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Frederick D Provenza

Acquired Aversions as the Basis for Varied Diets of Ruminants Foraging on Rangelands[1]

Frederick D. Provenza

Department of Rangeland Resources, Utah State University, Logan 84322-5230

ABSTRACT: Ruminants eat an array of plant species that vary in nutrients and toxins. This selection makes intuitive sense, but no theories adequately explain this diversity. Some maintain it reduces the likelihood of overingesting toxins, whereas others contend it meets nutritional needs. Nevertheless, herbivores seek variety even when toxins are not a concern and nutritional needs are met. I offer another explanation for this behavior, one which encompasses the avoidance of toxins and the acquisition of nutrients. A key concept in this theory is aversion, the decrease in preference for food just eaten as a result of sensory input (a food's taste, odor, texture, i.e., its flavor) and postingestive effects (effects of nutrients and toxins on chemo-, osmo-, and mechano-receptors) unique to each food. Aversions are pronounced when foods contain toxins or high levels of rapidly digestible nutrients; they also occur when foods are deficient in specific nutrients. Aversions occur even when animals eat nutritionally adequate foods because satiety (satisfied to the full) and surfeit (filled to nauseating excess) represent points along a continuum, and there is a fine line between satiety and aversion. Thus, eating any food is likely to cause a mild aversion, and eating a food too frequently or in excess is likely to cause a strong aversion. Aversions are involuntary and are not the result of conscious decisions by an animal. Aversions yield benefits (e.g., obtain a balanced diet, reduce ingestion of toxic foods, optimize foraging and rumination times, sample foods, maintain a diverse microflora in the rumen) that are often mistaken as the cause of varied diets. In this article, I discuss the subtle ways in which aversions diminish preference and cause animals to eat a variety of foods.

Key Words: Nutrients, Toxins, Aversions, Diets, Preference

Introduction

Ruminants select diets from an array of plant species that vary in nutrients and toxins. Some suggest this strategy reduces the likelihood of overingesting toxins (Freeland and Janzen, 1974). Others theorize that it meets nutritional needs (Westoby, 1978). Both of these theories are inconsistent with the tendency of herbivores to consume a diversity of foods even when toxins are not a concern and nutritional needs are met (e.g., Wilmshurst et al., 1995). For instance, lambs eat three foods even when one meets their nutritional needs (Provenza et al., 1996). Thus, neither the presence of toxins nor the lack of nutrients fully accounts for the preference for varied diets.

I offer another explanation, one that encompasses the avoidance of toxins and the acquisition of nutrients. A key concept in this theory is aversion, the decrease in preference for food just eaten as a result of sensory input (a food's taste, odor, texture, i.e., flavor) and postingestive effects (effects of nutrients and toxins on chemo-, osmo-, and mechano-receptors) unique to each food. In this article, I discuss the subtle ways in which aversions diminish preference and cause animals to eat a variety of foods. My primary interest is in ruminants, but details of their food selection are not always known. This requires that I occasionally refer to nonruminants for which mechanisms of food selection are better understood. The mechanisms used by nonruminants for selecting a diet are often similar to those used by ruminants (Provenza, 1994, 1995a,b).

Origins of Food Preference

Discussions of preference quickly lead to debates over which is more important, nature or nurture. But the argument is senseless because preference is a result of a dynamic interplay between nature and nurture throughout the lifetime of the individual and the existence of the species. At conception, nature (natural selection) provides each individual with a set of genetic instructions for its morphological and physiological development. Thenceforth, that morpho-physiology must conform to particular needs if the animal is to survive. To facilitate survival, nature has constructed genotypes in ways that enable nurture (experience) to structure individuals. Consider the development of the central nervous system: While gestating in utero, billions of neurons are produced; those that are used form elaborate networks one with another; those that are not used simply wither and die (Aoki and Siekevitz, 1988; Kalil, 1989; Shatz, 1992). Thus, the brain determines the structure of experience, but experience also determines the structure of the brain. In like manner, learning about foods involves neurological, morphological, and physiological changes (Provenza and Balph, 1990; Distel and Provenza, 1991).

Taste-Feedback Interactions

The dynamic interplay between nature and nurture is illustrated by the taste-feedback interactions associated with food preference. Food preference involves interactions between taste and postingestive feedback, which are determined by an animal's physiological condition and a plant's chemical characteristics (Provenza, 1996). Of course, taste (as well as smell and sight) allows animals to discriminate among foods and is a source of hedonic sensations. But other factors, especially postingestive feedback, calibrate a food's taste with its homeostatic utility. These biochemical mechanisms identify foods adequate in nutrients, thereby increasing an animal's preference. The same mechanisms decrease preference for foods deficient in nutrients, foods containing excess toxins, and foods containing too large a portion of rapidly digestible nutrients (Provenza, 1995a).

