per day.[76] Like modern humans, wild primates tend to be very selective feeders, eating only the most nutritious and digestible portions of particular wild foods, and dropping lower quality materials to the ground.[90]

Humans have carried this common primate pattern of high dietary selectivity to an extreme through the use of food preparation techniques (chopping, crushing, husking, cooking, leaching, brewing, and the like),[6,12,21] practices that serve to upgrade, refine, and modify many items of diet before they are ever brought into contact with the teeth and digestive tract of the human feeder.[6,12,29–31] This non-somatic "technologic barrier" between human digestive anatomy and most items of diet appears gradually to have resulted in the gut proportions characteristic of modern *Homo sapiens* as well as a reduction in the size of the dentition and face of modern humans in comparison with those of earlier members of the genus and/or species.[12,27,31,110]

The gradual shift in tooth size (and presumably, since guts do not fossilize, the size of certain sections of the gut), as well as the notable increase in brain size characteristic of the human genus and particularly our species, *Homo sapiens* (increasingly large brain size over the course of human evolution likewise pointing to a high-quality diet),[27–31] did not happen overnight. Rather, evidence from the human fossil and archaeologic record suggests a process involving increased dependence on technology and learning (manufacture and use of stone tools and hunting implements, techniques of food preparation, utilization of new foods) as well as social skills (division of labor, food-sharing, long period of offspring provisioning), much (but not all) of which probably took place over a period of some 2 million y or more.[19,29,31,110,111]

Unfortunately, it would appear that relatively recent human ingenuity has simultaneously both refined and consolidated some salient characteristics of wild foods (e.g., modified the sugar or starch content of many fruits, vegetables, or grains) and inadvertently reduced or removed certain essential nutrients from many foods (e.g., refined sugar, purified vegetable oils, a lower protein, vitamin, or mineral content in some cultivated fruits or vegetables relative to their wild counterparts; some essential nutrients can also be greatly reduced through features of food preparation though at times, the nutrient value of a food can also be increased). These manipulations as well as the general paucity of fresh fruits and vegetables in the diets of most present-day human populations and the low dietary diversity characteristic of many non-Western human populations may make it difficult for many individuals, particularly children, to take in the full complement of essential nutrients they require each day.[7,69,88] For example, an increase in daily calorie consumption in the US may not result in any notable improvement in nutritional status, as typically such calories come from foods high in fats or sugars, and such foods tend to be low in vitamins and minerals.

Meat eating would help to supply many essential micronutrients as well as provide high-quality protein,[88,104] but many present-day human populations (particularly in less industrialized nations), unlike prehistoric human populations or present-day hunter-gatherers, rarely have access to meat. In countries such as the US, where domesticated livestock is common, health implications of differences in the fat content and composition of domesticated livestock relative to wild ungulates have been noted[23,85] and there is also some concern about the effects on human health of various steroids and antibiotics involved in rearing livestock.[112]

In combination, the differences discussed above between the staple foods and dietary intake patterns of many present-day human populations as contrasted with those of extant primates may have produced a gradual cascade effect in humans, which is now manifesting itself in many of the diet-related health problems modern humans are increasingly experiencing. This effect probably relates to a host of other, as yet undiagnosed food-associated problems and conditions as well.

In summary, medical and nutritional scientists generally do not approach the study of diet-associated human health problems from an evolutionary perspective. But modern humans have ancestors and probably differ little from them biologically.[26] Modern humans also have close extant relatives in the primate order and are believed to have come from an ancestral lineage that was strongly herbivorous. Analysis of wild plant foods eaten by free-ranging primates shows that these foods are generally high in many nutrients regarded as essential for human health and well-being. Data suggest that, for their size, many wild primates routinely ingest greater amounts of many minerals, vitamins, essential fatty acids, dietary fiber, and other important dietary constituents than most modern human populations.

Furthermore, in wild primates, nutrients and myriad other chemical constituents of plants are eaten together, a fact that could have health implications that are as yet little investigated or understood. Increasingly, experimental data suggest positive synergistic effects from combinations of particular vitamins or minerals, or nutrients and vitamins, or nutrients and other chemical constituents.[5,79,80,113,114] For this reason too, greater attention to the dietary constituents of wild primate foods could help to guide research related to human diet and health. The increasingly strong recommendations made by both the medical and nutritional communities to consume more fresh fruits and vegetables each day[6,15–18] appear well supported by data presented previously and strengthen the assumption that closer attention to features of the natural diets of wild primates and study of their digestive physiology may provide valuable insights, which can eventually lead to better dietary practices for humans.

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