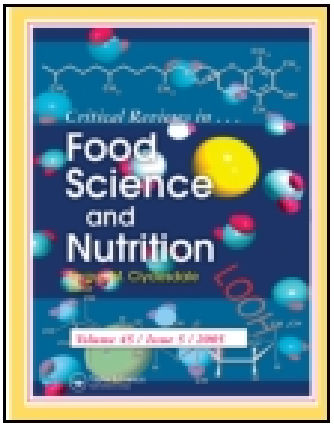

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Brain Evolution, the Determinates of Food Choice, and the Omnivore's Dilemma

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Brain Evolution, the Determinates of Food Choice, and the Omnivore's Dilemma

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A coevolutionary paradigm using a biocultural perspective can help to unravel the complex interactions that led to the contemporary pattern of eating. Evolutionary history helps to understand the adaptation of diet and its nutritional implications. Anatomical and behavioral changes linked to changing dietary patterns in the Paleolithic resulted in an adaptive framework that affects modern diet. The evolution of an expanding brain, a shrinking large intestine, and lengthening small intestine necessitated a demand for nutritionally dense foods. The key to these changes is an understanding of the response to the omnivore's dilemma. Omnivores in their search for new items to feed their varied diet (neophilia) have a challenge when they fear (neophobia) novel items that may be poisonous and can cause death. The inborn mechanism initiates palate fatigue (sensory-specific satiety) ensuring a variety of foods will be eaten. Variety will limit the impact of toxins ingested and provide a more balanced diet. The development of cuisine, a momentous event in history, mediated the conflict, and changed the course of human evolution. The cuisine, a biocultural construct, defines which items found in nature are edible, how these products are transformed into food, the flavors used to add a sensory dimension to foods, and rules of eating or etiquette. Etiquette defines how, when, and with whom we eat. Patterns of eating in the modern setting are the end product of the way that Homo sapiens evolved and resolved the omnivore's dilemma. Control of fire and cooking expanded the range of available foods by creating a class of foods that are "predigested." An essential element to the evolution of the human diet was the transition to agriculture as the primary mode of subsistence. The Neolithic revolution dramatically narrowed the dietary niche by decreasing the variety of available foods, with the shift to intensive agriculture creating a dramatic decline in human nutrition. The recent industrialization of the world food system has resulted in a nutritional transition in which developing nations are simultaneously experiencing undernutrition and obesity. In addition, an abundance of inexpensive, high-density foods laden with sugar and fats is available to a population that expends little energy to obtain such large numbers of calories. Furthermore, the abundant variety of ultraprocessed foods overrides the sensory-specific satiety mechanism leading to overconsumption.

Keywords Evolution, cuisine, Neolithic revolution, nutritional transition, food processing, diet

The biocultural approach (Durham, 1991; Goodman and Leatherman, 1998a, 1998b) has been an integrating force in anthropology (Armelagos, 2008). This perspective considers the coevolution of culture and biological features in the adaptive process (Laland et al., 2010). Studies that assimilate the coevolution of biology and culture have helped untangle the evolution of diet. Cultural factors shape the foods that we eat, and their consumption has biological consequences. For example, the introduction of swidden agriculture (slash and burn) for cultivating yams in West Africa created a breeding ground for the *Anopheles* mosquito, a vector for malaria. The biological response to the cultural practice of yam cultivation was a genetic change in the hemoglobin that altered the shape of the red blood cells causing them to sickle. Individuals with the sickle cell trait have a genetic abnormality that affects the structure of their hemoglobin, causing the disc-shaped red blood cell to collapse into a sickle-shaped with reduced oxygen pressure. The sickle-shaped cell morphology has multiple health consequences, including impaired functioning of the vascular and pulmonary organs. The intriguing part of the puzzle is how a gene that has such a negative effect on physiology could be maintained at a high frequency in some populations.

Individuals with sickle cell anemia frequently die before reaching reproductive age, essentially removing two genes from the population. Given this loss, one would expect the frequency for the sickle cell gene to be quite low. However, among some

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West African populations the frequency for the gene that controls sickling, Hb^s, reaches 0.4 (40%). Allison (1954) and Livingstone (1958) provided an answer to the riddle. The West African groups with the highest frequency of sickle cell anemia were yams growers who used slash and burn technology. They prepared the land by cutting trees and burning them (the iron axe introduced about 2000 years ago was the key to penetrating this forest habitat and the planting yams). The changes in the environment (the clearing of the land) exposing pooled water to sunlight and the use of thatch for houses created an ideal breeding ground for anopheline mosquitoes (Yasuoka and Levins, 2007). Since *Anopheles gambiae* breed in water in a sunny environment, land clearing gives them a reproductive advantage. The settlements near the burned areas with clusters of houses provided food (humans) for the mosquitoes. As the mosquitoes proliferated in the environment, malaria became endemic and created a new selection pressure for the sickle cell mutation (a single amino acid change), which provides a protective advantage for humans. The ensuing rapid selection for the gene provided protection for enough of the population that they could successfully exploit the forest, eventually leading to the widespread penetrance that we see today (Rosenthal, 2011).

The evolution of persistence lactose tolerance and the domestication of animals for milk represent a more direct link between biology (genes) and culture (milk as food). Mammals, except for *Homo sapiens*, trigger a shift from tolerance to milk to a state where lactose is not tolerated (Armelagos, 2010). Lactose intolerance (Beja-Pereira et al., 2003; Tishkoff et al., 2006; Ingram et al., 2009; Gerbault et al., 2011) results from a lack of the enzyme that is essential in hydrolyzing disaccharide lactose into galactose and glucose, which makes milk indigestible. Lactose intolerance is considered a disease, with 70% of the world's population lacking the lactase enzyme with milk consumption resulting in gas, bloating, and diarrhea. The gas in the large intestine is produced by *Escherichia coli* digesting the lactose. The persistence of lactase enzyme should be selected in populations where unprocessed milk is consumed after weaning. The difference in patterns of lactase persistence reflects difference in niche construction (Gerbault et al., 2011). The triangulation of genetic data, cultural practices, and archaeological evidence has been used to unravel the evolution of lactase persistence in Europe back to a single mutation (−213910*T).

CUISINE AS A MEDIATOR OF THE OMNIVORES DILEMMA

The omnivore's dilemma has its origins early in evolutionary development. It refers to the conflict in which an organism needs to seek new foods (neophilia) to meet their nutritional needs and the fear (neophobia) that what they are about to eat may be toxic, infectious, and deadly. Omnivory was an evolutionary adaptation of insects (Eubanks et al., 2003), but its adaptation by Eocene primates (Sussman, 1991) is the key to understanding its eventual occurrence in hominins. The omnivore's dilemma is illustrated in primate's use of the rain forest, which would seem an unlimited source of food for a primate given their ability to digest secondary compounds and vast amounts of fiber. The diversity of food in the rain forest requires taste discrimination and primates must select items carefully that are safe and worth harvesting (Jolly, 1985:57), as plant toxins such as morphine, caffeine, tannin, phenol, terpene, latex, phytohemagglutin, and saponin present a challenge to the primate diet (Janzen, 1978:73). Primates can distinguish quality in the food items selected and communicate this information with their calls sequences aiding the food search (Clay and Zuberbühler, 2011).

The strategy of Paleolithic foragers was to eat small amounts of a various foods to decrease the impact of toxin, poisons, or pathogens (Rozin and Rozin, 1981). The cuisine is a cultural system that defines the items in nature that are edible, how these items are extracted from the environment, eaten, or processed into food, the flavors used to enhance the taste of food and the rules about eating (Rozin, 1982). Cuisine was the solution to the omnivore's dilemma and remains an essential feature of human adaptation. Cuisine offers the advantage that at every meal the eater will not experience neophobia when making a dietary choice (Pollan, 2006) resulting in an expanding dietary repertoire.

Dietary variety in Paleolithic foragers, as with all omnivores, is biologically hard wired (Rolls et al., 1982). Eating a variety of foods makes it more likely that the species will get a balanced diet that includes the required micronutrients while simultaneously limiting the amount toxin ingested (Remick et al., 2009). Palate fatigue, sensory-specific satiety (Rollo and Marota, 1999), and monotony (Siegel and Pilgrim, 1958) assured the consumption of a varied diet and adaptively curbing food intake when necessitated by food scarcity (Remick et al., 2009). When food is scarce, survival is enhanced if intake is reduced, as eating smaller amounts of food conserves limited resources, especially proteins, assuring survival until food becomes plentiful again (Remick et al., 2009). Even when food becomes abundant, sensory-specific satiety and monotony ensures that humans will not fixate on a single food but instead ingest a varied diet and receive the needed nutrients.

