SUMMARY

We have attempted to review much of the data concerning evolutionary medicine—in particular material that was unavailable for the precursor to this volume (Trevathan, Smith, and McKenna, 1999). Both in sophistication of theory and in quality of evidence, we feel that the chapters in this volume show a maturation of the field. For the time being evolutionary medicine is likely to remain the province of a relatively small number of specialists working outside of clinical medicine, but we hope that our efforts and others by our colleagues of similar mind will push the awareness and imminent sensibility of an evolutionary approach into larger arenas. To be sure, only time will tell.

CHAPTER 2

Human Evolution, Diet, and Nutrition

When the Body Meets the Buffet

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As Turner and her colleagues argue so effectively here, modern humans are, indeed, omnivores, and, thus, our species has retained what they refer to as "fundamental physiologically mediated tendencies" to seek out and consume a "tremendous variety of foods." Attempting to find an answer to the question why we are so excessive in our eating (when the opportunities present themselves), they use the concept of "mouthsense" to help explain the degree to which understanding human eating patterns requires reference to cultural experiences against the backdrop of biology, which then helps us to appreciate more than ever how much more complex is the understanding of human eating patterns compared with other mammals. It is odd to think, as they point out, that as a species we lack innate knowledge as to what and how to eat. Instead, we must observe others eating in order to learn a "custom" on which our survival has come to depend. Moreover, the authors provide a view of the Paleolithic as regards what we can and cannot learn especially in trying to create a "Paleolithically correct" diet aimed at (so the promises go) restoring proper dietary balances. The critical perspective they leave us salivating over is, given our evolutionary past, how can we best determine (and then properly respond to) the "right proportions of various types of food categories as well as vitamin and mineral constituents." They make us think about how strange, on the one hand, it is that some contemporary people die because they haven't enough food, while many others ("Westerners") die because they have too much, or that some of us make so many poor selections and eat without (it would seem) caring or the ability to arrange reasonable proportions. Turner et al. end their chapter by warning us that there is no quick fix for teaching ourselves and getting ourselves to "eat right," only more choices to make about what we want to believe and feel about food, especially (at least for some of us) while foraging at our local, ever showcasing supermarkets.

INTRODUCTION

Although guidelines for a healthy diet are widely promoted in the United States, a substantial number of Americans do not consume a healthy diet. This has led to health problems including cardiovascular disease, hypertension, type 2 diabetes, obesity, osteoporosis, anemia, poor dental health, malnutrition, and some types of cancer (United States Department of Health and Human Services (HHS) and United States Department of Agriculture (USDA), 2005). In fact, most Americans are far outside the parameters of what is considered a healthy diet. In comparing data from a 2001–2002 National Health and Nutrition Examination Survey (NHANES) to the dietary standards of the current *Dietary Guidelines for Americans 2005*, the U.S. Department of Health and Human Services and the USDA found that American men and women consume far too few fruits, vegetables, whole grains, and dairy products and far too many saturated fats, starches, and refined sugars (HHS, 2005; USDA, 2004). If we as *Homo sapiens*, literally the "wise ones," are so intelligent, why do we make such bad dietary decisions? Based on their 1992 study, Murphy, Rose, Hudes, and Viteri (1992) suggest that the health community needs to better educate Americans about their food choices and engage in research that will effectively influence adults to improve their diets, a sentiment echoed in *Dietary Guidelines for Americans 2005*. However, given the extent of the problem, this nutritional crisis appears to be more than the result of poor education. Nutritional information is readily available to the public and has been since 1916, when the USDA published its first Food Guide. The many incarnations of the food pyramid that provide guidelines for a balanced diet are ubiquitous, and general nutritional information can be found on the packages of most of the items we consume. Even so, dietary health has not improved substantially in the United States (Morrill & Chinn, 2004) despite almost a century of nutrition education. Perhaps it is not the availability of information, but rather the kind of information, that is critical to changing modern American dietary practices. In this chapter we review literature in developmental psychology, neuroscience, nutrition, and anthropology with an explicitly biocultural focus in order to elucidate aspects of human dietary evolution that inform attempts to improve nutritional health in the United States and elsewhere in the industrialized world.

We present an evolutionary approach with a biocultural perspective (Armelagos, 1987) to help us understand the current dietary dilemma. We are living in a time characterized by soaring rates of obesity, heart disease, hypertension, and diabetes, a health crisis shaped in part by patterns of eating forced to keep up with a fast-paced lifestyle. The "time famine" experienced by dual income families in the United States has led to increased consumption of foods prepared away from the home, which are often nutritionally deficient. Foods prepared away from home are higher in calories, total fat per calorie, saturated fat, sodium, and cholesterol, and are lower in dietary fiber, calcium, and iron, than foods prepared and eaten at home (Guthrie, Lin, et al., 2002). Nowadays, families eat together less often, and more than a third of U.S. parents admit to eating more than one fifth of their meals in the car (Gardyn, 2002).

We as a species inhabit the full range of the earth's environments, with concomitant variation in amounts and types of available resources, which demonstrates that human populations can adapt their diet to widely differing ecological niches. In a cultural sense, many of us are adapted to an industrialized world. But nutritionally speaking, it appears

that the industrialized world, where various foods are plentiful on an unprecedented scale, is detrimental to our nutritional health. The relative uniqueness of the industrialized world in the grand theater of our evolutionary environments has prompted many to question whether or not humans are still choosing dietary items according to the biological needs and behaviors shaped by natural selection (Eaton, Eaton III, et al., 1997; O'Keefe & Cordain, 2004; Stinson 1992), and the degree to which cultural factors both reflect and override innate, evolved propensities.

In this chapter we discuss human genetic and developmental mechanisms that reflect an evolutionary history of encephalization, dietary generalism, and markedly increased social learning capabilities. These derived traits influence our diet, taste preferences, and nutrition in dynamic and complex ways. We also consider the two-way dynamic between the biology of food choice and cultural systems. This is a fruitful avenue to explore, given that eating is cross-culturally replete with symbolism, ritual, and performance and treated with great importance. We explore the dietary consequences of encephalization; the biology of taste, distaste, and regulatory mechanisms of feeding; aspects of food choice and the omnivore's dilemma; and the intersection of our Paleolithic legacy, evolutionary medicine, and modern lifestyles. To this end, we argue that the adaptive changes that enhanced our use of high-density food, which were important to survival in our early evolutionary history, now represent a dilemma in an environment were there is an overabundance of nutritionally dense foods.

