PALEOLITHIC HUNTER-GATHERERS’ DIETARY PATTERNS: IMPLICATIONS AND CONSEQUENCES

Al-Domi H¹*

Hayder Al-Domi

*Corresponding author email: h.aldomi@ju.edu.jo

¹Associate Professor of Nutrition and Dietetics, Department of Nutrition and Food Technology, Faculty of Agriculture, University of Jordan, Amman 11492, Jordan.
The human diet has passed through several revolutionary changes since the introduction of agriculture, which has led to substantial modifications in individuals’ nutrition behavior. Overwhelming evidence supporting that diet is a key environmental risk factor affecting the now rampant incidence of the diseases of affluence such as obesity, type 2 diabetes mellitus, cardiovascular diseases, and certain types of cancer. Findings on the health implications of low carbohydrate-high protein diet are inconsistent and controversial. Unlike modern humans, it was argued that the eating patterns of the Paleolithic hunter-gatherers could have beneficial effects on human health by reducing diet-induced chronic lifestyle diseases. Hence, the objective of this review was to outline the main aspects of Paleolithic hunter-gatherers’ dietary patterns and its main long-term health consequences. Paleolithic diet is based on the assumption that our hunter-gatherer ancestors were nourished on low carbohydrate-high protein diet. Yet, the majority of literature on Paleolithic diet is anecdotal and reflects two opposite viewpoints. First, advocates and proponents argued that human’s genome could have been modified a little since the early stages of agriculture. Thus, genetically, humans remain Stone Agers-adapted for a Paleolithic dietary regimen. As such, consuming a diet similar to that consumed during the Paleolithic era would be more compatible with our genetic makeup and might reduce the occurrence of diet-related lifestyle diseases. Second, critics asserted that the Paleolithic dietary recommendations and restrictions are not evidence-based. Adherents of Paleolithic nutrition claimed that modern populations who maintained Paleolithic lifestyle are totally free of the diseases of affluence. Nonetheless, information about the Paleolithic diet have been drawn from studies of surviving hunter-gatherer populations, archeological records, and analysis of wild plants and animals plus other methods. Recommendations of the Paleolithic nutrition are not based on interventional studies, thus the adoption of which could have negative health consequences. Hence, before adopting low carbohydrate-high protein diet, it seems logical to undertake a well-designed population-based longitudinal studies to evaluate the long-term health consequences of the Paleolithic nutrition.

**Key words**: Paleolithic, lifestyle, carbohydrate, protein, health
INTRODUCTION

The human diet has passed through several revolutionary changes since the introduction of agriculture, which has led to substantial modifications in individuals’ nutrition behavior [1]. The food industry has recently incorporated new technologies that permitted mass production of foods with longer shelf life, year round availability, and convenience. Hence, people in developing countries have been exposed to certain features of the affluent lifestyle, which is often accompanied by a shift in the availability and accessibility of foodstuffs. This has displaced local and traditional food items as well as food habits, which prompted possible negative impacts on health status leading to rampant rise in incidence of new lifestyle diseases including but not limited to obesity and type 2 diabetes mellitus [2].

Obesity is a serious global health problem contributing to the disease burden worldwide [3]. Many chronic health conditions, collectively known as lifestyle diseases, are associated with obesity include but not limited to type 2 diabetes, cardiovascular diseases and certain types of cancer [4, 5, 6]. Obesity does not merely reduce the individual’s quality of life, but also shortens life expectancy and entails heavy-associated healthcare costs [5, 7]. The dramatic increase in the prevalence of obesity worldwide over recent years can be restrictively explained, at one echelon, as classic gene-environment interplay wherein the individual phenotype is susceptible to environmental factors that affect energy intake and expenditure [8].

Obesity is a complex heterogeneous group of disorders, which develops predominantly from a polygenic multifactorial trait. It develops from a failure of complex interrelated homeostasis mechanisms that firmly control body-weight control mechanisms due to a complex interplay between both genetic and environmental risk factors mainly diet, and physical activity, which act by means of mediators of energy input and energy output [9, 10]. Mechanisms involved in the heritability of body weight-related phenotypes remain unknown. However, accumulating evidence has indicated that 6-85% of the variations in obesity-related phenotype is heritable and could be determined by genetic factors; thus far, a minimum of 127 candidates with multiple polymorphic genes for obesity have been identified and characterized [11, 12].