The first component of the cuisine is the foods selected from the environment. The selection of foods is based on availability and the efficiency by which the nutrients can be extracted from the environment. Hominins seek out the biggest "bang" for the "buck" (Speth, 2010). The optimal foraging models argue that an organism will select the nutrients that give the greatest benefit for the least energy expended in the search (MacArthur and Pianka, 1966). The diet must include a balance of nutrients that can provide energy and the eight essential amino acids: phenylalanine, valine, threonine, tryptophan, isoleucine, methionine, leucine, and lysine. The second component is the manner of preparation, which includes the processing of foods from the time the items are selected until they are consumed as food. The third component is the flavoring principle that a society uses to provide additional sensory input into their bland foods, and the fourth are the rules that govern eating. This includes the number and time of day when meals are eaten, whether they are eaten alone or with others, the setting of meals, the ceremonial use of foods, the observation of taboos, and the code of etiquette that govern the rules of eating.

FOOD SELECTION IN CONTEMPORARY FORAGERS AS A MODEL FOR THE PALEOLITHIC

There are a few examples from contemporary foragers that have been used to describe the cuisine of gatherer–hunters. The !Kung, foragers living in the Kalahari Desert typically described as a place of scarce resources, recognize 105 species of plants and 260 species of animals as edible from more than 500 species that have been identified as edible (Lee, 1984:36). Despite the large cache of foods identified as edible, the !Kung primarily rely on the mongongo nut and 13 other plants as their major food sources, providing up 75% of their diet (Lee, 1979:159). An additional 19 species of seasonally available plants are minor components of their diet. These minor items are famine foods that represent a critical survival feature of the !Kung cuisine. In periods of scarcity, an individual desperate for a meal can be assured that these less desirable foods can be consumed without fear.

The diets of foragers are as varied as the populations studied. The Ache of Paraguay are foragers who now reside at agricultural missions but continue to spend a quarter of their time on overnight forest hunting trips (Hill and Hurtado, 1989). While in the forest, meat from mammals comprises 46–66% of their diet, with honey providing up to 18% of their calories, and insects and plants contributing to 26% of their diet. Interestingly, the Ache exploits only about 50 of the 200 species of plants and animals available to them. Hill and Hurtado (1989) observed that over 98% of the calories from their foraging trips came from 17 resources. This suggests that they follow an optimal diet where foragers will seek resources whose return is higher than the average, relying primarily on the richest and most calorie dense for the energy expended (Hawkes and O'Connell, 1985; Hill and Hurtado, 1996).

FOOD SELECTION IN THE PALEOLITHIC

Even with information from observations of modern foragers, the composition of the early hominin diet is still a matter of debate (Hladik and Pasquet, 2002). It has been argued that meat was part of the menu of high density foods that characterized early hominins (Milton, 1999, 2003). Others have argued that plants, fruits, oil rich seeds, and tubers were more likely essentials of the early hominin diet (Wrangham et al., 1999; Wrangham and Conklin-Brittain, 2003). The diversity of opinions reflects the ambiguity of the evidence and the flexibility that characterizes the Paleolithic diet (Ungar, 2007).

There have been some interesting trends in the Paleolithic food choice. About three to four million years ago, australopithecines expanded their "buffet" to include a wider array of foods than were consumed by apes or other nonhuman primates (Gibbons, 2009). Changes in anterior dentition (Ward et al., 2010), isotopic analyses (Sponheimer and Lee-Thorp, 1999; van der Merwe et al., 2008), and microwear on dental enamel (Macho and Shimizu, 2010) provide evidence of this dietary shift.

The suggestion that *A. africanus* subsisted on a chimpanzee-like diet of fruits and leaves has been reevaluated. Stable carbon isotope analysis of *A. africanus* (Makapansgat) suggests that they consumed leaves and fruits similar to the ape diet but in addition ate large amounts of carbon-13-enriched foods including grasses and sedges (Cyperaceae) or animals that consumed these foods, or both (Sponheimer and Dufour, 2009; Lee-Thorp et al., 2010). Early hominids exploited relatively open grassy woodlands for food (Sponheimer and Lee-Thorp, 1999) consuming high-quality animal foods before the development of stone tools.

Dietary breadth increased from the Middle Pleistocene (<780,000 years ago) until the Late Pleistocene with the additional exploitation of aquatic species (<130,000 years ago) (Steele, 2010). Evidence from the Eurasian Middle Paleolithic to Upper Paleolithic forager sites suggests that hoofed animals were a primary source of meat. In the Upper Paleolithic, populations supplemented diets with a broader category of small animals. The behavioral changes associated with the Upper Paleolithic record signal a wider range of economic and technological roles in forager societies, suggesting shifts to a sexual division of labor and a diversified strategy for evening-out or sharing dietary risks (Stiner and Kuhn, 2009). Sites in southern Greece show two trends of increasing dietary breadth. Initially, the trend was the use of terrestrial resources and then with marine foods through the end of the Mesolithic period (Stiner and Munro, 2011). Interestingly, Neanderthal populations from different regions of Europe (≈120,000 to ≈37,000 BP) were top-level carnivores obtaining their dietary protein from large herbivores (Richards and Trinkaus, 2009).

The archaeological evidence for plant consumption includes starch grains from wild plants (ferns and cattails) on grinding tools surfaces from sites in Italy, Russia, and the Czech Republic (Revedin et al., 2010). The sites are from a variety of geographical and environmental settings dating to the Mid-Upper Paleolithic about 30,000 years ago. The evidence suggests flour processing and high-energy plant foods were part of the cuisine of mobile hunter–gatherers (Revedin et al., 2010). The flour of the cattail rhizome has the property of emmer wheat and would have had to be processed by cooking to be edible, indicating the early complexity of the cuisine toolkit.

A neglected area of the Paleolithic diet is the ingestion of commensal bacteria that are important in up regulating the immune system (Armelagos, 2009). The hygiene hypothesis (Strachan, 1989; Strachan et al., 1996) claims the lack of childhood exposure to infectious pathogens, parasites, and symbiotic microorganisms in developed nations results in an increase in the susceptibility to allergy, autoimmune, and other chronic diseases in adulthood. Using contemporary foragers as a model for commensal bacteria impact, Stig Bengmark speculates on the composition of Paleolithic forager's gut biome. He suggests that Paleolithic foragers would have been exposed to the many saprophytic mycobacteria that were present in the soil and decaying organic matter. Bengmark (2000:612) speculates on the difference between the Western and Paleolithic diet, the latter of which contained at least a billion times more nonpathogenic health-promoting bacteria such as *Lactobacillus* species.

Stomachs have bacterial communities (enterotypes) that are related to diet. Wu et al. (2011) identify nutrients that substantially affect the intestinal microbiota and found that higher fat intake and lower fiber intake were associated with particular bacterial groups. They found enterotypes associated with long-term diet. The *Bacteroides* enterotype was associated with animal protein and saturated fats, while the *Prevotella* enterotype was found in those whose diets were predominantly plant based with high carbohydrates intake and low meat and dairy consumption.

METHOD OF PREPARATION: COOKING AND CUISINE

The control of fire and cooking created adaptive advantages to hominins and their diet (Wrangham and Carmody, 2010). The crucial shift has been a defining event in human evolution and is so important in forming the human physiology that it described as a "biological trait" (Wrangham and Conklin-Brittain, 2003). Cooked foods allowed for the selection of smaller teeth and gut evolution resulting in faster food passage. These intestinal changes reduced the ability to digest uncooked fiber and to detoxify secondary compounds reducing potential dietary items.

Cooking processes inedible starches into high density food (Gibbons, 2007; Keller, 2009). The tubers and other starch rich foods are improved by cooking, which in a technological sense "predigests" foods (Milton, 2000). Cooking breaks down the skin, softens cellulose, denatures toxins, and reduces complex proteins while simultaneously enhancing sweetness and increasing the caloric intake of early hominines (Wrangham et al., 1999). Apes can discriminate levels of sugar (Hladik and Simmen, 1996) and cooking increases the susceptibility of starch to amylase degradation (Svihus et al., 2005; Tester et al., 2006).

