## Animal Source Foods and Human Health during Evolution<sup>1,2</sup>

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ABSTRACT Animal source foods (ASF) have always been a constituent of human diets. Their pattern of use, however, changed in dramatic ways over the course of human evolution. Before 2 million years ago (mya), meat in particular was acquired opportunistically via hunting of small or young animals and scavenging of animals killed by other species. At some point after that time, humans began to hunt cooperatively, making possible the acquisition of meat from large game. The marked increase in human heights between 2.0 and 1.7 mya may be linked to more efficient means of acquiring meat, namely through hunting. The final pattern of meat (and other ASF) use before the modern era is associated with the shift from hunting and gathering beginning  $\sim$ 10,000 y ago. This fundamental gamening beginning ~ 10,000 y ago. This fundamental sumption of meat and increased focus on domesticated ound the world reveals that this period in human dietary are of morbidity (poorer dental health, increased occlusal infection and bone loss). Human populations living in a lipid compositions that when eaten in excess promote my and eat more high fat foods, we can expect to see is of "civilization." J. Nutr. 133: 3893S–3897S, 2003. *animal source foods explores the changes in health with regard to what is known about dietary change, especially in the last 10,000 y, based on bout dietary change, especially in the last 10,000 y, based on the study of skeletal remains recovered from archaeological settings. A brief history of human diet Meat: it's what's for dinner.* Meat consumption has a long thistory in human evolution, likely going back to the earliest. dietary change resulted in a narrowing of diet, reduced consumption of meat and increased focus on domesticated grains. The study of archaeological human remains from around the world reveals that this period in human dietary history saw a decline in health, including increased evidence of morbidity (poorer dental health, increased occlusal abnormalities, increased iron deficiency anemia, increased infection and bone loss). Human populations living in developing and developed settings today rely on meats with lipid compositions that when eaten in excess promote cardiovascular disease. As humans become more sedentary and eat more high fat foods, we can expect to see increases in heart disease, osteoporosis and other diseases of "civilization." J. Nutr. 133: 3893S-3897S, 2003.

KEY WORDS: • evolution • diet • skeletons • health • animal source foods

The use of animal source foods in human diets has a long history, going back at least 5 mya. The pattern of meat consumption in human evolution can be divided into four time periods: 1) opportunistic hunting and perhaps scavenging; 2) full-scale hunting beginning perhaps as much as 2 mya; 3) the shift from hunting and gathering to domesticated food sources, both animal and plant, beginning  $\sim$ 10,000 y ago; and 4) the reliance on animal tissues with fatty acid composition deleterious to health, especially after World War II.

Meat provides a wonderful package of energy, high quality protein and key essential micronutrients (e.g., iron, zinc, vitamin A, vitamin B-12). It is not surprising, therefore, that humans would have focused on it, given the necessary tools for its acquisition and processing. With increasing population size beginning in the late Pleistocene Epoch some 10–12 thousand years ago (tya), humans began an abrupt and comprehensive dietary change-especially involving agriculture. This paper

history in human evolution, likely going back to the earliest known human-like ancestor living 5–7 mya (1–3). The pre-  $\aleph$ sence of primitive stone tools beginning at  $\sim 2.5$  mya in eastern  $\vec{\sigma}$ Africa indicates that early humans likely had the capability of cutting and processing meat from animals. For example, cutmarks made from stone tools on the bones of animal prey found in Kenya and Ethiopia indicate meat consumption (4,5). Before 2.5 mya, the archaeological record of meat consumption is nonexistent, but the commonality of hunting and meat eating by our nearest common ancestor, the chimpanzee, suggests that meat eating has an ancient history, extending before the appearance of a human-like primate some 6–8 mya (6).

Hunting and meat consumption. Although meat consumption has an ancient history, it was likely not a common food source until systematic hunting involving a technology focused on meat acquisition began, perhaps as long as two million years ago. In East Africa, large animals-the extinct species of giant gelada baboon, for example-were hunted and their tissues processed for food (7–9). The hunting of large prey by a group of cooperating adults provided humans with a regular and predictable access to protein and micronutrients.

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Perhaps the adoption of hunting strategies resulted in improved health in early hominids, thus explaining the increase in adult heights some 2.0–1.7 mya. McHenry and Coffing have documented a dramatic 44% increase in body mass for males (from 37 kg for *H. habilis* to 66 kg for *H. erectus/ergaster*) and a 53% increase for females (from 32 kg for *H. habilis* to 56 kg for *H. erectus/ergaster*) (10–12). This represents height increases of 33% for males (from 131 cm to 180 cm) and of 37% for females (from 100 cm to 160 cm) (10). So regular was meat consumption that by Neanderthal times in the later Pleistocene Epoch (100,000 y), animal source foods were a dominant dietary constituent (13).