To date, more than 40 genetic variants have been associated with obesity and fat distribution [13], whereas 30 % of this variation could be ascribed to the exposure to different environmental risk factors [14]. Yet, conclusive and reliable evidence consistently linking gene-environment interactions and energy homeostasis remains inadequately investigated [15]. Common single-nucleotide polymorphisms at candidate genes for obesity have been identified, which act as an effect modifier for environmental risk factors [16]. Hence, the sensation of hunger and satiety is a cascading function of signaling proteins activated by food restriction or consumption [17], provided that a number of genes play a primary function in uncovering the inter-individual dissimilarity in susceptibility or resistance to the environmental obesogenic risk factors [18].

Modern toxic food environment encourages passive overconsumption of caloric-dense diets, which causes a persistent imbalance between energy input and energy output,
which in turn leads to a chronic failure in various complex homeostatic mechanisms that firmly regulate body weight ultimately resulting in overweight and obesity [8, 19].

In fact, one of the earliest defining human traits is bipedalism, the upright gait. This characteristic evolved over four million years ago [20, 21, 22, 23]. Other essential human characteristics, such as a large and complex brain, the ability to make and use tools, the use of fire to cook food, and the capacity for language and culture developed more recently. Interestingly, many of what were considered higher traits, such as art, religion, and different expressions of cultural diversity emerged during the past 100,000 years [20, 21, 22, 23]. The prehistoric era Paleolithic period (about 2.5 million to 10,000 years ago) is characterized by the appearance of the genus Homo (man) who instituted the most primitive stone-made tools as the earliest type of technological development. Unlike modern humans, it was argued that the eating patterns of the Paleolithic hunter-gatherers could have beneficial effects on human health by reducing diet-induced chronic lifestyle diseases [24].

Anthropologists have linked morphological development to diet [25, 26, 27]. It could be speculated that interspecific differences in resource exploitation probably include a complex of both behavioral and morphological adaptations, which denote species evolutionary history and constructional limits forced on phylogeny [27]. It is accepted to suggest that perhaps the diet of the twentieth century could be incompatible with our genes, which could be attributed to a possible failure in the natural selection process to provide humans with the genes necessary to cope with a lifestyle that characterizes the affluent societies [28, 29].

The Paleolithic dietary approach attempts to mimic the diet of our ancestors during the Paleolithic times. The main principles of the Paleolithic dietary approach as well as the proportions of nutrients, and related lifestyle were drawn from various sources based mainly on observational studies. Among which: (1) anthropologic and ethnographic studies of surviving hunter-gatherers, archeological records, nutrient analysis of edible components of uncultivated plant foods and non-domesticated animals, (2) morphological changes such as cranio-dental features, and (3) comparative gut morphology [30, 31].

The majority of literature on Paleolithic nutrition is anecdotal and reflects two opposite viewpoints. First, advocates and proponents of the Paleolithic nutrition argued that consuming a diet similar to that consumed during the Paleolithic era could be more compatible with our genetic makeup, and might reduce the levels of diet-related lifestyle diseases [32]. Second, critics of the Paleolithic nutrition emphasized that the dietary recommendations and restrictions based on the Paleolithic diet are not based on interventional studies. Hence, adopting the Paleolithic nutrition as a dietary approach might be unsustainable and difficult to implement. Findings have indicated that long-term or negative impact of low carbohydrate diet-high diet based on animal source or ignorance of the nature and source increases the total mortality and risk of cardiovascular disease [33, 34, 35].
Anthropologists, food historians, epidemiologists, and nutrition science experts have been raising the question of why obesity, diabetes and other lifestyle diseases are increasing in prevalence, and whether a simpler, diets of Paleolithic and recent hunter-gatherers may represent a reference standard for modern human nutrition, and could be a means of reducing or at least ameliorating the incidence of the new lifestyle diseases [31]. Hence, the objective of this review was to delineate the main aspects of Paleolithic hunter-gatherers’ dietary patterns and their main long-term health consequences.