The link to changes in morphology that are claimed to be related to cooking are confounded by the evidence for the control of fire (Wrangham, 2009; Wrangham and Carmody, 2010). There are indications of the use of fire 1.9 million years ago. However, evidence of controlled fires in the form of the hearth is found between 800,000 (Goren-Inbar et al., 2004) and 250,000 years ago (Preece et al., 2006). The early hominins movement into northern latitudes of Europe necessitated the control of fire (Roebroeks and Villa, 2011). However, only from around 300,000 to 400,000 years ago did fire become a significant part of the hominin technology. While fire may have been a more recent event in human evolution, it certainly was a factor in increasing access to a variety of high-density foods though food processing by heat had little impact in completely transforming foods until the recent advent of ultra processing.

The issue of ultra processing has become a contested issue. Ultraprocessed food products are ready to eat or ready to heat products that require little or no preparation. These products are a third level of food of processing (Monteiro et al., 2010, 2011). According to the Monteiro's classification, processed items in the first level are slightly modified of single food item. A second level is the extraction of one specific component of a first-level processed food. Physical and chemical methods such as pressure, milling, refining, hydrogenation and hydrolysis, and the use of enzymes and additives, are used to produce edible and inedible foods that are different from the radically changed minimally processed foods. Ultraprocessed foods include salting, sugaring, baking, frying, curing, smoking, pickling, canning, and the frequent use of preservatives, cosmetic additives, synthetic vitamins and minerals wrapped in sophisticated packaging. Ultraprocessed foods used products from the second level in producing foods seldom including items from the first level of processing. The industrial processed fast foods are designed to be eaten anywhere are attractive, durable, accessible, convenient, ready-to-eat, or ready-to-heat foods with a "long shelf life." They are designed to be extremely palatable and can be habit-forming but have a durability that makes them transportable over long distances. They are designed to be consumed anywhere, at fast-food establishments, at home in place of domestically prepared and cooked food, while watching television, at a desk, at work, in the street, or while driving. Ultra processing can introduce tremendous variety into the diet. Differences in shape and flavor are distinct enough to give the eater a sense of variety that obscures the nutritional sameness (Rolls et al., 1982). The abundant variety at a meal by-passes the brains sensory specific satiety thus avoiding palate fatigue (Remick et al., 2009).

FLAVOR PRINCIPLE

The flavors used to enhance food as a defining feature of cuisine has generated some controversy. The debate has focused on the adaptive value of spices (Krebs, 2009). Although the suggestion that spices were used to mask rotting foods has been dispelled, antibacterial properties have been discovered (Sherman and Billing, 1999; Shan et al., 2009). The antibacterial consequences of the use of spices were likely a byproduct of their use as a solution to neophobia and to enhance dietary variety. Flavoring new foods provides a reassuring familiarity that blunts the fear of consuming an unfamiliar item. Interestingly, flavors can be manipulated to provide variety, for example, Indian curries can be combined in a number of ways to create, in the Rozins' terminology, themes and variations that help to solve the omnivore's dilemma (Rozin and Rozin, 1981; Armelagos, 1987). In children where neophobia is common (Wardle and Cooke, 2008) introducing the food with a familiar flavor such as ketchup can be instrumental in their acceptance of new foods (Pliner and Stallberg-White, 2000).

In a world of plenty, a varied diet may be maladaptive by stimulating appetite promoting excessive eating. Even the way Americans organize their meals by courses that are distinctively different maximizes food intake by overcoming the consumption-limiting effects of sensory-specific satiety (Rolls, 1979). The variety produces the "dessert effect" in which a satiated eater will rekindle their appetite when presented dessert, which is so different from the meal foods, making them palatable (Rolls et al., 1982; Remick et al., 2009).

BRAIN, GUT SIZE, AND FOOD CHOICE

The response to the omnivore's dilemma led to the coevolution of food choice and brain expansion. The selection for a larger brain in humans was related to a number of factors. Dunbar (1998) suggests the expansion of the neocortex was involved in social cognition associated with social interaction and memory. Although Dunbar and colleagues minimize the role of food choice in the enlarging brain, a high quality diet requires knowledge of how to extract patchily distributed resources that requires temporal and spatial memory (Snodgrass et al., 2009). Social networking of early hominins certainly was a force in developing an expanding brain with significant cognitive abilities (Dunbar, 2003; Dunbar and Shultz, 2007; Sol, 2009), and these neurological changes would have been important in dealing with the vagaries of the environment. The brain that comprises only 2% of the body's mass but consumes 20% of its use of energy (Magistretti, 2009). The resting human brain requires 25% more energy than that used by other primates in a similar state of inactivity. There is a problem of how do humans feed the brains expanded energy needs when the basal metabolism rate remains fixed. There must be a tradeoff where there can be a reduction in the energy needed to run another of the body's physiological systems, with the most likely candidate the digestive system.

Humans have a relatively smaller total gut size given their body size (Milton, 1999). The human small intestine makes up greater than 56% of the total gut, whereas the colon comprises up only 17 to 23% of its length. In comparison, the ape colon makes up greater than 45% of the total gut while the small intestines makes between 14 to 29% of its total (Milton, 1999, 2003). These changes represent an evolutionary trend in the relationship between gut morphology and brain size. When compared with other primates, humans are outliers in the size of their gut morphology. The evolution of human digestive system resulted in significant changes that altered human diet forever.

The human brain increased over three times what would be expected if a 143 pound man followed the trend of other primates (see Fig. 1). The gut size has decreased to 73% of what is expected from this trend. The expensive tissue hypothesis (Aiello, 1992; Aiello and Wheeler, 1995; Aiello et al., 2001) argues that the big brains in adults are fueled by the energy saved by having a smaller gastrointestinal tract. High-density and volumetrically concentrated foods are more easily digestible and provide added energy.

These changes in diet can act as a releaser or challenger with respect to diet (Babbitt et al., 2011). The release of energetic constraint is evident by ways in which energy-expensive tissues are reallocated in brain expansion. The need for high-density foods provides both an energetic and cognitive challenge. Given the "releaser" effect for an expanding brain, there is a metabolic challenge where genetic and molecular factors effecting diet and nutrition can provide some for adaptive advantage (Babbitt et al., 2011).

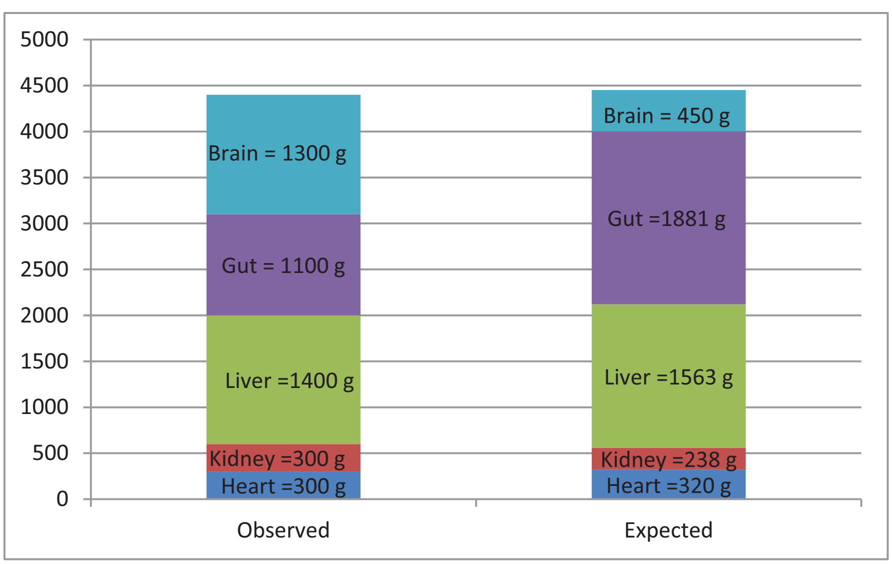

Figure 1 Observed organ mass for a standard 65-kg human compared with expected values for a typical primate. Modified from Figure 3, Aiello and Wheeler, 1995: 204. (Color figure available online.)

The changes in the gut would require high-quality, high-density foods, such as fruit, oil-rich nuts, tubers, and animal protein. Milton (2003: 3886S) argues that it is "highly unlikely" that early hominins could have achieved their large and complex brain without increasing their intake of animal protein. While plant material makes up from 87% to 99% of primates diet (Milton, 2003), the energy demand would require energy rich resources. Meat, seeds, and tubers would have provided hominins with needed energy. Children especially need "volumetrically concentrated, high-quality food" to feed their rapidly growing brain and relative small size of their guts (Milton, 2003).

