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Plant-animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherer diets[1,2]

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ABSTRACT Both anthropologists and nutritionists have long recognized that the diets of moderm-day hunter-gatherers may represent a reference standard for modern human nutrition and a model for defense against certain diseases of affluence. Because the hunter-gatherer way of life is now probably extinct in its purely un-Westernized form, nutritionists and anthropologists must rely on indirect procedures to reconstruct the traditional diet of preagricultural humans. In this analysis, we incorporate the most recent ethnographic compilation of plant-to-animal economic subsistence patterns of hunter-gatherers to estimate likely dietary macronutrient intakes (% of energy) for environmentally diverse hunter-gatherer populations. Furthermore, we show how differences in the percentage of body fat in prey animals would alter protein intakes in hunter-gatherers and how a maximal protein ceiling influences the selection of other macronutrients. Our analysis showed that whenever and wherever it was ecologically possible, hunter-gatherers consumed high amounts (45–65% of energy) of animal food. Most (73%) of the worldwide hunter-gatherer societies derived >50% (≥56–65% of energy) of their subsistence from animal foods, whereas only 14% of these societies derived >50% (≥56–65% of energy) of their subsistence from gathered plant foods. This high reliance on animal-based foods coupled with the relatively low carbohydrate content of wild plant foods produces universally characteristic macronutrient consumption ratios in which protein is elevated (19–35% of energy) at the expense of carbohydrates (22–40% of energy). *Am J Clin Nutr* 2000;71:000–000.

INTRODUCTION

Both anthropologists and nutritionists have long had an interest in the nutritional patterns of the earth's less-Westernized peoples and have recognized that the diets of modern-day hunter-gatherers may represent a reference standard for modern human nutrition and a model for defense against certain "diseases of civilization" (1–6). Although there is a vast and rich ethnographic record of many aspects of the diets of worldwide hunter-gatherers (7), there are few studies that have examined certain specific qualitative and quantitative aspects of the nutri-

ent composition of these people's diets with modern analytic procedures (8–11). The hunter-gatherer mode of life, which sustained humanity for all (99.6%) but the last 10 000 y of the ≈2.4 million y since the first appearance of our genus (*Homo*), is now probably extinct in its pure form (11–13). Unfortunately, not a single comprehensive nutritional study evaluating the macronutrient and trace nutrient contents of the wild plant and animal foods actually consumed in completely un-Westernized hunter-gatherer diets was ever conducted. Consequently, all future studies of the traditional diet of preagricultural humans must be evaluated indirectly by examining the ethnographic, fossil, or archaeologic records in conjunction with modern-day nutrient analyses of wild plant and animal foods.

The reconstruction of preagricultural human diets by using indirect procedures has only recently been attempted. In their seminal paper, Eaton and Konner (14) estimated the dietary macronutrient and trace nutrient contents of Paleolithic humans. These authors estimated the projected average dietary macronutrient composition (as % of energy) to be 21% fat, 34% protein, and 45% carbohydrate (14), which was recently updated to 22% fat, 37% protein, and 41% carbohydrate (15). Implicit in Eaton et al's (14–16) estimation of representative, or average, Paleolithic diets was an assumed ratio of plant to animal (P:A) energy subsistence of 65:35, which was based on Lee's compilation (11) of selected hunter-gatherer subsistence data taken from the *Ethnographic Atlas*, an ethnographic compendium of 862 of the world's societies (7). Because Lee did not sum animal foods derived from hunting and animal foods derived from fishing, P-A subsistence ratios of worldwide hunter-gatherers are not reported in Lee's analysis (11). Furthermore, the subsistence data from the *Ethnographic Atlas* are not reported as percentages of

energy, but simply as a percentage of the subsistence economy (7). Eaton and Konner's (14) model for projected Paleolithic diets accommodates P-A energy subsistence ratios other than 65:35, and these authors suggested that many macronutrient combinations are possible (14). Many other researchers (17, 18) indicated that the average hunter-gatherer subsistence pattern would have included more animal food than the 35% of energy originally estimated by Eaton et al (14–16).

We analyzed the economic subsistence data for all 229 hunter-gatherer societies using all 3 subsistence categories (gathered plant foods, hunted animal foods, and fished animal foods) contained within the updated and revised version of the *Ethnographic Atlas* (19). From these data, we estimated the likely dietary macronutrient intakes (as % of energy) for environmentally diverse hunter-gatherer populations. Additionally, we showed how different percentages of body fat in wild animals will alter the amount of available energy from protein, and how a maximal protein ceiling will influence the selection of other macronutrients.

METHODS

Ethnographic data analysis

The data used in this study to estimate P-A energy subsistence ratios are derived from Murdock's *Ethnographic Atlas* (7), in which various ethnographic data are summarized, based on extensive literature searches of 1267 of the world's societies. The Atlas is widely used to evaluate cultural differences among the world's peoples and multiple ethnographers have independently verified portions of Murdock's analysis (20). Gray's revision (19) of Murdock's data includes 105 specific ethnographic topics, arranged into coded columns. In the present study, the basis for inclusion as a hunter-gatherer society was a 100% dependence on hunting, gathering, and fishing for economic subsistence as rated in columns 1–5 of the Atlas (19). For each of columns 1–5, the Atlas assigns a value ranging from 0 to 9, representing the relative dependence on the 5 basic subsistence economies (column 1: gathering of wild plants and small land fauna; column 2: hunting, including trapping and fowling; column 3: fishing, including shellfishing and the pursuit of large aquatic animals; column 4: animal husbandry; and column 5: agriculture). Of the 1267 societies listed in the Atlas, 229 were defined as hunter-gatherers because of scores of 0 in both columns 4 and 5. The percentage of subsistence-dependence categories based on Murdock's 0–9 scoring system is depicted in **Table 1** (7). For instance, a score of 4 in column 3 would correspond to a subsistence dependence on fishing ranging from 36% to 45%. Although Murdock did not specify whether the subsistence-dependence categories were based on the energy content or weight of the food for each subsistence economy (gathered plant foods, hunted animal foods, and fished animal foods), examination of the >400 original references indicates that in many cases, estimates were made by weight. Ethnographic data are qualitative in nature and as such lack the precision of quantitative data; consequently, Murdock's subsistence-dependence categories, in almost all cases, represent subjective approximations by Murdock of the ethnographer's or anthropologist's original observation. In our model, we used the *Ethnographic Atlas* data to simply define reasonable boundaries or limits to the P-A subsistence ratios that would have been encountered by hunter-gatherer societies. The projected macronutrient estimations on the basis of energy con-

TABLE 1
Scoring of percentage economic subsistence dependence in the *Ethnographic Atlas*[1]

Score	Percentage of subsistence dependence
	%
0	0–5
1	6–15
2	16–25
3	26–35
4	36–45
5	46–55
6	56–65
7	66–75
8	76–85
9	86–100

[1] From reference 7.

tent were determined by applying mean energy density (kJ/g) values derived from wild plant and animal-food databases to the subsistence estimates (by wt) from the Atlas.