FEEDING A THINKING BRAIN

A biocultural approach to exploring the evolution of our diets calls for consideration of both physiological and behavioral factors in shaping how and why we eat what we eat. However, if the goal is to understand how the human diet is evolutionarily derived, it is insufficient to only look at the human species. The scope of variation in nonhuman primate diets is too broad to address here (the reader is referred to Milton & May, 1976, for more information on primate dietary patterns; Ankel-Simons, 2007; Chapman & Chapman, 1990; Chivers & Hladik, 1980); however, looking at key trends in our hominin lineage allows us to deduce several important evolutionary developments that took place as human feeding behaviors evolved from those of our hominin ancestors.

Among the suite of features unique to the human lineage is a very large brain. In proportion to our overall body size, we have considerably larger brains compared to our closest ape relatives, other primates, and other mammals in general. However, overall brain size is not the only issue here. Dunbar (1998) points out that what is important to human encephalization is the enlargement of the neocortex. The neocortex is a uniquely mammalian feature of the brain associated with social cognition, those aspects of perception, behavior, and memory associated with social interaction. Dunbar argues that in numerous primates and other social mammals, the size of the neocortex is strongly associated with group size and thus the complexity of social interaction. This association leads Dunbar to suggest that group sociality was a *causal* factor in the evolution of larger brains, especially in the human lineage. In other words, the fitness benefits of increased sociality, which depended on larger neocortices, were the selective factors that structured this evolutionary process. But the neocortex did not change alone—other researchers

have emphasized that the neocortex belonged to a suite of anatomical and life history traits that evolved together, feeding back on one another (Kaplan, Hill, et al., 2000). The challenge has been to explain and model these evolutionary feedback processes involving brains, bodies, and behaviors. This endeavor has produced important developments in life history theory.

Aiello and Wells (2002) note that among ancient African hominins, *Homo ergaster* (which they equate to early African *Homo erectus*) shows a dramatic increase in overall body size and cranial capacity compared to earlier *Homo habilis* and australopithecines. The authors interpret these anatomical changes as reflecting a substantial change in lifestyle, including such features as increased energy requirements, increased brain size, and delayed maturation. Charnov and Berrigan (1993) argue that an extended juvenile period entails a prolonged period of social learning and cognitive development and emphasize the importance of long juvenile periods among both chimpanzees and humans. Theoretically, the importance comes from the extra investment that is put into social learning and cognitive development, which pays off in the long run by equipping individuals to compete in a selective arena of steadily increasing sociality.

It therefore appears that social skills and cognitive development were "prime movers" in the evolution of increased encephalization as part of an adaptive complex geared toward learning and social cognition. In humans, this is especially apparent: the average human brain is almost five times the size one would expect given the average human body size (Aiello & Wheeler, 1995, p. 200). There is strong evidence that building and maintaining the neural information processing network of a large brain is metabolically costly (Laughlin, de Ruyter van Steveninck, et al., 1998). So where did the extra needed energy come from? Making the question even more complex, Aiello and Wheeler point out a seeming paradox: while human brains consume a substantial amount of energy, humans do not show a corresponding increase in basal metabolic rate (BMR). To resolve the question of how the human lineage has been able to feed their big brains without an increased metabolic output, Aiello and Wheeler propose the expensive tissue hypothesis (ETH) (see also Gibbons, 1998), which posits that the metabolic demands of an expanding brain are balanced by a decrease in another metabolically expensive organ, namely the gut.

This hypothesis is based on the fact that humans not only have larger than expected brains for the average body size but also smaller than expected guts. Based on fossil hominin morphology, Aiello and Wheeler extrapolate this relationship back to the emergence of early *Homo* approximately 2 million years ago. The authors argue that the *only* way these shifts in gut size could have occurred was if there was a substantial change in the diet. A larger gut serves to extract nutrients from low-quality, hard-to-digest foods such as mature leaves and fibrous plants. A shortening of the intestinal tract implies the opposite adaptation: a shift to easily digested, higher quality foods such as fruits, young plants, oil-rich seeds, and animal protein. Milton (1999, 2000) has also pointed out this fundamental association between gut size and dietary quality. Successfully seeking out these higher quality resources would have involved drastically altered, and possibly more complex, foraging strategies (Aiello & Wheeler, 1995, Fig. 5). In turn, these behavior changes imply increased cognitive activity and versatility.

The ETH does not posit diet as a prime mover in brain evolution: in this model, it was not a dietary change that *caused* an expansion in brain size. Rather, diet "permits a relatively small gut and liberates a significant component of BMR for the encephalized brain. No matter what was selecting for encephalization, a relatively large brain could not be achieved without a corresponding increase in dietary quality unless the metabolic rate was correspondingly increased" (Aiello & Wheeler, 1995, p. 211). In this model diet is a "prime releaser" (Aiello, 1997), giving the green light for brain expansion driven by causal factors having to do with fitness benefits of social cognition (Dunbar, 1998), thermoregulation (Falk, 1990), and maternal investment in big-brained, slow-maturing offspring (Hawkes, O'Connell, et al., 1998).

This research demonstrates the centrality of diet in the physiological and behavioral evolution of the human lineage. If we support the metabolic demands of our big, active brains while maintaining other bodily systems by consuming a high-quality diet, a key question follows: How do we obtain those high-quality foods? As discussed above, there are numerous elements of human diets that intertwine physiology and complex cultural behavior. We now turn to exploring these relationships in greater depth as a way to see how and why humans eat what they do, and when (over the life course and over the course of history) these patterns of behavior develop.

DOES BIOLOGY DETERMINE FOOD CHOICE?