PALEOLITHIC DIET AND GENETIC COMPATIBILITY

Genetic adaptation has its roots strongly embedded in the core of the evolutionary bases of the Paleolithic nutrition theory [36]. Advocates of the Paleolithic diet suggested that consuming a diet similar to that consumed by our ancestors during the Paleolithic era could be more compatible with our genetic makeup, thus it might reduce the magnitude of diet-related lifestyle diseases [37]. Nevertheless, the genetic code of humans has not changed substantially since the Paleolithic era, whereas many changes occurred in humans’ eating pattern and lifestyle, particularly since the introduction of agriculture and animal husbandry.

Compared to the vast majority of specie that predates humans by substantial periods, Homo sapiens are relatively young species and do not have as much time to add to genetic variation. Despite that, humans have a significant amount of common genetic information and the amount of biochemical individuality variation between two individuals is merely 0.1%; no two humans ever have been or will be genetically identical, save identical twins [29, 38].

The overwhelming changes in the environmental factors including diet, which began with the introduction of agriculture, happened too recently on an evolutionary time scale for the human genome to adjust [29]. Thrifty genes selected during the Paleolithic era are among the most examined genes. It has been implicated in the production of leptin hormone, a potent anorexigenic adipocyte-derived peptide that regulates adipose-tissue mass through hypothalamic effects on satiety and energy expenditure. Leptin exerts negative feedback effects on energy intake [39, 40].

Leptin loses its ability to inhibit energy intake and increase energy expenditure in obese individuals; eventually leptin receptors become desensitized to the effect of leptin leading to leptin resistant [39, 40]. Unlike modern humans, our hunter-gatherer ancestors encountered inconsistent food supply, the collection of which was highly dependent on vigorous physical activity. As such, it seems valid to argue that modern humans encounter irregular feast-famine and physical activity-rest cycles, which could overturn programmed biochemical balanced cycles, eventually leading to lifestyle-related diseases including obesity and type 2 diabetes mellitus [41].

LIFESTYLE OF THE MODERN HUNTER-GATHERERS

Anthropological studies (400,000-450,000 BC) revealed that the human diet consisted of considerable quantities of lean animal foods and unrefined plant derived foods [42].
Modern hunter-gatherers who were thought to be maintaining a diet and lifestyle similar to those of our Paleolithic ancestors have a dietary pattern high in antioxidants, fiber, vitamins, and photochemical as well as animal foods and/or gathered plant-foods as the dominant sources of energy [43]. Although fat intake was high, ranging from 28 to 58% of total energy requirements, qualitative differences in fat intake also existed compared to the present fat intake with relatively high levels of mono and polyunsaturated fatty acids and relatively low levels of saturated fat, and a lower ratio of omega-3 fatty acid [30].

Humans’ dietary requirements of macro and micronutrients have been determined [44], yet one in eight individuals worldwide is hungry [45], whereas approximately 2.3 billion adults will be overweight, and at least 700 million will be obese worldwide by 2015 [46]. Although agreed on the qualitative characteristics, proponents of the Paleolithic diet have not agreed on the relative proportions and amounts of macro and micronutrients. Whereas, advocates advised to consume suitable amounts of wild and grass-fed game meat as well as varieties of fresh vegetables, fruits, eggs, nuts and seeds. In addition, they recommend excluding foods that were not consumed in the Paleolithic era such as grains, legumes, dairy products, salt, refined sugars, flours, and processed oils [30, 43].

While hunter-gatherers populated much of the world until recent times, they became a small-marginalized minority, which retains characteristics of the social and cultural systems that were common during the Paleolithic period. There are currently about 235 to 265 hunter-gatherer groups scattered throughout the world; among best-known groups are the Australian Aborigines, Canadian and Alaskan Eskimos, Kung, and Tanzanian Hadza, and South American Indians [47].

