

More Than a Matter of Taste

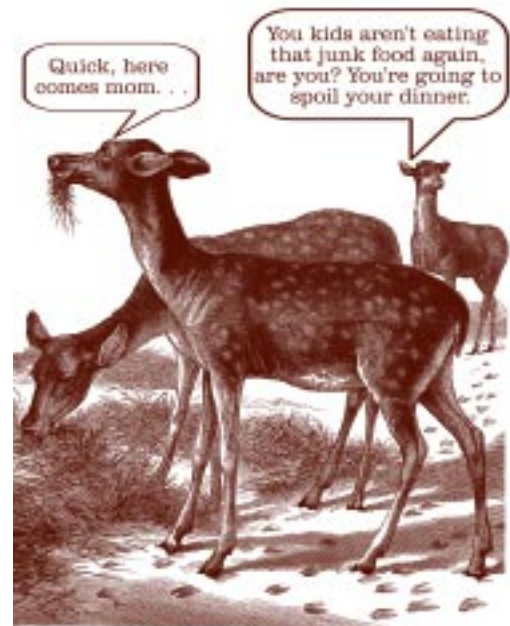
What are the origins of preference? Certainly, mother and peers play an important role in the acquisition of behaviors. By doing what mother does, young animals learn quickly what and what not to eat and where and where not to go. Diet and habitat selection patterns develop as a result of these interactions. But is that the whole story? As every parent knows, no matter how good the advice, offspring must try everything for themselves. This is certainly the case for young herbivores.

While mother and peers facilitate the acquisition of behaviors, continuation of the behaviors depends on the consequences to the individual. In the case of food ingestion, consequences depend on the postingestive effects of nutrients and toxins. Thus, social influences interact with individual experiences to generate behaviors. For example, young goat kids forage near mother even when a food they prefer is located elsewhere, which illustrates the influence of mother on offsprings' food and habitat selection. When given a choice of the two foods, however, the kids eat the food they prefer, which illustrates the influence of postingestive effects of nutrients and toxins on food selection. Likewise, young lambs that experience mild toxicosis while ingesting food their mother prefers do not continue to eat the food, which illustrates that the consequence of toxicosis to the lambs is more influential on diet selection than mother's preference. The same is true for humans. Young people who are lactose-intolerant stop drinking milk and eating yogurt and cheese because the consequences are aversive, even though their parents may eat the foods.

Thus, the origins of food and habitat preference involve interactions between the culture and the individual, as well as responses of the body to nutrients and toxins. Each cell and organ of the body is a world unto itself. These "worlds" interact and tell the palate which foods to like or dislike based on postingestive feedback from nutrients and toxins.

Palatability is more than a matter of taste

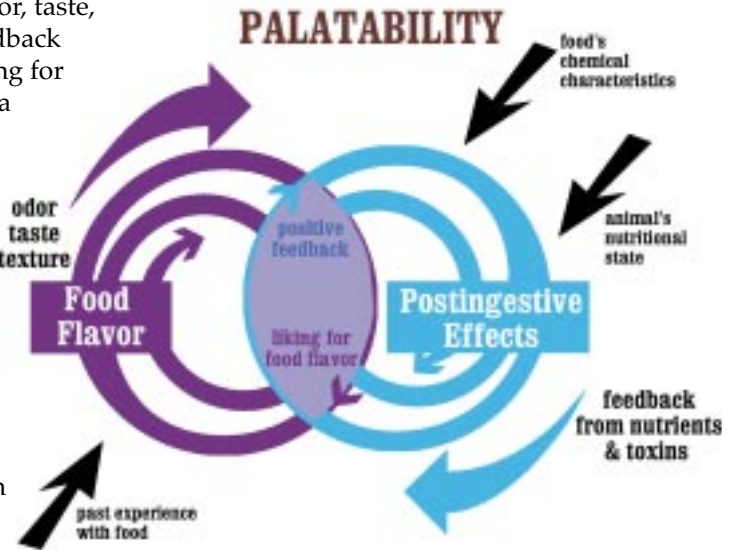
Preferences for foods are typically thought to be influenced by palatability. What is palatability? It is a narrowly defined term that has many meanings. Webster defines palatable as pleasant or acceptable to the taste and hence fit to be eaten or drunk. Animal scientists usually explain palatability as the hedonic liking or affective responses from eating that depend on a food's flavor and texture, or the relish an animal shows when consuming a food or ration. Conversely, plant scientists describe palatability as plant attributes that alter preference, such as chemical composition, growth stage, and associated plants. All popular definitions focus on either a food's flavor or its physical and chemical characteristics.