Human food selection, especially during very young ages, appears to be controlled by neural regulatory mechanisms that stimulate feelings of hunger and satiety. Rowland, Li, and Morien (1996) model these neural mechanisms according to a cascade of interactions between the medulla, pons, hypothalamus, and limbic forebrain. In this neurological cascade, numerous signal molecules are involved in the stimulation of hunger and feeding, including norepinephrine, neuropeptide Y, galanin, and opioids (Drewnowski, Krahn, et al., 1992; Rowland, Li, et al., 1996), while opoids, as well as other molecules such as serotonin, insulin, satietin, and corticotropin-releasing hormone, simulate feelings of satiety (Rowland, Li, et al., 1996). Often, feelings of hunger and satiety are stimulated well before an individual actually runs out of energy or consumes harmfully excessive amounts of food (Capaldi, 1996; Deutsch, 1987). This suggests greater complexity to physiological regulation of eating than is assumed by earlier homoeostatic models in which an individual's feeding behavior was in direct, immediate response to physiological deprivation or excess, in an attempt to return, nutritionally speaking, to a homeostatic state (Booth, 1987). Conspicuously absent from this suite of signaling molecules, however, are any that specifically limit fat intake (Phillipson, 1997), despite neural and visceral mechanisms limiting intake of dietary protein and carbohydrates (Friedman, 1989; Li & Anderson, 1989; Tordoff, 1989) and other nutrients (Bates, Sharkey, et al., 1998).

Also innate to human eating behavior are competing tendencies towards neophobia (suspicion of new foods as potentially harmful) and novelty (seeking variety in the diet) (Birch & Fisher 1996; Leathwood & Ashley, 1983). These behaviors are mediated by regulatory mechanisms such as sensory-specific satiety, a type of "palate fatigue" whereby preference for a specific food or taste declines as it is eaten, while preference for new foods and tastes remain unaffected (Drewnowski, 1995; Hetherington & Rolls, 1996).

Humans tend to exhibit several inborn taste tendencies influencing their food choices. These are broadly characterized as similarities in "mouthsense," defined as a suite of taste, textural, and odor perceptions that occur when chemical compounds from foods

interact with chemoreceptors in taste papillae on the tongue and odor receptors in the olfactory epithelium (Duffy & Bartoshuk 1996; Rozin, in Wysocki & Pelchat 1993). These receptors are distributed throughout the tongue and all recognize five basic tastes: sweet, bitter, sour, salty, and glutamate, or savory *(umami)* (Duffy & Bartoshuk 1996; Chaudhari, Landin, et al., 2000). Taste, textural, and olfactory signals are generated by these receptors and sent to key areas of sensory convergence in the brain, such as the left orbitofrontal cortex (de Araujo, Rolls, et al., 2003).

Facilitated by these neural sensory and regulatory mechanisms, humans exhibit broad but near-universal taste tendencies, including a persistent liking for sweet tastes and a disliking for bitter and sour tastes, and these tendencies are present at or before birth (Anderson, 1995; Blass, Shide, et al., 1989). Genetic variation in sensitivities to certain bitter compounds such as 6-n-propylthiouracil (PROP) and phenylthiocarbamide (PTC) does affect the degree of liking for bitter compounds and other tastes (Bankovi, Forrai, et al., 1993; Ly & Drewnowski, 2001; Yackinous & Guinard, 2001), especially in women after the onset of menarche (Duffy & Bartoshuk 1996). This genetic variation in taste sensitivity shows the potential for genetic mediation of food choice (Capaldi, 1996). Recent research has suggested an innate, inborn liking for glutamate *(umami)* taste, although not necessarily for its intrinsic taste properties but rather for its ability to enhance the palatability of the other four tastes (Beauchamp, Bachmanov, et al., 1998; Bellisle, 1999). Also, numerous studies show that preferences for the taste of sweet foods are significantly enhanced by adding texture from fat (Drewnowski 1989, 1995, 1997). In this sense, there is empirical evidence for what has been popularly called a "sweet tooth." With Drewnowski's research, we can add the term "fat tooth" to our dietary lexicon.

These complex and varied regulatory mechanisms, taste preferences, and behaviors all make sense when viewed in light of human evolutionary history, even those that may seem counterintuitive. The presence of satiety mechanisms for protein and carbohydrate intake, but not fat intake, was likely highly adaptive for much of human history, where human feeding behavior was more closely tied to resource seasonality, the unpredictability of hunting or scavenging, and the paucity of fat found in most plant foods (Phillipson, 1997). Consuming as much fat as is available is detrimental only when fat is constantly abundant, as it is in many modern food systems (Drewnowski, 1997). The presence of anticipatory hunger cues prior to any actual deficiency, and satiety cues prior to detrimentally high intakes, have obvious adaptive benefits in that actual starvation or excessive intake is avoided (Deutsch, 1987).

Understanding the biology of fat in the diet better elucidates its role in the Paleolithic. Speth and Speilman (1983) were among the first to provide an analysis of the cost and benefits of meat consumption. Their study found that during periods of marginal caloric intake, hunters and gatherers are likely to hunt large ungulates. Since these animals are also subsisting on declining resources, their reserves of body fat become depleted, and lean meat becomes a principal source of energy. The use of large quantities of lean meat has nutritional costs, including elevated metabolic rates, higher caloric requirements, and deficiencies in essential fatty acids. In many gathering and hunting societies, taboos prevent pregnant women from eating meat. Speth (1991) speculates that these taboos prevented excessive protein consumption (above 25% of total calories) that could be harmful to the fetus (see Fessler & Navarrete, 2003, for a cognitive explanation for meat taboos). Hunter-gatherers subsequently develop subsistence strategies that increase

carbohydrate and/or fat intake. Speth and Spielmann suggest three strategies that can achieve these results: (1) an increase in the selection and procurement of smaller animals with high fat content; (2) storage of fat-and carbohydrate-rich foods; and (3) an exchange of these items with other groups as an alternate way to procure needed food resources. Recent archeological research has revealed how these strategies played out in the late Paleolithic adaptations of human populations (Stiner, 2001; Stiner & Munro, 2002; Stiner, Munro, et al., 1999, 2000).

Proclivities for sweet and sweet–fat combinations and for glutamate taste enhancement are highly adaptive in guiding omnivores to safe (nonpoisonous), macronutrient-dense foods (Anderson, 1995; Yamaguchi and Ninomiya, 2000). Conversely, human newborns display an inborn dislike of bitter and sour tastes, but this dislike appears to be concentration dependent; bitter and sour solutions that are diluted below certain concentrations fail to elicit any response at all (Mennella & Beauchamp, 1998). This behavior makes sense in light of the fact that while many bitter compounds are in fact poisonous, some contain medicinally beneficial phytochemicals when eaten in small amounts (Dillard &German, 2000; Le Coutre, 2003), while vitamin-rich fruits are often sour when unripe (Laska, Scheuber, et al., 2003; Nishida, Ohigashi, et al., 2000). These studies illustrate the benefits of consuming some unpleasant-tasting foods within an adaptive complex in which potentially toxic substances are avoided. Finally, sensory-specific satiety as a physiological facilitator of variety seeking in food choice provides one adaptive mechanism for overcoming neophobia towards unfamiliar resources (Leathwood & Ashley 1983).