THE BIOLOGY OF TASTE

Food choice in humans is affected by hardwiring for certain tastes. Americans consume vast amount of sugar, averaging 22.2 teaspoons of additional sugar daily (355 calories), which represents the equivalent to over two and a half tons (5892 pounds) of added sugar over the course of a person's lifetime. There exists a biological basis for sweet substances (sucrose, simple carbohydrates, and sweet tasting amino acids, such as alanine) that gives humans a propensity for craving sweet foods. The hundreds of taste receptors on the tongue's 10,000 taste buds (Pfaffmann, 1959) (and in the gut) can detect sweetness diluted one part per 200. When these sweet receptors on tongue and gut are stimulated, impulses are sent to the hypothalamic region of the brain. This adaptive advantage of this neurological, tongue, and gut link ensures a search for rich energy sources. For millions of years, the sources of sweetness were limited. The abundant source of refined sugar is a recent blip in evolutionary time, as it was only with the industrialization of the food system that sugar became available to the masses and created the potential for overconsumption.

Our ability to taste bitter substances (PTC, phenylthiocarbamide and PROP, 6-n-propylthiouracil) (Johnston et al., 1966) coded by the TAS2R38 gene would have prevented foragers from consuming grotin, antithyroxin substances, (5-vinyloxazolidine-2-thione) (Wooding et al., 2010), or forced them to process them in a way to remove the bitterness (Johns, 1999). The intensity of this tasting ability is related to the number of fungiform papillae (Arvidson and Friberg, 1980; Essick et al., 2003). For contemporary populations, tasters have more food dislikes. A recent study showed that taste receptor sites on the respiratory cilia of the lung (Shah et al., 2009) are similar to those on the tongue, with bitter substances causing the cilia to increase motility to remove the substances from the airways (Kinnamon and Reynolds, 2009).

The taste sensitivity to PTC and or PROP may be related to dislikes of certain food, such as eggplant, cabbage, Brussels sprouts (Yackinous and Guinardf, 2003). Coffee and chocolate have bitter substances that are made palatable by the addition of sugar (Mintz, 1985). The sweetness and bitterness example show how cultural factors can interact with the biological underpinnings of taste and distaste on the tongue and in the brain. The coevolution of genes and taste perceptions illustrates the ways in which cultural factors impact diet. This cultural layering suggests that the nutritional failings of American cannot be solely tied to the biological factors opening an examination of another evolutionary trend that will provide a basis for our nutritional dilemma. There are two major events in evolutionary history that are at the basis of the contemporary dietary problems. The transition to primary food production (Aldenderfer, 2009; Cohen, 2009) and the industrialization of the food system (Grey, 2000) both reduced the food types available for human populations.

THE AGRICULTURAL TRANSFORMATION

The impact of agriculture on the infectious disease on the first farmers was expected (Wolfe et al., 2007), but the emergence of nutritional diseases (Cohen and Armelagos, 1984) was a surprise. The rise of social inequality (Armelagos et al., 2005), famine, seasonal hunger, blights, and trade increased the potential for a reduction in dietary resources. The transition from foraging to agriculture shows an array of pathologies that suggest a decline in health as populations transformed to primary food production (Cohen and Armelagos, 1984; Steckel and Rose, 2002). The rise of infectious diseases results from an increase in the size and density of sedentary populations (Barrett et al., 1998). The domestication of animals introduced emerging disease from the animals that are vectors for them (Wolfe et al., 2007). Even with the added disease burden, the postagricultural populations experienced a five-fold increase in population growth (Gignoux et al., 2011).

Empirically, agricultural populations experienced significant instances of nutritional deficiencies although they were able to produces surpluses that drove cultural development. The reduction of the dietary breadth was a product of the Neolithic revolution when there was often reliance on a limited number of domesticated plants, with plant blights and droughts interrupting the flow of food. Agriculturalist showed evidence of retarded and interrupted growth that had an impact on life expectancy. Surprisingly, primary food production resulted in dietary deficiencies that potentially exacerbated the disease profile. Agricultural subsistence invariable reduces the foods that are available to them (Armelagos, 1987) and frequently specialize in a central domesticate such a millet, rice, wheat, or maize that reduces the foods available to them. The reduction of the dietary niche (Katz, 1987) results in dietary deficiencies that can increase the impact of infectious disease. The combination of a complex society, increasing class inequalities, epidemic disease, and nutritional insufficiencies affect the stress levels in the population (Goodman et al., 1984).

Agriculture leads to a reduction in the dietary niche that creates a nutritional bottleneck. Only 3% of 5000 species of plants (150) that have been used as human food have become products of world commerce. Less than 20 plants provide most of the world's food supply. Wheat, rice, and corn account for 60% of the calories and 56% of the plant protein that humans consume, although the manner of preparation and the use of spices provide variety and reflect local cultural adaptations to these highly cultivated resources. About 90% of the total mammalian biomass is composed of humans and domesticated animals. Before the advent agriculture, 10,000 years ago, the mammalian biomass was 0.1% (Vince, 2011: 35).

THE INDUSTRIALIZATION OF THE FOOD SYSTEM

The industrialization of the food system has further reduced dietary breadth. The genetic diversity of crops has declined with industrial agriculture. According to FAO estimates, 75% of the genetic diversity of crop plants were lost in the last century (FAO, 1997). While the loss of the varieties of corn has been lost, the number of products made from this crop has increased. Of 45,000 food items products found in the modern super market, over 11,000 are made from corn (Pollan, 2006:19).

A justification of the industrial food system is its ability to produce enormous quantities of energy using minimal human energy. The technoenvironmental efficiency ratio measures the amount of human energy put in the food search or food production compared the amount of energy extracted from that activity (Harris, 1975: 203–217). Gatherers–hunters, for example, extract 9.6 calories for every calorie put into the system. Irrigation agriculturalists, meanwhile, extract nearly 54 calories for each calorie put into the system, and industrial farming shows a whopping 210 calories for every human calorie expended. However, the factory farming system is not just about the human energy expended, but also the subsidy of energy from fossil fuels placed into the system. For every 100 calories of energy put into factory farming, 13 calories are produced. We are in a sense "eating oil" (Green, 1978). The industrialization of the food system creates opportunities for incredibly dense food that can provide 65% more energy than is found in a typical family prepared home meal, but with minimal concern for issues of health.

Ludwig (2011) discussed the nutritional problem with ultraprocessed food showing that a 10-oz, 90-kcal portion of strawberries (cost $1.50) has 5 g of fiber, significant amounts of several vitamins (298% vitamin C, 18% foliate, 8% vitamin K) and minerals (58% manganese, 19% magnesium) (Selfnutritiondata, 2011) and dozens of phytochemicals (ellagic acid and flavonoids such as anthocyanins, catechins, quercetin, and kaempferol) (Hannum, 2004). For the same number of calories (90), a 1-oz portion of Fruit Gushers that cost 330% more ($.46), has 9-g sugar and 1 g of fat, but virtually none of the beneficial nutritional constituents of the real thing. There are no strawberries in the Strawberry Fruit Gusher. Instead, it is made from pears from concentrate, sugar, dried corn syrup, corn syrup, modified corn starch, fructose, and grape juice from concentrate. In addition, it contains (at 2% or less) partially hydrogenated cottonseed oil, maltodextrin, cottonseed oil, carrageenan, citric acid, glycerin, monoglycerides, sodium citrate, malic acid, vitamin C (ascorbic acid), natural flavor, potassium citrate, agar-agar, Red 40, xanthan gum (Anonymous, 2011).

Burger King has created the Meat Monster, introduced in Japan, which includes two beef patties, two slices of cheese, three strips of bacon, and a chicken breast fillet scrunched between two buns. Using Burger Kings Web site (Burger King, 2011) it contains 1310 calories, 29-g saturated fat, 275-mg cholesterol, 14-g sugar, 56-g carbohydrates, 80-g fat, 2-g trans fat, 94-g protein, and 2900-mg sodium. This one meal without drink or French fries represents 65% the RDA of calories, 145% of saturated fat, 109% of cholesterol, 126% of sodium, 18.6% of carbohydrates, and 188% of protein.

There is a link between the use of ultraprocessed fast foods and the economy. Statistician Ernst Engel in 1857 showed that as income rises, the share spent on food declines (Chakrabarty and Hildenbrand, 2011). As the food costs increase there is a change in the diet, further reflected by the linkage between income and dietary macronutrient composition. Higher income nations consume more added sugars and fats than those in lower income nations. Within rich nations, lower income consumers have lower-quality diets than higher income consumers (Drewnowski and Darmon, 2005b). A relationship between obesity and socioeconomic factors is related to dietary energy density and energy cost (Drewnowski and Darmon, 2005a). Adding refined grains, sugars, or fats are among the lowest-cost sources of dietary energy. High-energy dense foods are inexpensive; in addition, they taste good and are convenient to prepare for individuals living in the modern, fast-paced world. In addition, the more nutrient-dense lean meats, fish, fresh vegetables, and fruits generally cost more. An inverse relationship between energy density of foods (kilojoules per gram) and their energy cost (dollars per megajoule) means that the more energy-dense diets are associated with lower daily food consumption costs and may be an effective way to save money. Potato chips, for example, cost about $2.00/10 MJ (2388 kcal), whereas fresh carrots cost about $14.00/MJ (Drewnowski, 2003). Drewnowski and Darmon say that the economic decision to use high energy-dense food has biological consequences. Laboratory studies indicate that energy-dense foods and energy-dense diets have a lower satiating power and may result in passive overeating.

