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Research review

Our landscapes, our livestock, ourselves: Restoring broken linkages among plants, herbivores, and humans with diets that nourish and satiate

Frederick D. Provenza [a], [*], Michel Meuret [b], Pablo Gregorini [c]

[a] Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA
[b] INRA, UMR868 SELMET (Mediterranean and Tropical Livestock Farming Systems), 2 Place Pierre Viala, 34060 Montpellier Cedex 1, France
[c] Feed and Farm Systems Group, DairyNZ, Private Bag 3221, Hamilton 3240, New Zealand

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ABSTRACT

We contend that palates link herbivores and humans with landscapes and consider how these relationships have changed historically. An attuned palate, which enables herbivores to meet needs for nutrients and self-medicate to rectify maladies, evolves from three interrelated processes: flavor-feedback associations, availability of phytochemically rich foods, and learning in utero and early in life to eat nourishing combinations of foods. That occurs when wild or domestic herbivores forage on phytochemically rich landscapes, is less common when domestic herbivores forage on monoculture pastures, is close to zero for herbivores in feedlots, and is increasingly rare for people who forage in modern food outlets. Unlike our ancestors, the palates of many individuals are no longer linked in healthy ways with landscapes. Industrial farming and selection for yield, appearance, and transportability diminished the flavor, phytochemical richness, and nutritive value of fruits and vegetables for humans. Phytochemically impoverished pastures and feedlot diets can adversely affect the health of livestock and the flavor and nutritive value of meat and milk products for humans. While flavors of produce, meat, and dairy have become blander, processed foods have become more desirable as people have learned to link synthetic flavors with feedback from energy-rich compounds that obscure nutritional sameness and diminish health. Thus, the roles plants and animals once played in nutrition have been usurped by processed foods that are altered, fortified, and enriched in ways that can adversely affect appetitive states and food preferences. The need to amend foods, and to take nutrient supplements, could be reduced by creating phytochemically rich plants and herbivores and by creating cultures that know how to combine foods into meals that nourish and satiate.

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[*] Corresponding author.
E-mail address: fred.provenza@emeriti.usu.edu (F.D. Provenza).

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1. Introduction

Functional relationships with social and biophysical environments are the norm when wild or domestic herbivores forage on phytochemically rich landscapes, are less common when domestic herbivores forage on monoculture pastures, are close to zero for herbivores in feedlots, and are increasingly rare for many people who forage in modern food outlets. Many researchers, practitioners, and journalists now focus on the failure of people to eat nutritious foods, manifest in obesity and diet-related diseases. Our hypothesis for the disparity between herbivores and humans revolves around a discussion of the functionality of palatability – a palate in touch with the needs of a body – in mammalian herbivores and humans. Functional palates are guided by flavor-feedback interactions linked with the variety of foods on offer and how cultures learn to use them. We discuss how phytochemical richness and variety of foods affect appetite, intake, and satiety; how agricultural practices affect the quality of fruits, vegetables, meat, and dairy products for human consumption; how industrial-scale farming and food processing have converged to diminish phytochemical richness in foods that no longer satiate; and how synthetic flavors added to energy-dense processed foods obscure nutritional sameness and encourage overeating, obesity, and disease. We suggest that the desire to enrich and fortify foods, and to take nutrient supplements, could be reduced by recreating phytochemical richness in plants and herbivores and by creating cultures that know how to combine foods into meals that nourish and satiate. We conclude by discussing transgenerational linkages to landscapes where domestic herbivores and humans now forage and the conundrum of culture for humans. Our goal is to discuss how linkages among numerous factors in time (genetically and epigenetically) and space (ecologically, economically, and socially) generate patterns of behavior (Gamble, Gowlett, & Dunbar, 2013; Simoons, 1994). While we focus on domestic herbivores and omnivorous humans, as opposed to omnivorous chickens and pigs, the themes apply to all farm animals (Forbes, 2007a). They, too, face challenges as the ways they once foraged have changed from self-selecting diets while free-ranging to eating mixed rations in factory farms.

2. Challenges herbivores face in foraging

Herbivores face challenges when they forage on rangelands, grasslands, or pasturelands with copious species of grasses, forbs, shrubs, and trees, each physically and biochemically unique for different species and individual plants and plant parts (Provenza & Balph, 1990). Herbivores free to choose from this smorgasbord in diverse habitats may encounter well over one hundred plant species and often eat fifty or more plant species and parts in a day, though three to five items usually make up the bulk of any meal. In the process, they ingest thousands of phytochemicals that interact with one another and with cells in complex ways that are little understood.

Plants produce thousands of primary (energy, protein, minerals, and vitamins) and secondary (over 10,000 alkaloids, 25,000 terpenes, and 8000 polyphenols) compounds (Burrows & Tyrl, 2001; Rosenthal & Berenbaum, 1992; Rosenthal & Janzen, 1979). Each of the estimated 400,000 species of plants on earth makes hundreds to thousands of compounds. Biochemical themes are common within a species, but individual plants create variations within a theme as a result of interactions with the biophysical environment it encounters as a seed, seedling, and adult. A plant can be nutritious or toxic, depending on time of day and season and the resources in the environment (Bryant, Chapin, & Klein, 1983). By varying amounts of individual primary and secondary compounds, a plant with as few as twenty compounds can create millions of different blends. The consequences for a herbivore depend on its age, physiological state, past experiences with a plant, and the mix and sequence in which it eats plants. These conditions change from meal to meal, day to day, and season to season and they affect realized doses and interactions among ingested primary and secondary compounds.

As they came to appreciate these complexities, ecologists and animal nutritionists questioned the abilities of herbivores to select a diet from such a diverse and ever-changing biochemical array of plants (e.g., Grovum, 1988). They asked, appropriately, how can ruminants that deposit forages into four-chambered 'stomachs' discern the consequences of eating specific foods during various phases of different meals? During the past four decades, researchers made advances in understanding how herbivores make such associations. The findings highlight how a combination of flavor-feedback mechanisms, the physical and chemical characteristics of the forages on offer, and social interactions across generations can enable health through nutrition (Provenza, 2008; Provenza, Villalba, Dziba, Atwood, & Banner, 2003).

Researchers also learned herbivores are fallible: they can select forages that decrease performance and cause toxicosis (Provenza, 1997; Provenza & Cincotta, 1993; Provenza, Pfister, & Cheney, 1992). Their failings are often due to mismanagement. Moving wild or domestic animals to unfamiliar environments breaks transgenerational linkages to landscapes, which increases predation, malnutrition, over-ingestion of poisonous plants, and decreases reproductive performance. Over-stocking animals limits amounts of nutritious relative to toxic forages and causes losses to toxicosis. Over-feeding energy-dense foods like grains in feedlots also causes a host of illnesses. Herbivores also are susceptible to feedback traps: rapid positive effects from ingesting foods followed by aversive consequences – days, weeks, or even years later – from excesses of primary or secondary compounds or excesses or deficits of minerals.

3. Linking palates with foods

3.1. Flavor-feedback associations in herbivores

Palates link animals with landscapes through flavor-feedback associations (Provenza, 1995). These relationships involve primary and secondary compounds interacting with cells and organ systems in a dynamic network of communication that guides food selection. They are mediated by aroma and taste receptors linked by nerves, neurotransmitters, peptides, and hormones with organ systems throughout the body. Receptors for taste occur on membranes of cells throughout the body, including the tongue, gastrointestinal tract, pancreas, respiratory tract, heart, and brain (Depoortere, 2014; Janssen & Depoortere, 2013). The lining of the gut of mammals has a range of receptors, including those for odorants, nutrients, secondary compounds, and toxins (Furness, Rivera, Cho, Bravo, & Callaghan, 2013). Sensory information is transferred from the gut to the brain through four effector systems: intrinsic and extrinsic innervation of the gut; enteroendocrine hormonal; gut immune system; and local tissue defence systems.

These associations are further mediated by the microbiome. Scientists who study humans are just beginning to appreciate how the microbiome affects food preferences and health including inflammation (Alcock, Maley, & Aktipis, 2014; Maslowski et al., 2009; Norris, Molina, & Gewirtzc, 2013). However, scientists who study herbivores have long valued these relationships (Hungate, 1966). Most generally, high-grain diets select for bacteria that can digest starch; high-forage diets select for bacteria that can degrade cellulose; and diets rich in secondary compounds select for microbial populations that enable herbivores to eat plants they otherwise could not eat (Allison, Hammond, & Jones, 1990; Allison, Littledike, & James, 1977; Dearing, Foley, & McLean, 2005; Freeland & Janzen 1994).

A palate in touch with the needs of a body is manifest by the abilities of herbivores to meet needs for energy, protein, minerals, vitamins, and to self-medicate. Animals begin learning in utero to associate the flavors of foods in mother's diet with their post-ingestive consequences (Provenza & Villalba, 2006). After birth, they learn which foods to eat or avoid from foraging with mother (Mirza & Provenza, 1990; Thorhallsdottir, Provenza, & Balph, 1990). They associate unfamiliar (novel) foods with their consequences when eating different foods in a meal (Burritt & Provenza, 1991, 1997; Provenza, Lynch, Burritt, & Scott, 1994). They generalize from past flavor-feedback experiences to novel situations (Launchbaugh & Provenza, 1993). Positive or aversive consequences that occurred from eating foods in the past can influence an animal's responses to those foods days, weeks, or even years later (Burritt & Provenza, 1996).

All of these associations depend on an animal's needs relative to the chemical characteristics of foods, and they are updated as foods and needs change (Ginane, Bonnet, & Revell, 2015; Gregorini, Villalba, Provenza, Beukes, & Forbes, 2015). Animals need not optimize intake of every nutrient in a meal. Rather, homeostatic regulation needs only an increasing tendency, as a result of a steadily worsening imbalance, to generate behavior to correct a disorder (Forbes & Gregorini, 2015). The dynamics of these relationships have been captured in mechanistic models of food selection, based on two complementary theories – post-ingestive feedback and minimal discomfort (Gregorini et al., 2015). They also have been expressed mathematically for energy and protein for humans (Simpson & Raubenheimer, 2005) and herbivores (Raubenheimer, Machovsky-Capuska, Felton, & Simpson, 2014).

Livestock maintain a balance of energy and protein in their diets by associating the flavors of foods with nutrient-specific feedbacks. Lambs fed diets low in energy (or protein) will preferentially eat non-nutritive flavored food previously associated with feedback from ruminal infusions of energy (or protein); they also prefer sources of energy and protein that ferment at similar rates: excesses of one relative to the other can cause toxicity and thus reduce food intake (Villalba & Provenza, 1996; 1997a,b,c). Given an appetizer high in energy or nitrogen at the beginning of a meal, lambs subsequently prefer flavors of foods previously paired with nitrogen or energy, respectively, during the ensuing phase of a meal (Villalba & Provenza, 1999).