The pattern of acquisition of ASF takes on various forms in later human evolution, reflecting increased regional specializations in food acquisition in the late Pleistocene Epoch (20,000–11,000 y). It is during this time that animal herds, such as the extinct horse, were driven off of cliffs to acquire large amounts of meat. Most importantly, however, for the first time, there was widescale exploitation of marine resources derived from fishing and shellfish collection beginning in the late Pleistocene Epoch. This new exploitive strategy represents a major departure from the previous focus, lasting hundreds of thousands of years, on terrestrial ASF (14,15). Fish and shellfish provided valuable sources of protein, energy and micronutrients, but required new and innovative strategies of food collecting.

The agricultural revolution: less meat, more plants, less nutritional diversity. Within a short time of the arrival of essentially modern climates, human diets began to change in dramatic ways; people in select areas around the globe began to domesticate the plants and animals that heretofore had been wild (16). For some regions, domestic animal sources were important, especially for their meat, milk and skin products. Meat and milk provided food, whereas skins provided clothing and housing materials. In the Middle East, for example, cattle, sheep and goats were domesticated beginning some 8 or 9 tya. Pigs, chickens and other animals came under domestication somewhat later. For these and other regions of the globe, in the Americas, for example, plant domestication was much more important in the changing foodways.

What is so fascinating about domestication—and here, this article refers mainly to plant domestication because plants were so much more important than animals as a source of energy—is that it appeared in at least seven independent centers (16) and rapidly spread from these centers for lengthy distances. Although this article mainly considers the effect of this major change in diet on human health, it is nevertheless important to understand why it occurred. Some anthropologists speculate that it was a natural outcome of the warming trend that occurred after the retreat of the glaciers that covered vast areas of the globe. Others argue that perhaps it was linked to an overhunting of large animals, the ancestors of modern elephants and other animals that roamed Europe, Asia and the Americas during the Pleistocene Epoch. With the disappearance of these animals, perhaps some other means of acquiring food had to be developed.

The shift from food collection/hunting to food production likely reflects a combination of complex factors, including climate change involving a general warming and drying around the world, and the appearance of new plants and animals that could be domesticated. One thing that is attractive about domesticated plants as a food source is that they provide more calories per unit area of land than nondomesticated plants, at least in traditional settings.

The key point here is that the shift from hunting and gathering to agriculture resulted in an increasing focus on a limited variety of foods, with meat likely taking a back seat to plants. The remainder of this paper reviews what anthropologists have learned about the consequences of this fundamental dietary transition for human health.

Health consequences of shifting from hunting and gathering to agriculture. It has long been assumed by both the public and by scholars that the shift from a lifeway based on hunting and gathering to agriculture represented a major improvement in the human condition. After all, agriculture provided the foundation for what the modern world holds dear, what we call "civilization." Agriculture was the "great leap forward, the advance that catapulted us out of the hand-to-mouth, day-today existence of hunter-gatherers...and into the complex, cultured, literate existence of modern human beings" (17). The eminent archaeologist Robert Braidwood (18) captured the perspective of what it meant to be a hunter-gatherer >40 y ago when he said that "before (agriculture) most men must have spent their waking moments seeking their next meal, except when they could gorge after a great kill."

Some of the most compelling evidence from which to evaluate the consequences of the shift from hunting and gathering to agriculture on human health is derived from the study of ancient skeletons found in archaeological sites around the world. These skeletons tell us a number of things, especially what people ate in the past, the impact of chewing on our faces and jaws, the consequences of lifestyle changes for health and the alteration in lifestyle and consequences for skeletal maintenance.

