

Hunter-gatherer diets—a different perspective^{1,2}

Katharine Milton

Hunter-gatherer diets have long been a topic of interest and speculation (1–3). In this issue of the Journal, Cordain et al (4) attempt to estimate likely macronutrient intakes from plant and animal foods in the diets of “recent” (largely 20th century) hunter-gatherers. They conclude that most such societies likely derived more than half of their subsistence energy from animal foods and that because wild plant foods have a relatively low carbohydrate content, protein intake was elevated at the expense of carbohydrate (4). The take-home message seems to be that if we emulated such hunter-gatherers and derived more of our energy from animal foods, we might be able to avoid some of the “diseases of civilization” (eg, obesity, coronary heart disease, and type 2 diabetes). Such a suggestion, however well intentioned, seems ill advised given the high fat content of domesticated livestock relative to that of wild prey (2). Beyond this, however, both the approach of these authors and their conclusions require comment.

The hunter-gatherer data used by Cordain et al (4) came from the *Ethnographic Atlas* (5), a cross-cultural index compiled largely from 20th century sources and written by ethnographers or others with disparate backgrounds, rarely interested in diet per se or trained in dietary collection techniques. By the 20th century, most hunter-gatherers had vanished; many of those who remained had been displaced to marginal environments. Some societies coded as hunter-gatherers in the Atlas probably were not exclusively hunter-gatherers or were displaced agricultural peoples. Because most of the ethnographers were male, they often did not associate with women, who typically collect and process plant resources.

Finally, all the hunter-gatherers that were included in the Atlas were modern-day humans with a rich variety of social and economic patterns and were not “survivors from the primitive condition of all mankind” (6). Their wide range of dietary behaviors does not fall into one standard macronutrient pattern that contemporary humans could emulate for better health. Indeed, using data from the same *Ethnographic Atlas*, Lee (1) found that gathered vegetable foods were the primary source of subsistence for most of the hunter-gatherer societies he examined, whereas an emphasis on hunting occurred only in the highest latitudes.

Data on modern-day hunter-gatherers as well as hunter-gatherer-agriculturalists who consumed traditional diets indicate that such societies are largely free of diseases of civilization regardless of whether a high percentage of dietary energy is supplied by wild animal foods (eg, in Canadian Eskimos), wild plant foods (eg, in the !Kung), or domesticated plant foods taken primarily from a single cultivar (eg, in the Yanomamo) (7–11).

Furthermore, although humans can thrive on a diversity of diets, we know of few specific genetic adaptations to diet in our

species. Those few identified seem to be largely (although not exclusively) the result of regulatory mutations (eg, lactase synthesis in adulthood in some individuals) and unique selective pressures favoring such adaptations appear fairly well understood. Other than the occasional absence of intestinal sucrase, circumpolar peoples (or others with diets with a high animal food content) have not been shown to have special genetic adaptations that suit them for such diets (7, 11). In contrast, obligate carnivores, such as those of the cat family, show a range of specific metabolic adaptations to their all-flesh diets, including an unusually high requirement for protein for maintenance and growth, an unusual pattern of gluconeogenesis, and an inability to synthesize vitamin A and niacin from dietary precursors (12).

Food has played a major role in human evolution, but in a somewhat different manner than is generally appreciated. Humans are not self-made creations dietarily, but rather have an evolutionary history as anthropoid primates stretching back more than 25 million years (13), a history that shaped their nutrient requirements and digestive physiology well before they were humans or even protohumans (14, 15). In hominoids, features such as nutrient requirements and digestive physiology appear to be genetically conservative and probably were little affected by the hunter-gatherer phase of human existence. Neel et al’s (16) thrifty genotype hypothesis, for example, may embrace a range of common mammalian responses to particular environmental conditions; this hypothesis is also discussed in a different light by Allen and Cheer (17).

Hunter-gatherers were not free to determine their diets, rather, it was their predetermined biological requirements for particular nutrients that constrained their evolution. At the same time, these dietary needs apparently allowed for selection to favor increased brain size in the human lineage and the concomitant development of technologic, social, and other abilities directed at securing these nutrients (14, 15). In turn, cultural behaviors buffered hunter-gatherer biology from many selective pressures related to diet that other species must resolve largely through genetic adaptations. For example, the proportions of the modern human gut appear to reflect the fact that many foods are “predigested” by technology in one way or another before they ever enter the human digestive tract (14, 15).

¹From the Division of Insect Biology, the Department of Environmental Science, Policy and Management, University of California, Berkeley.

