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Review

Micronutrient intakes of wild primates: are humans different?*

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Abstract

Low micronutrient intake is implicated in a diversity of human health problems, ranging from problems associated with food insufficiency to those associated with food over-consumption. Humans are members of the order primates, suborder anthropoidea, and are most closely related to the great apes. Humans and apes are remarkably similar biologically. In the wild, apes and monkeys consume diets composed largely of plant foods, primarily the fruits and leaves of tropical forest trees and vines. Considerable evidence indicates that the ancestral line giving rise to humans (*Homo* spp.) was likewise strongly herbivorous (plant-eating). The wild plant parts consumed by apes and monkeys show moderate to high levels of many minerals and vitamins. The estimated daily intake of specific minerals, vitamin C and some other vitamins by wild primates is often quite high in comparison to intake levels of these same micronutrients recommended for humans. Are the high micronutrient intakes of wild primates simply a non-functional, unavoidable by-product of their strongly plant-based diets or might they actually be serving important as yet undetermined immunological or other beneficial functions? A better understanding of the basis for this apparent difference between humans and wild primates could help to clarify the range and proportions of micronutrients best suited for optimal human development, health and longevity.

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1. Introduction

Many current human health problems relate to diet and much remains to be discovered about the relationship between humans and their foods. At some point, the biochemical foundations for many human-food interactions will doubtless be better understood. The multifactorial nature of the genetic, cellular and physiological processes involved

for each individual may, however, make such understanding difficult (Williams, 1978; Bengmark, 1998; Lampe, 1999).

Broadly speaking, many diet-related health problems fall into one of two categories. In one category are problems particularly prevalent in low-income nations—these problems often relate to an insufficiency of higher quality foods, especially in infancy and childhood. Such insufficiency is manifested, for example, in the high incidence of linear growth retardation in young children in low-income nations (Calloway et al., 1992; Martorell, 1999; Berkman et al., 2002). In the other category are diet-related health problems especially prevalent in high-income nations—here many such

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problems relate not to food insufficiency but rather to its oversupply and/or the over-consumption of certain food types (Temple, 1994; Bengmark, 1998).

Critical examination of the many factors suggested to relate to the multitude of current human health problems stemming either from food inadequacy or food over-consumption is beyond the scope of this paper. For this reason, I focus on one factor strongly implicated in both sets of problems—namely, micronutrient intake. Using the comparative approach I examine available data on the content of various micronutrients in the foods of wild primates and compare these estimates with similar data on the micronutrient content of cultivated foods available in American super markets. I then compare the probable daily intake of some micronutrients by wild adult monkeys and apes with recommended dietary allowances (RDAs) suggested for adult Americans.

2. Background

Increasingly, clinical evidence suggests that micronutrients are involved in vast array of important biochemical processes. It has long been appreciated that an adequate intake of certain micronutrients relates to the prevention of classic deficiency diseases such as pellegra, scurvy and beriberi (Carpenter, 1981, 1986, 2000). An insufficiency of a particular micronutrient is also known to lead to other specific health conditions (e.g. lack of vitamin A and vision problems or blindness, lack of iron and anemia). However, of late, a new focus on micronutrients is occurring as many other health problems in both low- and high-income nations are now believed to relate, at least in part, to an insufficiency of certain micronutrients.

In low-income nations, for example, iron deficiency is now regarded not only in terms of anemia but also as a risk factor for cognitive defects in school-aged children (Berkman et al., 2002). A dietary study in Kenya designed to test the impact of three different diet supplements (i.e. energy, milk, meat) on cognitive development of school children, showed children receiving supplemental food with meat significantly outperformed all other children on the Raven's Progressive Matrix (Whaley et al., 2002). This outcome was suggested to relate, at least in part, to the many important micronutrients in meat, particularly iron and zinc.

The protein in meat also improves the bioavailability of iron and zinc from grain and some other plant foods—foods composing most of the diet in such communities (Kikafunda et al., 1998; Whaley et al., 2002). A study in Zanzibar likewise concluded that low dose iron supplementation significantly improved language and motor development of a community sample of rural preschool children (Stoltzfus et al., 2001). Zinc supplementation in Ugandan preschool children appeared to lower infection rates (Kikafunda et al., 1998). Indonesian preschoolers given vitamin A fortification had a significantly lower mortality rate and better growth rate than preschoolers not receiving such fortification (Edmonds, 1999). Many studies examining factors related to childhood health and development have reached similar conclusions regarding the importance of micronutrients (e.g. Calloway et al., 1992).