Frequency distributions were compiled for the 229 hunter-gatherer societies listed in the Atlas for each of the 10 categories of percentage subsistence dependence for the 3 hunter-gatherer subsistence economies (**Figure 1**, A–C). Then, an animal-food subsistence-dependence frequency distribution was derived by summing the frequency distributions for hunting and fishing (Figure 1, D). Although in the present analysis we assumed that gathering would only include plant foods, Murdock indicated that gathering activities could also include the collection of small land fauna (insects, invertebrates, small mammals, amphibians, and reptiles); therefore, the compiled data may overestimate the relative contribution of gathered plant foods in the average hunter-gatherer diet.

In addition, we compiled frequency distributions of subsistence dependence by latitude in worldwide (*n* = 229) hunter-gatherer societies for the 3 subsistence economies (**Figure 2**, A–C) and for hunting + fishing (Figure 2, D). Spearman's rho coefficients were calculated to examine the relation between latitude and subsistence dependence for each of the 3 subsistence economies in all 229 hunter-gatherer societies. Last, we tabulated mean subsistence economies by primary living environment in hunter-gatherer societies (*n* = 63) for which these data were available (**Table 2**).

Dietary macronutrient estimation

The estimation of average percentages of energy from dietary macronutrients derived from average P-A subsistence ratios by weight requires that values for both wild-plant-food and animal-food nutrients, consumed by hunter-gatherers, be known. Eaton and Konner (14) initially calculated the dependence on dietary macronutrients (as a %) using mean values for 44 wild plant and 21 wild animal species and suggested that the projected macronutrient composition of preagricultural diets could be determined by using the following equation:

$$A(C^a \times X) + B(C^p \times X) = \text{daily energy intake} \qquad (1)$$

where A and B are the mean energy contents (kJ/g) of a database of 21 wild animal foods (5.90 kJ/g) and 44 plant foods (5.40 kJ/g), respectively; C^a and C^p are the assumed proportions of animal and plant foods consumed, 0.35 and 0.65, respectively; and X is
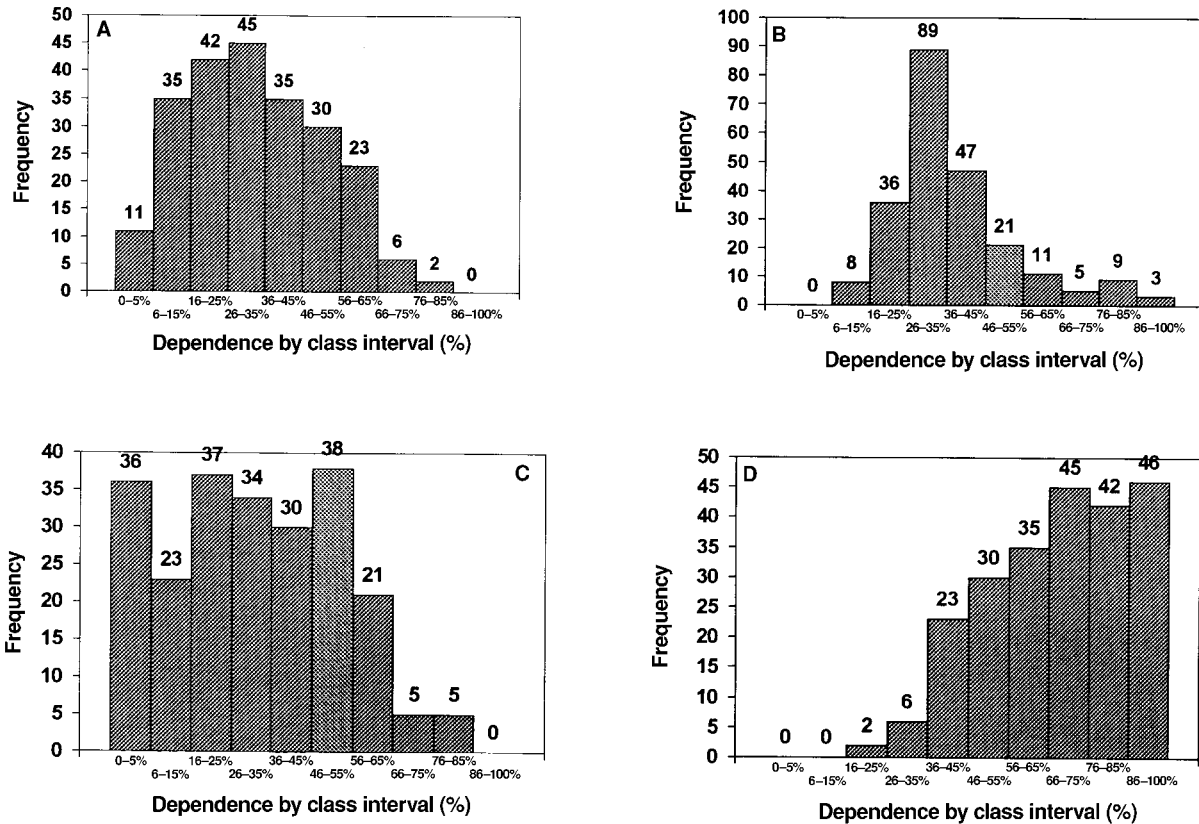
FIGURE 1. Frequency distributions of subsistence dependence of gathered plant foods (A: median, 26–35%; mode, 26–35%), hunted animal foods (B: median, 26–35%; mode, 26–35%), fished animal foods (C: median, 26–35%; mode, 46–55%), and fished + hunted animal foods (D: median, 66–75%; mode, 86–100%) in worldwide hunter-gatherer societies (*n* = 229).

the total number of grams required to provide any given amount of food energy.

In the present model, we used the same general approach that Eaton et al (14, 15) used, except that we made several important revisions. We *1)* added estimations of macronutrient energy for multiple P-A subsistence ratios representing most hunter-gatherer societies in the larger, revised Atlas; *2)* incorporated both hunted and fished animal foods in the animal portion of the P-A subsistence ratio; *3)* included various percentages of body fat of animals in the animal portion of the P-A subsistence ratio; and *4)* refined estimates of the amounts of energy from protein and fat in animal-based foods to reflect not merely mean energy values, but the cubic relations among these variables and percentage body fat (by wt).