Lambs choose a diet that maximizes growth when offered isocaloric foods that vary in protein. They eat less protein as they age and their need for protein declines (Kyriazakis & Oldham, 1993). Conversely, sheep increase intake of protein relative to energy as their needs for protein increase during the last trimester of gestation (Cooper, Kyriazakis, & Oldham, 1994), or when they are infected with parasites (Kyriazakis, Oldham, Coop, & Jackson, 1994). Intake declines with imbalances of energy relative to protein (Hill, Chapman, Cosgrove, & Parsons, 2009; Russell, O'Connor, Fox, Van Soest, & Sniffen, 1992; Sinclair, Garnsworthy, Newbold, & Buttery, 1993), and increases with appropriate ratios of energy to protein (Kyriazakis & Oldham, 1997). When fed protein or energy imbalanced diets, sheep forage in locations with foods that rectify the imbalances (Scott & Provenza, 2000). Dairy cows fed protein supplements during lactation subsequently avoid eating plants (e.g., legumes) and plant parts (e.g. new growth) high in protein when they forage on mixed swards (Emmick, 2007); conversely, they select plants and plant parts high in protein when they are fed energy-rich concentrates like corn grain during lactation (Emmick, 2007; Pinheiro Machado Filho, Martins D'Ávila, da Silva Kazama, Bento, & Kuhnen, 2014). Livestock thus sense dietary crude protein content and modulate short-term intake of flavored foods based on their protein requirements. Protein-restricted lambs distinguish among foods that differ in flavors and protein; they increase intake of umami-flavored foods, but this increase disappears if the food is low in protein (Bach, Villalba, & Ipharraguerre, 2012). Finally, lambs become averse to diets deficient in specific amino acids and they eat foods that rectify the amino acid deficit (Egan & Rogers, 1978; Rogers & Egan, 1975).

Minerals are required in lesser amounts than energy or protein, and needs for minerals often are met while consuming energy and protein. When deficient, however, sheep meet needs for Na, P, or Ca by discriminating among a poorly nutritious food (straw) in three flavors previously associated with ruminal infusions of each of those minerals (Villalba, Provenza, & Hall, 2008). Cattle and sheep with mineral deficits eat soil, lick urine patches, eat fecal pellets, and eat dead rabbits; non-deficient animals may sniff or lick these items, but they never eat them (Wallis de Vries, 1994; Villalba et al., 2008). Bighorn sheep use rodent middens as mineral licks (Coates, Schemnitz, & Peters, 1991), and Angora goats foraging on protein-deficient blackbrush shrubs eat urine-soaked vegetation high in nitrogen inside woodrat houses (Provenza, 1977). Wild herbivores with protein or mineral deficits may eat animals including live or dead lemmings, rabbits, and birds (caribou, red deer, and sheep); arctic terns, ptarmigan eggs (sheep); fish (white-tailed deer); and antlers (deer) (Bazely, 1989; Fumess, 1988; Sutcliffe, 1977). Conversely, sheep avoid excess minerals like NaCl (Villalba & Provenza, 1996) and sulfur when their mineral needs are met (Hills, Kyriazakis, Nolan, Hinch, & Lynch, 1999). Cattle stop eating bones when their blood Pi (inorganic phosphate) levels are in normal or excessive ranges (Blair-West et al., 1992; Denton, Blair-West, McKinley, & Nelson, 1986). These findings support the practice of offering minerals free-choice so animals can self-select minerals that are low in forages (Holliday & Helfter, 2014).

Herbivores can benefit from eating modest amounts of forages with secondary compounds like tannins, which alleviate bloat and improve protein use, immune responses, resistance to gastrointestinal nematodes, and reproductive efficiency (Min, Fernandez, Barry, McNabb, & Kemp, 2001; Min & Hart, 2003; Min, Pomroy, Hart, & Sahlu, 2004; Niezen et al., 2002; Waghorn, 1990). Goats limit intake of forages too high in secondary compounds like tannins (Provenza et al., 1990), and lambs reduce meal size (reach satiation sooner) and increase meal intervals (longer satiety) when their diets are high in terpenes (Dziba, Hall, & Provenza, 2006; Dziba & Provenza, 2007). Limits are set by rates of elimination of secondary compounds from the body (Foley & McArthur, 1994). Once sufficient levels are reached, animals stop feeding, and they resume eating only after concentrations in the body decline as a result of detoxification and elimination. These dynamics cause irregular patterns of intake of particular foods with peaks at low concentrations of particular secondary compounds in the body (Foley, Iason, & McArthur, 1999; Pfister, Provenza, Manners, Gardner, & Ralphs, 1997; Provenza, 1996).

Many secondary compounds are excreted in urine as conjugated amino acids, glucuronic acid, or sulfates; creating these compounds produces organic acids that can disrupt acid-base balance and deplete glucose and amino acids (Foley, McLean, & Cork, 1995; Illius & Jessop, 1995, 1996). Detoxification and elimination thus require additional energy, protein, and water. Supplemental energy and protein enable animals to eat more of foods high in secondary compounds (menthol, Illius & Jessop, 1996; terpenes, Banner, Rogosic, Burritt, & Provenza, 2000; Villalba, Provenza, & Banner, 2002a; tannins, Villalba, Provenza, & Banner, 2002b; saponins, Williams et al., 1992; terpenes, saponins, and flavones, Strickland et al., 1998; lithium chloride, Wang & Provenza, 1996). Lambs infused with terpenes, nitrate, tannins, or lithium chloride prefer foods with higher ratios of protein to energy; conversely, after infusions with cyanide, lambs prefer foods with higher ratios of energy to protein (Villalba, Provenza, & Bryant, 2002c).

Given the opportunity, taxa as diverse as insects, ruminants, and primates also learn to use secondary compounds to self-medicate (Huffman, 2011; Juhnke, Miller, Hall, Provenza, & Villalba, 2012; de Roode, Lefèvre, & Hunter, 2013; Villalba et al., 2013). Sheep fed acid-producing foods like grain ingest foods and solutions that contain sodium bicarbonate, which attenuates acidosis and restores acid-base balance (Phy & Provenza, 1998). Sheep learn to ingest polyethylene glycol (PEG) to attenuate aversive effects of tannins; they discriminate the benefits of PEG from non-medicinal substances, they ingest PEG after a meal high in tannins (Villalba & Provenza, 2001), and they titrate the dose of PEG in accord with the amount of tannin in the diet (Provenza, Burritt, Perevolotsky, & Silanikove, 2000). In the most complex studies to date, sheep learned to selectively ingest three medicines — sodium bentonite, polyethylene glycol, dicalcium phosphate — that attenuate illnesses from eating too much grain, tannins, or oxalic acid, respectively (Villalba, Provenza, & Shaw, 2006).

3.2. *Comparing flavor-feedback associations in herbivores and humans*

As with herbivorous animals, omnivorous people acquire likings through flavor-feedback associations, where the orosensory properties of food and positive consequences of nutrient ingestion lead to an acquired liking for the flavor of the food. These associations are influenced by the novelty of food, the amount of nutrients in the food, and the need of an individual for a particular nutrient in the food. Unlike with livestock, many studies with people fail to show changes in preference or intake after flavor-nutrient pairings. Yeomans (2012) considers how lack of experimental control and differences in study design might underlie these inconsistencies.

People learn to like foods that contain needed nutrients. Such flavor-nutrient learning, which begins in utero and early in life, affects food preference and intake throughout life. Scientists control experiences in utero and early in life in flavor-nutrient studies with livestock, but that is not possible with humans. Due to less history and greater malleability, young children more reliably increase preference compared with adults. Findings with adults are less consistent due to their long, diverse, and unknowable histories of eating habits. With children and adults, food novelty can decrease preference and intake as people prefer familiar to unfamiliar foods (Birch & Marlin, 1982; Sanudo et al., 2007).

Controlling for appetitive state and amount of nutrients consumed also is challenging in people because most studies use energy in attempts to condition preferences. Studies with people who typically eat large amounts of energy-dense foods, may condition only weak preferences or even aversions if people do not need additional energy. Good examples of appetitive state-dependent learning in humans occur where environmental circumstances create nutrient deficits, and hence cravings, for fat with lean-meat diets (Mowat, 2005); cod liver oil with rickets (Davis, 1928, 1939); fruit with scurvy (Lind, 1753); salt with salt deprivation (McCarron, Geerling, Kazaks, & Stern, 2009); and for people who exhibit pica, cravings for specific and often unusual 'foods' such as dirt when they are deficient in minerals (Rose, Porcerelli, & Neale, 2000).

Studies with herbivores control for appetitive state and amount of nutrients provided because even slight deficits or excesses relative to needs can condition aversions. For instance, when lambs are mildly deficient in energy they acquire strong preferences for flavors ingested just prior to ruminal infusions of the energy source propionate (infused as sodium propionate), a glucogenic volatile fatty acid produced by microbial fermentation in the rumen (Villalba & Provenza, 1996, 1997c). However, when lambs have free access to salt blocks as part of their daily ration, they avoid flavors paired with the small amounts of sodium infused during the trials with sodium propionate because they do not need the additional sodium. The same is true for other minerals, protein, energy, and fiber (Gregorini et al., 2015; Villalba et al., 2008; Villalba & Provenza, 1999).

With people, the relationships among appetitive state and nutrients differ from when our ancestors hunted and gathered (Armelagos, 2014). Foods now are altered (to reduce or remove existing nutrients or replace a nutrient with another substance), enriched (to add new nutrients), and fortified (to increase existing nutrients), and people take supplements (Tremblay & Arguin, 2013). These practices may adversely affect flavor-nutrient learning and health, if humans respond to excesses in a manner similar to herbivores. Taking additional β-carotene, vitamin A, and vitamin E, individually or combined with other antioxidant supplements increases risk of all-cause mortality (Bjelakovic, Nikolova, & Gluud, 2013; Hathcock, 1997; Miller et al., 2005). The risk is higher in developed countries, where use of supplements is popular (Rock, 2007), and individuals are more likely to meet needs from dietary sources (Mulholland & Benford, 2007; Ramakrishnan, 2002). Taking a multivitamin–multimineral supplement daily has no effect on mortality (Macpherson, Pipingas, & Pase, 2013).

Finally, Yeomans (2012) highlights how differences among individuals — regarding the novelty of a food and amount of nutrients in a food relative to the needs of an individual for those nutrients — affect flavor-nutrient learning. Studies with herbivores also illustrate the uniqueness of individuals (Provenza et al., 2003; Scott & Provenza, 1999). For instance, in a two-month study, no two individuals ever selected the same combination of foods from day to day when calves could choose among four foods — rolled barley, rolled corn, corn silage, and alfalfa hay (Atwood, Provenza, Wiedmeier, & Banner, 2001a). The average ratio of protein to energy ingested throughout the study was identical to that for a 'total-mixed-ration' – made by grinding and mixing the four foods in proportions formulated to meet the nutritional needs of the 'average' individual – balanced nutritionally to maximize growth at least cost. However, no calf was 'average' – each individual selected a diet with consistently higher or lower ratios of protein to energy. Even so, they all grew equally well compared with one another and with cattle fed the total-mixed ration. Calves could have selected imbalanced diets, developed acidosis, and died from eating too much barley or corn, but that never happened. When given time to learn about the aversive consequences of eating too much grain, calves and lambs learn to balance intake of grain and roughages to prevent acidosis (Provenza, Ortega-Reyes, Scott, Lynch, & Burritt, 1994; Scott & Provenza, 1999).