In high-income nations on the other hand, micronutrients are currently being viewed in a somewhat different light. Here inadequate micronutrient intake is of concern as it is hypothesized to relate not only to traditional deficiency diseases and developmental problems but also to DNA damage, cancer and other degenerative diseases (MacGregor, 1990; Block et al., 1992; Temple, 1994; Ames, 1989; Prasad et al., 1998; Victoroff, 2002). A recent review of studies examining the role of dietary factors in cancer risk, for example, determined that, overall, there is a considerably higher cancer incidence among people who consume fewer fruits and vegetables when compared with those who consume the most (Ames and Wakimoto, 2002). A dietary pattern rich in fruits and vegetables also appears to play a protective role in the prevention of cardiovascular disease and stroke (Bazzana et al., 2002).

These studies 'firmly establish' (Rimm, 2002) that the intake of fruit and vegetables lowers the risk of chronic disease but they do not identify the biological mechanisms responsible for this benefit (Prasad et al., 1998; Ames and Wakimoto, 2002). It is not clear which of the many chemical constituents in fruits and vegetables may be responsible for such protective effects. But there is strong evidence that certain micronutrient deficiencies cause DNA damage (Castro et al., 1992; Ames and Wakimoto, 2002) and diets deficient in fruits and vegetables are commonly low in folate, and vitamins C and E, among other micronutrients (Ames, 1989; Ames and Wakimoto, 2002).

Folate is an important component in DNA synthesis while vitamins C and E are generally regarded as potent antioxidants (Wardlaw and Insel, 1996; Ames and Wakimoto, 2002). It is currently estimated that approximately two and a half billion people are severely deficient in one or more micronutrients, even though they get adequate or marginally adequate macronutrients or calories each day (Beachy et al., 2002). Most Americans (i.e. 80% of children and adolescents, 68% of adults; Krebs-Smith et al., 1995) take in low levels of various micronutrients—levels lower than recommended by the National Cancer Institute and National Research Council (Murphy et al., 1992; Krebs-Smith et al., 1995) and likely insufficient for optimal health and longevity (Ames and Wakimoto, 2002; Lewis et al., 1998). Underconsumption of calcium, iron, magnesium, zinc, folate, and vitamins B-6, A, E and C has been reported for adults in the United States (US) (Murphy et al., 1992; Lewis et al., 1998; Ames and Wakimoto, 2002).

As low micronutrient intake is implicated in such a wide range of human health problems, it is of interest to examine the micronutrient content of a representative range of wild foods eaten by monkeys and apes and estimate their micronutrient intakes. As non-human primates, particularly the great apes, are extremely similar to humans biologically, it is logical to assume they should show similar micronutrient requirements (Portman, 1970).

3. Diets of wild anthropoids

A wide variety of field studies provide data on the daily diets of primates in the natural environment (Rodman, 1977; Wrangham, 1977; Milton, 1980; Calvert, 1985; Cords, 1987; Whiten et al., 1991; Tutin et al., 1991; Matsumoto-Oda et al., 1998). These studies show that both monkeys and apes feed primarily on plant foods, eating moderate to trace amounts of animal source foods (ASF), generally insects (Harding, 1981). For example, on average, African blue monkeys (*Cercopithecus mitis*) and red-tailed monkeys (*Cercopithecus ascanius*) are estimated to spend 73 and 75%, respectively, of their daily feeding time on plant foods (Cords, 1987) while for most baboon (*Papio* spp.) species, this figure is placed at >90% (Whiten et al., 1991). North Indian, forest-based rhesus macaques (*Macaca mulatta*) are reported

to take ‘almost the entire diet’ from plant foods, principally fruits (Lindburg, 1977). In the Neotropics, plant foods are estimated to make up >99% of the annual diet of wild howler monkeys (*Alouatta* spp.) and spider monkeys (*Ateles* spp.) (Milton, 1980, 1993a).

Among primates, the great apes are most closely related to humans and data suggest that humans and chimpanzees may have shared a common ancestor as recently as 7–5 million years ago (mya) (Wildman et al., 2002). The natural diets of wild orangutans (*Pongo pygmaeus*) and gorillas (*Gorilla gorilla*) are composed almost exclusively (>97%) of plant foods (Rodman, 1977; Calvert, 1985) while for common chimpanzees (*Pan troglodytes*), this figure is placed at 88.5 to ≥95%, depending on season and study site (Wrangham, 1977; Hladik, 1977; Stanford, 1999; Matsumoto-Oda et al., 1998). Though chimpanzees occasionally kill and eat vertebrate prey and often eat ants or termites, ASFs make up only a small proportion of the average chimpanzee diet, which is composed largely of ripe fruits (Hladik, 1977; Wrangham, 1977; Tutin et al., 1991; Stanford, 1999; Matsumoto-Oda et al., 1998). All great apes can therefore be regarded as very strongly herbivorous (plant-eating).