There are attempts to remedy the decline in nutrition of the poorer segments of the population. The United States Department of Agriculture (USDA) created The Thrifty Food Plan (TFP) (Carlson et al., 2007) to provide suggestions for low costs foods for Americans participating in the food stamp program (Drewnowski and Eichelsdoerfer, 2009). In 2002, the weekly cost of TFP for a family of four was $107.10 and by 2008 it reached $147.08 per week ($588.30 per month) (Drewnowski and Eichelsdoerfer, 2009. What the USDA failed to consider the time necessary to prepare the meals. The purchase, preparation, and consumption of a week of TFP meals requires from 9 to 16 hours per week, which for a women facing a time crunch is overwhelming. Women spend on the average about five hours per week preparing family meals and subsequently do not have the time to prepare low-cost nutritious foods and instead opt for to energy-rich but nutrient-deficient diets.

The use of ultraprocessed food may have a role in the obesity epidemic that has become global. Raynor et al. (2004) suggest that the increased variety in the food supply may contribute to the development and maintenance of obesity. Studies in animals and humans show an increase in consumption when there is more variety in a meal or diet. This variety, it should be noted, is based on added fat, sugar, salt, spices, shape, and texture.

Lifestyle factors that are influenced by economic considerations influence the families and individual's food choices that seriously impacts diet and nutrition. Half of parents depended on mealtime coping strategies in which fathers skip family meals, eat at work, or feed their families take-out meals (Devine et al., 2009). Mothers would skip breakfast and buy restaurant or prepared entrees instead of cooking. Devine et al. (2009: 365) showed that food prepared outside the home is lower in nutritional quality resulting in an unhealthier diet related to poor work conditions, heavy workloads, and increased demands at work.

We live in a land of feast and famine. American supermarkets stock over 50,000 items with 11,000 new items added every year (Nestle, 2002). Over 7000 of these new items are condiments, candy, snacks, baked goods, soft drinks, and ice cream novelties. Over 36 million Americans (12.2%) live in food insecure households and 11.9 million live with hunger (Cook, 2009:146–147). That food insecurity persists even with sizable federal food assistance (Chilton and Rose, 2009). Food security is defined "when all people at all times have access to sufficient, safe, nutritious food to maintain a healthy, and active life (FAO, 1996)." Food security means having a reliable source of food and sufficient resources to purchase it. A family is considered food secure when its members do not live in hunger or fear of starvation (United States, 2009).

The number of hungry people in the world will surpass one billion people, with twice that number facing intermittent food insecurity. This trend exists at a time when the flow of food aid is at a 20-year low according to the United Nations World Food Programme (Moszynski, 2009). Problems with global food security in the next 20 years will only become even more challenging as demand for food is projected to increase by 50% (United States, 2009). Ironically, this food insecurity coexists with rampant overnutrition, with half of adults Americans overweight and obese (Mokdad et al., 2001).

Save the Children estimates that each year four million babies are stillborn, dying between 22 weeks of pregnancy and birth, and another four million die before they reach the age of one month (STC, 2006). Half of all child deaths in the developing world are related to undernutrition. Chronic hunger and undernutrition primarily results from poverty—people who are poor often simply cannot afford to buy food. Hungry families spend over half their income to buy the food they need to survive. Global food security in the next 20 years will become more critical as the demand for food will increase by 50%, with the increased demand coming primarily from middle-income countries.

An unexpected additional nutritional stress has been added to the problem of undernutrition with an increase in obesity. The term nutrition transition was coined by Popkin (1994) to describe the simultaneous coexistence of obesity and undernutrition. These epidemiological changes were associated with dietary changes cardiovascular disease and type 2 diabetes. The growth of fast food outlets and global trade contributing to an increase in heart disease and other consequences of overnutrition in developing nations (Astrup et al., 2008).

CONCLUSION

The consequences of the omnivore's dilemma have come full circle. The solution to the dilemma in the early hominines in Africa was the development of the cuisine that could mediate the problem of dietary neophobia. Cuisine resolved the need for defining what is edible and expanded the range of high-density foods needed to satisfy the inherent need for dietary variety. Two events lead to the reduction of the variety of dietary plants and animals. The first, the Neolithic revolution, occurred in the Fertile Crescent, Asia (the Yangzi and Yellow River Basins), the Americas (Eastern United States, Central Mexico, and Amazonia), and New Guinea Highlands, all centers of complex domestication (Armelagos and Harper, 2005a, 2005b). Initially, domesticates increase the menu for the agriculturalist. However, with agricultural intensification the number of plants that was part of the diet decreased. Dietary variety was maintained by new manners of preparation and with the incorporation of spices. The second event was the industrialization of the food system that reduced the number of foods that were used to feed their populations. The variety of available foods through a myriad of methods of ultra processing that produces a large number of high-density foods featuring the addition of sugar and fats. The exportation of these high-density foods to the developing nations of Africa and Asia has created an unexpected scenario in which there is the coexistence of under- and overnutrition. The omnivore's dilemma solved the perplexing issue of neophobia, but the inherent need for variety has created problems in an industrial age that produces an overabundance of high-density foods that deliver salt, sugar, and fats to the masses. Highly processed food provides an over abundance of variety that overrides the sensory-satiating mechanisms that had controlled overconsumption of food.

The national and international nutritional dilemma derives from an evolutionary journey that began with hominins solution to the omnivore's dilemma. The development of the cuisine resolved the issue of neophobia allowed hominines to incorporate new food into their diet to satisfy the need for variety (neophilia). The pattern of eating served homines for millions of years but now has created a dilemma for modern human. The requirement of a variety of high-density food to meet the demands of an energy demanding brain and a shrinking gut set the stage for a nutritional crisis. It is only in the last half century with the evolution of an industrial food system that has been able to easily produce vast quantities of ultraprocessed inexpensive high-density food. The abundance of cheap high-density foods laden with fat and sugar is created in an American economic system that requires families to have both spouses in the work force. The dual income families not only face economic issues but also time crunches and not having time to meet their social obligations. The time crunch and the higher cost of preparing healthier food make eating at home a difficult choice. The problem of ultraprocessed food has become an international problem with the exportation of high-density foods to developing nations. The nutritional transition has created a problem in the poorer nations of the world where feast and famine coexist. Just as high-density food affects rich and poor in the United States, it has attained an international dimension that has it origin in our evolutionary history. Given the time depth for the development of our dilemma and the magnitude of problem, there is no easy solution to resolving it. The solutions are complex (Pinstrup-Andersen, 1993; Pinstrup-Andersen and Babinard, 2003) and require regional foci (Vorster et al., 2011). The imperatives of the world economic system may make it an irretraceable issue.

REFERENCES

Aiello, L. C. (1992). Body size and energy requirements. **In**: The Cambridge Encyclopedia of Human Evolution, pp. 41–45. Bunney, S., Jones, S., Martin, R. and Pilbeam, D., Eds., Cambridge University Press, Cambridge, UK.

Aiello, L. C., Bates, N. and Joffe, T. (2001). In defense of the expensive tissue hypothesis. **In**: Evolutionary Anatomy of the Primate Cerebral Cortex, pp. 57–78. Falk, D. and Gibson, K. R., Eds., Cambridge University Press, Cambridge, UK.

Aiello, L. C. and Wheeler, P. (1995). The expensive-tissue hypothesis: The brain and the digestive system in human and primate evolution. *Curr. Anthropol.* **36**(2):199–221.

Aldenderfer, M. (2009). Editorial: The continuing conversation about the origins of agriculture. *Curr. Anthropol.* **50**(5):585–585.

Allison, A. C. (1954). The distribution of the sickle-cell trait in East Africa and elsewhere, and its apparent relationship to the incidence of subtertian malaria. *R. Soc. Trop. Med. Hyg.* **48**:312–318.