4. Appetite, satiety, and food intake

Flavor-feedback associations are necessary to ensure health through nutrition, but herbivores and humans also must have access to phytochemically rich foods and learn how to eat combinations foods that nourish and satiate. The terms satiation and satiety are used in different ways by scientists who study herbivores and humans. While no consensus exists for humans (Blundell & Bellisle, 2013), many scientists define satiation as processes that bring a meal to an end and satiety as processes that inhibit eating between meals (Chapelot, 2013). These definitions do not deal with associations among the kinds and amounts of foods eaten within a meal and their relationships with satiation and satiety (Booth, 2009). While the focus in humans is often on primary compounds, studies of herbivores emphasize relationships among primary and secondary compounds as they affect selection of particular foods within and among meals.

4.1. Satiation and satiety in herbivores

Three hypotheses – one accenting food flavors, another nutrients, and yet another secondary compounds – account for why herbivores, given an opportunity, satiate from eating a variety of foods and foraging in different places within and among meals (Provenza, 1996). Each of these accounts is consistent with the notion that the mix of foods in time and space is critical, as no one food can meet the nutritional needs of animals while at the same time preventing toxicity.

Herbivores eat a variety of foods in part because they satiate on the flavors of foods (*flavor-specific satiety*). When sheep and cattle eat a flavored food, such as maple–or coconut-flavored grain or straw, for two hours on one day, they prefer food with a different flavor the next day (Atwood, Provenza, Wiedmeier, & Banner, 2001b). Livestock thus satiate on specific flavors and the degree to which their preference for a particular food declines depends on how adequate the food is relative to their needs (Early & Provenza, 1998).

Herbivores eat a variety of foods to meet needs for energy, protein, minerals, and vitamins as no plant contains all these nutrients in amounts animals require (*nutrient-specific satiety*) (Westoby, 1978). Eating forages high in energy or protein does not inevitably meet needs for minerals. Eating different species of plants, with different rooting depths and mineral acquisitions, enables herbivores to meet other needs as well. Being curious, opportunistic, and appreciating variety, herbivores often forage across landscapes. To diversify their diets in less botanically rich environments, cattle alternate among locations that contain different species of plants; conversely, in more botanically diverse environments, cattle often forage in the same general location for longer periods (Bailey, Stephenson, & Pittarello, 2015).

Herbivores also eat a variety of foods to avoid toxicity from secondary compounds (*secondary compound-specific satiety*) (Freeland & Janzen 1994). All plants contain secondary compounds that limit how much of each plant species an insect, fish, bird, or mammal can eat (Rosenthal & Berenbaum, 1992; Rosenthal & Janzen, 1979). By limiting intake of any one plant, secondary compounds cause animals to eat a variety of plants and to forage in a variety of places. Complementarities among secondary compounds, and the sequences in which they are ingested, markedly influence intake of forages. For instance, sheep first infused with saponins and then allowed to choose among alfalfa, trefoil, and tall fescue, decrease preference for alfalfa (high in saponins) and increase preference for trefoil (high in tannins) and tall fescue (high in alkaloids); conversely, sheep infused with alkaloids decrease preference for tall fescue (high in alkaloids), whereas sheep infused with tannins increase preference for tall fescue (Villalba, Provenza, Clemensen, Larsen, & Junke, 2011). Likewise, sheep first fed high-saponin alfalfa or high-tannin birdsfoot trefoil for 30 min, followed by a 3.5-h meal of either endophyte-infected tall fescue (alkaloids) or reed canarygrass (alkaloids), eat more and digest more dry matter, nitrogen, and energy than lambs not provided with an appetizer of alfalfa or trefoil (Owens, Provenza, Wiedmeier, & Villalba, 2012). These benefits are achieved when sheep eat less than 30% of their daily intake as alfalfa and less than 13% of their intake as trefoil. Cattle decrease time eating endophyte-infected tall fescue (high in alkaloids) when they first graze tall fescue alone for 30 min followed by birdsfoot trefoil (high in tannins), alfalfa (high in saponins), or alfalfa–trefoil combination for 60 min (Lyman, Provenza, Villalba, & Wiedmeier, 2011, 2012). Conversely, when the sequence is reversed, cattle forage actively for 30 min on trefoil, alfalfa, or trefoil-alfalfa combination and then continue to forage eagerly on fescue during the ensuing 60-min meal. Thus, to meet needs for energy and protein, herbivores must eat a variety of foods that differ in secondary compounds, each detoxified in different ways. Eating small amounts of plants with diverse arrays of phytochemicals enables health through nutrition (Provenza et al., 2007; Bailey & Provenza, 2008).

Each of these explanations accent one part of processes that are functionally integrated. The *satiety hypothesis* attempts to unite these hypotheses by ascribing changes in preference to transient aversions to the flavors of foods that arise as primary (e.g., energy and protein; Villalba & Provenza, 1999) and secondary (e.g., tannins, saponins, and alkaloids; Villalba et al., 2011) compounds interact to cause satiation and satiety (Moore, Wiggins, Marsh, Dearing, & Foley, 2015; Provenza, 1995, 1996). This view assumes feedback from eating combinations of forages resides along a continuum from requisite to surfeit that alters liking for particular foods (Forbes, 2007b; Provenza, 1996). Eating any combination of foods to satiety causes a decrease in liking for those foods. The decrease is stronger and more persistent when the foods are deficient or excessive in primary or secondary compounds relative to needs (Early & Provenza, 1998; Villalba et al., 2011).

Livestock prefer to eat different forages within meals and during the day. In any one meal, for instance, goats will eat around 20 of 60 edible species (Meuret & Bruchou, 1994), including species like leguminous shrubs that stimulate appetite (Meuret & Provenza, 2015a). Among meals, for instance, sheep prefer to eat clover in the morning and grass in the afternoon and they eat more when offered a combination of clover and grass than when offered either clover or grass alone (Parsons, Newman, Penning, Harvey, & Orr, 1994). Clover is more nutritious and digestible than grass, but after eating clover, sheep switch to grass; their mild aversion to clover subsides during the afternoon and evening and by morning they are ready for more clover. The transient aversion is due to feedback from primary (organic acids from soluble carbohydrates and ammonia from highly digestible protein) and secondary (cyanogenic glycosides) compounds (Cooper, Kyriazakis, & Nolan, 1995; Francis, 2003; Gregorini, 2012; Lobley & Milano, 1997). Relationships like these cause herbivores to eat foods with harmonizing phytochemical profiles and to track primary and secondary compounds in plants within and among meals (Bailey & Provenza, 2008; Carlson, Rothman, & Mitani, 2013; Gregorini et al., 2015; Scott & Provenza, 1998). These interactions also allude to the complexity, dynamism, and synergies among foods when herbivores eat diverse assortments of plants.

4.2. Modifying appetite in herbivores and humans

Skilled herders in France design grazing circuits at a meal scale to increase appetite and intake, to create synergies among meal phases, and to increase intake of abundant but less palatable forages (Meuret, 1996; Meuret & Provenza, 2014; 2015a,b). To do so, they partition landscapes into grazing sectors that are carefully sequenced within daily circuits. Meals are based on complementarity blends of terrain and plant communities within and among sectors, not on particular plants. Herders identify and ration various sectors into phases of a meal: appetite stimulator or moderator, first course, booster, second course, and dessert sectors. According to herders, animals develop a ‘temporary palatability scoring’ as they judge, in a comparative way, if the foods in an area are satisfactory. Herders can successfully modulate ‘palatability scoring’ by organizing access to sectors that enable minor foraging transitions over several days. Herders prevent the herd from having a much better foraging experience on one day than on others so the animals will not spend most days searching for favored forages and failing to use other forages. Conversely, offering the same foods repeatedly leads to ‘grazing weariness’. When repeatedly offered the same complementarity blends of locations and plant communities, livestock satiate on both the forages and the locations (Meuret & Provenza, 2015b). Given the same territory, breed of livestock, herd size and stock density, no two herders or herds will achieve the same degree of success, which will depend on a herder's ability to design, execute, and continually adjust grazing circuits and distinctive feeding habits of herds in time and space. The synergies herders enable depend on interactions among plant diversity, physical structure, and primary and secondary compounds, as shown in vivo and in virtualis through simulation models (Gregorini et al., 2015; Villalba, Provenza, Catanese, & Distel, 2015).

As with herders, people can organize meals by courses to stimulate appetite and intake. Offering a variety of foods in a meal consistently increases intake (Brondel et al., 2009; Hetherington, 1996; Sørensen, Møller, Flint, Martens, & Raben, 2003), the more different the foods are the greater the enhancement (Rolls et al., 1981), and desserts rekindle appetite when a person is presented with foods that differ from the appetizer and main courses (Remick, Polivy, & Pliner, 2009; Rolls, 1979; Rolls, Rolls, & Rowe, 1982). However, to prevent and manage obesity scientists are exploring ways to reduce food intake. Total food intake in a meal can decline when humans eat: 1) foods high in protein such as dairy products, red meat, or poultry; 2) some fishes high in unsaturated fats; 3) legumes and whole grains high in fiber; 4) fresh fruits and vegetables low in energy density and high in phytochemical richness; and 5) foods that contain phytochemicals such as caffeine and capsaicin (reviewed in Tremblay & Arguin, 2013). Foods high in protein (Johnstone, 2013), carbohydrates (Poppitt, 2013), and fats (Hennink & Maljaars, 2013) satiate, but when energy density (kcal/g of food) is held constant, the effects on satiety are similar for fat, carbohydrate, and protein (Rolls, 2009). Energy density thus influences satiety.

Decreasing energy density can reduce energy intake, and energy content and portion size of foods can be reduced without people noticing (Rolls, 2009, 2012). Eating a low-energy appetizer such as soup or salad or fruit can decrease energy intake in a meal (Rolls, Roe, & Meengs, 2004). Energy density also can be reduced by decreasing fat or sugar and flavor can be enhanced by adding herbs, spices, fruits, or vegetables to dishes. When the energy density of the main dishes served over a day is cut by adding puréed vegetables, both adults and preschool children consume fewer calories (Blatt, Roe, & Rolls, 2011; Spill, Birch, Roe, & Rolls, 2011). In these and other studies, people report similar ratings of hunger and fullness, even when energy intake is reduced by 25% over 2 days (Rolls, 2009). In year-long trials, people advised to reduce energy density by eating more fruits and vegetables, and reducing intake of fat, lost more weight than those advised merely to reduce intake of fat (Ello-Martin, Roe, Ledikwe, Beach, & Rolls, 2007).

Given a choice, neither herbivores nor humans eat only one food in a meal (Provenza, 1996; Rolls, 1986). Rather, they often eat meals in courses, they eat foods that vary in kinds and concentrations of primary and secondary compounds, and humans add herbs and spices to foods. Yet, we found no studies of how food combinations and sequences affect satiation or satiety in people. As with herbivores, primary compounds and secondary compounds in different foods likely contribute to satiation and satiety in humans beyond the effects energy, water, and fiber (Fardet, 2010). How do food combinations and sequences effect satiation and satiety?