²Address reprint requests to K Milton, ESPM, Division of Insect Biology, 210 Wellman Hall, University of California, Berkeley, CA 94720-3112. E-mail: kmilton@socrates.berkeley.edu.



The American Journal of Clinical Nutrition

Official Journal of The American Society for Clinical Nutrition

9650 Rockville Pike, Bethesda, MD 20814-3998

(301) 530-7038 Fax (301) 571-8303

WWW.AJCN.ORG

Humans come from a fairly generalized line of higher primates, a lineage able to utilize a wide range of plant and animal foods. There is general agreement that the ancestral line (Hominoidea) giving rise to humans was strongly herbivorous (14, 15). Modern human nutritional requirements (eg, the need for a dietary source of vitamin C), features of the modern human gut (haustrated colon), and the modern human pattern of digestive kinetics (similar to that of great apes) suggest an ancestral past in which tropical plant foods formed the basis of the daily diet, with perhaps some opportunistic intake of animal matter.

Although most wild anthropoids eat little animal matter, its digestion, at least to some point, does not pose a problem (14). The barrier to greater meat eating in anthropoids appears to be the high cost of prey acquisition in the natural environment. If they could circumvent this cost routinely, many wild anthropoids would surely eat more animal foods.

Archaeologic evidence shows that early humans did find such a means. Stone tools and cut marks on bones dating back more than 2 million years are evidence that animal carcasses were butchered (6). However, although these and later material remains indicate meat eating, they do not shed light on the energy contribution of animal compared with plant foods in the diet because plant foods do not leave such obvious traces.

Consumption of animal matter to satisfy requirements for protein and many essential micronutrients would free up space in the gut for carbohydrate-rich plant foods and allow for their use as fuel for the increasingly large human brain (14). Because humans initially evolved in Africa, where wild animals generally lack appreciable fat stores (2), it seems clear that they consumed a mixed diet of animal and plant foods, given the apparent limitations of human digestive physiology to secure adequate daily energy from protein sources alone (4).

When hunter-gatherers eventually extended their range into higher latitudes, where plant growth is greatly curtailed, they must have been forced to live largely or entirely on raw animal matter, including their own body fat. Alaskan Eskimos, for example, had an estimated total daily energy intake of 12 552 kJ (3000 kcal): $\approx 50\%$ from fat, $\approx 30\text{--}35\%$ from protein, and $\approx 15\text{--}20\%$ from carbohydrates, largely glycogen from meat (7).

However, because some hunter-gatherer societies obtained most of their dietary energy from wild animal fat and protein does not imply that this is the ideal diet for modern humans, nor does it imply that modern humans have genetic adaptations to such diets. It does, however, indicate that humans can thrive on extreme diets as long as these diets contribute the full range of essential nutrients.

Hunter-gatherer societies in other environments were doubtless eating very different diets, depending on the season and types of resources available. Hayden (3) stated that hunter-gatherers such as the !Kung might live in conditions close to the "ideal" hunting and gathering environment. What do the !Kung eat? Animal foods are estimated to contribute 33% and plant foods 67% of their daily energy intakes (1). Fifty percent (by wt) of their plant-based diet comes from the mongongo nut, which is available throughout the year in massive quantities (1). Similarly, the hunter-gatherer Hazda of Tanzania consume "the bulk of their diet" as wild plants, although they live in an area with an exceptional abundance of game animals and refer to themselves as hunters (18). In the average collecting area of an Aka Pygmy group in the African rain forest, the permanent wild tuber biomass is >4545 kg (>5 tons) (19).

Australian aborigines in some locales are known to have relied seasonally on seeds of native millet (2) or a few wild fruit and seed species (20) to satisfy daily energy demands. Some hunter-gatherer societies in Papua New Guinea relied heavily on starch from wild sago palms as an important source of energy (21), whereas most hunter-gatherer societies in California depended heavily on acorn foods from wild oaks (22).

These and similar data indicate that hunter-gatherer societies typically did not rely on many wild plant species specifically for energy. Rather, they had one or a few dependable wild staples (some also good sources of protein) that provided much of their energy needs. In nature, any dependable source of digestible energy is generally rare and when discovered is likely to assume great importance in the diet. Animal foods typically are hard to capture but food such as tree fruits and grass seeds are relatively reliable, predictable dietary elements. Furthermore, humans come from an ancestral lineage in which plant foods traditionally have served as the primary source of energy (14, 15). All else being equal, digestible carbohydrates are the most expedient way for humans to obtain glucose, the preferred fuel for the anthropoid brain and one source of glycogen. Humans are quick to appreciate the value of reliable energy-providing staples and will work hard to ensure a steady supply of them.