For wild primates as a class, fruit is by far the most commonly consumed category of wild plant food (Harding, 1981). Many primates also take some proportion of the daily diet from leaves, generally young leaves, but with a few exceptions only large-bodied or digestively specialized primates (e.g. Colobinae) eat notable quantities of leaves each day. Flowers, arils, seeds, bark, petioles, rhizomes and other plant parts are also eaten by some primates (Harding, 1981).

Most wild primates also eat moderate to trace amounts of ASFs each day, generally insects or other invertebrates and some species (e.g. chimpanzees, capuchin monkeys, baboons) will capture and eat smaller vertebrates. However, out of 131 primate species surveyed, none had ASFs as a major dietary component (Harding, 1981). Though ASFs can be an important source of micronutrients, particularly B₆, B₁₂, iron and zinc, I confine my examination below to the plant food portion of the wild primate diet. Any animal matter ingested would only increase micronutrient intake estimates.

The plant-based dietary focus of apes and monkeys appears evolutionarily quite ancient. The dentition of fossil apes more than 15 million years

old indicates a plant-eating, primarily frugivorous, way of life (Kay, 1977). There seems general consensus that the ancestral form giving rise to the human (*Homo*) lineage was likewise markedly herbivorous, a fact supported by the sacculated form of the modern human colon, the slow kinetic pattern of ingesta turnover which characterizes both humans and the great apes and the inability of humans (and all other anthropoids) to synthesize vitamin C—a trait found in only a few other highly herbivorous lineages (Milton and Jenness, 1987; Milton and Demment, 1988; Caton, 1999; Caton et al., 1999).

4. Micronutrient content of wild primate foods

Primates are believed to have evolved in tropical forests and even today most are highly arboreal. Therefore, the plant foods available to them over their long evolutionary history have been largely the leaves, fruits and flowers of tropical forest trees and vines. Remarkably little is known about the micronutrient content of such wild foods. Table 1 presents some comparative data on mineral levels of some wild fruit, leaf and flower species eaten by free-ranging monkeys, apes and bats and cultivated fruits and vegetables eaten by Americans and Samoans. As soil type and other environmental conditions can greatly affect the chemical composition of plants, data from several locales are given for the wild foods.

4.1. Minerals

Various wild plant foods compare favorably in levels of some minerals with cultivated plant foods (Table 1). Wild fruits from Panama, Venezuela, Gabon, Cameroon and Samoa show higher average values for calcium and phosphorous than cultivated fruits from the US and Samoa. Wild fruits from Panama, Cameroon and Samoa are also higher in potassium than cultivated fruits from the US and Samoa and higher in iron than cultivated fruits from the US. Table 1 also presents comparative estimates for 16 species of wild and 4 species of cultivated fruits from American Samoa (Nelson et al., 2000). All of the Samoan wild fruits, which are eaten by bats, are similar in type and composition to those eaten by wild primates. Wild Samoan fruits differed significantly from cultivated Samoan fruits in mean levels of copper, iron, sodium and calcium (Nelson et al., 2000). Wild

Samoaan fruits also showed more interspecific variation in mineral content than cultivated Samoan fruits.

Results are mixed for the mineral content of wild leaves (and flowers) when compared with those from cultivated foliar and other vegetable foods. Wild leaves from Panama and Cameroon, for example, average slightly higher calcium values relative to cultivated foods but wild leaves from Venezuela and Gabon are lower in calcium than similar cultivated foods. Cultivated leafy and vegetable foods from the US are higher in phosphorous and potassium than wild leaves from any site examined (Table 1).

Similar results have been found in other studies in which wild fruits, leaves or other wild plant parts eaten by humans were compared with locally available, cultivated plant foods in the same food category (Brand et al., 1983; Booth et al., 1992; Kuhnlein and Turner, 1991). These data indicate that wild plant foods of many types show moderate to high values for various minerals relative to their cultivated counterparts as well as high interspecific variation for particular minerals within sites. This latter feature is important because, for example, though most wild plant foods at a given locale may be low in a particular mineral, one or two are likely to be unusually high. By eating a variety of different plant foods each day (e.g. fruits and leaves from a number of different species), a characteristic feeding pattern of wild primates (Milton, 1987), a monkey or ape is more likely to get the optimal level of each micronutrient required (Nagy and Milton, 1979; Milton, 1999a).

4.2. Vitamins

There appears to be little information on the vitamin content of wild fruits and leaves from tropical forest tree species eaten by wild primates. One vitamin which has been fairly extensively examined in wild foods is vitamin C or ascorbate. Both leaves and fruits from wild plant species, including tree species, have been examined for ascorbate content in both tropical and temperate locales (Jones and Hughes, 1983; Dash and Jenness, 1985; Keshinro, 1985). This interest likely stems from the fact that vitamin C is of particular importance to humans. Unlike most mammals which synthesize their own ascorbate internally, all anthropoids, including humans, lack the enzyme L-gulonolactone oxidase (GLO, EC 1.1.3.8),

Table 1
Mineral content of wild and cultivated plant foods (mean ± S.D.)