Do complementarities exist: by binding to proteins, can tannins mitigate effects of gluten? To what degree do food combinations and sequences lessen hyperglycaemia and hyperinsulinemia in people (Jenkins et al., 2003)? Across meals during the day, a high-energy breakfast combined with low-energy dinner decreases hyperglycaemia throughout the entire day and increases GLP-1, a hormone that promotes insulin sensitivity, increases satiety, and reduces intake (Jakubowicz et al., 2015). Within a meal, eating whey protein as an appetizer, as well as altering the macronutrient composition of a meal, reduces glucose levels after a meal (Nuttall & Gannon, 2004; Frid, Nilsson, Holst, & Bjorck, 2005; Jakubowicz et al., 2014). We found only two studies, however, regarding the effect of food order on glycemia and insulinemia. Postprandial glucose and insulin levels are much higher when food order is carbohydrate (ciabatta bread and orange juice), followed 15 min later by protein (skinless grilled chicken breast) and vegetables (lettuce and tomato salad with low-fat Italian vinaigrette and steamed broccoli with butter) compared to when the food order is reversed (Shukla, Iliescu, Thomas, & Aronne, 2015; see also Imai & Kajiyama, 2010). Mean post-meal glucose levels decreased by 28.6%, 36.7%, and 16.8% at 30, 60, and 120 min, respectively, when vegetables and protein were eaten before carbohydrate. Postprandial insulin levels at 60 and 120 min also were lower when protein and vegetables were consumed first. The magnitude of these effects is comparable to pharmacological agents that target postprandial glucose and the findings also suggest this meal pattern may improve insulin sensitivity.

Do people who subsist on processed diets seek nutrients in short supply – and thus never satiate – because phytochemical richness and quality trump phytochemical sameness and quantity? Liebig's law of the minimum, developed by Carl Sprengel and popularized by Justus von Liebig, states that growth is controlled by the scarcest resource (van der Ploeg, Bohm, & Kirkham, 1999). From the standpoint of nutrition, the phytochemical richness of each meal is likely to be indispensable for reducing intake by providing all of the potentially limiting substances cells need. Livestock over-ingest energy to meet needs for protein and minerals (Provenza & Villalba, 2006; Webster, 1993) and, as discussed, calves offered four foods ate less, but grew equally well, compared with calves fed a total mixed ration made of these four foods. Humans, too, may over-eat foods to meet needs for limiting nutrients including minerals (Ames, 2006; Garcia, Long, & Rosado, 2009) and protein (Simpson & Raubenheimer, 2005). Protein intake now is roughly 15% of dietary energy intake; some contend that has facilitated obesity by causing humans to over-eat energy to meet needs for protein, which are closer to 30% of energy intake (Simpson & Raubenheimer, 2005). This notion is consistent with findings that humans will self-select a diet to meet needs for protein (Booth & Thibault, 2000; de Castro, 2000; Simpson, Batley, & Raubenheimer, 2003).

Healthy people often eat less of a food that provides more sensory pleasure than they do of a blander version of the food. In one study, satiation increased faster when people ate a soup spiced with chili as opposed to the base soup (Møller, 2013). Wanting more of the spiced soup decreased faster over time than wanting of the base soup, even though wanting of the spiced soup was higher initially. More rapid satiation and decrease in wanting when eating the spiced soup might obscure a wish to stop eating due to a lower appreciation of the spiced soup than of the base soup, but that was not the case: people better liked the spiced soup, which satiated them faster. Other studies also suggest that eating what a person likes induces a stronger decrease in wanting to eat, so it is not beneficial to restrict intake of liked foods to limit overall intake (Lemmens et al., 2009). These findings are consistent with the hypothesis that wants, likes, and needs are linked through phytochemical richness of foods. While some suggest eating a monotonous diet may induce satiation and help relieve obesity (Epstein, Carr, Cavanaugh, Paluch, & Bouton, 2011), eating a monotonous diet can induce cravings for liked foods. Indeed, energy intake can increase when foods are energy-dense but phytochemically poor (Møller, 2015; Pelchat, Johnson, Chan, Valdez, & Ragland, 2004).

Conversely, some conditions cause people to over-eat. Eating processed foods high in refined carbohydrates stimulates production of insulin, which boosts storage of energy in fat cells, thus depriving other organ systems of energy. In turn, that can cause people to over-eat because they are always hungry, despite the fact that metabolism and level of activity slow to conserve energy, which is being stored in fat cells (Ludwig & Friedman, 2014; Taubes, 2007). People with certain pathological states also over-eat. For instance, body mass index and activation of dopamine receptors in the striatum are inversely related. Dopamine modulates reward circuits and dopamine deficiency may cause pathological eating to compensate for diminished activation of these circuits (Wang et al., 2001).

Finally, the combinations of foods people eat in a meal can influence weight changes long-term (Smith et al., 2015). Interactions among protein- and carbohydrate-rich foods in a meal are important: protein reduces weight gain (Westerterp-Plantenga, Lemmens, & Westerterp, 2012), while high glycemic index (GI) and high glycemic load (GL) starches, refined grains, and sugars increase weight gain (Mozaffarian, Hao, Rimm, Willett, & Hu, 2011). The greater and more rapid rises in postprandial blood glucose and insulin induced by high GI and GL diets facilitate weight gain (Ludwig, 2002). Weight change is positively associated with foods higher in GI, especially refined grains, and inversely associated with foods lower in GI, such as whole grains, fruits, and vegetables (Liu et al., 2003; Koh-Banerjee & Rimm, 2003; Koh-Banerjee et al., 2004; Mozaffarian et al., 2011; Fogelholm, Anderssen, Gunnarsdottir, & Lahti-Koski, 2012). Higher protein, lower GI and GL diets also may confer an advantage during weight loss maintenance (Larsen et al., 2010), partly due to higher resting energy expenditure (Ebbeling et al., 2012). Compared with lower GI meals, higher GI meals satiate less, and they activate regions in the brain associated with reward and craving, thus leading to over-eating and weight gain (Lennerz et al., 2013). In adults, lowering the fat content of foods can lead to greater intake of carbohydrates, which can explain why weight gain usually is not different for low-versus high-fat versions of foods (Smith et al., 2015). Whether these findings in adults are applicable to all ages should be investigated given that children who consume more low-fat milk gain more weight than those who consume whole milk (Scharf, Demmer, & DeBoer, 2013).

5. Challenges humans face in foraging

During the past 10,000 years, humans have morphed from hunter–gathers into industrial-scale farmers and food manufacturers (Gamble et al., 2013). At the individual level, modern supermarket shopping is a return to the hunter–gatherer lifestyle as people forage for meats, produce, and processed foods in the isles of supermarkets. At the species/society level, ranching, farming, and feedlots are the local family/clan part of a division of labor that allowed settlements of hundreds to survive as hunters and agrarians traded fresh surplus in local markets and preserved surplus – including dried, salted, and fatty foods – locally and regionally to related clans during fall, winter, and spring. Those processes allowed some villages and towns to grow into large cities, but only after people involved with agriculture developed technologies of mass production and distribution and flexible economies. In the process, agribusiness and food manufacturing corporations became essential to the survival of large populations. But as we climbed the ladder to industrial and technological achievement, we removed many of the rungs that once linked us ecologically, economically, and culturally with the landscapes that sustain us.

5.1. The quest for nutritious fruits and vegetables without pesticides

Of roughly 400,000 species of plants on earth, humans eat only a few thousand, just a few hundred are cultivated, and only a dozen account for over 80% of the annual production of crops (Diamond, 1999). That constrained crop production to a few plants, relatively productive in a range of environments, rather than expanded diversity to include an array of plants valuable in local environments (Khoury et al., 2014). By focusing on a few species, people converted the phytochemically diverse plant world into a manageable domain that generally meets needs for energy and limits intake of toxins (Johns, 1990).

Like herbivores, however, contemporary humans still face challenges of detecting nutrients and avoiding toxins, but the forms these entities take differ now from those of our ancestors. Agricultural practices have increased yields of fruits, vegetables, and grains two-to three-fold in the past two centuries by selecting varieties with high yields, decreasing competition with non-crop weeds through cultivation and herbicides, using pesticides, and by increasing resource availability through irrigation and fertilization with off-farm sources of nitrogen, phosphorus, and potassium. But the increases in growth have come at the expense of phytochemical richness, which has declined 5%–40% in 43 fruits, vegetables, and grains in the past 40 years (Davis, 2009; Davis, Epp, & Riordan, 2004; Mayer, 1997). On the one hand, primary and secondary compounds often decrease when plants are given growth-promoting nutrients and water (Bryant et al., 1983; Reeve et al., 2015). On the other hand, farming practices that focus on improving soil health can increase phytochemical richness of vegetables and fruits and reduce risks from pesticides (Brandt, Leifert, Sanderson, & Seal, 2011).

People in the U.S., France, and many other countries are exposed to a range of pesticides in fruits and vegetables, many with known or suspected carcinogenic or endocrine-disrupting properties (Guyton et al., 2015). People are increasingly concerned about pesticide residues. Farmworkers are at greatest risk, because they routinely work with pesticides, as are children due their developing organ systems. Consumer Reports just published (May 2015) a guide to the risks of pesticide exposure from eating 48 fruit and vegetables. Conventionally grown and organic produce were given low-, medium-, or high-risk status according to type of produce and country of origin. Prohibiting use of synthetic pesticides under organic farming standards reduces by more than 4-fold the number of crops with pesticide residues (Baranski et al., 2014).

Despite these benefits, shifting farming practices from conventional to organic alone does not ensure that fruits and vegetables will be more phytochemically rich and flavorful. Vine-ripened produce is tastier than its counterparts picked green and ‘heirloom’ varieties taste better than many modern varieties (Bartoshuk & Klee, 2013; Klee & Tieman, 2013). Compared with varieties from before the post-World War II period of intensive breeding, modern cultivars have fewer phytochemicals that add flavor (Goff & Klee, 2006). In tomatoes, levels of glucose, fructose, citrate, and malate can vary several-fold, whereas levels of the over 400 flavor volatiles can vary 1000-fold or more among ‘heirloom’ varieties (Klee & Tieman, 2013). When targeted metabolomics and variation within 66 heirloom varieties of tomatoes were used to create a predictive model of liking, the most important contributor was sugar (Klee & Tieman, 2013). Volatile compounds also markedly affect liking and some volatiles make large contributions to perceived sweetness. For instance, the tomato variety Matina is perceived as twice as sweet as Yellow Jelly Bean, yet Matina has less sugar; each of seven volatiles that contribute to sweetness is at least twice as abundant in Matina as in Yellow JellyBean (Bartoshuk & Klee, 2013). The same is true for fruity volatiles such as citral, amyl acetate (banana), strawberry, peach, raspberry, passion fruit, and lychee (Bartoshuk & Klee, 2013). Thus, ‘sweetness’ and ‘complex flavor’ are most highly rated as favorable characteristics of both the ideal tomato (Tieman et al., 2012) and strawberry (Schwieterman et al., 2014). However, growers are paid for yield and appearance, not flavor, in large-scale production systems. Some researchers are now attempting to enhance the flavors of highly productive commercial cultivars (Klee & Tieman, 2013).