Although agriculture is relatively recent, most hunter-gatherer societies appear to have enthusiastically embraced it. For example, since well before the time of Columbus, tropical rain forests of South America have been inhabited not by hunter-gatherers but by hunter-gatherer-agriculturalists, small societies practicing shifting cultivation whose main crop was likely a single starchy carbohydrate. Contemporary ethnographers working in Amazonia noted that even when smoke racks are filled with game, if the carbohydrate staple becomes exhausted, the inhabitants say they have no food (23).

Medical examination has found little evidence of diseases of civilization in unacculturated Amazonian hunter-gatherer-agriculturalists (9, 10), even though such people appear to have obtained a high percentage of their daily energy from a single plant cultivar for hundreds of years. I suggest that it is the low energy density of most wild foods, both plant and animal, in combination with common features of human digestive physiology that have played the critical role in the lack of these diseases in such societies. Societies consuming a staple cultivar as well as wild foods likewise may have limited energy intakes because most cultivars lack many essential nutrients, necessitating the inclusion of other foods in the diet, and some are high in fiber (eg, cassava).

Because the human gut can hold only a limited amount of food and as the transit time of food through the human gut is protracted (averaging 62 h with low-fiber diets and 40 h with high-fiber diets), there is a clear upper threshold for the amount of such foods the human gut can process per day (14). In striking contrast to humans and all great apes, all extant Carnivora show a rapid turnover of ingesta. For example, a 370-kg polar bear takes ≈ 24 h to digest a seal carcass.

In the natural environment, energy-dense, highly digestible foods of any type are generally rare. When available, such foods often serve not so much to satisfy that day's energy demands but rather to provide fat stores for use as energy during times of low food availability or, in women, to help meet the extra energy demands of reproduction. Because humans have large brains, it is particularly important that they are adept at storing excess

Humans come from a fairly generalized line of higher primates, a lineage able to utilize a wide range of plant and animal foods. There is general agreement that the ancestral line (Hominidae) giving rise to humans was strongly herbivorous (14, 15). Modern human nutritional requirements (eg, the need for a dietary source of vitamin C), features of the modern human gut (haustrated colon), and the modern human pattern of digestive kinetics (similar to that of great apes) suggest an ancestral past in which tropical plant foods formed the basis of the daily diet, with perhaps some opportunistic intake of animal matter.

Although most wild anthropoids eat little animal matter, its digestion, at least to some point, does not pose a problem (14). The barrier to greater meat eating in anthropoids appears to be the high cost of prey acquisition in the natural environment. If they could circumvent this cost routinely, many wild anthropoids would surely eat more animal foods.

Archaeologic evidence shows that early humans did find such a means. Stone tools and cut marks on bones dating back more than 2 million years are evidence that animal carcasses were butchered (6). However, although these and later material remains indicate meat eating, they do not shed light on the energy contribution of animal compared with plant foods in the diet because plant foods do not leave such obvious traces.

Consumption of animal matter to satisfy requirements for protein and many essential micronutrients would free up space in the gut for carbohydrate-rich plant foods and allow for their use as fuel for the increasingly large human brain (14). Because humans initially evolved in Africa, where wild animals generally lack appreciable fat stores (2), it seems clear that they consumed a mixed diet of animal and plant foods, given the apparent limitations of human digestive physiology to secure adequate daily energy from protein sources alone (4).

When hunter-gatherers eventually extended their range into higher latitudes, where plant growth is greatly curtailed, they must have been forced to live largely or entirely on raw animal matter, including their own body fat. Alaskan Eskimos, for example, had an estimated total daily energy intake of 12552 kJ (3000 kcal): $\approx 50\%$ from fat, $\approx 30\text{--}35\%$ from protein, and $\approx 15\text{--}20\%$ from carbohydrates, largely glycogen from meat (7).

However, because some hunter-gatherer societies obtained most of their dietary energy from wild animal fat and protein does not imply that this is the ideal diet for modern humans, nor does it imply that modern humans have genetic adaptations to such diets. It does, however, indicate that humans can thrive on extreme diets as long as these diets contribute the full range of essential nutrients.