Plant macronutrient considerations

In the present model, we used a large wild-plant-food data-base (*n* = 829), which is characterized by plant-food type (17). Because of the substantial variation in energy density among the 12 plant-food types (**Table 3**), it is apparent that the relative inclusion of more energetically dense foods in the database nec-essarily increases the average energy density of the entire data-base, and conversely, the relative inclusion of less energetically dense food types will reduce the average energy density of all

foods. Consequently, the mean energy density of any wild-plant-food database used to estimate the percentages of energy from dietary macronutrients in humans will be influenced by the rela-tive contribution of any given plant-food type to the entire data-base. Studies of hunter-gatherers have shown that the various categories of plant foods were not randomly gathered, but were collected with a general prioritization that maximized the rate of energy capture relative to energy expenditure; this pattern of gathering is predicted by the "optimal foraging theory" (21–24). Although a hunter-gatherer society may have used ≥100 plant species, only a small percentage of these plants was regularly consumed and, generally, these plants provided the greatest ratio of energy capture to energy expenditure (21, 22).

The plant species used in the present analysis were identified and collected in association with Australian Aborigines, who recognized these plants as food resources. This database repre-sents by far the largest analysis of wild food eaten by a hunter-gatherer group. Percentages of macronutrients for the entire database were determined based on energy by using recom-mended methods of food analysis (17). In the present analysis, fruit represented 41% of the total number of food items, seeds and nuts represented 26%, and underground storage structures (tubers, roots, and bulbs) represented 24%. The remaining 9%
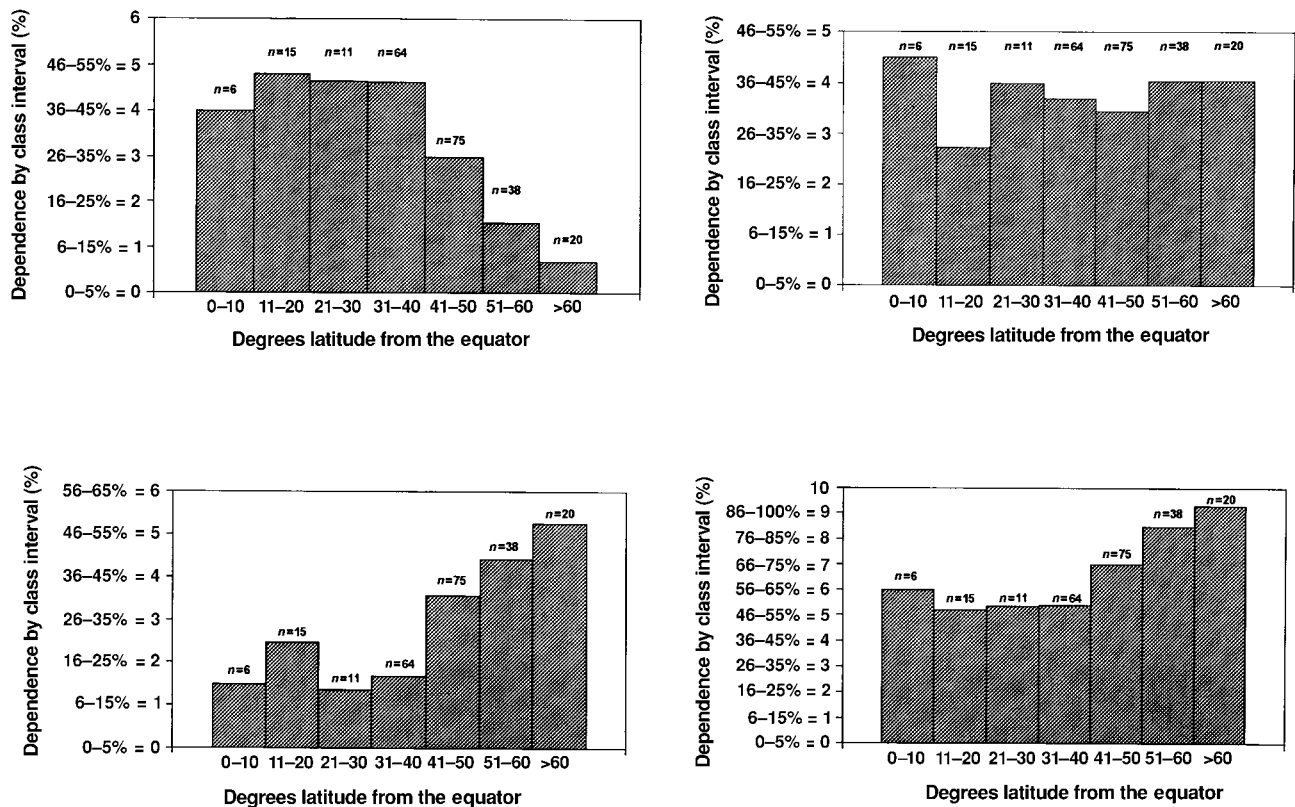
FIGURE 2. Mean subsistence dependence in worldwide hunter-gatherers ($n = 229$) by latitude for gathered plant foods (A), hunted animal foods (B), fished animal foods (C), and fished + hunted animal foods (D).

of the food items were leaves, dried fruit, flowers, gums, and miscellaneous plant parts. Therefore, our plant-food database maintains a weighting that is generally predicted by the optimal foraging theory (21, 23, 24) and that is consistent with observed plant-food choices in partially Westernized hunter-gatherers (22). Although we used a plant-food database derived entirely from Australian Aboriginal wild plant foods, our mean macronutrient values (62% of energy from carbohydrate, 24% from fat, and 14% from protein) were similar to those (68% of energy from carbohydrate, 19% from fat, and 13% from protein) derived from smaller wild-plant-food databases for worldwide hunter-gatherers (14). Clearly, there is no single plant-food weighting that represents all worldwide hunter-gatherer societies because plant-food resources vary by latitude, environment, and season. However, by and large, plant-food items with the greatest ratio of energy capture to energy expenditure would have provided most of the daily plant-food energy of worldwide hunter-gatherers (21, 22).

Animal macronutrient considerations

Previous models of reconstructed preagricultural diets have assumed that muscle tissue was the sole animal tissue consumed (14–16); however, many ethnographic reports of various hunter-gatherer societies showed that virtually all of the edible carcass was consumed (25–28). The edible carcass in hunter-gatherer diets has been estimated to range from 50% to 75% of the live animal weight (9, 21, 29). Estimates of edible carcass vary

depending on species, sex, and season. In ungulates in which the hooves, antlers, hide, and internal gastrointestinal contents were discarded, the remaining carcass represented 72% of the live weight (30). Because bone, except for marrow, is generally inedible, the total edible carcass of ungulates can represent 60–65% of the live weight (21). Consequently, virtually all of the potential fat contained in an animal's carcass—except for that in the hooves, hide, and horn—would generally have been consumed by hunter-gatherers (25–28). Even the fat contained within the matrix of bone was often extracted by boiling the bones (31).