Herbivores avoid eating plants that are poorly palatable/nutritious, which is one way plants defend themselves against herbivory (Coley, Bryant, & Chapin, 1985). Ironically, geneticists have selected for poorly palatable/highly defended fruits and vegetables based on appearance, uniformity, and transportability, not on richness of flavor. But flavor, not sight, is the arbiter of flavor–feedback relationships with cells and organ systems and many fruits and vegetables are uniformly unfit to eat. One way to diminish children's apparent dislike for vegetables is by flavor–flavor conditioning, where a vegetable is coated with a familiar sweet flavor like glucose or sucrose (Havermans, 2009). Adding a familiar flavor to a novel food increases intake of the unfamiliar food (Pliner & Stallberg-White, 2000). Another way to increase intake of vegetables is to hide them in prepared dishes (Blatt et al., 2011; Spill et al., 2011). Yet another way is to offer different vegetables in a meal (Meengs, Row, & Rolls, 2012). But the need to add sweet flavors to vegetables, hide vegetables in dishes, or offer multiple vegetables could be reduced if plant breeders increased phytochemical richness and flavor of vegetables and fruits. In so doing, flavor would once again be functionally linked with nutritional quality. In the meantime, consumers must learn to identify and purchase varieties of fruits and vegetables that are most phytochemically rich and flavorful (Robinson, 2013).

Finally, in many countries, people now navigate the isles of grocery stores stocked with thousands of processed foods made by extracting and purifying compounds in ways that amplify flavor–feedback relationships. They are attractively packaged and their energy-dense contents produce immediate positive flavor-feedback associations, which condition preferences, but delayed aversive effects that lead to obesity, diabetes, heart disease, and cancer. Ironically, as farming and plant selection practices were making the flavors of fruits and vegetables ever blander, people were making processed foods ever tastier (Schatzker, 2015). People learned to link synthetic flavors of fruits and spices with feedback from compounds rich in energy, which is required in large amounts and stored as a buffer (Galef, 1996; Lev-Ran, 2001). Differences in flavors are distinct enough to give consumers a sense of variety, which stimulates food intake, despite the nutritional sameness (Remick et al., 2009; Rolls, 1979; Rolls et al., 1982). These man-made feedback traps create preferences that diminish health (Drewnowski & Darmon, 2005a), and by adding compounds like sugar, make foods addictive (Avena, Rada, & Hoebel, 2008). People today crave foods and drinks high in sugar in multifarious guises. These slights-of-hand are illustrated by comparing real strawberries with artificially flavored strawberries (Ludwig, 2011). A 284 g (90-kcal) portion of strawberries (cost $1.50 U.S.) has 5 g of fiber, large amounts of minerals and vitamins and hundreds of phytochemicals (Schwieterman et al., 2014). A 28 g (90-kcal) portion of Fruit Gushers™ (cost $0.46 U.S. or 330% more than strawberries) has 9 g of sugar and 1 g of fat, but virtually none of the beneficial phytochemicals of strawberries because a Strawberry Fruit Gusher™ has no strawberries. Rather, it consists of pears (from concentrate), sugar, dried corn syrup, corn syrup, modified corn starch, fructose, and grape juice (from concentrate). While ‘low cost’ is touted as a reason people eat processed foods, the cost per unit of phytochemical richness is much less (330%) for a strawberry than for a Fruit Gusher™.

5.2. Herbivore diets, meat and milk for human consumptions

Meat, milk, and cheese reflect the climate, geography, and history of an area manifest through soil and plant chemistry, as illustrated when lamb meat was correctly classified for location of origin – England, Ireland, France, Germany, Italy, or Greece–in 78% of samples subjected to multi-element stable isotope ratio analyses (Camin et al., 2007). Ironically, while plant diversity and chemistry affect meat and dairy products, few studies have assessed how phytochemical richness of different mixtures of forages affects the flavor of meat or dairy products (Schatzker, 2010). While people often perceive ‘grass-fed’ beef and meat from wild game to have a ‘gamey’ flavor, the flavor, color, and quality of meat can be positively affected when herbivores eat phytochemically rich diets (Vasta, Nudda, Cannas, Lanza, & Priolo, 2008). The flavor and phytochemical richness of cheese are enhanced when dairy cattle can select a diet from botanically diverse pastures as opposed to eating a total-mixed ration made from a few cultivated forages and grains (Carpino, Home, Melilli, Licitra, & Barbano et al. 2004; Carpino et al., 2004). Compared with some studies of grass-fed beef (Van Elswyk & McNeill, 2014), consumers in the U.S. show higher liking for meat from cattle finished on grass-legume (fescue-sainfoin) pastures (Maughan et al., 2014; Maughan, Tansawat, Cornforth, Ward, & Martini, 2011). Tannins in plants like sainfoin reduce rumen bacteria that produce ‘off-flavors’ such as skatole that can adversely affect the flavor of meat (Priolo et al., 2009; Bjorklund, Heins, DiCostanzo, & Chester-Jones, 2014).

The forages herbivores eat can also affect human health. Eating the meat of a wild herbivore (kangaroo) foraging on native plants caused markedly lower postprandial inflammatory responses than eating meat of livestock (wagyu cattle) finished on grain in a feedlot (Arya et al., 2010). By design, diet and animal were confounded in this study and we could find no studies of how forage-versus grain-finishing of livestock affects inflammatory responses to meat or milk products in humans. Nor do epidemiological studies that assess the risks of eating red meat distinguish between meats from forage-as opposed to grain-fed livestock (Pan et al., 2012). Low-grade systemic inflammation – characterized by an increase in plasma levels of pro-inflammatory markers such as TNF-α, IL-6, and C-reactive protein – is strongly implicated as a cause of cancer and heart disease (Hotamisligil, 2006; O'Keefe & Bell, 2007). Given the prevalence of meat from cattle, pigs, and chickens fed grain-based rations in feedlots, and the many diet-related diseases, future studies should assess how phytochemical diversity of the diet of herbivores affects chemical characteristics of meat and dairy products and inflammation in humans.

The tissues of herbivores reflect the phytochemical richness of their diet (Descalzo & Sancho, 2008). The richness of phytochemicals in the meat and milk products that humans consume can enhance human health (Jacobs & Tapsell, 2007). While cells of humans and herbivores need energy, protein, minerals, and vitamins, they also use secondary compounds to reduce inflammation, improve brain and vascular functions, inhibit growth of cancer, boost immune function, and provide protection as antioxidants and anthelmintics (Catoni, Peters, & Schaefer, 2008; Craig, 1999; Crozier, Clifford, & Ashihara, 2006; Del Rio et al., 2013; Provenza & Villalba, 2010; Rathore, Saxena, & Singh, 2013). Consistent with these findings, livestock producers find that morbidity and mortality on cattle decrease when they switch from monocultures to diverse mixtures of plants (Jim Johnson, Noble Foundation, personal communication, 2015). The lack of research on this topic reflects the fact that livestock producers and researchers are just beginning to appreciate the value of plant phytochemical diversity above and below ground (Baskin, 2005).

Archaeological and anthropological evidence, along with studies of current hunter–gathers, show that human diets varied from plant-based in deserts and tropical grasslands to animal-based in northern coniferous forests and tundra (Brand Miller & Colagiuri, 1999; Cordain, Brand Miller, Eaton, & Mann, 2000a; Cordain, Brand Miller, Eaton, & Mann et al., 2000b; Milton, 2003). Hunter–gatherers had similar carbohydrate intake (30%–35% of total energy) over a range of latitudes from 11° to 40° north or south of the equator, but carbohydrate intake decreased (from 20% to 9% or less of total energy intake) as intake of meat increased with increasing latitudes from 41° to >60° (Ströhle & Hahn, 2011). The wild plants hunter–gathers ate were high in fiber and slowly digested; they yielded the low glycemic and insulin responses associated with less risk of heart disease and diabetes (Barclay et al., 2008; Ströhle & Hahn, 2011).

The diets of many hunter–gatherers were meat-based, but non-atherogenic, and they did not promote the formation of fatty plaques in arteries (Cordain, Eaton, Brand Miller, Mann, & Hill, 2002). Higher intake of red meat is cited as a cause of increased mortality from cardiovascular disease (CVD), so it is ironic that hunter–gatherers who derived most of their energy from animal foods had much lower mortality from CVD than people in other societies. Compared with Danes in Denmark, for instance, Inuit in Greenland had little CVD despite much greater intake of animal foods; their blood lipid profiles were lower in LDL, VLDL, and triglycerides (TG) and higher in HDL (Bang & Dyerberg, 1980). The lack of CVD was attributed to higher intake of omega-3s, but other factors likely were involved (discussed in Cordain et al., 2002). Protein intake was over twice as high for Inuit as Danes. Replacing carbohydrate isocalorically with protein or fat improves blood lipid profiles by reducing TG, LDL, and VLDL and by increasing HDL. For people of all ages and sexes, replacing saturated fats with refined carbohydrates increases risk of CVD, replacing saturated fats with small amounts of polyunsaturated fats reduces CVD, and eating monounsaturated fats is not associated with increased risk of CVD (Jakobsen et al., 2009).

The Ihalmiut of Canada, who subsisted on meat, craved fat, which they ate in a ratio of roughly 3 to 1 relative to red meat (Mowat, 2005). In addition to caribou, other foods were available in the Barrens—hares, whitefish, trout, graylings, and suckers—but the Ihalmiut did not rely on them. They were aware that hares and fish could not supply the fat they required. Fat serves several functions some more obvious than others. The liver and kidneys remove excess nitrogen when too much lean meat is eaten, but all of the nitrogen cannot be processed and accumulates to toxic levels in a body. The energy from fat is required as part of detoxification (liver) and elimination (kidneys) processes. While plants are good sources of omega-3 and omega-6 essential fatty acids, they also can be obtained from eating fat. Fat-soluble vitamins – A, D, E, and K – and calcium cannot be fully absorbed if eaten unaccompanied by fat.

The phytochemical richness of the diet a herbivore eats, which is reflected in its meat and fat (Descalzo & Sancho, 2008), can improve human health in other ways. For instance, pre-agricultural people had greater bone robustness and resistance to fractures (Ruff, Trinklaus, Walker, & Larsen, 1993), due to greater activity patterns, which increased bone loading (Bridges, 1995), and high intake of fruit and vegetables (Cordain et al., 2000a,b). Eating meats, hard cheeses, and cereal grains yield high renal acid loads, which cause metabolic acidosis (Barzel, 1995), but eating fruits and vegetables yields a net alkaline renal load (Cordain et al., 2002; Remer & Manz, 1995). Eating alkalinizing agents prevents the calciuria that normally accompanies high-protein diets such that acid-base balance is restored, calcium balance is improved, bone resorption is reduced, and bone formation is increased (Lutz, 1984; Sebastian, Harris, Ottaway, Todd, & Morris, 1994; Tylavsky, Spence, & Harkness, 2008). But peoples like the Ihalmiut had no access to fruits and vegetables, so how did they maintain acid-base balance and bone health? Obligate meat-eaters like the Ihalmiut obtained many phytochemicals from eating fat of herbivores, as well as their intestines and plant contents (Holston, 1963; Mowat, 2005). While potassium and bicarbonate in fruits and vegetables may be dually important for increasing buffering capacity to maintain acid-base balance, secondary compounds also absorb hydrogen ions, thus reducing acid loads, and are directly responsible for bone health (Muhlbauer, Lozano, Palacio, Reinli, & Felix, 2003; Muhlbauer, Lozano, & Reinli, 2002; Putnam, Scutt, Bicknell, Priestley, & Williamson, 2007).