	Ca (mg/g dry wt.)	P (mg/g dry wt.)	K (mg/g dry wt.)	Na (mg/g dry wt.)	Mg (mg/g dry wt.)	Fe (µg/g dry wt.)	Mn (µg/g dry wt.)	Cu (µg/g dry wt.)
<i>Wild Panama</i> ^a								
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 (2 species)	13.1 ± 0.6	1.3 ± 0.02	25.1 ± 1.4	0.5 ± 0	2.8 ± 0.4	52.5 ± 0.7	46.5 ± 10.6	4.2 ± 1.1
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
<i>Wild Venezuela</i> ^b								
Leaves (5 species)	2.9 ± 0.7	2.8 ± 0.6	–	–	–	–	–	–
Fruits (9 species)	6.4 ± 1.7	1.6 ± 0.5	–	–	–	–	–	–
<i>Wild Gabon</i> ^c								
Leaves (5 species) (4 species Na)	2.7 ± 1.1	1.9 ± 0.5	13.8 ± 2.2	3.3 ± 1.8	–	–	–	–
Fruits (8 species) (7 species Na)	3.2 ± 2.2	1.2 ± 0.5	11.7 ± 4.0	1.3 ± 0.5	–	–	–	–
Flowers (2 species)	3.4 ± 1.5	2.9 ± 0.01	19.3 ± 7.6	1.9 ± 1.3	–	–	–	–
<i>Wild Cameroon</i> ^d								
Leaves (5 species)	12.3 ± 11.5	1.8 ± 0.8	17.2 ± 8.5	0.2 ± 0.1	2.4 ± 1.6	260 ± 200	342 ± 131	14.0 ± 7.0
Fruits (6 species)	3.5 ± 4.5	1.3 ± 0.9	16.0 ± 11.0	0.1 ± 0.2	1.4 ± 0.6	250 ± 469	120 ± 147	12.0 ± 11.0
<i>Wild Samoa</i> ^e								
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
<i>Cultivated Samoa</i> ^f								
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
<i>Cultivated US</i> ^g								
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	–	–

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

^a Nagy and Milton (1979).

^b Oftedal (1991).

^c Hladik (1977).

^d Calvert (1985).

^e Nelson et al. (2000).

^f Nelson et al. (2000).

^g USDA, Nutritive Value of Foods, 10th ed., 1981.

Table 2
Ascorbic acid content of plant parts from different locales

Locale, kind of samples	Ascorbic Acid (mg/100 g fresh wt.)						Ref.
	No. Species	No. Specimens	Mean*	S.D.	Median	Range	
Panama							
Foliage	16	40	96.3	92.6	78	7–585	†
Foliage**	16	39	83.8	48.6	76	7–212	†
Fruit	10	14	62.4	72.0	37	6–268	†
Fruit***	10	13	46.5	42.6	33	6–128	†
Flowers	3	4				16–180	†
Venezuela							
Foliage****	4		197.5	86.1		119–300	+
Fruit juice****	4		85.0	32.6		55–118	+
Nigeria							
Fruit unusual	10		81.7	81.9		12–260	‡
Fruit common	8		73.6	88.5		17–289	‡
Wales (UK)							
Foliage	213	ca. 2500	161.7	109.4			§
New South Wales (Australia)							
Foliage (evergreen)	10	10	198.3	81.8		102–307	≠
Foliar cultivars	10		57.3	26.2			§
Plant food of							
hunter-gatherers	27		26.8				Δ

*Mean of all specimens for Panama material, mean of species for others. **Very young leaves of *F. yoponensis* excluded; ***Unripe fruit of *F. yoponensis* excluded; ****Lemon, orange, mango, papaya. † Milton and Jenness, 1987. + Marquez and Baumrucker, 1957. ‡ Keshinro, 1985. § Jones and Hughes, 1983. ≠ Dash and Jenness, 1985. Δ Eaton and Konner, 1985. (Reprinted from *Experientia* 43, Milton, K. and Jenness, R. Ascorbic acid content of neotropical plant parts available to wild monkeys and bats, pp. 339–342, 1987 with permission from Birkhauser Publishing).

which catalyzes the final step in ascorbate synthesis from glucose. For this reason, monkeys, apes and humans must ingest adequate vitamin C in the diet (Milton and Jenness, 1987).