Why are ice cream sundaes so palatable?
Most of us prefer them over celery.



Research during the past two decades shows that palatability is the interrelationship between a food's flavor and its postingestive effects. Flavor is the integration of odor, taste, and texture. Postingestive effects are a result of feedback from nutrients and toxins. Feedback influences liking for flavor. Flavor-feedback interactions are affected by a food's chemical characteristics, an animal's nutritional state, and its past experiences with the food. The senses—smell, taste, sight—enable animals to discriminate among foods and provide the pleasant sensations—liking for a food's flavor—associated with eating. Postingestive feedback calibrates the sensory experiences—like or dislike—in accord with a food's utility to the body.



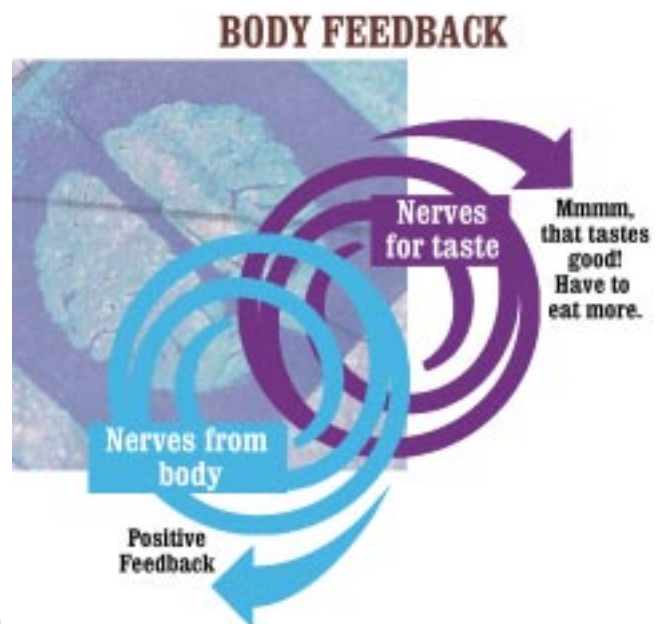
Feedback from the "body" to the senses is critical for health and well-being. Bodies are integrated societies of cells, organs, and organ systems all with nutritional needs. They interact with one another and with the external environment through feedback mediated by nerves, neurotransmitters, and hormones. In the case of flavor-feedback interactions, nerves for taste converge with nerves from the body at the base of the brain. These nerves interact as they relay throughout the central nervous system, from the brainstem to the limbic system to the cortex. Feedback from the body to the palate is how societies of cells and organs influence which foods and how much of those foods are eaten. Feedback from the body influences the senses—hedonics of taste, odor, sight—that are the interface between the body's internal environments and the external environments where animals forage.

The wisdom of the body

If palatability is more than a matter of taste, and it is, then how does the body discriminate among different foods based on flavor-feedback interactions during a meal? How does the body determine which foods have which postingestive effects?

The enteric (gut) and central (brain) nervous systems continually interact with one another and with the rest of the body to integrate a food's flavor with its postingestive effects. These interactions begin early in life. Because the body has a long memory, flavor-feedback interactions don't have to be re-learned each time an animal eats a food, any more than a human has to re-learn when different garden vegetables are ripe. Flavor-feedback relationships merely need to be updated when flavor or feedback change.

Several factors interact during these updates in which an animal's past experiences with a food are integrated with new information about food. These updates are based on the novelty of a food's flavor and the amount of each food eaten in a meal. Animals acquire aversions to novel foods when a meal of several familiar foods and a novel food is followed by toxicosis. Conversely, an animal that is nutrient deficient



associates recovery from the deficiency with a novel food after eating a meal of familiar and novel foods. The amount of each food eaten in a meal also enables the body to discriminate among foods in a meal. For example, when toxicosis follows a meal of blackbrush twigs, goats avoid either current-season or older-growth twigs depending on which they ate in the greater amount. Sheep must ingest a minimal amount of a novel food to discriminate among foods in a meal. Lambs offered novel foods for only 20 minutes a day actually preferred the less nutritious of two foods, presumably because it was most familiar, when they were eating a basal diet adequate in nutrients. However, the lambs quickly changed preferences to the most nutritious novel food when offered only the novel foods for 8 hours a day. Thus, lambs discriminated based on both the amount of food eaten and their nutritional state. Collectively, factors such as these influence palatability as food abundance, nutritional quality, and toxicity change daily and seasonally.