5.3. From ‘Magic Bullets’ to meal complexity to health

A one-compound focus in research enables people to transform diet data into marketing schemes based on the alleged ‘health benefits’ of compounds like omega-3s and antioxidants. For example, the meat of herbivores that consume forages as opposed to grains differs in ratios of omega-3s to omega-6s (Daley, Abbott, Doyle, Nader, & Larson, 2010). People have promoted the health benefits of omega-3s, which were thought to be anti-inflammatory, but findings are equivocal (Teng, Chang, Chang, & Nesaretnam, 2014). Early trials with fish oil in Italy (Gruppo Italiano per lo Studio della Sopravvivenza nell'Infarto Miocardico, 1999) and Japan (Yokoyama et al., 2007) were encouraging, but recent trials cast doubt on the benefits of omega-3s (The Risk and Prevention Study Collaborative Group, 2013; Chowdhury et al., 2014). Nor have omega-3s from fish oil – eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) – consistently affected heart disease in trials during the past 5–10 years (Kromhout, Giltay, & Geleijnse, 2010; Ramsden, Hibbeln, Majchzak, & Davis, 2010). Nor do EPA and DHA slow memory loss (Van de Rest et al., 2008; Dangour et al., 2010; Quinn et al., 2010), or progression of macular degeneration (The Age-Related Eye Disease Study 2 (AREDS2) Research Group

2013). Indeed, intake of omega-3s from sources other than fish was associated with increased risk of colorectal cancer when fiber intake was less than the median for people in the study (Kraja et al., 2015). Conversely, omega-6s were thought to be pro-inflammatory, but that was not evident in a rigorous review of the effects of linoleic acid in healthy people (Johnson & Fritsche, 2012), and some studies attribute lower pro-inflammatory markers to omega-6s (Forsythe et al., 2008). Weight loss is important: compared with lean individuals, overweight and obese people have much higher pro-inflammatory and lower anti-inflammatory cytokines (Teng et al., 2014). As Martijn Katan (2014) notes: “It's embarrassing, since we've been telling people to eat omega-3 fatty acids because they are wonderful for the heart … There have been heated discussions about how bad a high omega-6 to omega-3 ratio could be. Most of the evidence is from test-tube and rat experiments. There is little evidence that this ratio affects human health... [and omega-6s] may be better [than omega-3s for health] … I am not ready to give up on omega-3s yet, but you're better off getting them from fish, not fish oil capsules.”

Likewise, antioxidants are widely promoted as dietary supplements, ostensibly to counter the adverse effects of free radicals and prevent heart disease and cancer. Though initial studies suggested they might promote health, large clinical trials of antioxidant supplements including β-carotene, vitamin A, and vitamin E singly or in combinations show no effect and may even increase mortality (Bjelakovic et al., 2013). While not evident at low doses (Yfanti et al., 2010; Yfanti et al., 2012), at higher doses antioxidant supplements can shut down redox-sensitive cell signaling pathways and decrease synthesis of new muscle mitochondria and production of endogenous antioxidants (Feng et al., 2013; Hawley, Burke, Phillips, & Spriet, 2011; Kang, O'Moore, Dickman, & Ji, 2009; Strobel et al., 2011; Villanueva & Kross, 2012).

Other studies challenge assumptions about free radicals. Rather than kill, they may improve health, and the quest to neutralize them with antioxidants may do more harm than good (Ristow et al., 2009; Paulsen et al., 2014). Eating fresh fruits and vegetables promotes health, not necessarily because they protect from oxidative stress, but because the secondary compounds they contain induce mild stress. Secondary compounds work like hormetic stressors (Mattson & Calabrese, 2008), and eating plants that have struggled to survive may toughen us up as well (Howitz & Sinclair, 2008). Without regular stressors, including phytochemicals and exercise, the defences of cells are down-regulated; metabolism works less efficiently; and insulin resistance occurs. In essence, cells do not function as well as they might, which increases risk of disease. Implicit in this research is yet another criticism of highly processed foods: not only do they provide excess energy, they lack the phytochemicals that condition cells in ways that may prevent disease.

Nowadays, functional foods often are defined as dietary items with secondary compounds that can beneficially affect specific targets in the body, beyond providing adequate nutrition (Tremblay & Arguin, 2013). Functional foods of plant origins can be tailor-made genetically to increase specific phytochemicals with chemo-preventive traits. Processed foods also are being developed that incorporate new functional compounds or enhance the concentrations of existing ones. Ironically, geneticists historically selected for crops and forages with lower concentrations of secondary compounds that deterred humans and herbivores from eating particular vegetables, fruits, and forages, and people typically do not like the strong ‘gamey flavors’ of wild or domestic herbivores that forage on phytochemically rich landscapes. Our palates have been conditioned in utero and early in life to like ‘bland’ foods (Johns, 1990). Thus, increasing concentrations of secondary compounds in produce and meat is a major concern with the palatability of functional foods (Drewnowski & Gomez-Carneros, 2000).

Consistent with the findings of researchers who study herbivores, and with the experiential knowledge and practices of skilled French herders, Jacobs and Tapsell (2007) contend that combinations of foods with complex mixtures of primary and secondary compounds, and not individual foods or compounds, are etiologic in nutrition and health and for preventing many diseases in humans. Plant and animal tissues are exceedingly complex biochemically. A good assumption is that most of the compounds they contain interact to affect cells and organ systems of omnivorous consumers. The complexities of these relationships is evident by comparing the effects on health of specific compounds, combinations of compounds, individual foods, and various combinations of foods. These comparisons reveal why nutrition supplements and drugs are not always health promoting; why whole foods, not nutrients, should be the fundamental unit in nutrition; why combinations and sequences of foods are key to health through nutrition; and why people should eat a diverse array of whole (unprocessed) foods for health through nutrition.

Under some conditions people develop deficiencies and a perspective that focuses on a food sub-component can improve health: for instance, supplementing to prevent deficiency diseases such as scurvy or pellagra; supplementing folate during pregnancy to prevent congenital birth defects; supplementing B12 to vegetarians and the elderly; and supplementing in iron-deficiency anemia (Jacobs & Tapsell, 2007). However, these conditions represent only one area where nutrition intervention is required, which can be characterized as conditions of relative deficiency from dietary restriction, physiologic needs of pregnancy, or pathophysiological conditions. In most cases, extracting and purifying compounds from the broader phytochemical and ecological milieu in which they occur in plants, or creating synthetic analogues of compounds, amplifies effects in ways that are often detrimental longer term (Weil, 2004).

Yet, nutrition guidelines often are based on clinical trials of a single macronutrient or dietary supplement. Studies of β-carotene and B vitamins, along with total fat reduction, failed to reduce chronic disease risk, and in some cases increased risk (Jacobs & Tapsell, 2007). The failure of these trials suggests the original foods/combinations better promoted health than did the food sub-component. Epidemiological studies suggest a need to use complementarities among foods as the ‘variable’ of interest in disease risk. Among many examples, Jacobs and Tapsell (2007) use the lipid-based understanding of cholesterol and heart disease to make the case. Through this lens, the focus for diet and heart disease was on fat, protein, and carbohydrate. This emphasis on specific nutrients diverted attention from healthy foods with diverse phytochemicals. For instance, prospective observational studies suggest foods like fruits, vegetables, whole grains, nuts, olives, and high-fat fish, and combinations of foods reduce risk of chronic disease. These findings have biological coherence and consistency across many studies.

Some combinations of foods support bodies better than others. For instance, one study identified two dietary patterns using a principal components analysis of food intake data from a 131-item food frequency questionnaire; the prospective cohort followed for 8 years had 44,875 men aged 40–75 years who were free from cardiovascular disease and cancer when the study began (Hu et al., 2000). During the study, 1089 men developed coronary heart disease. The ‘prudent diet’ was based on a relatively higher intakes of vegetables, fruit, legumes, whole grains, fish, and poultry. The ‘Western diet’ was based on a relatively higher intake of red meat, processed meat, refined grains, sweets, and dessert, French fries, and high-fat dairy products. After adjusting for age and coronary heart disease risk factors, the relative risk (RR) for the highest versus the lowest quintile of the prudent diet was 0.70 (95% confidence interval 0.56–0.86; P < 0.0009). In contrast, the RR for the highest versus the lowest quintile of the Western diet was 1.64 (95% confidence interval, 1.24–2.17; P < 0.0001). Thus, combinations of foods yield information that can be readily translated into practice.

Food and nutrition scientists regard secondary compounds as the third functional component of food: the main function of food is to provide primary compounds; the secondary function is sensory attributes such flavor; and the tertiary function, presumed to be independent of the former two, is to use secondary compounds to prevent disease. But all three functions are linked. Primary and secondary compounds interact beneficially with one another and with cells throughout a body. At too high concentrations, any primary or secondary compound can deter feeding, but the dose makes the toxin and the combinations of foods herbivores and humans eat affects these interrelationships. Liking for foods – 'tastes' – changes within and among meals over time, as do the needs of a body. Needs for primary and secondary compounds vary with age and physical activity; they change throughout pregnancy; they increase when animals are infected with parasites or when they are ill. These changes may emerge gradually during pregnancy or as parasites increase, or they may occur quickly with shifts in physical activity or a change in the weather. Rather than hierarchically categorize these relationships into three distinctly different functional groups, is it not more integrative and comprehensive to posit that changes in 'taste' emanate from ever-changing needs of cells and organ systems? Changes in liking for tastes of wholesome foods is how a body gently guides a palate from birth to death to meet needs for macronutrients, minerals, vitamins, and the wide array of 'secondary' compounds in plant and animal tissues, which can promote health and diminish disease through nutrition.

6. Culture links herbivores and humans with landscapes

6.1. Transgenerational linkages to landscapes in herbivores

Herbivores begin to learn about foods in utero through exposure to flavors of foods in mother's diet, as illustrated in studies of sheep (Simitzis, Deligeorgis, Bizelis, & Fegeros, 2008). Onion and garlic, for instance, flavor amniotic fluid and milk, preparing lambs to eat onion and garlic plants (Nolte & Provenza, 1992; Nolte, Provenza, Callan, & Panter, 1992). After birth, offspring quickly learn what to eat from their mother. Six-week-old lambs fed whole-grain wheat with their mothers for as little as 1 h a day for 5 days ate much more wheat than lambs exposed to wheat without their mothers; even 3 years later, with no exposure to wheat beyond the 5 h early in life, intake of wheat was nearly ten times higher if lambs were exposed to wheat with their mothers than if lambs were exposed to wheat without their mothers or were not exposed to wheat (Green, Elwin, Mottershead, & Lynch, 1984). Lambs also learn from their mother to avoid potentially toxic foods (Thorhallsdottir et al., 1990). By eating foods mother eats, and cautiously sampling novel foods mother avoids, young animals are unlikely to die from eating poisonous plants (Provenza, Lynch, & Nolan, 1993), an outcome common when transgenerational linkages are broken by separating young animals from their mothers at a very early age and placing them in unfamiliar environments with poisonous plants (Provenza, 2003; Provenza et al., 1992).