Anonymous. (2011). http://www.foodfacts.com/NutritionFacts/Snack-Foods/Fruit-Gushers-Fruit-Snacks-Strawberry-Splash-oz/11014. Accessed September 9, 2013.

Armelagos, G. J. (1987). Biocultural aspects of food choice. **In**: Food and Evolution, pp. 579–594. Harris, M. and Ross, E., Eds., Temple University Press, Philadelphia, PA, USA.

Armelagos, G. J. (2008). Biocultural anthropology at its origins: Transformation of the new physical anthropology in the 1950. **In**: The Tao of Anthropology, pp. 269–282. Kelso, A. J., Ed., University of Florida Press, Gainesville, FL, USA.

Armelagos, G. J. (2009). The Paleolithic disease-scape, the hygiene hypothesis, and the second epidemiological transition. **In**: The Hygiene Hypothesis and Darwinian Medicine, pp. 29–43. Rook, G. A. W., Ed., Switzerland Birkhauser Publishing, Basel, Switzerland.

Armelagos, G. J. 2010. The omnivore's dilemma: The evolution of the brain and the determinants of food choice. *J. Anthropol. Res.* **66**(2):161–186.

Armelagos, G. J., Brown, P. J. and Turner, B. (2005). Evolutionary, historical and political economic perspectives on health and disease. *Soc. Sci. Med.* **61**(4):755–765.

Armelagos, G. J. and Harper, K. N. (2005a). Genomics at the origins of agriculture, part one. *Evolutionary Anthropology: Issues, News, and Reviews* **14**(2):68–77.

Armelagos, G. J. and Harper, K. N. (2005b). Genomics at the origins of agriculture, part two. *Evolutionary Anthropology: Issues, News, and Reviews* **14**:109–121.

Arvidson, K. and Friberg, U. (1980). Human taste: Response and taste bud number in fungiform papillae. *Science* **209**:807–808.

Astrup, A., Dyerberg, J., Selleck, M. and Stender, S. (2008). Nutrition transition and its relationship to the development of obesity and related chronic diseases. *Obes. Rev.* **9**(Suppl. 1):48–52.

Babbitt, C. C., Warner, L. R., Fedrigo, O., Wall, C. E. and Wray, G. A. (2011). Genomic signatures of diet-related shifts during human origins. *Proc. Royal Soc. B: Biol. Sci.* **278**(1708):961.

Barrett, R., Kuzawa, C., McDade, T. and Armelagos, G. J. (1998). Emerging and re-emerging infectious diseases: The third epidemiologic transition. *Annu. Rev. Anthropol.* **27**:247–271.

Beja-Pereira, A., Luikart, G., England, P. R., Bradley, D. G., Jann, O. C., Bertorelle, G., Chamberlain, A. T., Nunes, T. P., Metodiev, S. and Ferrand, N. (2003). Gene-culture coevolution between cattle milk protein genes and human lactase genes. *Nat. Genet.* **35**(4):311–313.

Bengmark, S. (2000). Bacteria for optimal health. *Nutr. Clin. Prac.* **16**:611–615.

Burger King. (2011). Menu and nutrition. Available from http://www.bk.com/en/us/menu-nutrition/category1/menu-item1/index.html. Accessed November 5, 2011.

Carlson, A., Lino, M., Juan, W., Hanson, K. and Basiotis, P. P. (2007). Thrifty Food Plan. (CNPP-19). U.S. Department of Agriculture, Center for Nutrition Policy and Promotion, Washington, DC.

Chakrabarty, M. and Hildenbrand, W. (2011). Engel's law reconsidered. *J. Mathem. Econom.* **47**(3):289–296.

Chilton, M. and Rose, D. (2009). A rights-based approach to food insecurity in the United States. *Am. J. Public Health* **99**(7):1203–1211.

Clay, Z. and Zuberbühler, K. (2011). Bonobos extract meaning from call sequences. *PLoS ONE* **6**(4):e18786.

Cohen, M. N. (2009). Introduction: Rethinking the origins of agriculture. *Curr. Anthropol.* **50**(5):591–595.

Cohen, M. N. and Armelagos, G. J., Eds. (1984). Paleopathology at the Origins of Agriculture. Academic Press, Orlando, FL.

Cook, J. T. (2009). Food security and insecurity in the United States and their consequences for child health. **In**: Critical Food Issues: Problems and State-of-the Art Solutions: Environment, pp. 143–156. Phoenix, L. E., Eds., Santa Barbara: ABC-CLIO.

Devine, C. M., Farrell, T. J., Blake, C. E., Jastran, M., Wethington, E. and Bisogni, C. A. (2009). Work conditions and the food choice coping strategies of employed parents. *J. Nutr. Educ. Behav.* **41**(5):365–370.

Drewnowski, A. (2003). Fat and sugar: An economic analysis. *J. Nutr.* **133**(3):838S–840S.

Drewnowski, A. and Darmon, N. (2005a). The economics of obesity: Dietary energy density and energy cost. *Am. J. Clin. Nutr.* **82**(1 Suppl):265S–273S.

Drewnowski, A. and Darmon, N. (2005b). Food choices and diet costs: An economic analysis. *J. Nutr.* **135**(4):900–904.

Drewnowski, A. and Eichelsdoerfer, P. (2009). Can low-income Americans afford a healthy diet? *Nutr. Today* **44**(6):246–249.

Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews* **6**(5):178–190.

Dunbar, R. I. M. (2003). The social brain: Mind, language, and society in evolutionary perspective. *Annu. Rev. Anthropol.* **32**(1):163–181.

Dunbar, R. I. M. and Shultz, S. (2007). Evolution in the social brain. *Science* **317**(5843):1344–1347.

Durham, W. H. (1991). Coevolution: Genes, Culture, and Human Diversity. Stanford University Press, Palo Alto, CA, USA.

Essick, G. K., Chopra, A., Guest, S. and McGlone, F. (2003). Lingual tactile acuity, taste perception, and the density and diameter of fungiform papillae in female subjects. *Physiol. Behav.* **80**(2–3):289–302.

Eubanks, M. D., Styrsky, J. D. and Denno, R. F. (2003). The evolution of omnivory in heteropteran insects. *Ecol. Disease* **84**:2549–2556.

FAO. (1996). Report of the World Food Summit. 13–17 November 1996. FAO, Rome. Available from http://www.fao.org/docrep/003/w3548e/w3548e00.htm. Accessed October 1, 2011.

FAO. (1997). The State of the World's Plant Genetic Resources for Food and Agriculture. Food and Agricultural Organization of the United Nations, Rome.

Gerbault, P., Liebert, A., Itan, Y., Powell, A., Currat, M., Burger, J., Swallow, D. M. and Thomas, M. G. (2011). Evolution of lactase persistence: An example of human niche construction. *Phil. Trans. Royal Soc. B: Biol. Sci.* **366**(1566):863.

Gibbons, A. (2007). Food for thought. *Science* **316**(1558–1560).

Gibbons, A. (2009). What's for dinner? Researchers seek our ancestors' answers. *Science* **326**(5959):1478.

Gignoux, C. R., Henn, B. M. and Mountain, J. L. (2011). Rapid, global demographic expansions after the origins of agriculture. *Proc. Natl. Acad. Sci.* **108**(15):6044–6049.

Goodman, A. H. and Leatherman, T. L., Eds. (1998a). Building a New Biocultural Synthesis: Political-Economic Perspectives on Human Biology. The University of Michigan Press, Ann Arbor, MI.

Goodman, A. H. and Leatherman, T. L. (1998b). Traversing the chasm between biology and culture: An introduction. **In**: Building a New Biocultural Synthesis: Political-Economic Perspectives on Human Biology, pp. 3–41. Goodman, A. H. and Leatherman, T. L., Eds., The University of Michigan Press, Ann Arbor, MI.

Goodman, A. H., Martin, D., Armelagos, G. J. and Clark, G. (1984). Indications of stress from bones and teeth. **In**: Paleopathology at the Origins of Agriculture, pp. 13–49. Cohen, M. N. and Armelagos, G. J., Eds., Academic Press, Orlando, FL.

Goren-Inbar, N., Alperson, N., Kislev, M. E., Simchoni, O., Melamed, Y., Ben-Nun, A. and Werker, E. (2004). Evidence of hominin control of fire at Gesher Benot Ya'aqov, Israel. *Science* **304**:725–727.

Green, M. B. (1978). Eating Oil: Energy Use in Food Production, pp. xviii, 205. Westview Press, Boulder, CO.

Grey, M. A. (2000). The industrial food stream and its alternatives in the United States: An introduction. *Hum. Organ.* **59**(2):143–150.