Hunter-gatherer societies in other environments were doubtless eating very different diets, depending on the season and types of resources available. Hayden (3) stated that hunter-gatherers such as the !Kung might live in conditions close to the "ideal" hunting and gathering environment. What do the !Kung eat? Animal foods are estimated to contribute 33% and plant foods 67% of their daily energy intakes (1). Fifty percent (by wt) of their plant-based diet comes from the mongongo nut, which is available throughout the year in massive quantities (1). Similarly, the hunter-gatherer Hazda of Tanzania consume "the bulk of their diet" as wild plants, although they live in an area with an exceptional abundance of game animals and refer to themselves as hunters (18). In the average collecting area of an Aka Pygmy group in the African rain forest, the permanent wild tuber biomass is >4545 kg (>5 tons) (19).

Australian aborigines in some locales are known to have relied seasonally on seeds of native millet (2) or a few wild fruit and seed species (20) to satisfy daily energy demands. Some hunter-gatherer societies in Papua New Guinea relied heavily on starch from wild sago palms as an important source of energy (21), whereas most hunter-gatherer societies in California depended heavily on acorn foods from wild oaks (22).

These and similar data indicate that hunter-gatherer societies typically did not rely on many wild plant species specifically for energy. Rather, they had one or a few dependable wild staples (some also good sources of protein) that provided much of their energy needs. In nature, any dependable source of digestible energy is generally rare and when discovered is likely to assume great importance in the diet. Animal foods typically are hard to capture but food such as tree fruits and grass seeds are relatively reliable, predictable dietary elements. Furthermore, humans come from an ancestral lineage in which plant foods traditionally have served as the primary source of energy (14, 15). All else being equal, digestible carbohydrates are the most expedient way for humans to obtain glucose, the preferred fuel for the anthropoid brain and one source of glycogen. Humans are quick to appreciate the value of reliable energy-providing staples and will work hard to ensure a steady supply of them.


Although agriculture is relatively recent, most hunter-gatherer societies appear to have enthusiastically embraced it. For example, since well before the time of Columbus, tropical rain forests of South America have been inhabited not by hunter-gatherers but by hunter-gatherer-agriculturalists, small societies practicing shifting cultivation whose main crop was likely a single starchy carbohydrate. Contemporary ethnographers working in Amazonia noted that even when smoke racks are filled with game, if the carbohydrate staple becomes exhausted, the inhabitants say they have no food (23).

Medical examination has found little evidence of diseases of civilization in unacculturated Amazonian hunter-gatherer-agriculturalists (9, 10), even though such people appear to have obtained a high percentage of their daily energy from a single plant cultivar for hundreds of years. I suggest that it is the low energy density of most wild foods, both plant and animal, in combination with common features of human digestive physiology that have played the critical role in the lack of these diseases in such societies. Societies consuming a staple cultivar as well as wild foods likewise may have limited energy intakes because most cultivars lack many essential nutrients, necessitating the inclusion of other foods in the diet, and some are high in fiber (eg, cassava).

Because the human gut can hold only a limited amount of food and as the transit time of food through the human gut is protracted (averaging 62 h with low-fiber diets and 40 h with high-fiber diets), there is a clear upper threshold for the amount of such foods the human gut can process per day (14). In striking contrast to humans and all great apes, all extant Carnivora show a rapid turnover of ingesta. For example, a 370-kg polar bear takes ≈ 24 h to digest a seal carcass.

In the natural environment, energy-dense, highly digestible foods of any type are generally rare. When available, such foods often serve not so much to satisfy that day's energy demands but rather to provide fat stores for use as energy during times of low food availability or, in women, to help meet the extra energy demands of reproduction. Because humans have large brains, it is particularly important that they are adept at storing excess

dietary energy as fat because ketones can serve as an alternative fuel for the brain. Recent technology has circumvented this natural energy barrier by processing or otherwise altering both plant and animal foods such that much more energy can be ingested per day (15, 24). In addition, most Westerners lead sedentary lifestyles, whereas the hunter-gatherer-agriculturalists I am familiar with work an average of ≥ 8 h/d, much of this work involving strenuous activities.

In conclusion, it is likely that no hunter-gatherer society, regardless of the proportion of macronutrients consumed, suffered from diseases of civilization. Most wild foods lack high amounts of energy and this feature, in combination with the slow transit of food particles through the human digestive tract, would have served as a natural check to obesity and certain other diseases of civilization. Yet today, all non-Western populations appear to develop diseases of civilization if they consume Western foods and have sedentary lifestyles (24). Given these facts, in combination with the strongly plant-based diet of human ancestors, it seems prudent for modern-day humans to remember their long evolutionary heritage as anthropoid primates and heed current recommendations to increase the number and variety of fresh fruit and vegetables in their diets rather than to increase their intakes of domesticated animal fat and protein. 

