Estimation of the diet-dependent net acid load in 229 worldwide historically studied hunter-gatherer societies[1,2]

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ABSTRACT

Background: Nutrition scientists are showing growing interest in the diet patterns of preagricultural (hunter-gatherer) humans. Retrojected preagricultural diets are reportedly predominantly net base producing in contrast to the net acid-producing modern Western diets.

Objective: We examined the dietary net acid load [net endogenous acid production (NEAP)] for 229 worldwide historically studied hunter-gatherer societies to determine how differences in plant-to-animal (P:A) dietary subsistence patterns and differences in the percentage of body fat in prey animals affect the NEAP.

Design: With the use of *1)* ethnographic data of dietary P:A ratios of hunter-gatherer populations, *2)* established computational methods, and *3)* knowledge that fat densities of animal foods consumed by hunter-gatherers varied between 3% and 20%, we computed the NEAP for the diets of 229 populations in 4 different models of animal fat densities (model A, 3%; model B, 10%; model C, 15%; model D, 20%).

Results: As P:A ratios decreased from 85:15 to 5:95, the NEAP increased from −178 to +181 mEq/d (model A) and from −185 to +120 mEq/d (models B and C). Approximately 50% of the diets consumed by the 229 worldwide hunter-gatherer populations were net acid producing (models B and C). In model D, 40% of the diets were net acid producing.

Conclusions: Our data confirm that the NEAP of hunter-gatherer diets becomes progressively more positive as P:A ratios decline. The high reliance on animal-based foods of a worldwide sample of historically studied hunter-gatherer populations renders their diets net acid producing in ≈40–60% of subgroups of P:A ratios. Only further investigations can show the implications of these findings in determining the NEAP of human ancestral diets.   *Am J Clin Nutr* 2010;91:406–12.

INTRODUCTION

Since anthropologists S Boyd Eaton and Melvin J Konner published their seminal 1985 article "Paleolithic Nutrition" (1), interest in an evolutionary perspective on the optimal human diet has grown (2–6). Proponents of a program called "evolutionary health promotion" suggest that information about diets consumed by preagricultural *Homo sapiens* might contribute importantly to nutrition science through the application of evolutionary principles. They propose that the nutritional patterns of our ancestors who lived in the African Paleolithic Age (Old Stone Age, which began ≈2.6 million y ago), before the introduction of

agriculture about 10,000 y ago, represent a reference standard for the optimal diet of modern humans (2, 3, 7–13). Various attempts to retroject the diets of preagricultural hunter-gatherers both qualitatively and quantitatively (1, 14–18) all rely on indirect procedures that, to a considerable extent, examine the ethnographic records of historically recent hunter-gatherer populations.

Although contemporary foragers do not represent "living fossils" (19), they provide the most relevant models for at least late Paleolithic humans (20). With adjustment for the likelihood that no single universal hunter-gatherer diet existed, Cordain et al (3) and Eaton (11) summarized the likely characteristics of preagricultural diets. One such feature consists of estimates of the net systemic acid load supplied by the diet [net endogenous acid production (NEAP)]. In contrast to the characteristically net acid-producing modern Western diet, which ranges over an order of magnitude of +10 to +150 mEq/d (21–25), nearly all preagricultural hunter-gatherer diets were estimated as net base producing [ie, negative NEAP (3, 11, 26)].

That characterization of the acid-base yield of the Paleolithic diet would seem to have important public health implications, because net base-yielding diets have shown multiple health benefits (12, 13, 27). The inference that ancestral preagricultural diets yield net base is based in part on calculations reported by Sebastian et al (26). Their estimations depend on assumptions about the ratio of plant-source foods to animal-source foods in the diet, because the former tend to yield net base on metabolism and the latter net acid.