Changes in palatability are automatic

Changes in palatability through postingestive feedback occur automatically without the need for any overtly recognized (cognitive) association or conscious memory of the feedback event. The same is true for digestive processes. We don't have to tell the pancreas to release a dose of insulin after we eat a candy bar. Even when animals are deeply anesthetized or tranquilized, postingestive feedback still causes changes in the palatability of a food eaten just prior to anesthesia. When sheep eat a nutritious food and then receive a toxin dose during deep anesthesia, they acquire an aversion to the food because feedback changes palatability automatically in the absence of conscious awareness.

The body is typically unobtrusive in "instructing the creature" what and what not to eat. People consciously remember only those blatant feedback events that were traumatic, such as becoming violently ill from food poisoning. Through vomiting and nausea-induced decreases in palatability, the body tells us not to eat the food again. But the body typically works subtly and at a non-cognitive level to indicate its needs. If it didn't, animals would spend all their time figuring out what to eat, how to digest it, and how to change preferences based on ongoing changes in needs. It is remarkable to consider that so many complex interactions occur without a bit of thought.

The non-cognitive nature of flavor-feedback interactions is why palatability changes, even when food aversions make no rational sense. For example, humans often acquire strong aversions to foods eaten just prior to getting nauseated even in cases where the person knows for a fact that flu or wave-induced seasickness—not food—was responsible for the decrease in palatability.



Carlos Rodriques (right), NRCS resource conservationist, assists in feeding Corriedale sheep on a ranch in Charlo, Mission Valley, Montana. Research shows that lambs discriminate among foods based on both the amount of food eaten and their nutritional state.



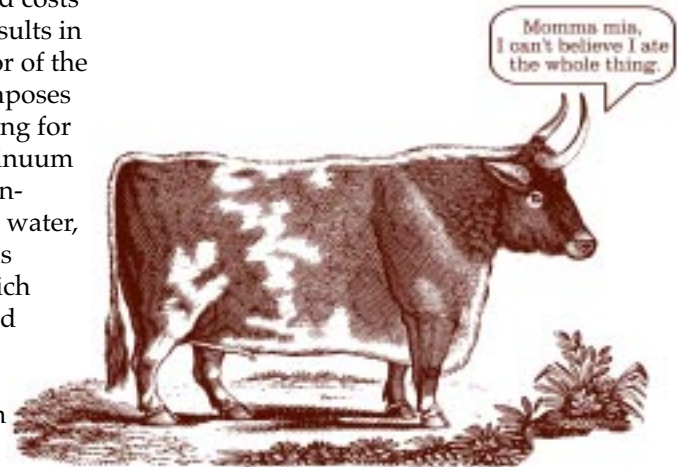
As an animal eats, it is unaware of the thousands of messages traveling between the brain, the senses, and organs and between all the cells of the body.

Excesses and deficits

Satiety and malaise are the experience of the benefits and costs of eating. Ingesting nutrients in appropriate amounts results in benefits, experienced as satiety and a liking for the flavor of the food. Conversely, ingesting excess nutrients or toxins imposes physiological costs, experienced as malaise and a disliking for the flavor of the food. Palatability operates along a continuum to influence preference because virtually everything, if ingested in high enough doses, is toxic, including oxygen, water, and all nutrients. As the Swiss-born alchemist Paracelsus observed, “All substances are poisons; there is none which is not a poison. The right dose differentiates a poison and a remedy.”

Animals typically show little preference for foods low in nutrients. Likewise, they eat limited amounts of foods too high in nutrients. Excesses or deficits of nutrients—protein, energy, minerals—decrease palatability. Humans experience this excess-nutrient effect when we eat high-energy foods that are too rich or high-sodium foods that are too salty. Research shows that herbivores experience these effects when they are forced to eat foods with excessive levels of minerals like phosphorus, sodium, sulfur, or macronutrients. For example, protein is required in moderate amounts every day, but excess protein causes dramatic decreases in palatability and intake because of excess production of ammonia, which is toxic. Energy is also a major nutrient, needed daily in far greater amounts than any other nutrient. However, too much energy from readily available sources of carbohydrates in foods like grains can cause malaise—acidosis—and diminish palatability. Both the ratio of protein to energy and the rates at which different sources of protein and energy ferment in the rumen have a strong influence on intake and palatability. Palatability declines if there is too much protein relative to energy or if the rates at which protein and energy ferment are not similar.