What people ate and how we know. Up until recently, most of our understanding of past diets was based on the remains of plants and animals found in archaeological sites. These data sources provide a laundry list of what people ate, but not in their relative proportions. The former presents a picture of diet, whereas the latter reflects nutrition, which is really what we want to know. New insights into nutrition are provided by chemical signatures of diet found in bones and teeth of earlier humans (19). Some of the best information is based on analysis of stable isotopes of carbon [ratios of <sup>13</sup>C/<sup>12</sup>C ( $\delta^{13}$ C)] and nitrogen [ratios of <sup>15</sup>N/<sup>14</sup>N ( $\delta^{15}$ N)] extracted from human bone. Analysis of carbon isotope ratios tell us about the use of  $C_3$  plants versus  $C_4$  plants in diet, because the isotope ratios of these plants are different (and, hence, the tissues of the humans consuming these plants).  $C_3$  plants are those mostly from temperate climates, whereas  $C_4$  plants are the tropical grasses. Maize is one of the key C<sub>4</sub> plants eaten by millions of people in the past and present in the Americas. Maize played an important part in the development and rise of complex societies in this area of the globe before Columbus. Soon after Columbus's arrival in the New World, the plant transported back to Europe and rapidly became a key staple throughout the Old World. Other C4 plants are millet in Europe and Asia and sorghum in Africa. The dietary signatures of and relative importance in human diets are discernable via the study of skeletal remains.

Nitrogen isotope values identify a number of dietary aspects, but are especially useful for identifying the amount of seafoods versus the amount of terrestrial foods in diet, the former representing fish, marine mammals and shellfish, and the latter representing animals and plants that are land based, especially plants. Stable isotope ratios of nitrogen are also useful for identifying the relative contributions of plant versus animal sources of protein or the position of the organism consumed in the food chain (the trophic level) (13). The relative measures of stable isotopes of carbon and nitrogen also provide information on the importance of plant source food consumption versus animal source food consumption.

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These methods of identifying foods eaten by people in the past are important because they inform our understanding of the relative nutritional standing of past populations. Consumption of maize on such as grand a scale as it was in many parts of the Americas before Columbus and throughout the world after tells us that populations likely had reduced access to animal protein as an energy source. It also tells us that: 1) they focused on a food lacking essential amino acids (lysine and tryptophan) and key micronutrients; 2) they likely had a narrower dietary breadth; 3) they had an increased exposure to phytate in diet and poor calcium and iron status; and 4) they lived in circumstances that promoted the spread of infectious disease.

There are a number of regions where we now know a great deal about dietary change. For example, in the southeastern U.S. Atlantic coast (Georgia and Florida), we have documented a simultaneous decrease in the use of marine foods and an increase in the use of maize (19). The overall consumption of meat probably declined. For the Atlantic coastal setting, although marine sources declined with agriculture, they remained important in the nutriture of populations. In Neolithic Greece and in some other coastal settings where agriculture became important, marine sources appear to have been greatly reduced (or even eliminated), at least as they are identified by stable isotope analysis (21). In general, the emerging picture suggests that there was a reduction in ASF in diets in the last 10,000 y of human evolution.

Chewing and its implications for oral health. The shift from hunting and gathering to agriculture involved not only an alteration in the kinds of foods eaten, but also in their consistency. In particular, the advent of agriculture also involved the invention of ceramic vessels and the ability to cook foods, plants in particular, from tough to soft consistencies. Studies of laboratory animals and observations of living humans show that those who eat hard foods tend to have longer skulls than those who eat soft foods (22-24). More importantly, for human health, the shift to softer foods results in a reduction in the bony areas of the facial skeleton that support and anchor the teeth in the jaws. Tooth size has undergone remarkable reduction in size throughout human evolution, but the jaws have reduced dramatically in the last 10,000 y. This means that increasingly over time there has been less room for the growing dentition, resulting in the rise in occlusal abnormalities and malocclusion generally in humans, especially in the last millennium. Thus, it is no mystery why orthodontics is such a booming business today.

Other implications for oral health are directly linked to the foods consumed. For example, the consumption of soft carbohydrates, such as maize, would have meant increased opportunities for the metabolism of carbohydrates by oral flora resulting in dental decay (caries) (25). For many regions of the world where domestic grains were utilized, dental caries increased in a dramatic fashion, such as with maize in the New World. In settings involving consumption of rice, preliminary evidence suggests that caries did not increase (26–28).

Other health consequences: implications of population crowding and sedentism. An indirect outcome for health in the shift from hunting and gathering to agriculture is the impact of sedentism and population size increase and concentration (29). Basically, agriculturalists in the past became more concentrated, higher in number, and less mobile than were their foraging forebears. From the epidemiological perspective, this reconfiguration of humans on the landscape created new circumstances that facilitated the evolution and breeding of the microbes responsible for infections and infectious disease. Indeed, most studies of skeletal remains by physical anthropologists show that prehistoric populations living in crowded settings had in general more skeletal infections identified as lesions called periosteal reactions. Periosteal reactions are nonspecific responses with no clear cause, but at least some were caused by specific infectious diseases, such as treponematosis. Many periosteal reactions were caused by localized infections, such as from soft tissue wounds (23). In the settings where populations were living in reduced sanitary conditions, chances for infection would have increased. At least some of the major infectious diseases humans are experiencing today got their start in the setting of crowding, made possible by the agricultural revolution. At least some of these diseases, the zoonotic diseases, derived originally from contact with domestic animals. Regardless of their origins, infectious diseases and infections generally were exacerbated by poor diets and compromised nutrition.