The presence of many of these inborn tendencies among rats, chimps, and other omnivores supports arguments that human food choice is indeed a complex suite of adaptive traits reflecting our mammalian evolutionary history (Bellisle, 1999; Nishida, 1989; Ulijaszek, 2002). The key question that remains, however, is how many of these traits are actually genetically "hard-wired"? As will be discussed below, extensive research suggests surprisingly few. Within the past two decades, human food choice has been increasingly conceptualized around the primacy of learning and the near-constant contingencies of environmental and social contexts. Contrary to homeostatic models of food choice in which humans seek out foods based primarily on innate drives (Beidler, 1982), numerous studies of rats (Leathwood & Ashley, 1983), guinea pigs (Hudson & Distel, 1999), and human children (Birch, 1987; Birch & Fisher, 1996) suggest that there is no such thing as the "wisdom of the body" whereby foods are selected in direct response to physiological needs for specific nutrients such as sodium (Beauchamp, 1989) or animal-based protein (Simoons, 1994).

Moreover, while omnivores tend to seek out and express preferences for diets that are balanced in nutrient composition, it seems clear that what is actually mediating this tendency is the association of sensory properties, including taste, odor, texture, irritant qualities, and even color (Clydesdale, 1993) with positive or negative postingestive consequences (Leathwood & Ashley, 1983). In essence, an animal will not seek out a dietary regime that is balanced so much as one that makes it feel good; diets that are deficient in key nutrients such as protein will not be avoided because they are deficient, but rather because the animal suffers the symptoms of malnutrition. These associated taste properties and postingestive consequences may or may not have any relation to the macronutrient and micronutrient properties of the foods themselves (LeMagnen, 1987; Tordoff, 1989). The strengths of these learned associations show in the rapidity, intensity, and

duration of aversions to tastes and even food odors that are associated with negative postingestive consequences such as nausea, allergy, anaphylaxis, or gastric distress (Bernstein, 1999). This can occur to the extent that foods or food odors that were once liked can become disgusting if they are associated with nausea or vomiting (Pelchat & Rozin, 1982), whether or not they had any causal role in the associated ill effects.

Even the mechanisms regulating hunger and satiety are shaped by expectations of meal frequency and duration, meal size and importance, to the extent that feelings of hunger and fullness may occur independent of any physiological deprivation or repletion (Capaldi, 1996; Ramsay, Seeley, et al., 1996). Aside from broad similarities in basic taste perception, preferences for and avoidances of specific foods are typically learned within contexts of social interaction. Indeed, animal studies suggest that most omnivores may be incapable of learning how to select adequate diets early in life unless they are able to observe and learn the feeding behaviors of other, often related, conspecifics (Galef, 1989, 1996). Even innate dislikes of irritant or bitter foods, such as chili pepper and black coffee, displayed by nonhuman primates and dogs are overcome without incentive within human-mediated social contexts (Rozin & Kennel, 1983).

The primacy of social learning in food preferences is especially clear in humans, for whom eating is rarely divorced from social and cultural spheres. Numerous studies point to factors like ethnicity (Hudson & Distel, 1999; Rozin, 1996), family experience (Birch, 1987; Rozin & Millman, 1987), and cultural practices (Lupton, 1994; Mela, 1999; Messer, 1986; Simoons, 1994) as more immediately salient to shaping taste preferences and food choices than biological drives or innate tendencies.

Additional research suggests that many highly salient, learned taste associations and resultant eating behaviors are shaped very early in development. Flavors from foods ingested by pregnant women, including garlic, mint, vanilla, carrot, anise, and alcohol, are present in amniotic fluid and breastmilk (Mennella & Beauchamp, 1998; Schaal, Marlier, et al., 2000) in addition to other compounds normally found in breastmilk such as citric, lactic, and pyruvic acids, salts, urea, amino acids, and sugars (Mennella & Beauchamp, 1996). Rather than acting as passive flavor receptacles, fetuses actively retain and associate liked and disliked flavors, even those related to maternal electrolyte depletion (Crystal, Bowen, et al., 1999), in ways that are known to influence postnatal taste preferences and guide feeding behaviors (Barker, 1982). Following birth, infants are exposed to flavors in breastmilk that further shape acceptance of flavors and flavor variety and willingness to try new foods well into childhood (Blass, Shide, et al., 1989; Hudson & Distel, 1999; Wright, 1987). In turn, food exposure and preferences established during critical periods of social learning in childhood have lasting effects on neophobic tendencies, preferences, and choices throughout life (Birch & Fisher, 1996; Casey & Rozin, 1989).

FOOD CHOICE AND THE OMNIVORE'S DILEMMA: A LEGACY OF EVOLUTION

The shift from viewing hard-wired tendencies to learned behaviors as most critical in shaping taste preferences and food choice does not require abandoning the notion that these learned behaviors are adaptive in an evolutionary sense. The omnivorous behavior that characterizes many primates, including humans, is highly adaptive in that it expands

a given species' foraging range and accommodates seasonal variation. Reliance on an omnivorous diet, typically a pattern of collecting with some predation and at least rudimentary sharing, likely shaped the dietary patterns of our hominin ancestors and carry over in part to our own diet.

Although taste preferences and aversions are clearly developed through experiential learning, their adaptive significance remains clear. The ability to quickly recognize a harmful substance by taste or odor and permanently retain that association, despite a delay between ingestion and effect, is clearly adaptive to a variety-seeking omnivore. Likewise, the ability to learn substance avoidance through observing the aversions of others is clearly beneficial to an omnivore (Schafe & Bernstein, 1996). The development of preferences based in part on learning from conspecifics cuts a great deal of trial-and-error out of risky food selection (Galef ,1996), thereby enhancing success in consuming the wide variety of safe foods that satisfy human nutrient needs (Armelagos, 1987). As an example, no unequivocal relationship has been found between modern, cross-cultural pregnancy cravings and nutrient appetites, or between prenatal aversions and food toxins (MacClancy, 1992; Pelchat, 1997; Profet, 1992; Rodin, 1989). Nonetheless, there may be some adaptive significance to these preferences and aversions, especially aversions to easily spoiled foods such as meat (Fessler, 2002). In fact, the heightened taste sensitivity alone could serve as an adaptive and protective behavior through increased maternal scrutiny of any and all potential foods during pregnancy.