However, the contribution of animal-source foods to preagricultural hunter-gatherer diets merits further consideration, in light of Cordain et al's (18) published analysis of the most recent ethnographic compilation of plant-to-animal (P:A) subsistence patterns in historically recent worldwide hunter-gatherer pop-

ulations. Cordain et al (18) found that most of the members of worldwide historically studied hunter-gatherer societies ($n = 133$; 58%) consumed higher amounts of animal-source foods than previously thought (1, 16, 28). Because the consumption of animal-source foods might increase the net acid load (29), one might question whether historically studied hunter-gatherer diets generally yield a net base load. On the other hand, Cordain et al (18) also proposed that the hunter-gatherers consumed the fat-rich components of hunted and fished animal-source foods, which would lessen the acid load of a given quantity of animal-source food.

Although there have been a number of quantitative studies on preagricultural diets (1, 14, 16–18, 26), none have examined the NEAP for all of the historically studied worldwide hunter-gatherer societies. In this article we therefore report estimates of net systemic acid load (NEAP) for 229 worldwide hunter-gatherer population diets and compare them with that of contemporary Western diets. Furthermore, as introduced by Sebastian et al (26), we show how differences in the percentage of body fat in prey animals would alter the NEAP in hunter-gatherer diets.

METHODS

With the use of recent ethnographic data of P:A subsistence patterns of hunter-gatherer populations and established computational methods, we computed the NEAP for all the diets of 229 worldwide forager populations as follows:

1) Ethnographic data. The data of P:A energy subsistence ratios came from an analysis of a revised version (30) of the *Ethnographic Atlas* (31), carried out by Cordain et al (18). In their analysis of this cross-cultural index, which summarized various ethnographic data of 1267 of the world societies, Cordain et al (18) identified 229 hunter-gatherer societies. All of their economic subsistence depended exclusively on hunting (which included trapping and fowling), gathering (wild plants and small land fauna), and fishing (which included shell fishing). In accordance with Cordain et al (18) we assumed in our present analysis that gathered food would only include plant foods, whereas Murdock (31) stated that gathering activities could also include the collection of small fauna. We also followed the assumption of Cordain et al (18) whereby the P:A subsistence ratio based on weight in the *Ethnographic Atlas* can be taken as identical to the P:A subsistence ratios based on energy.

2) General algorithm for the estimation of the diet's daily NEAP. The estimations of the NEAP were based on the validated model of Sebastian et al (26). According to this model, the NEAP can be computed from the sum of (A) the production rates of sulfuric acid, plus (B) a fraction of the total endogenous organic acid production that contributes to the NEAP, minus (C) the potential bicarbonate yielded from diet.

Factor (A) was calculated from reported values of the amino acids methionine and cysteine (32), which contain sulfur, with the assumption that the fractional intestinal absorption of protein is 0.75 (33, 34) and that there is a complete metabolism of the intestinally absorbed protein's cysteine and methionine sulfur

content to sulfur acid. Factor (B) was quantifiable as the daily urinary excretion rate of organic anions (21). Organic anions that are not excreted yield bicarbonate on metabolism, which back-titrate the protons released during organic acid generation and, hence, do not contribute to the NEAP. Because organic anion excretion (mEq/d) is predictable from the unmeasured anion content (mEq/d) of the diet (35), it is possible to estimate endogenous organic acid production from the composition of the diet:

$$\begin{aligned} \text{Diet organic anion excretion (mEq/d)} = 32.9 \\ + 0.15 \times [\text{sodium (mEq/d)} + \text{potassium (mEq/d)} \\ + \text{calcium (mEq/d)} \\ + \text{magnesium (mEq/d)} - \text{chloride (mEq/d)} \\ - \text{phosphorus (mEq/d)}] \end{aligned} \quad (1)$$

with the valence of phosphorus taken as 1.8.

Factor (C) was computed from the inorganic ion composition of the diet as follows:

$$\begin{aligned} 0.95 \times \text{sodium (mEq/d)} + 0.8 \times \text{potassium (mEq/d)} \\ + 0.25 \times \text{calcium (mEq/d)} \\ + 0.32 \times \text{magnesium (mEq/d)} - 0.95 \\ \times \text{chloride (mEq/d)} - 0.63 \times \text{phosphorus (mEq/d)} \end{aligned} \quad (2)$$

where the coefficients indicate average fractional intestinal absorption of the ion, and the valence of inorganic phosphorus is taken as 1.8 (33, 34). For particulars about the calculations of the NEAP and the physiologic background, *see* Sebastian et al (26) and Frassetto et al (36).