Data on ascorbate values of fruit and leaves from wild and cultivated plant species from various locales are presented in Table 2. The mean for ascorbate values for the edible portion of ten Nigerian wild fruit species was higher than that for eight commonly consumed Nigerian cultivated fruit species (Keshinro, 1985). Panamanian fruits routinely eaten by wild monkeys contain notable amounts of ascorbate (Milton and Jenness, 1987). One species of Panamanian wild fig, *Ficus yoponensis*, showed an ascorbate level in fruits (2340 mg ascorbate per 100 g fresh wt.) that appears to be one of the highest reported (Milton and Jenness, 1987). Wild Panamanian leaves averaged a higher ascorbate content than cultivated fruit juices and wild leaves, both tropical and temperate, are excellent sources of ascorbate, better, for example, than cultivated leafy vegetables (Jones and Hughes, 1983; Booth et al., 1992).

Because vitamin K is involved in photosynthesis, wild leaves should also be a good source of

vitamin K (Booth et al., 1992). Many wild fruits eaten by monkeys and apes have brilliant yellow or orange flesh, at times oily flesh (e.g. Palmae), and would appear to be good sources of bioavailable carotenoids (Booth et al., 1992; Pee et al., 1998). Though wild plant food sources of primates do not appear, as yet, to have been analyzed for other vitamins, it is likely that many of the fruits, arils, seeds, leaves, flowers and buds wild monkeys and apes consume are good sources of various other micronutrients.

Worthington (2001) recently carried out an extensive review of the nutrient content of organic vs. conventional crops. Similar to many results for wild plant foods, her results showed that organic plant foods contained significantly more iron, magnesium, phosphorous and vitamin C than conventional crop foods.

5. Micronutrient requirements and intake by wild primates

5.1. Requirements

As pointed out by Nicolosi and Hunt (1979), due to the many variables involved, it is difficult

Table 3
Estimated daily mineral intakes of wild howler monkeys and humans (all units mg)

Mineral	Estimated intake-adult wild howler monkey per kg per day	Total daily intake-7 kg adult wild howler monkey	Total daily RDA-adult human male	Estimated assim. rate per kilogram-adult wild howler monkey	Estimated assim. rate per kilogram-adult human male
Calcium, mg	653	4571	800	20	4
Phosphorus, mg	104	728	800	6	9
Potassium, mg	917	6419	1600–2000	393	27
Sodium, mg	26	182	500	12	16
Chloride, mg	254	1778	750	102	24
Magnesium, mg	189	1323	350	9	2
Iron, mg	5.5	38.5	10.0	0.92	0.45
Manganese, mg	2.6	18.2	2.0–5.0	0.01	–

Modified from materials in Nagy and Milton (1979). Intakes and assimilation estimates derive from feeding trials and observations of wild howler monkeys eating a typical leaf and fruit diet. See Nagy and Milton (1979) for details of feeding trials and analytical protocols. Assimilation rates in humans estimated from assimilation percentages given by the National Research Council (1968), Passmore et al. (1974) and Williams (1974).

to be precise about the nutrient requirements of non-human primates and this is particularly true in the case of micronutrients. Despite the important and varied role of minerals in physiological processes, few studies have concerned themselves with the mineral requirements of non-human primates (Nicolosi and Hunt, 1979). Vitamin requirements for non-human primates have been somewhat better investigated, but are still not well-defined for most vitamins. Such studies generally establish the minimum level of a particular mineral or vitamin required by a given primate species to prevent deficiency disorders rather than determine the optimal level. Perhaps for this reason, estimates for both minerals and vitamins for non-human primates often appear to err on the side of caution, being higher than would be predicted by body weight (Portman, 1970). Deficiency studies show that non-human primates require an intake of many of the same minerals and vitamins as humans but it seems difficult to specify daily requirements. Portman (1970), Kerr (1972), Nicolosi and Hunt (1979) and Oftedal (1991) offer summaries of data available on recommended nutrient intake levels for non-human primates, including micronutrients.

5.2. Intake

The daily *intake* of particular micronutrients by wild primates can be crudely estimated from detailed information on feeding behavior in the natural environment and knowledge of the micro-

nutrient content of important wild foods. For example, data on the feeding behavior of wild adult howler monkeys in Panama, in combination with analyses of some wild foods, allow an estimate of their daily intake of some minerals. As shown in Table 3, howler monkeys appear to take in very high levels of many minerals each day relative to RDAs suggested for humans (Nagy and Milton, 1979). Values for the calcium, phosphorous and potassium content of important wild fruits in the diet of Gabonese chimpanzees (Table 1), in combination with my conservative estimate of the daily fruit intake of adult wild chimpanzees (i.e. 700 g dry wt.) indicate that these apes take in high levels of all three minerals. These estimates relate to only the fruit portion of the diet—chimpanzees also eat other plant parts and some ASFs (Hladik, 1977; Wrangham, 1977). By analogy, it would appear that most free-ranging monkeys and apes eating wild fruits and leaves of similar mineral content to those in Table 1 take in high levels of many minerals each day.