Intraspecies percentages of body fat in wild mammals vary with age, sex, season, and the health of the animal, whereas interspecies percentages of body fat vary according to body size and, hence, fat-free mass (FFM) (32). FFM was shown to strongly correlate ($r = 0.86$) with percentage body fat when this relation was evaluated for 47 species of wild animals (32). Consequently, Pitts and Bullard (32) showed that the percentage body fat of a mammalian species can be estimated from its relative size:

$$\text{Percentage body fat} = 1.5 \times \text{FFM}^{0.20} \text{ (in g)} \qquad (2)$$

For example, body fat in a group of 23 North American white-tailed deer (*Odocoileus virginianus*) that varied by sex, age, and season of slaughter was determined by whole-carcass chemical analysis to range from 2% to 18% ($\bar{x}$: 10 ± 5%) (33). If the mean value obtained from the whole-carcass, chemically extracted FFM (30.6 kg) is applied to the equation of Pitts and Bullard (32), the predicted value is 12% body fat. In contrast, smaller mammals

TABLE 2
Mean economic subsistence dependence in worldwide hunter-gatherer societies ($n = 63$) by primary living environment

Environment	Dependence on gathered plant foods	Dependence on hunted animal foods	Dependence on fished animal foods
	%		
Tundra, northern areas ($n = 6$)	6–15	36–45	46–55
Northern coniferous forest ($n = 14$)	16–25	26–35	46–55
Temperate forest, mostly mountainous ($n = 6$)	36–45	16–25	36–45
Desert grasses and shrubs ($n = 11$)	46–55	36–45	6–15
Temperate grasslands ($n = 11$)	26–35	56–65	6–15
Subtropical bush ($n = 2$)	36–45	26–35	26–35
Subtropical rain forest ($n = 4$)	36–45	46–55	6–15
Tropical grassland ($n = 4$)	46–55	26–35	16–25
Monsoon forest ($n = 2$)	36–45	26–35	26–35
Tropical rain forest ($n = 3$)	26–35	26–35	36–45

(FFM: 189.0 ± 18.9 g; $n = 9$) such as squirrels (*Tamiasciurus hudsonicus*) have been shown to have actual percentages of body fat of 2%, which is reasonably close to their predicted mean value of 4%. Taken together, the data show that the average size of hunter-gatherer prey species will likely influence the total amount of fat obtained from animal-food sources. Therefore, larger animals will usually supply more total dietary fat than will smaller animals on both a relative and an absolute basis.

Except for the liver and possibly the kidney and tongue, there is virtually no carbohydrate available for consumption in the carcass of postmortem mammals. Additionally, because of the relative constancy of the protein content of FFM (32, 34), the energy density of a mammal's edible carcass is almost entirely dependent on the percentage of body fat. The linear relation between percentage body fat and energy density (as determined by whole-body chemical carcass analysis) in an ungulate species is shown in **Figure 3**. The third-order polynomial relation ($r^2 = 0.99$, $P < 0.001$) between percentage body fat by weight and percentage body fat by energy and the relation between percentage body fat by weight and the percentage protein by energy are shown in Figure 3. These linear and cubic relations between percentage body fat, energy density, percentage of energy from protein, and percentage of energy from fat are universally apparent in vertebrates, with only slight differences between phylogenetic orders. Similar cubic relations between the percentage of fat by weight and the percentages of energy from protein and fat of the edible flesh of fresh and saltwater fish are shown in **Figure 4**. Thus, in hunter-gatherer societies in which the bulk of daily animal energy intakes is derived from vertebrates, it is possible to estimate the relative contributions of both protein and fat energy on the basis of percentage body fat by weight of the species.

The present model

In the present model, we did not use a single P-A energy subsistence ratio but rather a series of P-A energy subsistence ratios (35:65, 45:55, 50:50, 55:45, and 65:35) that fall within the range of most (58%; $n = 132$) of the hunter-gatherer societies considered in this analysis. Within each of these categories, we calculated the overall dietary macronutrient energy ratio for 5 different whole-body fat percentages in both fish and mammalian prey species (2.5%, 5%, 10%, 15%, and 20%). This range of percentage body fat was chosen because it represents the most likely range that would have been found in historical hunter-gatherers. Because previous analyses of the *Ethnographic Atlas* (11, 36) as well as the present analysis indicate that hunted animal food makes up $\approx 35\%$ of the subsistence base for worldwide hunter-gatherers regardless of their resident latitude or environment, we used this constant figure. The remainder of the animal food, when the percentages of animal food exceeded 35% of energy, was assumed to be either fresh or saltwater fish. Consequently, in the present model, with decreasing animal-food (hunted + fished) intakes, fish-food intakes decrease as plant-food intakes increase and hunted-animal-food intakes remain constant. This inverse relation between fish and plant foods is consistent with a previous compilation of certain portions of hunter-gatherer data derived from the *Ethnographic Atlas* (37) as well as with the present analysis of the Atlas. We used the average plant macronutrient values of 62% of energy from carbohydrate, 24% from fat, and 14% from protein based on the previously analyzed database of 829 wild plant foods (17). Because of the similarity (3.5% difference) in the mean energy density of wild plant (6.99 kJ/g) and animal foods (7.24 kJ/g) in our database, we assumed that the P-A subsistence ratio based on weight in the *Ethnographic Atlas* would be virtually identical to the P-A subsistence ratios based on energy.