Unlike indigenous people throughout the world who continued to defend their traditional lifestyle, culture, and lands in which they preserve 80% of the world’s biodiversity, modern hunter-gatherers have incorporated various elements of modern civilization into their traditional lifestyle, which has led, among other health risk factors, to a semi-sedentary lifestyle. Consequently, the transition in the lifestyle of the modern hunter-gatherers has caused a dramatic increase in the prevalence of lifestyle-related diseases [48].

Indeed, lifestyle diseases were uncommon and almost unknown within the traditional hunter-gatherer societies [48]. For instance, Australian aborigines who lived as hunter-gatherers were extremely healthy with no evidence of the chronic diseases that now afflict them. Modern acculturated Australian aborigines have a life expectancy of approximately twenty years less than non-native Australians, which is due to the now rampant incidence of chronic lifestyle diseases as compared to Western populations. For instance, the prevalence of diabetes mellitus among native Australians aged 25 to 54 years old is one of the highest in the world. Similarly, the mortality rate of heart diseases is up to fourteen times higher than the general rate. Moreover, premature death from chronic lifestyle diseases is more prevalent among native Australians at much younger ages than that among Western populations [49, 50].
HEALTH IMPLICATIONS OF THE PALEOLITHIC DIET

Arguably, the Paleolithic diet confers positive health effects including glycemic, and lipid profile as well as cardiovascular risk factors such as blood pressure [30, 31, 32]. In addition, discordance between human’s ancient genetically determined systems and the affluent lifestyle has led to increasing prevalence of various lifestyle diseases [43]. The adoption of the modern diet and high intake of refined cereal flours, sugar, sweets, and canned goods by first generation of modern hunter-gatherers has detrimental developmental changes in dental arch, facial features, immunity, and brain development [51]. Nonetheless, long-term consumption of low-carbohydrate-high protein diets without consideration of the type of carbohydrates or proteins are significantly associated with increased risk of cardiovascular diseases [34]. Unlike low-carbohydrate diet based on vegetable sources, low-carbohydrate diet from animal sources was associated with all-cause mortality rate in both males and females [33].

Paleolithic nutritional characteristics were based on the presumption that our ancestors were nourished by animal derived foods containing no carbohydrates and high protein and/or high fat foods [52]. Agricultural revolution with efficient production of grains, legumes, and potatoes, which are the very foods prohibited by the Paleolithic diet and discontinuation of a diet of mostly animal foods, believing that our ancestors actually did, marks the dawn of civilization that encompasses our advanced state of intellectual, cultural, and material development [52].

Food processing introduced during the Neolithic and Industrial eras primarily changed seven key nutritional characteristics of the hunter-gathers’ diets: (1) glycemic load, (2) fatty acid composition, (3) macronutrient composition, (4) micronutrient density, (5) acid-base balance, (6) sodium-potassium ratio, and (7) fiber content [23]. Nevertheless, eating practices of modern humans are considerably affected by both social factors and cultural practices [43].

Abundance of energy-dense foods and beverages has led to a pervasive passive overconsumption of energy dense foods, and an environment that limits opportunities for physical activity, which has led to an almost a universal sedentary state [19]. This toxic food environment has led to now rampant prevalence of obesity and obesity-related lifestyle chronic diseases worldwide [3, 44]. This could be justified by classic gene-environment interplay wherein the individual phenotype is susceptible to environmental risk factors that affect energy intake and expenditure [53].

It was estimated that calcium intake of our Paleolithic ancestors was as high as 2000 mg/day as compared with the current dietary recommendations of 740 mg/ day [43]. As rates of colon cancer and cardiovascular diseases have risen over the recent past few decades, could it be that lower calcium intake levels are part of the problem? Findings showed that dietary calcium in excess of absorptive needs, such as the case during Paleolithic times, binds bile acids in the gut thus sparing the colon epithelium from damaging effects of bile acids and at the same time lowering plasma cholesterol [43]. This could in part account for the increasing rates of colon cancer and cardiovascular diseases that have accompanied the falling rates of calcium intake [54].
Furthermore, the amount of carbohydrates that human consumed was raised sharply by the beginning of the agricultural revolution. However, traditional carbohydrate foods have low glycemic index and produced only modest increases in plasma insulin. The industrial revolution radically changed the quality of dietary carbohydrates; milling of cereals made starch more digestible and postprandial glycemic and insulin responses increased two to three fold compared with coarsely ground flour or whole grains, which led to insulin resistance and hyperinsulinaemia common to many modern day diseases.