In the estimation of the essential factors (A), (B), and (C) of the NEAP algorithm described in the section above, we followed the methods published by Sebastian et al (26). According to these methods, the diet database for calculation of the NEAP for a given P:A energy ratio included 53 food items from among the major groups likely to have been consumed by preagricultural humans: 9 meats (which included 4 wild game meats) and 44 plant foods assigned to 6 groups (roots, nuts, tubers, fruit, leafy green vegetables, and vegetable fruit). Cereal grains and legumes were excluded because of their late (mostly postagricultural) incorporation into the human diet (37, 38). For all calculations, unless otherwise specified, the combined energy intake from animal and plant foods was maintained at 12,552 kJ/d (3000 kcal/d). On the basis of this and the (simplified) assumption that all animal foods consumed by hunter-gatherers are characterized by the same NEAP as for meat, we were able to calculate the NEAP of different P:A ratios and the corresponding NEAP of the diets of $n = 229$ hunter-gatherer populations. Because the fat content of animal foods eaten by hunter-gatherers varied between 3% and 20% of whole-body fat (18), we generated 4 different NEAP models (model A: 3% body fat of animal food; model B: 10% body fat of animal food; model C: 15% body fat of animal food; and model D: 20% body fat of animal food). With the use of those models and with consideration of the P:A ratios of the diets of $n = 229$ hunter-gatherer diets from the *Ethnographic Atlas*, it was possible to calculate the NEAP for the different diets.

RESULTS

The findings of the computations for different P:A ratios of hunter-gatherer diets are summarized in **Table 1**. According to these findings, there is a linear relation between the energy ratio from plant and animal food and the measure of the NEAP, depending on the percentage of body fat of the edible carcass that was consumed (**Figures 1–4**). Therefore, the dependent variable NEAP can be predicted from the P:A ratio and the whole-body fat content following the 4 linear systems of equations:

$$f(x_A) = 422.8x - 241.7 \qquad (3)$$

$$f(x_B) = 369.73x - 241.8 \qquad (4)$$

$$f(x_C) = 355.35x - 244.22 \qquad (5)$$

$$f(x_D) = 328.53x - 241.87 \qquad (6)$$

Equation 3 describes the association between the percentage of energy from animal food (x) by giving a whole-body fat content of $\approx 3\%$ (lean meat), equivalent to an animal-fat content of $\approx 26\%$ of animal food energy (39) and the NEAP of model A. Accordingly, Equations 4, 5, and 6 describe the same associations by giving a whole-body fat content of $\approx 10\%$ ($\approx 51\%$ of animal food energy; moderate-fat meat model B), $\approx 15\%$ ($\approx 62\%$ of animal food energy; higher-fat model C), and $\approx 20\%$ (72% of animal food energy; high-fat model D), respectively. As the results of our calculations in Table 1 show, historically studied hunter-gatherer diets, which are characterized by P:A ratios that declined from 35:45 to 5:95, were net acid producing in model A, and those with P:A ratios that declined from 25:65 to 5:95 were net acid producing in models B, C, and D.

Because we were interested in the NEAP of the entire collective of the hunter-gatherer diets, we calculated the overall NEAP for each of the 229 P:A subsistence ratios. The frequency distributions of the estimated NEAP of these P:A categories are shown in **Table 2**. Depending on the fat content of the hunted animals, a wide range of interval values were shown. For model A, NEAP = –178 to – 140, to +160 to +181 mEq/d (median and mode: +33 to +71 mEq/d); for model B, NEAP = –186 to –153, to +109 to +128 mEq/d (median and mode: –2 to +32 mEq/d); for model C, NEAP = –190 to –159, to +90 to +111; and for model D, NEAP = –193 to –163, to +70 to +87.