TABLE 3
Relative contribution of plant-food type to the wild-plant-food database[1]

Rank	Plant-food type	n	Percentage of total number	Energy density
			%	kJ/g
1	Fruit	317	41.3	3.97
2	Tubers	86	11.2	4.06
3	Other seeds	74	9.6	12.38
4	Nuts	74	9.6	12.80
5	Roots	51	8.5	3.93
6	Acacia seeds	55	7.2	14.73
7	Bulbs	30	3.9	6.78
8	Leaves	28	3.6	2.55
9	Flowers	16	2.1	3.56
10	Miscellaneous	14	1.8	3.81
11	Dried fruit	7	0.9	12.18
12	Gums	2	0.3	9.96

[1] $n = 768$ From reference 17.
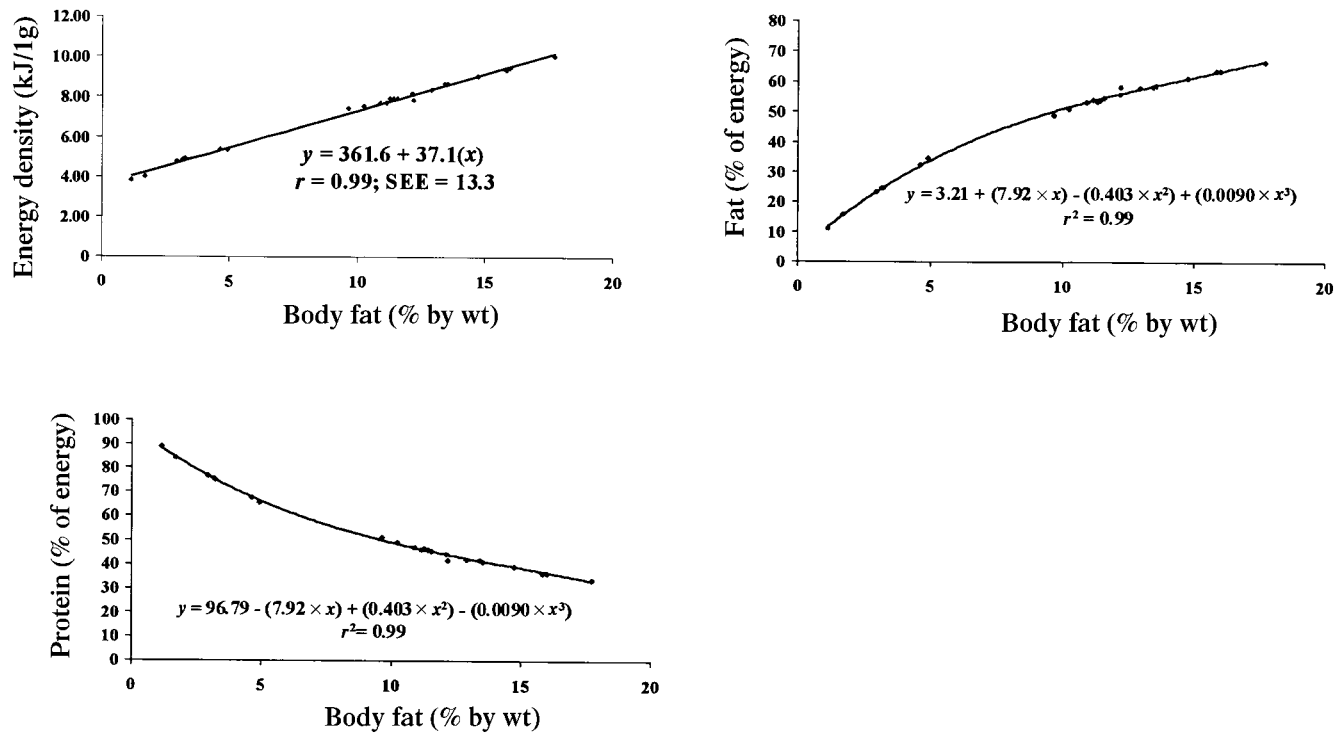
FIGURE 3. Regression of whole-carcass percentages of body fat on energy density, fat, and protein in white-tailed deer ($n = 23$). Adapted from reference 33.

Example calculation

For an assumed P-A subsistence ratio of 40:60 and an energy intake of 12552 kJ [the mean daily energy requirements for hunter-gatherer males (38)], plant protein would contribute 703 kJ ($0.14 \times 0.40 \times 12552$ kJ), plant fat would contribute 1205 kJ ($0.24 \times 0.40 \times 12552$ kJ), and plant carbohydrate would contribute 3113 kJ ($0.62 \times 0.40 \times 12552$ kJ). Hunted animal food would contribute a constant 35% of the total energy intake, or 4393 kJ (0.35×12552 kJ). The relative contribution of fat energy from hunted animal food was determined by using the equation from Figure 3; thus, an animal with 10% body fat would derive 51% of its energy from fat, or 2243 kJ (4393 kJ $\times$ 0.51). The relative contribution of protein energy from hunted animal food was also determined by using the equation from Figure 3; thus, an animal with 10% body fat would derive 49% of its energy as protein, or 2155 kJ (4393 kJ $\times$ 0.49). At a P-A energy subsistence ratio of 40:60, total energy from animal food (hunted + fished) would be 7531 kJ (0.60×12552) and total energy from animal food derived from fish would be 3138 kJ (7531 kJ − 4393 kJ). With a percentage body fat of 10% by weight for fish, the equation from Figure 4 yields a percentage of fat by energy of 56%, or 1757 kJ (0.56×3138 kJ). With use of the equation from Figure 4, a constant percentage body fat of 10% by weight yielded a percentage of energy from protein of 44%, or 1381 kJ (0.44×3138 kJ). Total energy from protein was 4239 kJ (703 kJ + 2155 kJ + 1381 kJ), or 34% of energy (4239 kJ/12552 kJ $\times$ 100). Total energy from fat was 5205 kJ (1205 kJ + 2243 kJ + 1757 kJ), or 41% of energy (5205 kJ/12552 kJ $\times$ 100). Total energy from carbohydrate was 3113 kJ, or 25% of energy (3113 kJ/12552 kJ $\times$ 100).

RESULTS

Hunter-gatherer plant-animal subsistence ratios

Figure 1 (A–C) displays the respective frequency distributions of economic subsistence dependence on gathered, hunted, and fished foods in the 229 hunter-gatherer societies listed in the *Ethnographic Atlas.*. These compiled data indicate that the most representative (median and mode) subsistence dependencies are divided approximately equally among the 3 subsistence categories of hunting, fishing, and gathering. However, it is evident from Figure 1D that most (73%) of the worldwide hunter-gatherers derived >50% (≥56–65%) of their subsistence from animal foods (hunted and fished), whereas only 13.5% of worldwide hunter-gatherers derived >50% (≥56–65%) of their subsistence from gathered plant foods. Of the 229 hunter-gatherer societies listed in the *Ethnographic Atlas*, 58% ($n = 133$) obtained ≥66% of their subsistence from animal foods in contrast with 4% ($n = 8$) of societies that obtain ≥66% of their subsistence from gathered plant foods. No hunter-gatherer population is entirely or largely dependent (86–100% subsistence) on gathered plant foods, whereas 20% ($n = 46$) are highly or solely dependent (86–100%) on fished and hunted animal foods.