It seems clear that on an individual basis, humans have a complex suite of physiological mechanisms by which they become familiar with new foods, distinguish "good" versus "bad" in exploring potential food resources, and commit to memory an extensive and dynamic database of food-related information. At the group level, where knowledge, values and experience are exchanged and shared, humans have equally complex cultural toolkits used to better exploit available food resources. Among these toolkits are culturally constructed systems of food acquisition, preparation, and eating known as cuisines. Paul Rozin (1976) suggests that cuisines are cultural inventions that mediate biological nutritional needs within groups that share knowledge and values. The cuisine of a given group is an analyzable system of shared knowledge and values, which exists amidst a social and natural ecology. Researchers can seek to answer questions of, for instance, why certain changes occur in a group's food selection, preparation, and consumption habits (Farb & Armelagos, 1982). Changes in the dietary system can occur differentially in what Elizabeth Rozin (1982) calls the four components of a cuisine: The foods selected from the environment, the manner of preparation, the flavor principles employed, and rules established for eating. Viewed in this way, change in the environment, or change in any of these four components, influences the entire system in interesting feedback loops. Functionally speaking, one role of a cuisine is to balance neophobia and sensory-specific satiety through the incorporation of novel foods in familiar gustatory contexts (Farb & Armelagos, 1980).

Cuisines represent codified, structured, culturally constructed, and socially learned practices that are complex, highly variable, and contingent on available resources. Cuisines are also highly adaptive in that they allow human groups to efficiently manipulate, and sometimes even create, the food resources around them in ways that are attuned to local environmental constraints. For example, the use of milk and ghee but not of beef in some Indian cuisines permits a sustainable use of cows well adapted to India's climatic

and economic landscape (Harris, 1978). Another example, widespread and intensive use of spices in many tropical cuisines, may reflect the adaptive use of antimicrobial plant products (Billing & Sherman, 1998) and an adaptive reversal of apparently innate dislikes of bitter tastes (Rozin, Ebert, et al., 1982). Spices also allow what Rozin and Rozin (1981) describe as theme (consistency in flavor) and variation (variety) in food combinations. For example, to an uninitiated palate, the flavor of curry may seem to be a single taste. However, populations who customarily use curry blends in their cuisine vary the spices to provide a different taste, resulting in a multitude of curries that help avoid palate fatigue. In addition to flavor principles, particular processing techniques are nutritionally very useful and sometimes mandatory in avoiding ill effects. These include soaking or cooking to remove toxins from otherwise inedible foods such as bitter manioc (Dufour, 1995), fermenting soy to make it edible while retaining its nutrients (Barnes, 1998), and mixing complementary amino acids through combinations of rice and legumes or lime-processed corn (Farb & Armelagos, 1980; Katz, 1982; Stinson, 1992). The complex suites of rules, techniques, and combinations that characterize the myriad cuisines worldwide clearly represent behavioral adaptations used to maximize the ways in which human populations exploit available resources in the varied environments in which they live.

In sum, there are complex neurological, psychological, and cultural mechanisms by which humans have been able to learn about, associate, manipulate, and create food resources in ways that are highly adaptive. Most of these mechanisms are not hard-wired in the sense that most of them are learned at various points in an individual's life. Within this broad adaptive framework, however, it is possible, and useful, to generalize about the costs and benefits of different subsistence patterns (ways of procuring food) employed by humans throughout our evolutionary history and to use the insights gained to inform our own modern dietary patterns. As we will show, some of the most widespread and popular dietary solutions in the United States attempt to map out lifestyle plans based on the postulated diets of our Neolithic, Paleolithic, and earlier hominin ancestors. A number of these studies follow rigorous scientific methods and have been highly influential in shaping what we know about variety, change, benefits and costs of prehistoric diets. Unfortunately, these scholarly works have been used to create numerous popular publications that claim the same degree of scientific validity. These popular publications have misinterpreted the findings of scientific investigations in evolutionary medicine and have to a large extent ignored our evolutionary history as generalists and omnivores. Molding diets after those of our ancestors is a prime example of the culturally constructed nature of cuisine. While popular diets based on ancestral diets aim to be more adaptive, misinformation and simplification often prevents them from achieving such a goal.

THE SEARCH FOR A TRUE HUMAN DIET

There has in recent decades been a major reinterpretation of human dietary evolution based on reconstructions of dietary patterns during the Paleolithic and Neolithic periods. In the late 1970s, empirical evidence emerged that suggested the transition to agriculture during the Neolithic period brought about significant biological costs, such as stunted growth, increased susceptibility to infectious disease, and increased risk of famine (Cohen & Armelagos, 1984). To theorists at the time, this seemed counterintuitive. Many

theorists and the public alike assumed that agriculture, though toilsome, is superior to other modes of production in meeting the nutritional needs of humans on a grand scale. In his influential book, *The Food Crisis in Prehistory*, Cohen (1977) argued that changes at the end of Pleistocene led to larger, more sedentary human populations that soon ran out of their foraged food resources. This supposedly resulted in a nutritional crisis that forced populations to shift to primary food production (i.e., farming), as opposed to foraging, in order to have enough food. This theory led to hypotheses that can be tested in various archaeological contexts throughout the Old and New Worlds. If Cohen's theory was the case, then evidence of nutritional deficiencies such as skeletal lesions or growth disruptions caused by nutritional insults should be apparent in different settings directly *before* local origins of agriculture. In turn, the same kind of evidence would be expected to decline after agriculture was fully implemented (but see Armelagos & Harper 2005). However, the archaeological record did not provide such evidence.

In fact, emerging empirical evidence suggested a decline in health *with* the shift to agriculture. Populations that underwent a subsistence shift to primary food production showed an increase in infectious and nutritional diseases (Cohen, 1989; Cohen and Armelagos, 1984). The rise in infectious disease was predictable, since populations were becoming sedentary, denser, and larger, and these demographic changes would lead to more exposure to pathogens that are more easily transmitted (Armelagos 1990, 1998). Moreover, with the reliance on single grains to provide the bulk of dietary calories and nutrients, groups became more susceptible to famine as the result of blights and droughts in an unpredictable climate from year to year. In addition, rising social inequality with increasing population density and sedentary life increased the potential for nutritional deficiencies in lower, more vulnerable social strata (Armelagos & Brown, 2002).

