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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

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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: flavorfeedback 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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#### 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 varving 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

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