Provided that all the animal-source foods in the hunter-gatherer diets came from the lean muscle tissue of wild animals, which typically contains about 3% fat by weight (18), it is evident from Table 2 that most ($\approx 70\%$; $n = 160$) of the diets consumed by historically studied worldwide hunter-gatherers were net acid producing (NEAP = > 0 to $\leq$ +181 mEq/d). Similarly, by examination of the effects of the 229 hunter-gatherer diets substantially moderate in animal fat densities (10–15% fat by weight), $\approx 50\%$ ($n = 133$) of the foragers consumed a net acid-producing diet (NEAP = >0 to $\leq$ +128 mEq/d).

This net acid load of the aggregated diets reflected the sum of sulfuric and organic acid production rates exceeding bicarbonate production rates because of the high meat intake as the only net acid-producing food group in preagricultural diets. In contrast, only $\approx 30\%$ (model A) and $\approx 40\%$ (model B) of the 229 hunter-gatherer societies listed in the *Ethnographic Atlas* consumed a diet that showed net base-producing effects. However, as the results of our NEAP calculations in the high-fat model (D) show, only 38% of the worldwide hunter-gatherer diets were characterized as net acid producing (NEAP: ≥ 5 to $\leq$ +87 mEq/d).

DISCUSSION

The subsistence diets of preagricultural and historically studied hunter-gatherers is a debated topic (28, 40–51), and various attempts have been made to reconstruct such diets quantitatively (1, 14, 16–18, 26). It is clear that there was a wide range of dietary behaviors among hunter-gatherer societies, depending on geographic, climatic, and ecologic circumstances; therefore, no single diet could represent all foragers (20, 41, 50, 51), although some researchers (3, 11, 27) have tried to summarize the universal characteristics of hunter-gatherer diets. Because the effect of diet on acid-base balance and health is widely accepted (52–54), one characteristic of preagricultural diets that has generated increasing interest is the net systemic acid load. On the basis of calculations of the NEAP of 159 hypothetic retrojected preagricultural diets by Sebastian et al (26), the notion

TABLE 1
Effect of the ratio of plant-food energy intake to animal-food energy intake (P:A ratio) on net endogenous acid production (NEAP) for preagricultural Paleolithic diets with variations in the body fat of the hunted animal foods[1]

				P:A ratio					
	85:15	75:25	65:35	55:45	45:55	35:65	25:75	15:85	5:95
NEAP (mEq/d)									
Model A	−178	−136	−94	−51	−9	+33	+75	+118	+160
Model B	−186	−149	−112	−76	−38	−2	+36	+72	+109
Model C	−190	−155	−120	−85	−49	−15	+20	+56	+99
Model D	−193	−160	−127	−94	−61	−28	+5	+37	+70

[1] The cubic relation between the percentage of fat by weight and the percentage of energy from fat is [$f(x) = 0.009x^3 - 0.403x^2 + 7.92x - 22.79$, where x represents percentage body fat by weight (39)]. Model A: animal-fat energy = 26% of animal-food energy, which is equivalent to $\approx 3\%$ whole-body fat content; model B: animal-fat energy = 51% of animal-food energy, which is equivalent to 10% whole-body fat content; model C: animal-fat energy = 62% of animal-food energy, which is equivalent to 15% whole-body fat content; model D: animal-fat energy = 72% of animal-food energy, which is equivalent to 20% whole-body fat content.
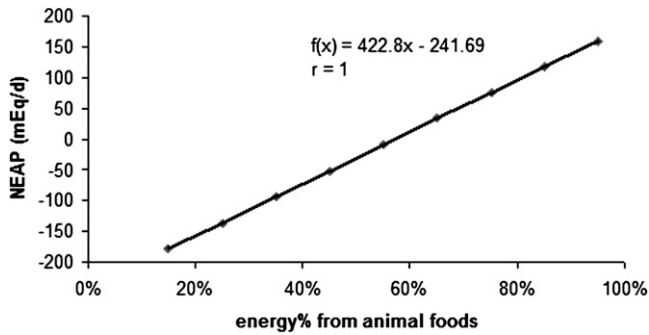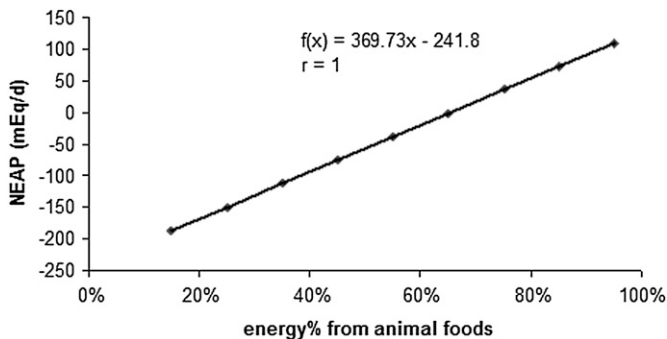
FIGURE 1. Association between net endogenous acid production (NEAP) and plant-to-animal ratios depending on body fat content of animal food (model A: 3% fat by weight).