By interacting with the genome during development, social and biophysical environments influence form and function through gene expression and behavioral responses. Lambs exposed to saltbush in utero grow faster and handle a salt load better than lambs whose mothers grazed on pasture without saltbush; they excrete salt more rapidly, drink less water, and eat more saltbush (Chadwick, Vercoe, Williams, & Revell, 2009). These behavioral changes are enabled by changes in kidney form and function. Likewise, pregnant cows that eat high-fiber forages in winter, a time when their needs for energy are only marginally met, prepare their fetus to use high-fiber forages: compared with naïve offspring, experienced animals eat more and better digest high-fiber forages and they grow better (Wiedmeier, Villalba, Summers, & Provenza, 2012). Experiences early in life further enhance performance, as illustrated in a study where calves were exposed to straw with their mothers for 2 months; as adult cows 5 years later, they were fed straw as a major part of their diet from December to May for 3 years (Wiedmeier, Provenza, & Burritt, 2002). Throughout the study, experienced cows ate more straw, gained more weight, maintained better body condition, produced more milk, and conceived sooner than cows not exposed to straw. The importance of learning is underscored by the fact that heritability of dry matter intake and digestibility of high-fiber forages is only 20% in cattle (Wiedmeier, Walters, & Cockett, 1995). Likewise, sheep reared on poor-quality grass eat more grass and digest grass better than naïve sheep, in part because they are better able to recycle nitrogen, which helps microbes in the gut (rumen) digest grass (Distel, Villalba, & Laborde, 1994).

Foraging behaviors, which develop as a function of history, need, and chance, can become part of a culture, as illustrated in studies to evaluate the ability of goats to rejuvenate blackbrush-dominated landscapes (Provenza, 1977). From January through March for 3 years, 15 goats browsed in each of two pastures that were 1, 2, or 4 ha in size. The first winter, Angora goats from the Navajo Nation did not perform well due to their lack of familiarity with the poorly nutritious blackbrush. The goats lost weight, but they lost more weight in the 1-ha and 4-ha pastures (>20%) than in the 2-ha pastures (<10%). Goats should have lost weight as a function of pasture size (1 ha > 2 ha > 4 ha), assuming less available browse in smaller pastures. However, goats in one of the 2-ha pastures learned to eat wood rat houses, which appear to be even less nutritious than blackbrush. But inside the houses was densely packed vegetation soaked in urine. The goats had discovered a source of non-protein nitrogen, which can be synthesized to protein by rumen microbes, thus providing more aminogenic and glucogenic nutrients to goats that eat blackbrush. Of most interest, only one of those six groups of goats learned to eat wood rat houses the first winter, and over the ensuing two winters, out of eighteen groups of goats of different breeds and from different locations, only that one group of goats ever learned to use wood rat houses. These findings illustrate the peculiar ways herbivores learn dietary habits, the importance of peers learning from one another to forage in the 2-ha pasture, and how such behaviors then become part of the foraging culture of a group (Howery, Provenza, Banner, & Scott, 1996, 1998; Ralphs & Provenza, 1999; Thorhallsdottir et al., 1990).

The ability to learn to use forages high in secondary compounds is illustrated by cross-fostering studies with two breeds of goats: Damascus goats prefer high-tannin species of woody plants while Mamber goats do not (Glasser et al., 2009). Offspring from one breed (Damascus) were reared from birth by females from the other breed (Mamber) and vice-versa. Mamber kids, whose Damascus foster mothers preferred high-tannin browse, learned to eat much more high-tannin browse than did Damascus kids whose Mamber foster mothers did not eat high-tannin browse. Likewise, goats reared from 1 to 4 months of age with their mothers on blackbrush-dominated rangeland ate 2.5 times more blackbrush than did goats naive to blackbrush, a shrub high in fiber and tannins (Distel & Provenza, 1991). When allowed to choose between blackbrush and alfalfa pellets, experienced goats ate 30% more blackbrush than did naïve goats at any level of alfalfa pellet availability, which ranged from 20% to 100% of *ad libitum*. Gut (rumen) volume and ability to cope with tannins were higher for goats reared on blackbrush than for naïve goats. Similarly, cattle exposed to sagebrush in utero and early in life eat more sagebrush, a shrub high in terpenes, and maintain better body weights than do their naive counterparts (Petersen, Provenza, & Villalba, 2014).

Livestock also learn to eat forages in sequences that are complimentary (Meuret & Provenza, 2015b). For example, researchers at the U.S. Sheep Experiment Station in Idaho identified sheep that ate large amounts of sagebrush, a shrub high in terpenes. They created a flock of sagebrush-eating sheep, which presumably differed in form and function from sheep that did not eat sagebrush. However, sheep that preferred sagebrush had learned to eat bitterbrush, a shrub high in tannins (Seefeldt, 2005). Bitterbrush as an appetizer helps sheep eat sagebrush, findings consistent with studies that show sheep eat more food with terpenes when they first eat food with tannins (Mote, Villalba, & Provenza, 2008). By binding with compounds like terpenes and alkaloids, tannins in shrubs like bitterbrush, or forbs like birdsfoot trefoil and sainfoin, enable herbivores to cope with terpene- and alkaloid-rich plants. Likewise, compared with naïve sheep, experienced sheep learn to eat much more of three complementary foods that contain tannins, terpenes, or oxalates, and they do so even when they have *ad libitum* access to nutritious alternatives (Villalba, Provenza, & Han, 2004; Shaw, Villalba, & Provenza, 2006a,b).

Social groups fashion a balance between stability (mother) and creative exploration (offspring), which can enable cultures to evolve as environments change from generation to generation. Offspring create new relationships with social and biophysical landscapes as they explore foods and environments not used by mother. For instance, when nanny goats that originated on different islands in the French Indies were all moved to one island, which had a smorgasbord of forages found on each of their home islands, the foraging behaviors acquired by the adults on the different islands did not change (Biquand & Biquand-Guyot, 1992). The original nannies from different islands influenced foraging behaviors of their offspring for more than two generations, but as time passed, the offspring were increasingly affected by peers from the other islands, and over four generations the peers converged on more similar diets.

Such experiences in utero and early in life affect food and habitat preferences in taxa as diverse as insects, fish, birds, and mammals (Davis & Stamps, 2004). Thus, what constitutes 'high-quality' diets or habitats can differ for animals of the same species reared in different environments. Unlike their wild counterparts, livestock often are conceived in one locale, born in yet another, and then moved one or more times to unfamiliar settings. These practices sever transgenerational linkages with landscapes, which explains why domestic and wild herbivores placed in unfamiliar environments often suffer from predation, malnutrition, overingestion of poisonous plants, and poor reproductive performance (Provenza, 2003). Usually, three years are required for mature adults to change food and habitat selection behaviors and they change only when forced to do so after being moved to unfamiliar localities or when management changes radically in a familiar haunt (Provenza, 2003). Declines in performance can be mitigated by management. Skilled herders, for instance, use dedicated grazing practices and social models with experience of the grazing conditions and forages to teach naïve sheep about conditions they have not formerly encountered (Meuret & Provenza, 2015b). All of the aforementioned findings regarding herbivores raise a question: What price do we pay when we ignore transgenerational linkages to social and biophysical environments in humans and the animals in our care?

6.2. Transgenerational linkages to landscapes in humans

By experiencing the cuisine of their culture in utero and early in life, humans learn to eat locally available plant and animal foods in ways proven to ensure survival through cycles of plenty and scarcity (Mennella & Beauchamp, 2010). Traditionally, people learned to eat combinations of foods that met nutritional needs and to use foods for medicines (Johns, 1990). They developed social norms and rituals around food gathering, cooking to increase digestibility of fiber and decrease secondary compounds, and eating (Armelagos, 2014; Johns, 1990; Nabhan, 2004; Wrangham & Conklin-Brittain, 2003). The phrase 'predictive adaptive response' refers to processes, which begin in utero and early in life, that act through developmental plasticity to modify form, function, and behavior (Gluckman, Hanson, & Spencer, 2005). They confer survival advantages when the environment of rearing matches that where a person lives, which will be so if the behavior of mother is appropriate for the post-weaning environment and if that environment does not change radically during the life of the offspring.

Studies of human infants illustrate how flavor-nutrient learning, availability of wholesome foods, and culture can interact to enable health through nutrition. In the 6-year study, Clara Davis became the 'mother' for 15 infants who selected nutritionally adequate diets when offered 34 foods of animal and vegetable origins (Davis, 1928, 1939). The infants initially sampled all of the foods, which could be procured fresh in the market year-round, but soon came to prefer some over others. No two children ever selected the same foods and no child ever selected the same mix of foods from day-to-day. They ate several foods in any meal, and often preferred brains, raw beef, bone jelly, and bone marrow, foods repulsive to adults who have not learned to eat them. As Davis points out, their patterns of selection developed due to "sensory experience and doubtless the feeling of comfort and well-being that followed a meal." If selected in appropriate combinations, these foods provided necessary fats, carbohydrates, amino-acids, minerals, and vitamins, though the children could have become deficient by selecting wrong combinations of foods. Throughout the study, no child became nutrient deficient. Rather, they all developed normally and were in fine health. She concluded that the 'trick' in her studies was in the foods she offered: "confined to natural, unprocessed and unpurified foods, and without prepared dishes of any sort, it reproduced to a large extent the conditions under which hunter–gatherers in many parts of the world had sound diets and excellent nutrition."

While not all hunters and gathers were well fed all the time, most fared well most of the time. As anthropologists like Lancy (2008) point out, the transition from hunting and gathering to farming adversely affected peoples. An unintended consequence was lower diet variety and human fecundity, documented by archaeologists. In the southwest U.S., for instance, where human remains span the change from hunter–gathers to farmers, anthropologists found that nutrition and health declined. The amount of meat and wild plant foods in everyone's diets declined as maize became the dietary mainstay. The lesser amount of protein in women's diets may have created impoverished nutrition and poor health, particularly during pregnancy and lactation. As women's nutritional status declined, so did the health of their unborn and newly born children. Children's poor health was manifest as a pervasive pattern of high infant mortality, malnutrition, and disease infestation. Demand for farm labor created a need for more children that lead to shorter inter-birth intervals, earlier weaning, and higher infant mortality.

During the transition from hunting and gathering to farming, people adapted to an energy-rich food supply (Patin & Quintana-Murci, 2008). Populations that eat high-starch diets now have more salivary amylase than those that maintained an ancestral pre-agricultural way of life (Perry et al., 2007). Some individuals in populations can also tolerate refined carbohydrates. Insulin-stimulated glucose uptake varies in people with normal glucose tolerance (Hollenbeck & Reaven, 1987). Roughly 25% of people have a greatly blunted response to glucose: they do not produce much insulin following a glucose challenge. Conversely, another 25% of people respond to a glucose challenge by producing far too much insulin: they are hyperinsulinemic. The other 50% of people are on a continuum between these two extremes. This suggests that 25% of the population is well adapted to a diet of refined carbohydrates, while 25%, highly responsive to glucose, is at high risk of obesity and diabetes.