Hunter-gatherer plant-animal subsistence ratios by latitude

When the subsistence dependencies of hunter-gatherers were analyzed by latitude (Figure 2, A–D), it was shown that subsistence supplied by hunted animal foods was relatively constant (26–35% subsistence), regardless of latitude (Figure 2B). Not surprisingly, plant food markedly decreases with increasing latitude, primarily at a threshold value of >40° N or S (Figure 2A). Because hunted land

animal-food subsistence generally does not increase with increasing latitude (Figure 2B), then the reduction in plant-food subsistence is replaced by increased subsistence on fished animal foods (Figure 2C). As indicated in Figure 2D, the subsistence dependence on combined hunted and fished animal foods is constant in hunter-gatherer societies living at low-to-moderate latitudes (0–40° N or S) and the median value falls within the 46–55% subsistence class interval. For societies living at >40° N or S, there is an increasing latitudinal dependence on animal foods (Figure 2D), which is primarily met by more fished animal foods (Figure 2C). Significant relations exist between latitude and subsistence dependence on gathered plant foods ($\rho = -0.77$, $P < 0.001$) and fished animal foods ($\rho = 0.58$, $P < 0.001$), whereas no significant relation exists between latitude and subsistence dependence on hunted animal foods ($\rho = 0.08$, $P = 0.23$).

Hunter-gatherer macronutrient intakes

Our estimated macronutrient intakes by energy for 5 P-A subsistence ratios (35:65, 45:55, 50:50, 55:45, and 65:35) at 5 different percentages of animal body fat (2.5%, 5%, 10%, 15%, and 20%) are shown in **Table 4**.. These P-A subsistence ratios fall within class intervals that encompass 58% ($n = 133$) of the hunter-gatherer societies listed in the *Ethnographic Atlas*. The 2.5–20% range of percentage body fat was chosen because it represents values in typically encountered prey species.

DISCUSSION

The diets of historically studied hunter-gatherer populations provide important information regarding the limits and boundaries of the diets to which humans are genetically adapted. Our data clearly indicate that there was no single diet that represented all hunter-gatherer societies. However, there were dietary trends that transcend geographic and ecologic boundaries and represent nearly all the world's hunter-gatherers. These nutritional trends, when analyzed under the scrutiny of modern nutritional theory, may have important implications for the mediation of nutritionally related, chronic diseases of Westernized societies.

The data presented in this analysis represent a detailed revision of the basic model that Eaton et al originally used to estimate the nutrient intake of Paleolithic humans (14–16). The present model estimates the relative dietary macronutrient intake by energy in a greater number of hunter-gatherer societies than used by Eaton et al (14–16) and additionally incorporates various P-A subsistence ratios that use various body compositions of prey species (Table 4). By analyzing and displaying multiple combinations of P-A subsistence ratios and percentages of body fat of various prey species, we refined our analysis and gained insight into the dietary combinations that would have been physiologically possible for historically studied hunter-gatherers.

Major findings

Dietary protein was estimated to have comprised between 19% and 50% of total energy intake, depending on the P-A subsistence ratio and the percentage body fat by weight in the prey animals. However, humans may not tolerate diets that contain >35–40% protein by energy. Previous indirect reconstructions of preagricultural human diets have not considered the modulating influence of dietary protein intake on the selection of dietary fat and carbohydrate (14–16). The avoidance of the physiologic effects of excess protein has been an important factor in shaping the subsistence

strategies of hunter-gatherers (39–41). Many historical and ethnographic accounts have documented the deleterious health effects that have occurred when humans were forced to rely solely on the fat-depleted lean meat of wild animals (39). Excess consumption of dietary protein from the lean meats of wild animals leads to a condition referred to by early American explorers as "rabbit starvation," which initially results in nausea, then diarrhea, and then death (39). Clinical documentation of this syndrome is virtually nonexistent, except for a single case study (42). Despite the paucity of clinical data, it is quite likely that the symptoms of rabbit starvation result primarily from the finite ability of the liver to up-regulate enzymes necessary for urea synthesis in the face of increasing dietary protein intake. Rudman et al (43) showed that the mean maximal rate of urea synthesis (MRUS) in normal subjects is 65 mg N·h^{-1}·kg body wt$^{-0.75}$ (range: 55–76 mg N·h^{-1}·kg body wt$^{-0.75}$) and that protein intakes that exceeded the MRUS resulted in hyperammonemia and hyperaminoacidemia. Using Rudman et al's (43) data (assuming 16% N/g protein), we calculated the mean maximal protein intake for an 80-kg subject to be 250 g/d (range: 212–292 g/d). For a 12552-kJ energy intake, the mean maximal dietary protein intake would be 35.1% of energy (range: 29.7–40.9% of energy). Therefore, dietary protein intakes greater than values in this range may result in hyperammonemia and hyperaminoacidemia, which in turn likely cause some of the clinical symptoms responsible for the rabbit starvation syndrome described by explorers.

Muscle tissue of wild ungulates typically contains ≈2.0–3.0% fat by weight (14–16, 35). Lean muscle meat of ungulates (2.5% fat by wt)
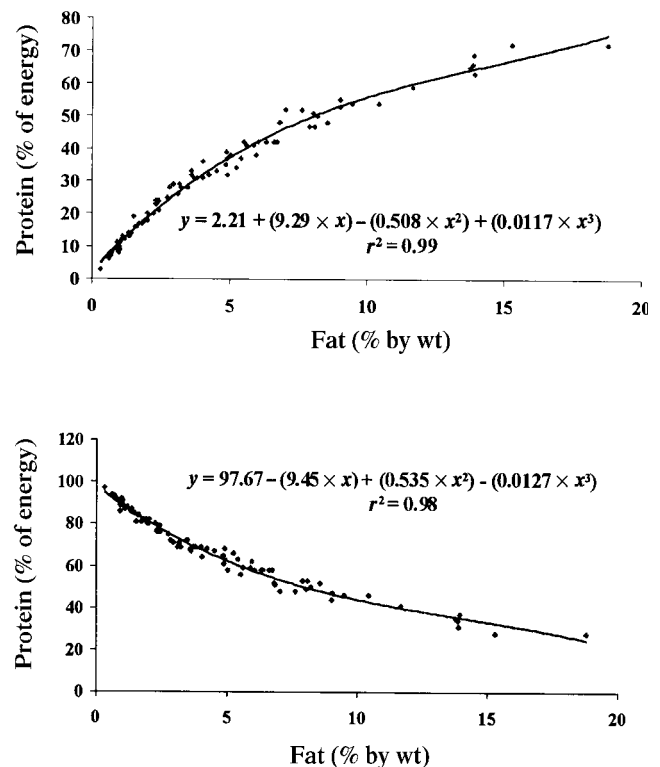
FIGURE 4. Regression of percentages of body fat on fat and protein in raw fish ($n = 94$). Adapted from reference 35.