Wild primates also take in notable levels of vitamin C (ascorbate). A 7 kg adult wild howler monkey in Panama, for example, is estimated to consume approximately 600 g of fruit and 400 g of leaves, wet weight per day. With the average ascorbate content given in Table 2, intake is estimated at 279 mg of ascorbate from fruit and 335 mg from leaves for a total of 614 mg or 88 mg/kg/day. Wild Panamanian spider monkeys, which average 7 kg when adult, eat considerably more fruit per day than howler monkeys, some

1600 g wet wt./day. This would furnish 106 mg/kg/day of ascorbic acid or a total of 744 mg of ascorbate per day (Milton and Jenness, 1987) and spider monkeys also eat some leaves each day.

Bourne (1949) estimated that wild gorillas consuming approximately 9 kg of wild 'green foods' per day might take in more than 4 g of ascorbate. Similar high ascorbate intake seems unavoidable for wild chimpanzees and orangutans with their strong focus on ripe fruits in the diet as well as for many monkeys. Mammals from other plant-eating orders are likewise reported to take in or even require very high levels of ascorbate each day. Levine (1986), for example, pointed out that guinea pigs (like anthropoids a lineage that requires a dietary source of vitamin C), needed approximately 10 times more vitamin C to maintain general health than was required to prevent scurvy.

The current RDA for vitamin C for the average adult American is approximately 1 mg/kg/day. Thus a 70 kg adult would take in approximately 70 mg of vitamin C per day—far less than a 7 kg wild howler or spider monkey would be taking in *per kilogram* of body weight per day. Humans therefore appear to take in far less ascorbate per day than most wild primates, including similar-sized wild apes.

6. Micronutrient levels offered captive primates

What micronutrient levels are offered to captive non-human primates? Bilby (1968) presented comparative data on levels for several minerals offered captive primates. There was notable variation. For example, the mean calcium level per kilogram body weight for monkeys at the London Zoo was 34 mg (range 26–120 mg) while 400 mg/kg was offered captive monkeys in Purina chow and 112 mg/kg was offered captive monkeys at Monkey Hill (Bilby, 1968).

In terms of ascorbate intake, a level of 0.5–1.0 mg of ascorbate/kg/day, is suggested for captive rhesus monkeys (*M. mulatta*) and 7.5–10 mg of ascorbate/kg/day for captive squirrel monkeys (*Samiri scurrius* Nicolosi and Hunt, 1979). Portman (1970) suggests 25 mg/kg/day of ascorbate for captive non-human primates in general.

Kallman (1989) calculated the daily intakes per kilogram body weight for 15 micronutrients for a 7 kg monkey consuming a commercial chow diet and compared these estimates to human RDAs for

a 70 kg adult male. The mean of the ratios of monkey intake per kilogram body weight to recommended human intakes per kilogram body weight for the same 15 micronutrients was 23—on average, the chow-fed monkeys were offered 23 times as much of a given micronutrient per kilogram body weight in chow as was recommended for an adult human male (Kallman, 1989). No specific studies had been carried out to determine micronutrient levels for the monkey chow—rather a safety factor had been added to minimum estimates derived from deprivation or other studies and present-day levels had resulted (Kallman, 1989).

7. Discussion

It seems unlikely, though not impossible, that humans differ from other anthropoids in micronutrient requirements (with body mass and other variables held constant). Humans, apes and monkeys are known to differ in some aspects of nutrient requirements (e.g. dietary requirement for vitamin D₃ by Neotropical primates; Nicolosi and Hunt, 1979) and nutrient-associated physiology (e.g. serum lipoprotein profiles; Nelson et al., 1984). Regardless, it is the case that both wild and captive non-human primates appear to take in very high levels of some micronutrients relative to human RDAs. These levels do not appear harmful to the non-human primates—in the case of captive primates eating chow diets, such levels are regarded as 'optimal' (Kallman, 1989) and in the case of wild primates, such daily levels are the norm. Yet potential risks or no obvious benefits are believed to be associated with high intakes of some micronutrients by humans (Victoroff, 2002).