Over-ingesting toxins such as terpenes, alkaloids, and cyanogenic glycosides causes palatability to decrease. Research with toxic compounds shows that delivering high doses of toxins via a stomach tube—oral gavage—following food ingestion causes strong aversions to the food eaten just prior to toxicosis. When herbivores forage, however, over-ingestion of toxins is seldom a problem. Rapid postingestive feedback from toxins enables animals to limit the rate and amount of most toxic foods ingested, apparently in accord with the rates of detoxification they can sustain. Thus, the concentration of toxins in foods sets limits on the amount of a particular food animals can ingest. As toxin concentrations in a plant decline, intake of the plant increases. That is why, given a choice, herbivores are able to select more of foods that are high in macronutrients and low in toxins.



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These Missouri cows stand in water trying to cool themselves down from fever brought on by toxic alkaloids. Grazing endophyte-infected fescue caused the over-ingestion of alkaloids.

Fred Provenza

All forages are not created equal

Pasture managers typically attempt to increase animal production by planting forages that maximize nutrient intake, but they don't always succeed. For instance, Greg Baer, a livestock producer in Missouri, planted a mixture of legumes, and nutritional analyses showed that the pastures were very high in energy and protein. To Greg's dismay, forage intake was low and cattle were losing weight. The animals even preferred moldy hay and endophyte-infected tall fescue high in toxic alkaloids to the forage legumes. The plants evidently contained excess protein and cyanogenic glycosides, which resulted in strong food aversions. When Greg planted strips of grass in the legume pastures, the abnormal feeding behaviors ceased and production improved because cattle were able to select a more balanced diet. Biochemical diversity adds spice to life for livestock, improves economic viability for producers, and maintains the ecological integrity of agricultural landscapes. To meet nutritional requirements, animals need a variety of foods.

The kinds and mixtures of plant species influence food intake and animal performance. Offering animals a variety of foods on pastures and rangelands helps each individual to meet its nutritional needs. Individual herbivores, when given a variety of foods, balance the ratio of macronutrients in their diet to meet their nutritional needs. Turnips in ryegrass pastures and grass-legume mixtures can help livestock maintain a better ratio of energy to protein while minimizing effects of toxic compounds in plants. Providing a variety of foods that differ in macronutrients also allows for changes in nutritional needs, such as changing demands for milk production and daily variation in activity and weather.

When foods contain different kinds of toxins that are complementary—that is they operate on the body and are detoxified in different ways—they may have a positive influence on food intake and animal performance. Forages like white clover contain cyanogenic compounds that limit intake by herbivores. Endophyte-infected tall fescue produces alkaloids that adversely affect food intake and livestock performance. Cattle in Missouri performed better on fescue and clover pastures than on legume-only pastures because the mixture contains complementary toxins. It may be beneficial to plant forbs like sanfoin that contain tannins together with legumes like alfalfa that cause bloat. That's because tannins and proteins that cause bloat form stable complexes in the intestinal tract, thereby reducing the amount of foams that cause bloat.

We have much to learn about how animals might mix their diets to reduce toxicosis. We also have much to learn about biochemical complementarity among plants in mixture and how concentrates fed in confinement affect selection of forages in pasture. No doubt our lack of knowledge contributes to observations that a plant is palatable under some conditions and unpalatable under others. Palatability depends on biochemical interactions among the mix of foods available.



Gary Neuenwander

Missouri livestock producer, Greg Baer, was puzzled as to why his cattle were losing weight on carefully planted pasture that offered a mixture of legumes high in energy and protein.



Mary Donahue

Here in Greg Baer's pasture in central Missouri, Bob Herschbach, NRCS grazing lands specialist, shows the variety of plant species that helped cattle to increase forage intake and gain weight.

Nutritional state

There is growing understanding that animals respond to specific nutrients. Thus, what's palatable depends on an animal's nutritional state.

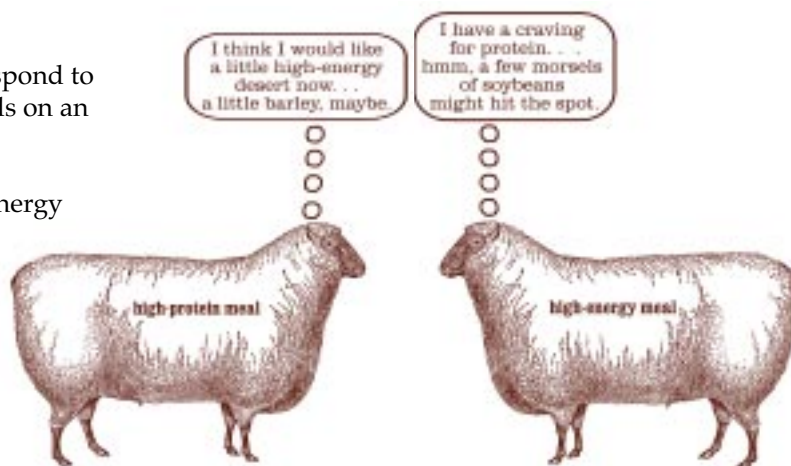
Animals maintain a relatively constant ratio of energy to protein in their diets—when they can select from foods varying in macronutrients—because the body discriminates between feedback signals from energy and protein. Preference for food high in energy increases after a meal high in protein, while preference for food high in protein increases after a meal high in energy. Animals also increase intake of protein relative to energy as their needs for protein increase, for example, during growth, pregnancy, or parasite infections. Animals require nearly 5 times more energy than protein, and they can store excess energy in the form of fat. Thus, palatability is always strongly influenced by energy.

