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Introduction

The last 10,000 years of human history have been marked by profound changes in virtually all aspects of human culture, occurring primarily as a result of the agricultural and industrial revolutions, whereas for the few million years prior to this period lifestyles for the genus *Homo* were relatively constant. Evolutionary theory and empirical evidence indicate that the human genome is not capable of adapting to the rapid pace of cultural change with which modern human populations have been faced (1). It is thus that living men and women are, in a manner of speaking, temporally dislocated, and equipped with physiologies that are in some respects poorly adapted to their present environments. The patterns of behavior, especially of nutrition and physical activity, which can be associated with our prehistoric ancestors, therefore constitute a reference range against which current practices may be compared. Such a comparison is illustrative both because it facilitates understanding of the so-called "diseases of civilization", which together account for most of the total disease burden in developed nations, and because it confirms certain aspects of current nutritional recommendations as well as suggesting some respects in which these recommendations might be improved. Because detailed information regarding prehistoric diets and activity patterns is largely unavailable, a surrogate may be found in modern groups that most closely adhere to prehistoric traditions, namely hunter-gatherer tribes and other pre-industrial peoples. This review discusses the results of such comparisons and their implications for public health.

Plant/Animal Ratios

A cursory reflection on the resource circumstances experienced by hunter-gatherers (and presumably by prehistoric humans) reveals that, of necessity, they consumed relatively large quantities of wild game and uncultivated vegetables and fruits, but few grains and no dairy products. A more precise characterization of hunter-gatherer nutrition, however, requires an estimation of the relative quantities of animal and plant matter consumed (P:A ratio), as well as their types and average nutritional content. Early estimates of P:A ratios for typical hunter-gatherer tribes indicate diets composed of 65% plant matter and 35% percent animal tissue (2). More recent analyses based on Murdock's *Ethnographic Atlas* (3) have, in contrast, suggested that most (73%) of hunter-gatherer societies derived >50% of their calories from meat (including wild game and fished foods), while only 14% of societies derived >50% of their calories from plants (4). Extreme P:A ratios of 1:4 or 1:9 (respectively, the Ache of Paraguay (5) and Alaskan Eskimo tribes (6)) have been described, consistent with the hypothesis that humans are adapted to consuming large quantities of animal flesh. Naturally, variability of P:A subsistence ratios among hunter-gatherers was quite high, depending on latitude, climate, location, and seasonal variations in the food supply (1). Furthermore, hunter-gatherer P:A ratios are not likely to be completely representative of those consumed by Paleolithic humans, as modern tribes have been relegated to marginal habitats, and the herds of large ungulates on which Paleolithic humans probably depended have been largely depleted over the course of the last few thousand years.

Meat

At a superficial level, the suggestion that hunter-gatherer tribes consumed large amounts of meat seems at odds with modern nutritional recommendations, which suggest that meat-particularly red meat-should comprise only a small part of a person's diet. The basis for such

recommendations, however, is the fact that the modern meat supply is relatively high in fat and saturated fat, such that consumption of domesticated meats correlates closely with one's risk of cardiovascular disease. The fat content of the wild-game species consumed by worldwide hunter-gatherers was quite low, however, and in such animals most existing fats are polyunsaturated, structural fats (7). Largely as a result of this fact, the estimated total fat intake of hunter-gatherers is lower both than current average American consumption and US government recommendations.

In surprising contrast, the total cholesterol consumed by hunter-gatherers was as high as, if not higher than, that consumed by modern Americans. This is due to the fact that cholesterol levels in wild-game and domesticated livestock are not substantially different. Nonetheless, it has been suggested that hunter-gatherers were better able to tolerate high dietary cholesterol, primarily because of low saturated fat intake. Indeed, total serum cholesterol levels in several hunter-gatherer tribes have been shown to be quite low; this is consistent with the observation that the incidences of atherosclerosis and coronary heart disease in non-aculturated hunter-gatherer groups (as well as most primitive agriculturalists) are much less than in affluent societies (8).

Hunter-gatherer protein intake is estimated to be quite high, between 19% and 50% of total energy intake (4). In contrast, modern dietary recommendations suggest that protein provide no more than 12% of one's daily calories. While historical evidence suggests that humans cannot tolerate diets containing more than 35-40% protein because of limitations on the rate of urea synthesis in the liver, the above evidence nonetheless suggests that modern recommendations may be excessively restrictive. Interestingly, however, many hunter-gatherer tribes may have been nutritionally limited by high protein intake, requiring extensive efforts to obtain other sources of calories. This involved consumption of only the fattest parts of killed animals, the pursuit of larger animals (which have a higher fat content), and increased plant consumption (9). Nonetheless, the reported incidence of renal disease (which may be aggravated by excessive dietary protein) in hunter-gatherer groups was negligible, presumably because of the elimination of other causative factors, such as diabetes mellitus (10).

Plants

Except for groups located in high latitudes where botanical diversity is limited, most hunter-gatherer peoples relied on a wide variety of plants for food. As dictated by the optimal-forager hypothesis, calorie acquisition for hunter-gatherers was heavily dependent on physical effort, and the maximization of caloric acquisition was desirable; thus foraging efforts were focused primarily on those plant materials with the highest energy content. Recent analysis has shown that on average fruit represented 41% of hunter-gatherer diets, seeds and nuts 26%, underground storage structures (tubers, roots, and bulbs) 24%, and other plant tissues (flowers, gums, leaves) the remaining 5% (4).