These bioarchaeological and paleodemographic studies all led to the realization that the transition from hunting and gathering to agriculture during the Neolithic had significant, negative effects on human populations. This in turn led to research, grounded in the emerging field of evolutionary medicine (Williams & Nesse, 1991), that suggested there was much to learn about our American dietary trends by comparing them to those of contemporary hunter-gatherers. In a seminal paper, S. Boyd Eaton and Melvin Konner (1985) championed what they called the Paleolithic diet. Eaton and coworkers used the archaeological record and recent foragers' patterns of subsistence to analyze the nutritional properties of wild game and "uncultivated" vegetable foods. The authors' goal was not to constrain a specific diet or even set of diets that encompassed all human populations throughout our evolutionary history. Rather, they were clear in their objective to outline broad nutritional similarities between widely varied hunter-gatherer diets, such as micronutrient content, amounts and types of fats, proteins and sugars, and fiber content. References to a "Paleolithic average" should therefore be interpreted in terms of general nutritional characteristics, not in terms of actual foodstuffs. Within this framework, Eaton and Konner provided a strong contrast between the "average" preagricultural forager diets, based largely on wide varieties of collected wild plants and hunted lean meat with minimal processing, and the "average" American diet (Eaton & Konner, 1985, Table 5). Modern foragers consume about 55% fewer calories from dietary fat (20% vs. 36%), more than 600% more fiber (100 vs. 15 g/d), and have 55% less body fat on average as measured by skinfolds (9.6 vs. 17 mm) compared to modern Americans. Eaton and coworkers have expanded their database to include more nutritional information on game

animals and what they call "wild" vegetables (Eaton, Eaton III, et al., 1997, 1999), including the amounts of fiber (Eaton, 1990), calcium (Eaton and Nelson, 1991), and a host of important micronutrients in these foods. Importantly, Eaton and colleagues emphasize the inertia of biological evolution: in the 10,000 or so years between the shift from hunting and gathering to agriculture, there has been insufficient time for any genetic adaptations to the rapid changes in human diets. Therefore, no matter how much our dietary *behavior* has changed over the past 10 millennia, *biologically* human populations have remained the same. Eaton and colleagues used this disconnect to characterize modern humans as "Stone Agers in the fast lane" (Eaton and Konner, 1986; Eaton, Konner, et al., 1988). Importantly, the authors note that evolved gustatory behaviors, such as strong proclivities for sweet and salty tastes and fatty textures, convey selective benefits to hunter-gatherers. This is because food sources with these characteristics tend to be calorically dense and relatively scarce in environments where game animals are lean, water possibly scarce, and plant foods low in sugars. However, in modern, industrialized food systems where sugars, salts, and fats are in endless, easy supply, these same evolved behaviors can lead to overconsumption, obesity, and metabolic diseases. Humans have only had a regular surplus of food for the past century, yet the effects of this surplus on health are immediately obvious. In 2004, 65% of the adult American population was overweight and obese (Stein & Colditz, 2004) and in 2005, an estimated 30.5% of U.S. adults were clinically obese (Li, Bowerman, et al., 2005).

This increased attention to the disparity between modern and Paleolithic dietary patterns, and the notion that many modern humans are eating against the evolutionary grain, so to speak, led to a more intensive reexamination of both the modern foragers' and modern Americans' diets. Eaton and colleagues' original 1985 article captured the attention of physicians and nutritionists, and the authors (Eaton, Eaton III, et al., 1997) have continually updated the key elements and merits of the diet that patterned the nutrition of our Paleolithic ancestors. Eaton, Shostak, and Konner (1988) expanded their model in *The Paleolithic Prescription*, which provides a program of diet, exercise, and "design for living" that was highly adaptive for Paleolithic populations. In fact, they argue that the dietary characteristics of our remote ancestors may serve as a reference standard for modern human nutrition—"a model for defense against certain 'diseases of civilization'" (Eaton & Konner ,1985, p. 288).

Contrasting with Eaton and Konner's modeled Paleolithic diet is the average American lifestyle. As of 2001, 72% of married Americans with children under 18 were employed outside the home (Jabs & Devine, 2006). Americans today have more stringent time constraints and increasingly purchase prepared foods. While in the 1960s, 65% of the American family food dollar went to grocery stores, in 1997 only 50% did (Park & Capps, 1997). Because both parents work, little time is invested in preparing foods, and as a recent *Time Magazine* article explained, the shared family meal has become a "quaint kind of luxury" (Gibbs, 2006).

Many families believe that long work hours, inflexible schedules, and overtime work leave them without the necessary energy to prepare meals that meet their nutritional ideals. People cope by adopting different food-procurement strategies such as keeping the home stocked with microwavable foods, cooking large meals on Sundays to be reheated throughout the week, or stretching a large pot of soup through several meals by adding ingredients each night (Devine, Conners, et al., 2003; Jabs and Devine 2006). In addition, the American public has demonstrated a desire to spend less time cooking, and the food industry has responded with more prepared foods, takeout meals, and devices such as microwaves, rice cookers, and other options to decrease cooking time. Despite the increasingly limited time spent on preparing meals at home, these meals are likely still more nutritious than counterparts purchased away from home. Families that eat meals together tend to consume less soda and fried foods and far more fruits and vegetables (Gibbs, 2006).

However, another modern food-procurement strategy involves extensive consumption of foods prepared outside of the home. Eating out has increased from 10% of all food expenditure in 1960 to 47% in 1998 (Beale, 2000; Caplan, 1997). Between 1970 and 1990, the typical dual income family increased their annual market work by 600 hours, and this may account for why consumption of food away from home increased from 18% to 32% of total calories between 1977–78 and 1994–96 (Finkelstein, Ruhm, & Kosa, 2005). Since 1985, fast food sales have increased at a faster rate, growing annually at a rate of 6.8% and comprising 34.2% of all food purchased outside the home in 1997 (Jekanowski, 1999). More than a third of U.S. parents say they eat takeout food regularly and one fifth of all meals are consumed in a car (Gardyn, 2002). Foods prepared outside the home, and often chosen for meals eaten "on the run," are usually high in dietary fat, sodium, and calories and low in fruits, vegetables, fiber, calcium, and iron. Because of the time famine dual income families experience, many are consuming more ready-prepared meals, eating fewer family meals at home, and eating more meals away from home, all of which may lead to nutrient deficiencies and negative effects on their health (see Chapter 3).