Hannum, S. M. (2004). Potential impact of strawberries on human health: A review of the sciences. *Crit. Rev. Food Sci. Nutr.* **44**(1):1–17.

Harris, M. (1975). Culture, People, Nature: An Introduction to General Anthropology, pp. 22, 694. Crowell, New York, USA.

Hawkes, K. and O'Connell, J. F. (1985). Optimal foraging models and the case of the! Kung. *Am. Anthropol.* **87**(2):401–405.

Hill, K. and Hurtado, A. M. (1989). Hunter-gatherers of the new world. *Am. Sci.* **77**(5):437–443.

Hill, K. and Hurtado, A. M. (1996). Ache Life History: The Ecology and Demography of a Foraging People. Aldine de Gruyter.

Hladik, C. M. and Pasquet, P. (2002). The human adaptations to meat eating: A reappraisal. *Hum. Evol.* **17**:199–206.

Hladik, C. M. and Simmen, B. (1996). Taste perception and feeding behavior in nonhuman primates and human populations. *Evol. Anthropol.* **5**(2):58–71.

Ingram, C. J. E., Mulcare, C. A., Itan, Y., Thomas, M. G. and Swallow, D. M. (2009). Lactose digestion and the evolutionary genetics of lactase persistence. *Hum. Genet.* **124**(6):579–591.

Janzen, D. H. (1978). Complications in interpreting the chemical defenses of trees against tropical arboreal plant-eating vertebrates. **In**: Ecology of the Arboreal Folivores, pp. 73–78. Montgomery, G. G., Ed., Cambridge University Press, Cambridge, UK.

Johns, T. (1999). The chemical ecology of human ingestive behaviors. *Annu. Rev. Anthropol.* **28**(1):27–50.

Johnston, F. E., Hertzog, K. P. and Malina, R. M. (1966). Phenylthiocarbamide taste sensitivity and its relationship to growth variation. *Am. J. Phys. Anthropol.* **24**(2):253–255.

Jolly, A. (1985). The Evolution of Primate Behavior. Macmillan, New York, USA.

Katz, S. H. (1987). Food and biocultural evolution: A model for the investigation of modern nutritional problems. **In**: Nutritional Anthropology, pp. 41–63. Johnston, F. E., Ed., Alan R. Liss, Inc., New York, USA.

Keller, A. (2009). The cooking ape. *Science* **325**:394–395.

Kinnamon, S. C. and Reynolds, S. D. (2009). Using taste to clear the air(ways). *Science* **325**(5944):1081–1082.

Krebs, J. R. (2009). The gourmet ape: Evolution and human food preferences. *Am. J. Clin. Nutr.* **90**(3):707S.

Laland, K. N., Odling-Smee, J. and Myles, S. (2010). How culture shaped the human genome: Bringing genetics and the human sciences together. *Nat. Rev. Genet.* **11**(2):137–148.

Lee, R. B. (1979). The !Kung San: Men, Women, and Work in a Foraging Society. Cambridge University Press, New York, USA.

Lee, R. B. (1984). The Dobe !Kung. Case Studies in Cultural Anthropology. Holt, Rinehart and Winston, New York, USA.

Lee-Thorp, J. A., Sponheimer, M., Passey, B. H., de Ruiter, D. J. and Cerling, T. E. (2010). Stable isotopes in fossil hominin tooth enamel suggest a fundamental dietary shift in the Pliocene. *Phil. Trans. Royal Soc. B: Biol. Sci.* **365**(1556):3389–3396.

Livingstone, F. B. (1958). Anthropological implication of sickle cell gene distribution in West Africa. *Am. Anthrol.* **60**:533–562.

Ludwig, D. S. (2011). Technology, diet, and the burden of chronic disease. *JAMA* **305**(13):1352–1353.

MacArthur, R. H. and Pianka, E. R. (1966). On the optimal use of a patchy environment. *Am. Natural.* **100**(916):603–609.

Macho, G. A. and Shimizu, D. (2010). Kinematic parameters inferred from enamel microstructure: New insights into the diet of Australopithecus anamensis. *J. Hum. Evol.* **58**(1):23–32.

Magistretti, P. J. (2009). Low-cost travel in neurons. *Science* **325**(5946):1349–1351.

Milton, K. (1999). Nutritional characteristics of wild primate foods: Do the diets of our closest living relatives have lessons for us? *Nutrition* **15**(6):488–498.

Milton, K. (2000). Hunter-gatherer diets-a different perspective [editorial; comment]. *Am. J. Clin. Nutr.* **71**(3):665–667.

Milton, K. (2003). The critical role played by animal source foods in human (Homo) evolution. *J. Nutr.* **133**:3886S–3892S.

Mintz, S. (1985). Sweetness and Power: The Place of Sugar in Modern History. Penguin Books, New York, USA.

Mokdad, A. H., Bowman, B. A., Ford, E. S., Vinicor, F., Marks, J. S. and Koplan, J. P. (2001). The continuing epidemics of obesity and diabetes in the United States. *JAMA* **286**(10):1195–2000.

Monteiro, C. A., Levy, R. B., Claro, R. M., Castro, I. R. R. and Cannon, G. (2010). A new classification of foods based on the extent and purpose of their processing. *Cadernos de Saúde Pública* **26**(11):2039–2049.

Monteiro, C. A., Levy, R. B., Claro, R. M., de Castro, I. R. R. and Cannon, G. (2011). Increasing consumption of ultra-processed foods and likely impact on human health: Evidence from Brazil. *Public Health Nutr.* **14**(1):5–13.

Moszynski, P. (2009). Hunger poses the "world's greatest health risk" as aid deficit bites, says UN. *BMJ* **339**, September 18:b3849.

Nestle, M. (2002). The soft sell: How the food industry shapes our diets. Nutrition Action Health letter. http://www.questia.com/library/1G1-90980246/the-softsell-how-the-food-industry-shapes-our-diets. Accessed September 6, 2013.

Pfaffmann, C. (1959). The sense of taste. **In**: Handbook of Physiology, Section 1, Volume 1 Neurophysiology, pp. 507–533. Field, J., Magoun, H. W. and Hall, V. E., Eds., American Physiological Society, Washington, DC, USA.

Pinstrup-Andersen, P. (1993). Integrating political and economic considerations in programs and policies to improve nutrition: Lessons learned. **In**: Political Economy of Food and Nutrition Policies, pp. 225–235. Pinstrup-Anderson, P., Ed., Johns Hopkins University Press, Baltimore, MD, USA.

Pinstrup-Andersen, P. and Babinard, J. (2003). Globalization and human nutrition: Opportunities and risks for the poor in developing countries. *Afr. J. Food, Agric., Nutr. Develop.* **1**(1):9–18.

Pliner, P. and Stallberg-White, C. (2000). Pass the ketchup, please': Familiar flavors increase children's willingness to taste novel foods. *Appetite* **34**(1):95–103.

Pollan, M. (2006). The Omnivore's Dilemma: A Natural History of Four Meals, p. 450. Penguin Press, New York, USA.

Popkin, B. M. (1994). The nutrition transition in low-income countries: An emerging crisis. *Nutr. Rev.* **52**(9):285–298.

Preece, R. C., Gowlett, J. A. J., Parfitt, S. A., Bridgland, D. R. and Lewis, S. G. (2006). Humans in the Hoxnian: Habitat, context and fire use at Beeches Pit, West Stow, Suffolk, UK. *J. Quaternary Sci.* **21**:485–496.

Raynor, H. A., Jeffery, R. W., Tate, D. F. and Wing, R. R. (2004). Relationship between changes in food group variety, dietary intake, and weight during obesity treatment. *Int. J. Obes. Relat. Metab. Disord.* **28**(6):813–820.

Remick, A. K., Polivy, J. and Pliner, P. (2009). Internal and external moderators of the effect of variety on food intake. *Psychol. Bull.* **135**(3):434–451.

Revedin, A., Aranguren, B., Becattini, R., Longo, L., Marconi, E., Lippi, M. M., Skakun, N., Sinitsyn, A., Spiridonova, E. and Svoboda, J. (2010). Thirty thousand-year-old evidence of plant food processing. *Proc. Natl. Acad. Sci.* **107**(44):18815–18819.

Richards, M. P. and Trinkaus, E. (2009). Isotopic evidence for the diets of European Neanderthals and early modern humans. *Proc. Natl. Acad. Sci.* **106**(38):16034–16039.

Roebroeks, W. and Villa, P. (2011). On the earliest evidence for habitual use of fire in Europe. *Proc. Natl. Acad. Sci.* **108**(13):5209.