Unlike modern humans, hunter-gatherers made no significant use of cereal grains, suggesting that current practices (11), and the recommendation that grains provide the bulk of a person's caloric intake may be misguided. In contrast to the plant materials utilized by hunter-gatherers, cereals have relatively low amounts of micronutrients and phytochemicals, and consequently may not provide the same protective effects against chronic and degenerative diseases as other plant foods. While the currently accepted recommendation that Americans increase their intake of fruits and vegetables to 3-5 servings of each per day is commendable, it may be insufficient by

hunter-gatherer standards. Indeed, the high amounts of dietary fiber and phytochemicals consumed by most hunter-gatherer groups may explain the relatively low incidence of cancer (e.g., colon cancer) documented for such peoples (6).

Micronutrients

Largely because hunter-gatherers relied heavily on raw or incompletely processed food sources and consumed relatively large amounts of meat, fruits, and vegetables, it is likely that their intake of most vitamins and minerals was quite high. While an examination of all such nutrients is beyond the scope of this review, it has been shown that hunter-gatherer levels of most major micronutrients exceeded modern equivalents (and in some cases, modern nutritional recommendations), by several times (12). Hunter-gatherer intake of calcium, for instance, was estimated as roughly twice current values (10) largely due to greater consumption of vegetables and fruits. Hunter-gatherer consumption of electrolytes was essentially the inverse of modern tendencies, with relatively elevated levels of potassium and greatly reduced (by nearly an order of magnitude) intake of sodium. This observation is explained both by the high potassium content of wild game and uncultivated plants and the fact that hunter-gatherers typically had no access to sodium chloride other than that contained in their primary foods (12). The relatively high ratio of potassium to sodium contained in the hunter-gatherer diet is significant because it may explain the virtual absence of essential hypertension and age-related elevations in blood pressure in those groups; furthermore, it corroborates the results of clinical studies which suggest that the development of hypertension in westernized persons is linked to excessive sodium consumption.

Average Caloric Requirements and Physical Activity

Most analyses of hunter-gatherer diets assume caloric intakes of approximately 3000kcal/day (1,4) a surprisingly large figure that exceeds typical contemporary intakes. The level of energy expenditure necessitated by pre-agricultural lifestyles, however, was much greater than that for average modern individuals. For instance, total energy expenditure in the !Kung and Ache peoples averaged 206kJ/kg/d, compared to roughly 134kJ/kg/d for contemporary humans (13). This difference is accounted for both by the fact that hunter-gatherers had, on average, higher resting metabolic rates, due to greater proportions of lean to adipose tissue, as well as greater levels of vigorous physical activity. Typical !Kung and Ache males have been estimated to expend an average of 105kJ/kg/d in the course of their regular occupations; to compete with such a figure, the sedentary male of today would have to walk approximately 19km/d in addition to his other pursuits (12).

It is probably as a result of their increased energy throughput (moderately elevated caloric intake coupled with greatly increased energy expenditure) that the health consequences of metabolic imbalance occurred only rarely in non-acculturated hunter-gatherers. Unlike contemporary Americans, hunter-gatherer groups practicing traditional lifestyles showed little tendency toward obesity, non-insulin dependent diabetes mellitus, and other associated disorders (8). The process of acculturation, however, has been found to greatly increase the prevalence of such diseases in hunter-gatherer groups, as indicated by the recent experiences of Australian Aborigines (14), the Pima Indians of the American southwest (15), and others.

Conclusions

Examination of the patterns of diet and physical activity inherent to the lifestyle of hunter-gatherers provides a means of assessing the conditions to which the human species is genetically adapted, and thus a comparison of hunter-gatherer practices with those of contemporary populations reveals some of the respects in which the latter deviate from our evolutionary heritage. These deviations are significant in that they suggest potential causes for many of the chronic, degenerative diseases that plague industrial societies, and corroborate the results of clinical and epidemiological research concerning such diseases in those populations. An effort to modify current patterns of behavior to accord more closely to those of hunter-gatherers might serve to improve individual health, and should be reflected in clinical and nutritional recommendations, where important differences exist.

Naturally, however, the situation is not so simple as that. An evolutionary perspective on nutrition and exercise may be useful, but it also suggests that efforts to change existing behavioral modes are likely to be fruitless. Indeed, current patterns of food consumption and the minimal levels of exercise attained by most individuals could be predicted from an analysis of prehistoric humans and their non-agricultural, non-industrial forebears. As discussed above, hunter-gatherer peoples practiced optimal foraging techniques, and in general attempted to maximize caloric intake while minimizing physical activity; such tendencies had obvious survival advantages, and presumably have been incorporated into our genetic makeup. But while prehistoric humans' instincts to pursue foods with the greatest caloric density, to consume large quantities of said foods when possible, and to conserve the energy obtained in the process by minimizing extraneous physical activity, were counterbalanced by the exigencies of their environments, this is not the case in industrial societies, where, in general, foods of high quality can be obtained in large quantities with minimal effort. The diseases that currently plague modern civilizations are as much a product of our retention of old patterns of behavior as they are of changes in our basic way of life. Therefore, as long as affluent societies continue to exist, the individuals who inhabit them should continue to suffer from their own inheritance.

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