TABLE 4
Estimates of dietary macronutrients in worldwide hunter-gatherer societies (*n* = 229) with varying plant-animal subsistence ratios and with varying animal (hunted + fished) body compositions

Subsistence ratio	Protein	Carbohydrate	Fat
		% of energy	
35:65			
20% animal fat	21	22	58
15% animal fat	28	22	50
10% animal fat	35[1]	22	43
5% animal fat	47[1,2,3]	22	32
2.5% animal fat	56[1,2,3]	22	23
45:55			
20% animal fat	20	28	52
15% animal fat	26	28	46
10% animal fat	32[1]	28	40
5% animal fat	42[1,2,3]	28	30
2.5% animal fat	49[1,2,3]	28	23
50:50			
20% animal fat	20	31	49
15% animal fat	25	31	44
10% animal fat	31[1]	31	38
5% animal fat	39[1,2]	31	30
2.5% animal fat	46[1,2,3]	31	23
55:45			
20% animal fat	19	34	47
15% animal fat	24	34	42
10% animal fat	29	34	37
5% animal fat	37[1,2]	34	29
2.5% animal fat	43[1,2,3]	34	23
65:35			
20% animal fat	19	40	41
15% animal fat	22	40	37
10% animal fat	26	40	34
5% animal fat	32[1]	40	28
2.5% animal fat	37[1,2]	40	23

[1] Exceeds low value (29.7% of energy from protein) for the range of maximal hepatic urea synthesis.

[2] Exceeds mean value (35.1% of energy from protein) for the range of maximal hepatic urea synthesis.

[3] Exceeds high value (40.9% of energy from protein) for the range of maximal hepatic urea synthesis.

is composed of 79.8% of energy as protein and 20.2% as fat. Consequently, consumption of lean ungulate meat as the sole daily energy intake would rapidly exceed the ability of the liver to eliminate nitrogen as urea and, hence, produce symptoms of rabbit starvation.

In Table 4, we showed how variations in the body composition of prey animals (both hunted and fished) influenced the protein intakes at different P-A subsistence ratios. Relatively lower P-A subsistence ratios require that fatter animals be consumed to maintain protein intakes within physiologic limits imposed by maximal hepatic urea synthesis rates. The data indicate that if lean muscle tissue (2.5% body fat) were isoenergetically consumed as the sole component of animal-food intake, it would exceed the mean MRUS for the P-A subsistence ratios for 86% (*n* = 198) of the hunter-gatherer societies listed in the *Ethnographic Atlas*. Clearly, this could not have been the case. Because the *Ethnographic Atlas* data indicate that the most representative subsistence dependence on total animal food for worldwide hunter-gatherers would have fallen within the 66–75% class interval (Figure 1D) or the 46–55% class interval, if the confounding effect of latitude is considered (Figure 2D), it

becomes apparent that animals with ≥10% body fat would have been required to maintain protein intakes below the maximal MRUS (Table 4). For an animal with 10% body fat by weight, fat would comprise 51% of the available carcass energy and protein would comprise the remaining 49% (Table 3).

To circumvent the dietary protein ceiling, hunter-gatherers generally would have had several options. They could have *1*) increased their P-A energy subsistence ratios by eating more plant-food energy; *2*) hunted larger animals because percentage body fat increases with increasing body size (32); *3*) hunted smaller animals during the season in which body fat is maximized; *4*) selectively eaten only the fattier portions of the carcass, including lipids boiled from the cancellous tissues of bones, and discarded the rest; *5*) increased their intake of concentrated sources of carbohydrate such as honey; or *6*) implemented ≥2 of the 5 options. To exploit various worldwide environments, one or more of these strategies must have been used. For example, with increasing latitude, plant-food resources become seasonally limited, thereby requiring the inclusion of more animal food (Figure 2D). The inclusion of more animal food requires increasingly greater inclusion of fat or carbohydrate to prevent protein toxicity (Table 4). As indicated in Table 2, hunter-gatherer subsistence strategies vary not only with latitude, but with primary living environment.

Although the adoption of an increased P-A subsistence ratio by increasing plant-food consumption appears to be the simplest solution to the dietary protein ceiling, data from the *Ethnographic Atlas* (Figure 1A) clearly indicate that this approach was not the preferred solution by worldwide hunter-gatherers, even when plant-food resources would have been available year round at lower latitudes (Figure 2, B and D). The answer to this seeming paradox lies in the "optimal foraging theory." Multiple studies have shown that animal foods almost always result in a higher ratio of energy capture to expenditure than do plant-based foods (21, 23, 44). Consequently, the solution preferred by most worldwide hunter-gatherers to circumvent excess dietary protein would likely have been a relative increase in total dietary fat from animal foods. Of the options available to achieve this goal, the selective consumption of fatty portions of the carcass while discarding leaner portions of the carcass would have been quite costly on the basis of the ratio of energy capture to energy expenditure (21–25). The selection of larger prey species, when ecologically and technologically possible, may have been the preferred option. This strategy would provide not only more energy simply from the increased mass of the larger species, but also from the greater available energy per unit mass (Figure 3) because of the increased percentage body fat that occurs with increasing species mass (32).

For worldwide hunter-gatherers, the most plausible (values not exceeding the mean MRUS) percentages of total energy from the macronutrients would be 19–35% for protein, 22–40% for carbohydrate, and 28–58% for fat (Table 4). For the entire sample of hunter-gatherer societies, subsistence dependence on animal food (hunted + fished) fell within the 66–75% subsistence class interval. For an animal subsistence dependence of 65%, the projected range (not exceeding the mean MRUS) of percentages of total energy would be 21–35% for protein, 22% for carbohydrate, and 43–58% for fat. Because our sample contained more societies (*n* = 133) located above 40° N or S latitude than below it (*n* = 96) and because there was a substantial increase in combined (hunted and fished) animal-food subsistence dependence (Figure 2D) at the expense of plant foods (Figure 2A) in those

living above 40° N or S latitude, the median value for animal-food subsistence was positively skewed. With use of a more conservative subsistence dependence on animal foods (hunted + fished) of 50%, a value that falls within the median class interval (46–55%) for animal-food subsistence values for hunter-gatherer societies living from 0 to 40° N or S latitude (Figure 2D), the projected ranges of percentages of total energy (not exceeding the mean MRUS) would be 20–31% for dietary protein, 31% for carbohydrate, and 38–49% for fat.