Rollo, F. and Marota, I. (1999). How microbial ancient DNA, found in association with human remains, can be interpreted. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **354**(1379):111–119.

Rolls, B. J. (1979). How variety and palatability can stimulate appetite. *Nutr. Bull.* **5**:78–86.

Rolls, B. J., Rolls, E. T. and Rowe, E. A. (1982). The influence of variety on human food selection and intake. **In**: The Psychobiology of Human Food Selection, pp. 101–122. Baker, L. M., Ed., AVI, Westport, CT, USA.

Rosenthal, P. J. (2011). Lessons from sickle cell disease in the treatment and control of malaria. *N. Engl. J. Med.* **364**(26):2549–2551.

Rozin, E. (1982). The structure of cuisine. **In**: The Psychobiology of Human Food Selection, pp. 189–203. Barker, L. M., Ed., AVI Publishing Company, Inc., Westport, CT, USA.

Rozin, E. and Rozin, P. (1981). Culinary themes and variation. *Nat. Hist.* **90**:6–14.

Selfnutritiondata. (2011). Strawberries, raw. Available from http://nutritiondata.self.com/facts/fruits-and-fruit-juices/2064/2. Accessed July 6, 2011.

Shah, A. S., Ben-Shahar, Y., Moninger, T. O., Kline, J. N. and Welsh, M. J. (2009). Motile cilia of human airway epithelia are chemosensory. *Science* **325**(5944):1131–1134.

Shan, B., Cai, Y.-Z., Brooks, J. D. and Corke, H. (2009). Antibacterial and antioxidant effects of five spice and herb extracts as natural preservatives of raw pork. *J. Sci. Food Agric.* **89**:1879–1885.

Sherman, P. W. and Billing, J. (1999). Darwinian gastronomy: Why we use spices. *BioScience* **49**(6):453–463.

Siegel, P. S. and Pilgrim, F. J. (1958). The effect of monotony on the acceptance of food. *Am. J. Psychol.* **71**(4):756–759.

Snodgrass, J. J., Leonard, W. R. and Robertson, M. L. (2009). The energetics of encephalization in early hominids. **In**: The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence, pp. 15–29. Hublin, J.-J. and Richards, M. P., Eds., Springer, New York, USA.

Sol, D. (2009). Revisiting the cognitive buffer hypothesis for the evolution of large brains. *Biol. Lett.* **5**(1):130–133.

Speth, J. D. (2010). Big-Game Hunting in Human Evolution: The Traditional View. The Paleoanthropology and Archaeology of Big-Game Hunting, pp. 39–44. Springer, New York.

Sponheimer, M. and Dufour, D. L. (2009). Increased dietary breadth in early hominin evolution: Revisiting arguments and evidence with a focus on biogeochemical contributions. **In**: The Evolution of Hominin Diets, pp. 229–240. Hublin, J. -J. and Richards, M. P., Eds., Springer, Netherlands.

Sponheimer, M. and Lee-Thorp, J. A. (1999). Isotopic evidence for the diet of an early hominid, Australopithecus africanus. *Science* **283**(5400):368–370.

STC. (2006). State of the Worlds Newborns. Save the Children. Available from http://www.healthynewbornnetwork.org/sites/default/files/resources/SOWN%20Report%20Color.pdf. Accessed September 6, 2013.

Steckel, R. H. and Rose, J. C. (2002). The Backbone of History: Health and Nutrition in the Western Hemisphere, pp. xx, 633. Cambridge University Press, Cambridge, UK.

Steele, T. E. (2010). A unique hominin menu dated to 1.95 million years ago. *Proc. Nat. Acad. Sci.* **107**(24):10771.

Stiner, M. C. and Kuhn, S. L. (2009). Paleolithic diet and the division of labor in mediterranean eurasia. **In**: The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence, pp. 157–169. Hublin, J.-J. and Richards, M. P., Eds., Springer Science + Business Media B.V., Dordrecht, Netherlands.

Stiner, M. C. and Munro, N. D. (2011). On the evolution of diet and landscape during the Upper Paleolithic through Mesolithic at Franchthi Cave (Peloponnese, Greece). *J. Hum. Evol.* **60**(5):618–636.

Strachan, D. P. (1989). Hay fever, hygiene, and household size. *Br. Med. J.* **299**:1259–1260.

Strachan, D. P., Taylor, E. M. and Carpenter, R. G. (1996). Family structure, neonatal infection, and hay fever in adolescence. *Arch. Dis. Child.* **74**(5):422.

Sussman, R. W. (1991). Primate origins and the evolution of angiosperms. *Am. J. Primatol.* **23**:209–223.

Svihus, B., Uhlen, A. K. and Harstad, O. M. (2005). Effect of starch granule structure, associated components, and processing on nutritive value of cereal starch: A review. *Anim. Feed Sci. Technol.* **122**:303–320.

Tester, R. F., Qi, X. and Karkalas, J. (2006). Hydrolysis of native starches with amylases. *Anim. Feed Sci. Technol.* **130**:39–54.

Tishkoff, S. A., Reed, F. A., Ranciaro, A, Voight, B. F., Babbitt, C. C., Silverman, J. S., Powell, K., Mortensen, H. M., Hirbo, J. B. and Osman, M. (2006). Convergent adaptation of human lactase persistence in Africa and Europe. *Nat. Genet.* **39**(1):31–40.

Ungar, P. S. (2007). Evolution of the Human Diet: The Known, the Unknown, and the Unknowable, pp. xiv, 413. Oxford University Press, Oxford, UK.

United States DoS. (2009). Global Hunger and Food Security Initiative Consultation Document. United States Department of State. Available from http://www.state.gov/s/globalfoodsecurity/129952.htm. Accessed June 14, 2011.

van der Merwe, N. J., Masao, F. T. and Bamford, M. K. (2008). Isotopic evidence for contrasting diets of early hominins Homo habilis and Australopithecus boisei of Tanzania. *S. Afr. J. Sci.* **104**:153–155.

Vince, G. (2011). An epoch debate. *Science* **334**(6052):32–37.

Vorster, H. H., Kruger, A. and Margetts, B. M. (2011). The nutrition transition in Africa: Can it be steered into a more positive direction? *Nutrients* **3**:429–441.

Ward, C. V., Plavcan, J. M. and Manthi, F. K. (2010). Anterior dental evolution in the Australopithecus anamensis–afarensis lineage. *Philos. Trans. Royal Soc. B: Biol. Sci.* **365**(1556):3333–3344.

Wardle, J. and Cooke, L. (2008). Genetic and environmental determinants of children's food preferences. *Br. J. Nutr.* **99**(Suppl S1):S15–S21.

Wolfe, N. D., Dunavan, C. P. and Diamond, J. (2007). Origins of major human infectious diseases. *Nature* **447**(7142):279–283.

Wooding, S., Gunn, H., Ramos, P., Thalmann, S., Xing, C. and Meyerhof, W. (2010). Genetics and bitter taste responses to goitrin, a plant toxin found in vegetables. *Chem. Senses* **35**(8):685–692.

Wrangham, R. W. (2009). Catching Fire: How Cooking Made us Human. Basic Books, New York, NY, USA.

Wrangham, R. and Carmody, R. (2010). Human adaptation to the control of fire. *Evolutionary Anthropology: Issues, News, and Reviews* **19**(5):187–199.

Wrangham, R. and Conklin-Brittain, N. L. (2003). Cooking as a biological trait. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **136**(1):35–46.

Wrangham, R. W., Jones, J. H., Laden, G., Pilbeam, D. and Conklin-Brittain, N. (1999). The raw and the stolen: Cooking and the ecology of human origins. *Curr. Anthropol.* **40**:567–594.

Wu, G. D., Chen, J., Hoffmann, C., Bittinger, K., Chen, Y.-Y., Keilbaugh, S. A., Bewtra, M., Knights, D., Walters, W. A., Knight, R., Sinha, R., Gilroy, E., Gupta, K., Baldassano, R., Nesse, L., Li, H., Bushman, F. D., Lewis, J. D. (2011). Linking long-term dietary patterns with gut microbial enterotypes. *Science* **334**(6052):105–108.

Yackinous, C. A. and Guinardf, J.-X. (2003). Relation between PROP (6-n-propylthiouracil) taster status, taste anatomy and dietary intake measures for young men and women. *Appetite* **38**(3):201–209.

Yasuoka, J. and Levins, R. (2007). Impact of deforestation and agricultural development on anopheline ecology and malaria epidemiology. *Am. J. Trop. Med. Hyg.* **76**(3):450–460.