FIGURE 3. Association between net endogenous acid production (NEAP) and plant-to-animal ratios depending on body fat content of animal food (model C: 15% fat by weight).
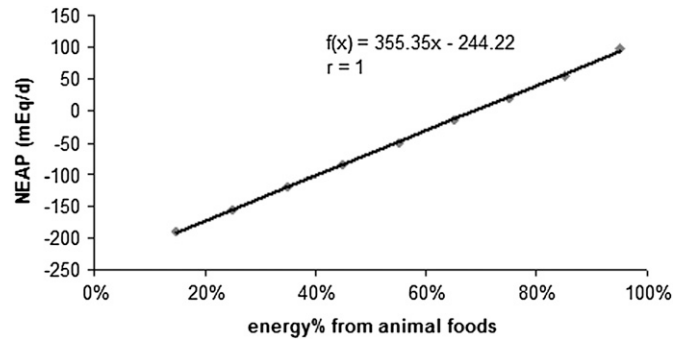
that nearly all such diets were net base producing has attained axiomatic status in the nutrition community (3, 11, 25, 55). However, as our present analysis of the diets consumed by the 229 historically studied hunter-gatherer societies listed in the *Ethnographic Atlas* clearly indicates, a high proportion of historically studied hunter-gatherer diets are characterized by a net acid load.

By analyzing and displaying a larger variation of P:A ratios and percentages of animal body fat, our data on the NEAP of historically studied hunter-gatherer diets conflict with those reported by Sebastian et al (18). Whereas their estimations of the net acid load for different hypothetic preagricultural diets were based on the assumption that the P:A energy subsistence ratios varied between 95:5% and 40:60%, we observed plant-source energy intakes as low as 0–5%, and animal-source energy intakes as high as 86–100% when we systematically analyzed the economic subsistence data for all 229 historically studied hunter-gatherer societies. According to their different dietary behaviors (20, 41, 50), which showed wide ranges of P:A subsistence patterns [gathered plant food: 0–5% to 76–85%; animal food: 16–25% to 86–100% (18)], we observed great variations in the NEAP for the different historically studied hunter-gatherer diets. The net acid load of these diets was estimated to have fallen between −178 and +181 mEq/d (lean-meat model A) and between −185 and +120 mEq/d (moderate-fat meat models B and C, respectively). Interestingly, even in the very-high-fat model (D), ≈40% of the hunter-gatherer diets were characterized as net acid producing.

These findings reflect the high reliance on animal-based foods of most of the worldwide historically studied hunter-gatherer

societies. For all 229 hunter-gatherer populations, the median subsistence dependence on animal foods was 66–75% (18). In addition, a compilation of the few available quantitative nutrition studies in historically studied hunter-gatherers shows a relatively low average P:A subsistence ratio of 35:65% (56, 57) and 41:59 (58).