The modern American lifestyle has wrought changes not only to the diet, but to activity patterns as well, which the *Dietary Guide for Americans 2005* (HHS and USDA, 2005) emphasizes as equally important to overall health. Jeffery and Utter (2003) and Stein and Colditz (2004) found that over the past 20 years, Americans have increasingly used private vehicles for transportation, and there has been a commensurate decline in use of bicycles, public transportation, and walking. Inactive leisure activities involving television viewing, video games, and home computers require decreased amounts of physical activity, and many labor-saving devices such as lawn mowers, television remote controls, and garage door openers have further decreased normal daily activity levels. These two studies also link these sedentary activities to greater weight in children and adults, due either to a corresponding decrease in physical activity or an increase in related food consumption. Stein and Colditz determined that in 2004, 60% of the U.S. population did not participate in regular physical activity and that 25% of the population was almost completely sedentary.

It is not our objective to imply that Paleolithic subsistence is inherently superior to that in industrialized countries such as the United States, nor is it our objective to imply that the modern American diet is wholly unhealthy. The increased capabilities for food production, transport, and storage that characterize industrialized food systems have contributed, in many nations, to a life expectancy of over 70 years, far beyond Eaton and Konner's Paleolithic average. However, the modern American dietary pattern does differ substantially from the diets of our Paleolithic ancestors, as do food-procurement strategies, in that the American diet is based primarily on refined carbohydrates and fats, limited in both nutrient quality and breadth, and requiring almost no physical activity

whatsoever to obtain. Reliance on this dietary pattern has increased within the last 50 years, translating our abundance of food into a health crisis.

EVOLUTIONARY MEDICINE AND DIET: *CAVEAT EMPTOR*

Eaton and colleagues provide an intriguing hypothesis that many current health problems, including obesity, diabetes, heart disease, hypertension, and osteoporosis, can be explained at least in part by our deviation from the dietary pattern that characterized much of our evolutionary history. However, the authors also temper their interpretations by cautioning that formal dietary recommendations based on a Paleolithic model are premature, emphasizing that an "awareness of Paleolithic nutritional patterns should generate novel, testable hypotheses grounded in evolutionary theory" (Eaton & Eaton III, 2000, p. 67). This rigorous analytical perspective has been echoed by Cordain, Eaton, Sebastian, et al. (2005), Cordain, Gotshall, Eaton, and Eaton III (1998), Cordain, Watkins, and Mann (2001), and Somer (2001), in attempts to assess and apply the Paleolithic diet to contemporary populations and offer practical dietary solutions (Cordain, 2002; Cordain & Friel, 2005).

With these scholarly studies, however, has come a flood of popular publications, including *NeanderThin: A Cave Man's Guide to Nutrition* (Audette & Gilchrist, 1995), *Nourishing Traditions: The Cookbook That Challenges Politically Correct Nutrition and the Diet Dictocrats* (Fallon & Enig, 1999), *Charley Hunt's Diet Evolution: Eat Fat and Get Fit* (Hunt, Eades, et al., 1999), *Health Secrets of the Stone Age* (Goscienski, 2003), and *Metabolic Man: Ten Thousand Years from Eden* (Wharton, 2001). These authors do not engage in the level of research that characterizes the work of Eaton and coworkers, Cordain and associates, and Somers. Instead, they have relied on the on catchy titles and promotional materials.

These popular books show that, unfortunately, evolutionary medicine has spawned for-profit dietary prescriptions that are scientifically vacuous and theoretically sterile (Armelagos, 2004). A prime example of this phenomenon is the book *Eat Right 4 Your Type* (D'Adamo & Whitney, 1996). In this book, the authors present individualized diet plans based on a person's ABO blood type, customizing diets to different ABO blood groups that they claim represent separate trajectories in the course of human evolution. For example, they argue that blood type O is the earliest to have evolved and dates back to the origin of Cro-Magnon populations, and that type O populations were and still can be characterized as optimal meat eaters. Conversely, blood type A populations were originally cultivators who emerged about 25,000–50,000 years ago and have a evolved a sensitive digestive tract that is best adapted to a vegetarian diet. Blood type B reflects the evolution of nomadic ancestors who migrated out of Africa to Europe, Asia, and the Americas about 15,000– 10,000 years ago, and individuals with type B blood are advised to include dairy products in their diet. The AB blood type first appeared about 1500 A.D. through the recent intermingling of various groups, and type AB individuals are advised to eat a blend of the type A and type B diets.

In examining D'Adamo and Whitney's evolutionary scenario, it is difficult to find a single fact that can be used to support their arguments about the typological nature of blood groups or the relationship of the blood groups to diet. In fact, studies of ABO blood

type distribution across human populations have found strong associations to infectious disease prevalence, *not* to dietary needs. Aho et al. (1980) predict differential susceptibility to influenza according to blood type, while Koda et al. (2001) suggest that the frequencies of alleles coding for different blood types are shaped by natural selection. Seymour et al. (2003) are even more specific, modeling the distribution of the ABO blood system according to distinct selective pressures from bacterial and viral pathogens. The distribution of ABO blood types in populations therefore reflects disease risk, not subsistence pattern. Nonetheless, D'Adamo and Whitney present their "evolutionary" argument for the ABO diet types as established science and have convinced readers of its validity. *Eat Right 4 Your Type* has been so successful (over a million copies have been sold and it has been translated to into 40 languages) that D'Adamo and Whitney have published companion books, such as *Cook Right 4 Your Type* (1998) and *Live Right 4 Your Type* (2001). When advice such as this is sold as evolutionary medicine, it surely has an impact on popular perceptions of the paradigm. Those readers that recognize these books as scientific nonsense could not only reject it, but also reject evolutionary medicine and the evolutionary paradigm altogether. Or worse, they will have bought into a perversion of evolutionary medicine that is built on assumptions and "facts" that have no scientific basis (see Armelagos, 2004).