For example, data suggest that the human body becomes saturated with vitamin C at intakes greater than approximately 150 mg/day (Wardlaw and Insel, 1996) and that excess ascorbate is excreted from the body. A high intake of vitamin C can cause various health problems for humans including stomach inflammation and diarrhea. Perhaps for this reason, at megadose intakes of vitamin C, the human body is suggested to develop enzyme systems that rapidly metabolize ascorbate (Wardlaw and Insel, 1996). Yet, as noted, guinea pigs, which, like anthropoids, obtain their ascorbate from dietary sources, require a daily intake of ascorbate 10 times higher than that needed to prevent scurvy to remain in good health. Animals

that synthesize their own ascorbate (almost all mammals other than anthropoids, guinea pigs and few others), often make it in very large amounts. A hog produces 8 g of ascorbate per day though it is not known what benefit this high synthesis provides. (Wardlaw and Insel, 1996). As ascorbate synthesis incurs a cost to the producer, it would seem that such high synthesis would not take place if the end product were not of value to the animal producing it.

Several explanations, that are not mutually exclusive, can be suggested to account for the apparent difference in micronutrient intakes recommended for humans and those of non-human primates.

(1) A high intake of certain micronutrients by wild primates may be an unavoidable by-product of their heavily plant-based diets. Here the argument would be that high micronutrient intake occurs because it cannot be avoided and non-human primate physiology has adapted to this 'superfluous' micronutrient load. In this explanation, high micronutrient levels would be regarded as a non-functional, unavoidable by-product of the typical wild primate diet.

(2) Micronutrients in plant parts eaten by wild primates may have low bioavailability. Thus what looks like a very high intake might in fact just net a sufficiency for the primate feeder. Experimental data show, for example, that wild howler monkeys are poor assimilators of various minerals in their wild plant diets (Table 3). They appeared to assimilate only approximately 3–4% of the calcium and magnesium, 6% of the phosphorous and 15% of the iron in the wild foods offered them in feeding trials in Panama (Table 3; Nagy and Milton, 1979). Such estimates are lower than those for various other non-primate, plant-eating vertebrates (Nagy and Milton, 1979).

(3) Though assimilation estimates for wild howler monkeys are low, this is relative to the very large quantities of particular minerals animals take in each day in their wild plant foods. Howlers actually assimilate considerably more of some minerals per unit mass than adult humans (Table 3). For example, though assimilating only 20 mg of calcium per kilogram body weight from their wild foods (Table 3), a 7 kg adult howler monkey would assimilate an estimated 140 mg of calcium per day. A 70 kg adult human male (with an estimated assimilation efficiency for dietary calcium of $\approx 35\%$ and taking in the RDA of 800 mg)

assimilates 4 mg of calcium per kilogram of body weight per day or a total of 280 mg. For its metabolic body weight, a 7 kg howler monkey (metabolic body wt. = 4.3 kg) is assimilating approximately 3 times as much calcium per kilogram per day as a 70 kg adult human male (metabolic body wt. = 24.2 kg). Captive juvenile rhesus macaques (*M. mulatta*) ≥ 1 year of age, fed prepared rations containing 166 mg calcium/kg/day stored an estimated 80 mg/kg/day, showing an assimilation efficiency of almost 50% (Greenberg, 1970). For a 3 kg juvenile monkey this would be a total of 240 mg of calcium assimilated per day—in other words, the captive 3 kg juvenile monkey is assimilating almost as much calcium per day as the 70-kg adult human male.

Unlike most other monogastric primates, howler monkeys eat a high percentage of tree leaves each day (Milton, 1980, 1993b). Wild leaves are often protected against consumption by herbivore feeders by distasteful or potentially harmful allelochemicals—some of which are known to reduce the availability of nutrients or are energetically costly to detoxify (Milton, 1979, 1993b; Marriott, 2000). Unlike howler monkeys, most wild primates (excluding digestively specialized forms such as the Colobinae) tend to fill up on ripe fruits rather than leaves. As edible fruit pulp is elaborated by trees to attract seed dispersal agents such as monkeys and apes, the bioavailability of micronutrients in ripe fruits is predicted to be higher on average than values for leaves.

It is the case, however, that wild plant foods tend to be higher in potentially toxic or digestibility-reducing chemicals than cultivated plant foods. High micronutrient intakes by wild primates could function to lower potentially harmful effects of some chemicals present in wild foods. Vitamins C and E, for example, are a potent antioxidants which should facilitate the metabolism or excretion of undesirable plant compounds (e.g. phenols, terpenes; Dash and Jenness, 1985; Milton and Jenness, 1987). In humans and guinea pigs, a deficiency of ascorbate leads to reduced ability to detoxify foreign chemicals (Dash and Jenness, 1985). As humans now eat cultivated plant foods, the argument would be that they simply do not require similar high levels of micronutrients as their dietary conditions have altered and they no longer have to deal with high levels of undesirable constituents in wild foods.