Over the last 50 years, the rapid rise of convenience and take away fast foods among other changes in the food supply has exposed most all populations-regardless of age, sex, race, ethnicity, socioeconomic status, education level, or geographic region-to caloric intakes far in excess of daily energy requirements, which has led unprecedented marked rise in the rates of obesity, insulin resistance, and obesity-related chronic lifestyle diseases [55].

**SUITABILITY OF THE PALEOLITHIC DIET TO MODERN HUMANS**

Rather than a strictly vegetarian diet, consumption of lean meat, fish, vegetables, and fruits might be optimal in the prevention of affluent lifestyle diseases [32]. Despite the importance of plant foods to hunter-gatherers diet, they ate as much vegetable foods and meat as they could [56].

The Paleolithic diet is the most recent and popular approach to weight loss, improved health, and longevity, which is accomplished by consuming large amounts of animal-derived foods [52]. Metabolic processes surely helped ancient people and current hunter-gatherers to thrive and survive during harsh environmental conditions and the scarcity of food sources during famines. Whereas, people in the affluent societies still have thrifty genes working, the affluent diet and lifestyle provided a constant and homogeneous food supply with minimal work needed to obtain and consequently reduced physical activity [41].

As such, under these circumstances, the same thrifty genes might be expected to enhance the development of same lifestyle diseases [41]. Yet, Paleolithic dietary recommendations are popular, perhaps due in part to romantic notions as well as huge commercial promotions. Their popularity was coloring the objectivity of such research, and the evidence base is relatively weak, giving the absence of several thousand years of data on its actual characteristics and health effects [57].

Skeptics of the Paleolithic nutrition ask: if modern humans are eating poor food, then why do they live so much longer today than Paleolithic ancestors did? Although there is evidence indicating that hunter-gatherers died at early age mainly due to injury and infection, archeological records showed that a few individuals were able to live apparently healthy lives sometimes until their seventh decade [42]. Recent rise in the life expectancy of humans attributed is mainly to the success in combating communicable diseases, improvements in hygiene, and food safety [58].
Modern population densities and lifestyle require easy storage of foodstuffs, food availability, and rapid preparation and consumption. Providing the greatest proportion of our energy from carbohydrates namely grains, wheat, rice, and maize is much more economical apart from their nutritious value and high fiber content. Effective adjustments to the diet require immediate perceived advantages to the consumer in order to reduce anxiety of dealing with the endless choices of the available excess food energy and not just long-term health benefits, rather than the consumption of specific novel foods of the Neolithic underlies the rinsing rates of the diseases of affluence [42].

CONCLUSIONS AND FUTURE IMPLICATIONS

Overlooking the Paleolithic diet debate, there is overwhelming evidence supporting that unhealthy diet is a key environmental risk factor affecting the now rampant incidence of the diseases of affluence. Food can have social and possibly political consequences of both regulating and harmonizing food production and consumption. The nutritional requirements specific to human health, age, and lifestyle will be addressed with regard to population, group, or individual genetic makeup [59].

It is assumed that systems biology, nutrigenomics and metabolomics could provide means for individualized diet. Merging both nutritional and metabolomics findings to humans’ phenotyping can enable researchers to understand the process by which genes interact with food. The variation of individuals’ genetic that act as an effect modifier for environmental risk factors [15], and its effect on metabolic processes will allow healthcare providers to use person-specific diets to sustain health and prevent the occurrence of diet-related diseases [60].

The recommendations of the Paleolithic nutrition are not based on interventional studies, and therefore the adoption of which could have health consequences. Therefore, before adopting low carbohydrate-high protein diet, it seems logical to undertake well-designed population-based longitudinal studies to evaluate the long-term health consequences of the Paleolithic nutrition.

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