Another outcome of sedentism that is documented in the developing world, where water sources are contaminated with parasites (e.g., hookworm), is iron deficiency anemia. Millions today are affected by this debilitating disease. Although poor diets are a factor, it is really the water contamination by parasites that is the root cause of iron deficiency anemia where these parasites are endemic (30). Thus, it comes as little surprise that in many Holocene populations where crowding was present, there were elevated levels of skeletal evidence of iron deficiency anemia (29). On the other hand, populations with abundant marine resources express relatively low prevalence of skeletal manifestations of iron deficiency in the form of pitting in the bone of the eye orbits and flat cranial bones called cribra orbitalia and porotic hyperostosis, respectively. For example, on the Atlantic coast of the southeastern United States, late prehistoric maize-eating populations had low frequencies of cranial pitting linked to iron deficiency (20). This finding is consistent with the clinical evidence showing better iron status in populations who combine maize and fish in their diets (31).

Lifestyle and its implications for skeletal health. The change in how food was acquired resulted in major alterations in workload and physical activity. Study of living populations shows that some traditional agriculturalists work very hard, whereas others work less hard. In comparing hunter-gatherers with agriculturalists, this literature does not suggest a clear pattern of how food production patterns affect human workload. However, study of articular disease (osteoarthritis) and bone form (biomechanics) provides key insight into the work patterns and behavioral adaptations of earlier societies.

Osteoarthritis (also called degenerative joint disease) is caused by the mechanical wear and tear on the joints of the body, especially the joints involved in manipulation of objects (e.g., the hands), lifting (the back), carrying (the arms and shoulders), and walking or running (the hips, legs and feet). Osteoarthritis is expressed most commonly in the form of bony spicules that build up along joint margins or less often as deterioration of joint surfaces (23). In a number of settings, comparison of earlier hunter-gatherers with later agriculturalists reveals a dramatic decline in osteoarthritis (20). This suggests that workload also decreased with the shift to dependence on food production. In the southeastern U.S., with the arrival of Europeans and the establishment of mission centers, there were dramatic increases in osteoarthritis. This later change reflects the increased work demands and labor excesses placed on exploited native populations by Spanish colonizers.

The application of biomechanics to the analysis of skeletal morphology provides additional perspective on the effects of workload and activity for different types of dietary regimes (32). Bones adapt themselves during the life of the individual so as to be able to resist breakage from excessive activity; bone is placed where it is needed and taken away where it is not. In human societies that use their limbs and bodies in heavy work and physical activity, bones are larger and more developed. On the other hand, in societies where workload and activity are minimal, bones are smaller and less developed. In some settings, such as in situations of extended bed rest or space travel, there can be considerable bone loss, resulting in a condition called osteoporosis. Osteoporosis can result in pathological fracture. In our own sedentary society, at no other time has the prevalence of osteoporosis been so high, which is linked in large part to inactivity.

Our analysis of bone size and structure, via the measurement of what engineers call cross-sectional geometric properties, reveals that in some settings, bones are "stronger" in hunting and gathering regimes and "weaker" in agricultural regimes. This is the case on the southeastern U.S. Atlantic coast (33), but not in pre-Columbian Alabama (34). In the latter setting, there was an increase in bone strength reflecting an increase in workload. These differences suggest that the transition to agriculture had different effects on workload and activity levels from one region to another.

Therefore, the skeletal response in relation to activity must have varied from one region to another. However, by and large, there has been a weakening of human bones over the last 10,000 y that is related to lifestyle. As humans became less involved in labor and activity associated with the food quest, the skeletal system became adapted for lower-intensity activity. There is also evidence to suggest that osteoporosis may have increased. Humans are living longer in recent history, which explains to some extent the remarkable increase in osteoporosis in recent times compared to humans living thousands of years ago. But it is also the case that the shift in lifestyle and diet, especially increased sedentary behavior and greater emphasis on carbohydrates and fats, set the stage for the current epidemic of this potentially debilitating disease (35).