As several authors have pointed out (18, 59–62), it seems unlikely that lean muscle tissue (≈3% body fat) was the sole component of animal-food intake in hunter-gatherers who showed a high reliance on hunted foods. This is because such diets would exceed the mean maximal rate of urea synthesis (65 mg N · h^{-1} · kg body weight$^{-0.75}$) because of their high protein content. Accordingly, Cordain et al (18) calculated that most of the hunter-gatherers had to have consumed animals with ≥10% body fat to avoid deleterious health effects ["rabbit starvation" (59)]. The possibility of the intake of toxic amounts of protein could have been averted by emphasizing the consumption of fatty portions of the carcass, such as organ meats and viscera, whereas leaner portions were discarded (62). Given this, model A seems to have overcalculated the NEAP for those hunter-gatherers who showed a P:A ratio of <40:>60% energy. Models B, C, and D seem to reflect a more realistic situation. It seems therefore most plausible that 40–50% of the entire sample of the 229 historically studied hunter-gatherers consumed net acid-producing diets, rather than 70%, as calculated in our lean-meat model A. Although these higher fat percentage ranges (10–20% fat by weight) for animal foods may at first appear to be intuitively incorrect because of the lean nature of wild animals, ethnographic descriptions of hunter-gatherers indicate that
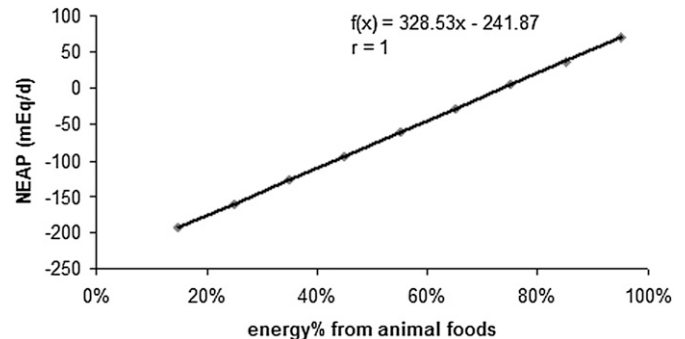

FIGURE 2. Association between net endogenous acid production (NEAP) and plant-to-animal ratios depending on body fat content of animal food (model B: 10% fat by weight).

FIGURE 4. Association between net endogenous acid production (NEAP) and plant-to-animal ratios depending on body fat content of animal food (model D: 20% fat by weight).

TABLE 2
Frequency distribution of the estimated net acid load of the diet in 229 hunter-gatherer societies with variations in the body fat of the hunted animal foods[1]

P:A ratio (%) by class interval[2]	Absolute frequency	Relative frequency	NEAP			
			Model A	Model B	Model C	Model D
	No. of societies	*% of societies*		*mEq/d*		
≤5 to ≥95	11	4.8	160 to 181	109 to 128	90 to 111	70 to 87
6–15 to 85–94	35	15.3	118 to 156	72 to 106	56 to 90	37 to 67
16–25 to 75–84	42	18.3	75 to 113	36 to 69	20 to 54	5 to 34
26–35 to 65–74	45	19.7	33 to 71	−2 to 32	−15 to 19	−28 to 1
36–45 to 55–64	35	15.3	−9.2 to 29	−38 to −5	−49 to −17	−61 to –32
46–55 to 45–54	30	13.1	−51 to −13	−76 to −42	−85 to −52	−94 to –64
56–65 to 35–44	23	10.0	−94 to −56	−112 to −79	−120 to −88	−127 to –97
66–75 to 25–34	6	2.6	−136 to −98	−149 to −116	−155 to −123	−160 to –130
76–85 to 15–24	2	0.9	−178 to −140	−186 to −153	−190 to −159	−193 to –163
Median	—	—	33 to 71	−2 to 32	−15 to 19	−28 to 1
Mode	—	—	33 to 71	−2 to 32	−15 to 19	−28 to 1

[1] Body fat of the hunted animal foods: ≈3% by weight for model A, ≈10% by weight for model B, ≈15% by weight for model C, and ≈20% by weight for model D. P:A ratio, ratio of plant-food energy intake to animal-food energy intake; NEAP, net endogenous acid production.