Limitations of the model

In the present model, we used a fixed plant-food macronutrient value of 62% of energy from carbohydrate, 24% from fat, and 14% from protein, derived entirely from Australian Aboriginal plant foods. Plant-food types in hunter-gatherer diets obviously vary by season, latitude, and geographic locale; consequently, variations in plant-food macronutrient composition by plant type will influence the overall estimated dietary macronutrient energy values. Despite these potential confounders, previous estimates (14) of the percentages of energy derived from plant-food macronutrients in preagricultural human diets were 68% of energy from carbohydrate, 19% from fat, and 13% from protein, which are similar to the values we derived.

For our analysis, we also assumed a constant hunted animal-food intake (35% of energy) that was based on previous estimates (11, 36) and the present ethnographic data (Figure 2B). Certainly, there are small numbers of hunter-gatherer populations, such as nonfishing societies, who do not necessarily conform to this assumption. Within animal-food (fished + hunted foods) subsistence dependence, we assumed the same percentages of body fat for both hunted and fished animals; however, these values may not be linked. Obviously, these and other variables not factored into the model can subtly and occasionally overtly influence the outcome of our projected estimates.

Perhaps the most important variable influencing the estimation of the dietary macronutrient ratio in hunter-gatherer populations, when indirect procedures are used, is the validity of ethnographic data. Other ethnographers who compiled hunter-gatherer data from the *Ethnographic Atlas* noted that the scores Murdock assigned to the 5 basic subsistence economies are not precise, but rather are approximations (11, 36, 37) generally based on raw weights of the dietary items (36). Although estimations of energy by weight of wild plant and animal foods may sometimes yield results similar to actual values, there is considerable room for error. The present analysis indicates that if the mean plant-food energy density for 829 wild plant foods (6.99 kJ/g) is contrasted with the energy density (7.24 kJ/g) of an average white-tailed deer with 10% body fat, there would only be a 4% difference between actual energy values and those estimated by weight. However, if the mean energy density of wild fruit (3.97 kJ/g) or wild tubers (4.06 kJ/g) were contrasted with that of a white-tailed deer with 17.7% body fat (10.17 kJ/g), there would be a 60–61% difference between actual energy values and those estimated by weight. Obviously, not all ethnographic estimations of energy intake in hunter-gatherer populations based on food weight would necessarily be this extreme. This example does indicate the imprecise nature of qualitative ethnographic data; however, it does not rule out its important use as a data source to test hypothetic models. The *Ethnographic Atlas* does provide reasonable dietary trends that have been cross-validated in a general sense by other independent anthropologic and archaeologic procedures (36, 37).

The dietary macronutrient ratios shown in Table 4 do not rely on the *Ethnographic Atlas* data for their derivation, but rather only on the boundaries or limits to the P-A subsistence ratios provided by the *Ethnographic Atlas*. The projected macronutrient estimations are based on analytic values for carbohydrate, fat, and protein contained in wild foods consumed by hunter-gatherers and by analytically determined macronutrient relations in wild animals based on different percentages of body fat. Consequently, the ethnographic data provided us with general boundaries to the P-A energy subsistence ratios in food consumed by most worldwide hunter-gatherers.

Comparison of hunter-gatherer macronutrient intakes with modern diets

The most plausible (values not exceeding the mean MRUS) percentages of total energy would be 19–35% for dietary protein, 22–40% for carbohydrate, and 28–58% for fat. In the United States, the third National Health and Nutrition Survey showed that among adults aged ≥20 y, protein contributed 15.5%, carbohydrate 49.0%, fat 34.0%, and alcohol 3.1% of total energy intake (45). Consequently, the range of percentages of energy for carbohydrate and protein in the diets of most hunter-gatherer societies worldwide (Table 4) falls outside the average value found in Western diets (45) and in recommended healthy diets [15% of energy from protein, 55% from carbohydrate, and 30% from fat (46)]. Our macronutrient projections for worldwide hunter-gatherer diets indicate that these diets would be extremely high in protein (19–35% of energy) and low in carbohydrate (22–40% of energy) by normal Western standards, whereas the fat intake would be comparable or higher (28–58% of energy) than values currently consumed in modern, industrialized societies. However, the types and balance of fats in hunter-gatherer diets would likely have been considerably different from those found in typical Western diets (47, 48).

It should be pointed out that the types of plant and animal foods that together comprise the macronutrient composition of hunter-gatherer diets are substantially different from those commonly consumed by Westernized societies. In the United States, the 1987–1988 National Food Consumption Survey indicated that cereal grains contributed 31%, dairy products 14%, beverages 8%, oils and dressings 4%, and discretionary sugar and candy 4% of the total energy intake for all individuals (49). Virtually none of these foods would have been available to hunter-gatherers (14–16, 47). Cereal grains represent the highest single food item consumed on the basis of energy content in both the United States (49) and the rest of the world (50); however, they were rarely consumed by most hunter-gatherers (37, 47), except as starvation foods or by hunter-gatherers living in arid and marginal environments (37, 51). Although cereal grains, dairy products, beverages, oils and dressings, and sugar and candy comprise >60% of the total daily energy consumed by all people in the United States (49), these types of foods would have contributed virtually none of the energy in the typical hunter-gatherer diet.

The average P-A subsistence ratio for all people in the United States is currently 62:38 (49) with a corresponding mean intake of 15.5% from protein, 49.0% from carbohydrate, and 34.0% from fat. Only 13.5% (*n* = 31) of the world's hunter-gatherer societies maintained P-A subsistence ratios ≥62:38; however, even in these societies the macronutrient ratios would have been quite different from those found in Western populations. Total fat intakes would have been similar or higher; however, under all

circumstances, protein intakes would have been higher and carbohydrate intakes would have been lower (Table 4). These differences are due, in part, to the high reliance of Western societies on cereal grains, dairy products, beverages, oils and dressings, and sugar and candy in lieu of meat and fruit and vegetables.

Anthropologic and medical studies of hunter-gatherer societies indicate that these people were relatively free of many of the chronic degenerative diseases and disease symptoms (52) that plague modern societies and that this freedom from disease was attributable in part to their diet (14–16, 47, 52). Therefore, macronutrient characteristics of hunter-gatherer diets may provide insight into potentially therapeutic dietary recommendations for contemporary populations.

Conclusions

Whenever and wherever it was ecologically possible, hunter-gatherers would have consumed high amounts (45–65% of total energy) of animal food. Most (73%) hunter-gatherer societies worldwide derived >50% (≥56–65%) of their subsistence from animal foods, whereas only 13.5% of these societies derived more than half (≥56–65%) of their subsistence from gathered plant foods. In turn, this high reliance on animal-based foods coupled with the relatively low carbohydrate content of wild plant foods produces universally characteristic macronutrient consumption ratios in which protein intakes are greater at the expense of carbohydrate.

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