REFERENCES

- Lee RB. What hunters do for a living, or how to make out on scarce resources. In: Lee RB, DeVore I, eds. *Man the hunter*. Chicago: Aldine Publishing Co, 1968:30-48.
- O'Dea K. Traditional diet and food preferences of Australian aboriginal hunter-gatherers. *Philos Trans R Soc Lond B Biol Sci* 1991; 334:233-41.
- Hayden B. Subsistence and ecological adaptations of modern hunter/gatherers. In: Harding RSO, Teleki G, eds. *Omnivorous primates: gathering and hunting in human evolution*. New York: Columbia University Press, 1981:344-421.
- Cordain L, Brand-Miller J, Eaton SB, et al. Plant-animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherers. *Am J Clin Nutr* 2000;71:682-92.
- Murdock GP. *Ethnographic atlas: a summary*. *Ethnology* 1967; 6:109-236.
- Isaac GLI, Crader DC. To what extent were early hominids carnivorous? An archaeological perspective. In: Harding RSO, Teleki G, eds. *Omnivorous primates: gathering and hunting in human evolution*. New York: Columbia University Press, 1981:37-103.
- Ho KJ, Mikkelsen B, Lewis LA, Feldman SA, Taylor CB. Alaskan Arctic Eskimos: responses to a customary high fat diet. *Am J Clin Nutr* 1972;25:737-45.
- Truswell AS. Diet and nutrition of hunter-gatherers. In: *Health and disease in tribal societies*. New York: Elsevier, 1977:213-26. (Ciba Foundation Symposium 49.)
- Neel JV. Health and disease in unacculturated Amerindian populations. In: *Health and disease in tribal societies*. New York: Elsevier, 1977:155-77. (Ciba Foundation Symposium 49.)
- Salzano FM, Callegari-Jacques SM. South American Indians: a case study in evolution. Oxford, United Kingdom: Clarendon Press, 1988.
- Draper HH. The aboriginal Eskimo diet in modern perspective. *Am Anthropol* 1977;79:309-16.
- Morris JC, Rogers OR. Comparative aspects of nutrition and metabolism of dogs and cats. In: Burger IR, Rivers JPW, eds. *Nutrition of dog and cat*. Cambridge, United Kingdom: Cambridge University Press, 1989:35-66. (Waltham Symposium 7.)
- Kay RF. Diet of early Miocene hominoids. *Nature* 1977;268:628-30.
- Milton K. A hypothesis to explain the role of meat-eating in human evolution. *Evol Anthropol* 1999;8:11-21.
- Milton K. Nutritional characteristics of wild primate foods: do the natural diets of our closest living relatives have lessons for us? *Nutrition* 1999;15:488-98.
- Neel JV, Weder AB, Julius S. Type II diabetes, essential hypertension, and obesity as "syndromes of impaired genetic homeostasis": the "thrifty genotype" hypothesis enters the 21st century. *Perspect Biol Med* 1998;42:44-74.
- Allen JS, Cheer SM. The non-thrifty genotype. *Curr Anthropol* 1996;37:831-42.
- Woodburn J. An introduction to Hazda ecology. In: Lee RB, DeVore I, eds. *Man the hunter*. Chicago: Aldine Publishing Co, 1968:49-55.
- Hladik CM, Hladik A. Food resources of the rain forest. In: Hladik CM, Bahuchet S, de Garine, eds. *Food and nutrition in the African rain forest*. Paris: UNESCO/MAB, 1990:14-8.
- Gould RA. *Living archaeology*. Cambridge, United Kingdom: Cambridge University Press, 1980.
- Dwyer PD, Minnegal M. Hunting in lowland, tropical rain forest: toward a model of non-agricultural subsistence. *Hum Ecol* 1990; 19:187-212.
- McCarthy H. Managing oaks and the acorn crop. In: Blackburn TC, Anderson K, eds. *Before the wilderness: environmental management by native Californians*. Menlo Park, CA: Ballena Press, 1993:213-28.
- Milton K. Protein and carbohydrate resources of the Maku Indians of northwestern Amazonia. *Am Anthropol* 1984;86:7.
- O'Dea K. Clinical implications of the "thrifty genotype" hypothesis: where do we stand now? *Nutr Metab Cardiovasc Dis* 1997; 7:281-4.



The American Journal of Clinical Nutrition

Official Journal of The American Society for Clinical Nutrition

9650 Rockville Pike, Bethesda, MD 20814-3998

(301) 530-7038 Fax (301) 571-8303

WWW.AJCN.ORG