[2] Class intervals refer to P:A subsistence ratios, divided into 10 categories, as formulated by Cordain et al (18).

preferential butchering was commonly practiced, in which the leanest portions of the carcass were discarded in favor of the fattier elements [marrow, brains, retro-orbital fat, tongue, etc (59, 60, 63)], which can contain between 50% and 90% fat content (64, 65).

Regardless of the model used, our data presented here clearly show that a high proportion of the nonagriculturally based diets of historically studied hunter-gatherer societies were net acid producing. However, because ≈40–50% of the hunter-gatherer diets were characterized by negative or neutral NEAP values, there is no universal NEAP representative of preagricultural diets in general. Given that, as Cordain (18) asserts, "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' " (p 682), our results might be interpreted to indicate that it is not possible to identify a characteristic value range of the NEAP that contemporary humans could adopt for better health. Hence, on the assumption of the validity of Cordain's (18) assertion, the approach to the question of NEAP values associated with health benefits or risks based solely on data from historically studied hunter-gatherer diets might not to be feasible.

An important limitation is the use of ethnographic data from an analysis (18) of the *Ethnographic Atlas* (30). It is known that ethnographic data are subjective and qualitative in nature (28, 66); thus, the validity of the different P:A ratios is questionable. However, as Cordain et al (18) have stated, "The *Ethnographic Atlas* does provide reasonable dietary trends that have been cross-validated in a general sense by other independent anthropologic and archeologic procedures" (p 690). In addition, a compilation of the few available quantitative nutrition studies in hunter-gatherers (56, 57) showed a remarkable agreement between these quantitative P:A ratios and the ethnographic data used in this work.

Another limitation of the present analysis is the assumption that gathered food would only include plant foods, whereas Murdock (31) had stated that gathering activities could also include the collection of small fauna. As in the case of the analysis of Cordain (18), our calculations may be based on

overestimates of the relative contribution of gathered plant foods in the hunter-gatherer diets. Therefore, the compiled calculations presented here might underestimate the net systemic load of acid of retrojected preagricultural diets.

A further limitation of our study is that the P:A subsistence ratios of historically studied hunter-gatherers cannot with certainty be considered representative of the P:A subsistence ratios of the *Homo* species throughout the Paleolithic Age (27, 51), so any conflict between the data of the present study and those reported by Sebastian et al (26) must remain unresolved. With respect to P:A subsistence ratios, one cannot assume that worldwide historically studied hunter-gatherers serve as a valid representation of preagricultural hunter-gatherers and, in particular, those preagricultural African hunter-gatherers who lived for millions of years in geographic, climatic, and ecologic conditions much more narrowly restricted than those of the widely geographically distributed historically studied worldwide hunter-gatherers. Latitude of hunter-gatherer living sites plays an important role; Cordain et al (18) have shown differences in intake of hunted and fished animal foods between equatorial and nonequatorial regions. Sebastian et al (26) assumed an African equatorial Paleolithic. Likewise, worldwide historically studied hunter-gatherers have had a much longer time to develop methodologies for securing animal-source foods (hunting techniques and weapons; fishing techniques and tools). The present findings, therefore, cannot invalidate the conclusion of Sebastian et al (26) that ancestral preagricultural hunter-gatherers consumed P:A subsistence ratios that yielded net base-producing diets habitually or at least for considerable periods of time during any given year.

In conclusion, our data do not suggest that hunter-gatherer diets necessarily have net base-producing effects. In contrast, the high reliance on animal-based foods of modern worldwide hunter-gatherer populations produced net acid effects in a high proportion (40–50%) of the forager diets. The health effects of the reliance of historically studied hunter-gatherers on a net acid-producing diet require further investigation, in particular because reviews of the literature suggest that even small amounts of net acid perturb the systemic acid-base status in humans and

that such perturbations in the acidward direction have pathogenic significance (12, 13).

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