Limited evidence suggests that mineral needs also influence palatability. Managers have used salt to limit intake of macronutrient supplements for years. Research shows that when their mineral needs are met, sheep strongly prefer flavored straw alone to flavored straw paired with an oral gavage of NaCl. Conversely, when animals need salt, they strongly prefer mineral licks and trace-mineral salt blocks. Herbivores respond to deficits of sodium, phosphorus, and sulfur. In general, though, carefully conducted research is needed to determine if herbivores can rectify deficits of other required minerals.

Interactions between nutrients and toxins

When animals eat foods high in toxins, their nutrient needs increase. When supplemented with needed nutrients, they are better able to ingest foods high in toxins. For example, sheep and goats eat more sagebrush, a shrub high in terpenoids, when they receive supplemental macronutrients, especially protein. The need for protein also increases when animals eat diets high in tannins. Conversely, animals supplemented with energy are better able to eat foods high in toxins like cyanogenic glycosides, which increase needs for energy.

Diets high in toxins increase mammals' acid loads. That has led to the idea that intake of foods with toxins is regulated by the rate of formation and disposal of hydrogen ions responsible for acidosis. Maintaining acid/base balance and excreting toxins increase amino acid catabolism and glucose depletion. Thus, the capacity to ingest toxins depends on an animal's macronutrient status because animals must biotransform and excrete toxins.



Fred Provenza

This research found that when the mineral needs of sheep are met, they strongly preferred flavored straw alone to flavored straw paired with an oral dose of NaCl.



Mary Donahue

Gerald Menard, a rancher near Abbeville, Louisiana, explains how he likes to grow turnips with ryegrass to provide an energy source that complements the protein in the grass.

Helping weed eaters

In the United States, the cost of controlling undesirable plants—so-called weedy and invasive species—is estimated at \$12 billion annually. It is little wonder that weed specialists, range scientists, and plant ecologists are seeking ecologically viable ways to suppress undesirable plants and encourage more desirable species. The public is rightly concerned over the adverse environmental effects of herbicides, and specialists are concerned that herbicides alone cannot prevent the spread of weeds. On the other hand, interest is growing in using livestock to reduce the abundance of undesirable plants on pastures and rangelands.

Livestock have been used to control weeds and brush under a variety of conditions, even in urban areas. The city of Laguna Beach, California, each year pays nearly \$2,700 per square kilometer for 500 to 800 goats to graze a 68-square-kilometer “fireproof moat” in chaparral vegetation around the city. Goats and sheep are even being used as weed eaters in cities like Denver and Vail, Colorado.

Livestock can be herded or fenced with temporary electric fencing, they recycle nutrients (urine and feces), and they pose no environmental hazards when managed

properly because grazing is a natural process. In many cases, livestock can be used “surgically” to reduce plant species abundance by altering competitive relationships between less and more desirable plant species.

Contrary to the popular belief, getting livestock to eat undesirable plant species does not involve greater deprivation of food but better nutritional status. The better off nutritionally herbivores are, the more toxins they can handle in the plants they eat. The sheep above have eaten all the leafy spurge outside the fence.



Fred Provenza



Bob Nichols, 1997, USDA Natural Resource Conservation Service

Trinete Bell (right), NRCs soil conservationist, assists Maeoloe Barber with fencing around a livestock area in South Carolina.

sagebrush, which is high in terpenoids, and bitterbrush, which is high in tannins. Intake of these foods was nearly doubled in feeding trials when sheep and goats received supplemental energy and protein. These findings are counter-intuitive and suggest that understanding the nutritional and physiological needs that underlie the behaviors of herbivores grazing weeds can lead to more effective, efficient, and sustained weed control by livestock.