ASSESSING THE EVOLUTION OF HUMAN DIETS

At this point we can revisit a key question, namely: Why do we in the modern world make such unhealthy dietary choices? We know that part of what makes human food choice so adaptive is that it is highly varied and that much of it is contingent on external influence and learning. As a species, humans are able to eat an incredible variety of resources; through processing techniques we can even turn poisonous plants into nutritious foods, and through cuisines we can create endless resource combinations. We also know that there are a few tendencies, such as a preference for sweet tastes and fatty textures, that appear to be inborn and lifelong, and that in our modern world where sugars and fats are consistently abundant, these inborn tendencies can create harmful effects on our health. Similarly, we know that for much of our evolutionary history, human populations had diets that, however varied, were very different from the prepared foods that make up the base of our modern diets. How can we use this knowledge to address the modern nutritional crisis, while avoiding the pitfalls of bogus "evolutionary" diets?

Perhaps one way is not to focus on just the types of foods, but the *variety* of foods in our diets. Perhaps we should view the capacities for negotiating and shaping our gustatory environment as more significant in an evolutionary sense than hard-wired tendencies such as our sweet tooth or fat tooth (Ramsay, Seeley, et al., 1996). In this sense, the Paleolithic diet becomes significant not only for its high fiber content and paucity of sugars, but also for its wider breadth: Cordain, Brand Miller, Eaton, et al. (2000) note that modern hunter-gatherer populations, who are often relegated to marginalized lands, utilize varying percentages of over 100 food resources each. In the modern world, it seems that there are more choices than ever in what to eat, but the vast majority of foods in the American diet are different combinations of the same few ingredients, such as corn,

sugar, and animal fat. Sidney Mintz (1996, p. 118) cites the USDA's list of 10 major sources of calories in the United States as "whole and lowfat milk; white bread, white flour, rolls, and buns; soft drinks, margarine and sugar; and ground beef and American cheese," while the Food and Agriculture Organization (FAO) reports that over the past 30 years American intake of oils and sugars has doubled (FAO/Earthscan 2003). In 1996, the average American ate 152 pounds of caloric sweeteners per year (USDA, 1998). This reliance on a few staple foods is potentially as significant to our poor dietary health as the staples themselves.

What may then be maladaptive about dietary habits in the modern world is not the excessive consumption of calorically dense foods but a dramatic narrowing of dietary breadth; the causal arrow is not drawn just to innate proclivities run amok but to another innate capacity, that of extreme omnivory, suppressed. The gustatory plasticity and generalist subsistence strategies displayed by humans was and is well suited to varied and fluctuating environments, which human populations have faced throughout their evolutionary history (Colson, 1979; Eaton, Eaton III, et al., 1997, 2002; Nestle, 1999; Nishida, 1989; Ulijaszek, 2002). What may be selected, therefore, is hard-wired flexibility in various capacities for learning food preferences during early development (Barker, 1982; Hudson & Distel, 1999; Mennella & Beauchamp, 1996) and through social interaction (Galef, 1996; Ramsay, Seeley, et al., 1996; Rozin, 1982, 1996; Nestle, Wing, et al., 1998). This hypothesis fits well with more general models that show the selective benefits of phenotypic and behavioral plasticity during human evolution (Potts, 1998) and omnivory in general (Galef, 1989; Rodman, 2002).

It should be noted that a handful of population-level adaptations have arisen in response to limited food resources, including the ability to digest lactose into adulthood (Simoons, 1982), although some, such as favism, are as much in response to endemic disease as to food resources (Stinson, 1992). Overall, however, we argue that to habituate and socialize one's taste preferences to a narrow range of foods, thereby winnowing one's diet to a few processed macronutrients to the near exclusion of dietary variety, is what makes modern food choices so maladaptive. The modern American diet, with its reliance on fast food, processed fats, and carbohydrates, and marginal inclusion of unprocessed plant foods, could therefore be seen as not only too fatty and too loaded with "carbs" but also entirely too narrow.

Adding to this problem is the plethora of diet plans centered on weight loss or weight management through dietary restriction. Americans perceive restrictive diets to be the most effective, turning to books that advise cutting out all flour and sugar (Gott & Donovan, 2006) or eating disproportionate quantities of rice (Gurkin Rosati & Rosati, 2006), grapefruits and cider vinegar (Dunford, 2002), or cabbage soup (Danbrot, 2004). However, if we look at humans as omnivores who evolved to learn about, manipulate, and consume a wide array of resources, the shortcoming of these diets is immediately obvious: there is no dietary variety. Our emphasis on breadth as a critical component of a healthy diet underscores the potentially substantial role that dietary monotony, through the prodigious marketing efforts of the modern food industry, has on derailing long-term health. Assessments of modern diet plans would benefit from critical scrutiny based on our evolutionary history of consuming widely varied food resources.

CONCLUSION

We have provided a number of biocultural avenues for understanding the dilemma of what many consider the dietary crisis in the United States. The ways in which food and the body interact provide some key pieces to the puzzle of why we eat what we eat. Our physiology and phylogenetic history have developed complex interactions with food, made even more complex by our capacity to learn about and manipulate food resources. As we have shown, biological checks and balances are easily manipulated or overridden by social and cultural factors, in this case with deleterious health effects. Our reliance on high-density foods, relatively scarce for much of our evolutionary history, can easily be made maladaptive in an industrial food system that provides such foods in unprecedented abundance. As important, our reliance on substantial dietary breadth has become distorted in a modern food system, our diets paradoxically limited by our reliance on thousands of prepared foods made from a few high-density ingredients.

It is therefore clear that an evolutionary and biocultural perspective is of critical importance when exploring the causes of and solutions to the growing dietary crisis in the United States. Examining the mechanisms of human feeding behavior while elucidating the evolutionary events that have shaped them allows us to better understand how our modern eating habits fit in, or not, to the rest of our evolutionary history. Ultimately, quick-fix diet fads, especially those that claim a basis in evolutionary medicine, must be replaced in popular publication with rigorous scientific research and sound biocultural models if the epidemics of diabetes, obesity, and other health problems are to be effectively addressed. Contextualizing human diets and human food choice within an evolutionary, interdisciplinary, and biocultural framework is, as we hope to have shown here, the most powerful way to understand and alter our modern dietary patterns to achieve better health.