**Recent historical trends in heights: implications for health** and diet in human evolution. Heights provide an important perspective on health trends in the recent historical past. In the big sweep of human evolution, as pointed out above, heights greatly increased somewhere between 2 and 1.7 mya. From then on, height and body mass were more or less equivalent with that of recent humans (10–12). Study of archaeological samples shows fluctuations in the heights of modern humans. These fluctuations are linked to access to high quality nutrition that presumably included meat. In a number of settings worldwide, the shift to agriculture saw a decline in heights, which reflects the shift in orientation to include domesticated plants, probably less meat, and certainly reduced nutrition overall (29).

Some of the best anthropometric historical data on heights is derived from the analysis of military and other records where height data are abundantly available. Costa and Steckel (36) have analyzed height data of military recruits in North America for the eighteenth through twentieth centuries. The record shows a steady increase in heights by an inch or so from 1710 to 1830, followed by a drop of two inches through the remainder of the nineteenth century. Beginning in about 1890 or so, heights rebounded and showed a steady rise to the present day. A variety of factors likely explain the decrease in the nineteenth century, but access to ASF and their micronutrients likely was important, reflecting a shift from life on the farm to life in an urban setting. Sanitation, health care and other factors were also important, but the access to ASF must have been an important factor.

Interestingly, socioeconomic differences in colonial Americans were relatively small, especially in comparison with Europeans living at the same time. Colonial European populations show strong disparities in heights, presumably reflecting differences in access to ASF by social class (37). In addition, during the time that Americans were seeing declines in height through much of the nineteenth century, Europeans were generally increasing their heights (38).

Within other subsets of recent human populations, access to meat appears to have engendered better health, at least as it is measured by heights. Equestrian Plains tribes from North America, for example, are among the tallest compared with any other Native American population (39). These populations were nomadic and dispersed, thus would have experienced limited levels of infectious disease. In addition, their access to buffalo and other game was greatly facilitated by the use of horses in hunting and subsequent food distribution.

In the twentieth century, the association between meat intake and increased heights is illustrated in Belgium (40), among other developed countries. From the mid-1950s to 1978, meat consumption per capita increased from 60.8 kg/y to 98.0 kg/y, representing a 50% increase. At the same time, grain consumption declined and fruit consumption increased. Heights showed dramatic increases. This trend was repeated globally in developed and developing nations after World War II (41).

The study of skeletal remains from archaeological settings around the world indicates that health in humans remained largely robust until the shift from hunting and gathering to agriculture, a dietary transition documented for the last 10,000 y of human evolution (29,40,42-44). The primary change in body size involving an increase in height may have been linked to more efficient means of ASF acquisition, probably involving hunting. This dramatic change in body size is the only development that is discernable in the study of the past before 10,000 y ago. The shift from foraging to farming involved a decrease in meat consumption. The health declines summarized in this article are unlikely to be tied to a decline in meat consumption, but rather, they are mostly linked to an increased emphasis on foods (plants) that have a poor nutrient content, especially with regard to key micronutrients. That said, grains do provide certain health benefits (14,45–47), such as lowering the risk of coronary heart disease.

In general, the evidence of the skeletal record provides a compelling picture of decline in health with the replacement of a varied diet, which included significant meat consumption, by a diet focused on a few domesticated grains. Studies of traditional hunter-gatherers in the first half or so of the twentieth century showed that they are generally free of cardiovascular disease (14,47–50). These diets were in many ways similar to those consumed for much of the history of humankind, certainly before 10,000 y ago.

The reason for the low prevalence of cardiovascular disease in traditional hunter-gatherers is likely due to the fact that the animal tissues they consumed contained the same amount of fat as consumed by humans living in developed settings today, but the fat eaten by traditional hunter-gatherers was high in monounsaturated and polyunsaturated fatty acids (14,50). Moreover, the level of physical activity was markedly greater than what is observed in developed (and many developing) countries. Thus, although hunter-gatherers consumed fat, it was not of the variety that promotes cardiovascular disease as seen in modern populations. Herein, then, lies another key point: if meat consumption is to be significant in living populations in the developed and developing world, the lipid characteristics should more closely approximate the lipid characteristics of meats (e.g., ruminants) consumed by traditional hunter-gatherers and our prehistoric forebears (14,50).

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Most importantly, at no other point in our history as a species do we know so much about nutrition and how nutrition and diet affect our health and well being. With this knowledge in hand, we should be able to develop a pattern of food consumption that is beneficial to the health and well being of our species. The decisions we make now about our diets are surely as important as decisions made by our ancestors about theirs.

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