Nowadays, many offspring are being 'prepared' to eat highly-processed foods, even to the extent of being born with a suite of metabolic disorders (Archer, 2014; Gonzalez-Bulnes, Ovilo, & Astiz, 2014). Maternal obesity and diabetes during pregnancy increase the risk of obesity and type II diabetes in offspring (Levin & Govek, 1998; Levin, 2000; Martin-Gronert & Ozanne, 2005; McMillen & Robinson, 2005; Plagemann, 2006; Taylor & Poston, 2007; Gluckman, Hanson, Cooper, & Thornburg, 2008; Iozzo et al., 2014). Insulin-producing cells in the pancreas of a fetus of a diabetic mother are stimulated to grow in size and number due to high levels of blood sugar in mother's diet. That, in turn, causes the fetus to produce more fat, which causes fat babies in a malicious cycle. The greater a woman's weight gain during pregnancy, the higher the risk her child will be overweight by 3 years of age and continue to be overweight into adolescence and adulthood (Kral et al., 2006; Smith et al., 2009).

Historically, people living in higher income nations ate more refined carbohydrates than people in lower income nations, and within richer nations, people with lower incomes ate more highly processed foods than people with a higher income (Drewnowski & Specter, 2004; Drewnowski & Darmon, 2005a,b). In the short-term, people with a lower income maximize intake of energy-dense foods at 'low cost,' but society pays a high price. Obesity and diet-related diseases now cost $123 billion annually in the U.S., half of which is paid by peoples' tax dollars through Medicare and Medicaid. These patterns and associated costs are increasingly common globally: overweight and obesity, estimated to affect 1.5 billion adults worldwide in 2008, are now projected to be 2.16 billion (overweight) and 1.12 billion (obese) by 2030 (Popkin, Adair, & Ng, 2012). Because obesity rates reflect an unequal distribution of incomes and wealth, ending obesity is linked with curtailing poverty. Nourishing foods can be inexpensive, but people on a limited budget will struggle to eat healthier foods unless they depart from social norms and embrace unfamiliar eating habits by learning to eat 'less palatable' foods, which can score low on taste, variety, enjoyment, and convenience (Drewnowski & Darmon, 2005b). As people learn what to eat in utero and early in life, policies must address ways to change acquired preferences.

6.3. *Conundrum of culture for humans*

Herbivores and modern humans differ in three ways regarding diet selection. Biophysical environments set physical (plant form) and biochemical (secondary compounds) limits that cause herbivores to eat a variety of phytochemically rich forages; human food environments facilitate eating energy-dense processed foods with little or no physical or biochemical limits to moderate intake. Herbivores maintain balanced diets by responding to excesses and deficits; many humans take supplements in attempts to prevent maladies long-term. Humans study and attempt to understand consequences of eating particular foods or compounds; herbivores, hunter–gatherers, and peoples in some cultures learn to eat combinations of foods that nourish and satiate.

Ironically, as a result of the penchant for analysis and prevention, many people in the U.S. believe food is as much a toxin as a nutrient and eating is nearly as dangerous as not eating (Rozin, 1989, 1996). Their anxiety is based in part on medical literature that suggests the key features of food that influence longevity have to do with chemical composition, including levels of fat and salt, rather than with social norms and attitudes toward food and on the supposed longer life of people in southern Europe who live on a traditional 'Mediterranean Diet' (Rozin, Fischler, Imada, Sarubin, & Wrzesniewski, 1999). Yet, historically, people in central and northern Europe ate diets high in fat and lived longer than people in southern Europe (Samuelson, 1990). The angst over food in the U.S. contrasts with a more pleasure-oriented attitude toward food among the French. Several studies link pleasure and good health and stress and poor health (Netter, 1996). Moreover, 86% of a sample of French adults derived more than 30% of their energy from fat and 96% ate a diet that exceeded past U.S. recommendations for less than 10% of calories from saturated fats (Drewnowski et al., 1996). Many people in the U.S. believe even trace amounts of fats are unsafe (Mozaffarian & Ludwig, 2015; Rozin, Ashmore, & Markwith, 1996), though cardiovascular disease occurs at much lower rates in France than in the U.S. (Renaud & de Lorgeril, 1992).

Consistent with what appears to be a belief that most health differences can be traced to particular compounds or foods, searches for 'the answer' to the 'French paradox' have focused on finding protective components such as red wine in the French diet (Renaud & de Lorgeril, 1992; Criqui & Ringel, 1994). Little regard is given for alternative accounts including different patterns of food intake or stress in relation to eating. Most of the French are more concerned about cuisine – food freshness, variety and balance of foods, quality as opposed to quantity, and smaller portions – while most Americans are more concerned about nutrition (Rozin et al., 1999; Rozin, Kabnick, Pete, Fischler, & Shields, 2003). Ironically, more than any other group Americans worry about diet and modify their diet in ways they perceive to be healthful based on studies of what and what not to eat, but they are least apt to consider themselves healthy eaters (Rozin et al., 1999).

Gluten illustrates another issue related to the alleged adverse effects of eating particular compounds/foods. As with the 'toxic' effect of fat, many people have adverse reactions to gluten, not because they are physiologically harmed by gluten, but because they think gluten is harmful, as illustrated when people cycled through high-gluten, low-gluten, and no-gluten diets, without knowing which diet they were eating (Biesiekierski et al., 2013). Throughout the study, people in each treatment, including the no-gluten diet, experienced pain, bloating, nausea, and gas to a similar degree, indicating strong nocebo effects. While several maladies certainly can occur with gluten – including autoimmune (celiac disease, dermatitis herpetiformis, gluten ataxia), allergic (wheat allergy), and possibly immune-mediated (gluten sensitivity) responses (Sapone et al., 2012) – most people are not affected physiologically. And rather than gluten-wheat, some of these issues may be caused by fermentable carbohydrates in gluten-containing cereal grains or by non-gluten proteins (Junker et al., 2012; Biesiekierski et al., 2013).

Peoples' trepidations are fueled by endless changes in nutrition recommendations specifically and science generally (Arbesman, 2013). We assume the scientific research that underlies decisions about health-related issues is unbiased and accurate, but the conclusions of industry-sponsored scientific research often are biased (Bekelman, Li, & Gross, 2003; Washburn, 2006; Lesser, Ebbeling, Goozner, Wypij, & Ludwig, 2007; Bes-Rastrollo, Schulze, Ruiz-Canela, & Martinez-Gonzalez, 2013). Repeatedly, compounds once thought to promote health are shown to be harmful (e.g., high doses of supplemental vitamins; trans-fats in margarine); foods once thought to be harmful are shown to be healthy (e.g., salt: McCarron et al., 2009; red meat and saturated fat: Chowdhury et al., 2014; Jakobsen et al., 2009; Pan et al., 2012; Rohrmann et al., 2013; Siri-Tarino, Sun, Hu, & Krauss, 2010); and relationships between diet and weight loss are elusive (e.g., Johnston et al., 2014). As a case in point, the 2015 U S. Dietary Guidelines eliminated cholesterol and fat as nutrients of concern and removed the upper limit for intake of fat (Mozaffarian & Ludwig, 2015). A primary concern with dietary guidelines is that one size never fits all. Virtually all advice, based on the 'average' individual in a population, ignores the tremendous variation that exists among individuals in response to eating different foods and diets. In some respects, the ever incomplete, regularly conflicting, and often misguided understanding of foods and compounds in health, and the presumed adverse or beneficial consequences of eating them, is worse than no knowledge at all. That is not to say the quest to understand is needless: it is now vital given how cultures have adversely modified foods during the past century.

But as scientists delve ever deeper into genomics, proteomics, metabolomics, anatomy, physiology, biochemistry, pharmacology, and related topics, people reflect ever less on the 'wisdom of the body' as the originator, integrator, and manifestation of all these processes. In so doing, we fail to consider a crucial point, one the body of every wild insect, bird, fish, and mammal who ever roamed the planet 'comprehends' from personal experience: the body was the first geneticist, molecular biologist, physiologist, nutritionist, pharmacist, and physician. A healthy body knows what to do regarding foods and diets, given appropriate choices and social models. And while humans are arguably intelligent, brainy is not wise, and our 'immoderate greatness' has mostly wreaked havoc on peoples and other species on this planet (Ophuls, 2012).

7. Conclusions

Our ancestors' palates were linked with the landscapes they inhabited through the hunting of animals and the gathering and growing of plants. An attuned palate enabled them to meet needs for nutrients and self-medicate. Access to phytochemically-rich foods, which are combined to make meals that nourish and satiate, enables an attuned palate. While most people no longer hunt or gather, and few people are involved with agriculture, we can still eat nutritious varieties of wholesome foods, grown on fertile soils. We can also grow gardens, a modest act that can profoundly affect health and well-being by linking people with soil and plants.

Aldo Leopold (1949) captured the essence of this notion nearly 70 years ago in *A Sand County Almanac*: "There are two spiritual dangers in not owning a farm. One is the danger of supposing that breakfast comes from the grocery, and the other that heat comes from the furnace. To avoid the first danger, one should plant a garden, preferably where there is no grocer to confuse the issue. To avoid the second, he should lay a split of good oak on the andirons, preferable where there is no furnace, and let it warm his shins while a February blizzard tosses the trees outside."

In addition to nurturing the health and well-being of people, growing gardens instead of lawns could greatly reduce use of natural resources in countries that engage in such behaviors. For example, the amount of lawn in the U.S. is 40.5 million acres and the total amount of money spent on lawns is $30 billion annually. Three million tons of fertilizer is used annually on lawns. Use of nitrogen fertilizer could be cut in half by leaving clippings on lawns to build healthy soil. Over 30 thousand tons of synthetic pesticides are used on lawns annually at a cost of well over $2 billion. Over 800 million gallons of gasoline is burned annually caring for lawns. For perspective, the amount of gas spilled annually refilling gasoline lawn mowers is 17 million gallons – 1.57 times the amount spilled by the Exxon Valdez off the shores of Alaska. Finally, residential water use outside the home is 30%–60% of total water use. Depending on the estimate, 7 billion to 9 billion gallons of water are used each day for suburban irrigation.

As human populations transformed – from people who learned how to hunt, gather, and grow food into city dwellers who learned how to grow lawns – meat, produce, and dairy became less flavorful and processed foods became more desirable. Thus, the roles that animals and plants once played in nutrition were usurped by processed foods that were altered, fortified, and enriched. The need to amend foods, and take nutrient supplements, could be eliminated by recreating phytochemical richness in meat and produce and by refashioning cultures that know how to combine foods into meals that nourish and satiate. Though unlikely, that could change the emphasis on diet recommendations – from an endless stream of writings and commercial ads offering the latest advice on which foods and supplements to eat or avoid – to simply eating a variety of wholesome foods and letting our body gently guide our choices, as Clara Davis did as 'mother' to orphaned infants, as skilled shepherds do with their flocks, as hunter–gatherers did for millennia, and as wild creatures have done since the advent of life on earth.

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