However, numerous novel chemical compounds occur in human foods today, compounds which differ from the plant toxins, tannins and other natural environmental hazards wild primates have apparently developed means to deal with during their long evolutionary association with a wild plant food diet. Most humans today are also exposed to a wide array of air pollutants and other chemical substances new to their biology, which may require detoxification or call for enhanced immunological or other defenses. Ironically, humans may require high levels of antioxidants and other micronutrients today to help counter the effects of these new environmental hazards (but see Ames and Gold, 1997).

8. Conclusions

Comparative data suggest that wild primates take in higher levels of various vitamins and minerals each day than those suggested for humans. In the fresh plant foods monkeys and apes eat, unlike fortified foods or supplements, each nutrient is embedded in its natural organic matrix, permitting normal synergistic, additive or inhibitory biochemical effects to occur (Lampe, 1999; Prasad et al., 1998; Thompson et al., 2002; Marriott, 2000). It may be normal for human as well as ape and monkey blood and body tissues to be saturated continuously with many of the vitamins and minerals common in wild plant foods and for large quantities to be flushing continuously through the body (Bourne, 1949). This may produce quite different physiological benefits than the short-term oxidative or other effects derived from vitamin (Moller and Loft, 2002) or mineral supplements or from generally low levels of many micronutrients in the body due to inadequate dietary sources.

The suggestion that modern humans (and all living humans are anatomically modern *Homo sapiens sapiens*) increase their daily intake of fresh fruits and vegetables seems sound even if we were to base this recommendation purely on our knowledge of the probable foodways of pre-human ancestors and the present-day diets of wild apes and monkeys. It seems unlikely that consuming more lean meat or other ASF each day at the expense of fresh fruits and vegetables would provide the same health benefits for the average adult westerner. This is not to imply that humans should eat like apes. Over evolutionary time, the human

gut has come to differ in certain respects from the guts of extant apes and no longer appears suited to large quantities of indigestible plant material (Milton, 1986, 1987, 1993b, 1999b, 2002). For this reason, all modern humans must eat higher quality diets than all great apes (Milton, 1986, 1987, 1993b, 1999b, 2002).

In high-income nations at present, the general human tendency to upgrade and improve dietary quality has been carried to a new extreme as numerous foods are now refined and condensed to levels unimaginable to human populations even as recently as 100 years ago. All daily energy requirements can now be met with a relatively small amount of food. Unfortunately, many individuals in high-income nations tend to fill up each day on these highly refined, energy-dense foods, foods often demonstrably low in many micronutrients relative to similar unrefined foods, (Temple, 1994; Bengmark, 1998). For this reason, it is not surprising that problems associated with low micronutrient intake occur today in high-income nations (Murphy et al., 1992; Lewis et al., 1998; Ames and Wakimoto, 2002).

In low-income nations in contrast, millions of people rely for most of their daily energy on a single grain cultivar. These important cereal foods, analogous to over-refined foods in high-income nations, provide largely energy to the consumer. However, in striking contrast to refined western foods, cereal foods typically are less concentrated volumetrically. Small children in particular, with their characteristic human gut proportions and food transit times but accelerated requirements for energy and nutrients would be hard pressed to meet nutritional requirements on such foods, even if these were available in unlimited quantity (Milton, 1999b, 2002). For this reason, ASF, which generally are highly digestible and also macro- and micronutrient dense, are of particularly strong positive value to young children in such dietary circumstances (Milton, 1999b; Whaley et al., 2002). Cereal foods can then be used primarily as an energy source.

The current dietary situation for many humans in both high- and low-income nations does not seem compatible with human biology. Human biology evolved initially in conjunction with the quality and anti-quality components of a pre-human, largely wild plant-based diet. Human evolution marked a departure from the pre-human dietary pattern in that ASFs from vertebrates as

well as new modes of food processing (both of which up-graded dietary quality and thereby reduced the total volume of food needed per day to meet nutrient requirements) became the norm (Milton and Demment, 1988; Milton, 1993b, 1999a). However, these adaptations in the human lineage appear to relate more to the physical properties of foods than their chemical properties. For this reason, humans and great apes likely still require the same micronutrients in the diet—they just use different dietary strategies to obtain them.

Though the bioavailability of micronutrients to wild primates is almost totally unstudied, a high intake of various micronutrients (e.g. vitamins C and E, provitamin A, calcium) appears to be the norm. The difference between the estimated intake of certain micronutrients by wild primates and humans is striking. This difference is of particular interest today because a large number of recent studies strongly indicate health benefits to humans from increasing amounts of fresh fruits and vegetables in the diet (Block et al., 1992; Temple, 1994; Ames and Wakimoto, 2002). A better understanding of the possible health implications of such intake differences seems imperative due to the strong biological similarity of humans to other higher primates and the growing realization that micronutrients may play far more important roles in human development, health and longevity than formerly have been appreciated.

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