Taste-Feedback Interactions Are Not Cognitive or Rational

Taste-feedback interactions occur automatically, in the absence of any cognitive association or memory of the feedback event, every time food is eaten. Thus, after food ingestion, preference changes even if an animal is deeply anesthetized (Roll and Smith, 1972; Bermudez-Rattoni et al., 1988; Provenza et al., 1994b), tranquilized (Forthman Quick, 1984), or when its electrocortical activity is depressed (Davis and Bures, 1972; Buresova and Bures, 1973). The noncognitive nature of taste-feedback interactions is the reason preference changes despite knowledge of the cause of the feedback event. For instance, people acquire aversions to foods eaten prior to becoming seasick, even though they know the sea was the cause. Thus, *food preference* depends on the automatic processing of taste-feedback interactions, processes etched into the brain stem and limbic system during the past 300 to 500 million years of evolution; on the other hand, *food selection* involves cognitive choices among alternatives, processes involving the cortex that evolved during the past 3 to 4 million years (Jerison, 1973; Llinas, 1990; Decker, 1992). Thus, the cortex enables animals to respond to changes in preference, but it is not necessarily the origin of preference (Kihlstrom, 1987).

Role of Experience in Taste-Feedback Interactions

An animal's experiences early in life exert a profound influence on preference (Provenza 1994, 1995b). Animals acquire preferences for familiar foods, and they are reluctant to eat novel foods or familiar foods whose flavors have changed (Provenza et al. 1993a, 1995a). Animals search for preferred foods in unfamiliar environments (Gluesing and Balph, 1980; Gillingham and Bunnell, 1989), and they show the greatest decreases in intake when they are offered novel foods in novel environments (Burritt and Provenza, 1996a).

Accordingly, familiarity controls preference. When animals become ill after eating a meal of familiar and novel foods, they avoid the novel foods, and novelty can even override temporal contiguity when illness develops after foods are eaten in sequence (Burritt and Provenza, 1989a, 1991). For instance, lambs typically avoid the food eaten just before illness after eating foods in succession (Provenza et al., 1993b), unless one of the foods is novel, in which case they avoid the novel food regardless of sequence (Revusky and Bedarf, 1967). Furthermore, when animals become ill after eating a meal consisting of only novel foods, they avoid the foods that are most novel (Kalat, 1974; Launchbaugh et al., 1993; Provenza et al., 1994a). For instance, lambs consume small amounts of barley (familiar food) containing different levels of a novel flavor; if they receive a mild dose of toxin after eating, they avoid the barley with the highest concentration of the flavor (i.e., the barley most different from plain barley). Conversely, when animals become ill after eating familiar foods, they avoid foods eaten most frequently or in excess (Provenza et al., 1994a; Phy and Provenza, 1996), and foods that made them ill in the past (Burritt and Provenza, 1996b).

Importance of Aversions in Taste-Feedback Interactions

Food aversions operate in subtle ways to diminish preference for familiar foods (Barker et al., 1977; Braveman and Bronstein, 1985; Burish et al., 1985). Aversions do not typically involve any overt

behavioral signs (i.e., emesis, toxicosis, infirmity). Aversions are usually specific to a particular food, even though an animal has eaten a meal of several foods (Burritt and Provenza, 1991, 1996b; Provenza et al., 1994a). An aversion can occur within minutes of eating or gradually over days and weeks (Garcia, 1989). Aversions can be acquired in a single trial, even when malaise does not occur for hours after food is consumed (Garcia and Kimeldorf, 1957; Burritt and Provenza, 1991). Unlike other sensory systems (i.e., eyes, ears, nose) involved in conditioning, taste and feedback become more sensitive to stimulation with time, as titers of nutrients and toxins (excesses of nutrients or toxins or deficits of nutrients) in bodily fluids change (Garcia et al., 1985; Garcia, 1989). In contrast, if an animal does not smell, see, or hear something immediately, increasing the duration of exposure will not enhance detection, and these senses become less responsive with time (i.e., they habituate).

Aversions result from specific combinations of sensory input (a food's distinctive flavor) and feedback signals (a food's particular nutritional or toxicological effects on chemo-, osmo-, and mechano-receptors, Anil et al., 1993; Mbanya et al., 1993) unique to each food. Aversions ensue from a cascade of events that involve various physiological signals (Provenza, 1995a) along gustatory and visceral nerves that converge in the brain stem, then branch to the limbic system, and thence to the cortex (Glenn and Erickson, 1976; Norgren, 1983; Novin, 1983). Lesions along these pathways impede an animal's ability to integrate taste and visceral signals and thereby modify preference (Anil and Forbes, 1980, 1988; Louis-Sylvestre et al., 1983; Crawley et al., 1984; Cox and Smith, 1986; Spector et al., 1992).

Toxins and nutrients in foods can both cause aversions, but most toxins impose greater limitations on intake (Provenza, 1995a). As Garcia (1989) suggests, "That may be the way chemical protection gradually evolves; those organisms which can quickly induce satiety in foragers stand a better chance of having their kind survive. Perhaps it is no accident that many phytochemicals such as caffeine, nicotine and digitalis cause a loss of appetite in vertebrates including humans, thus providing an excellent protection against continued munching by foragers." Excesses of toxins (Aldrich et al., 1993) and nutrients (Provenza et al., 1994c) and deficits of nutrients (Gietzen, 1993) all cause aversions, and there is some evidence that aversions result from stimulation of the emetic system of the midbrain and brain stem (Seynaeve et al., 1991; Mitchelson, 1992); the emetic system can be activated by excesses of nutrients or toxins from various locations in the body, including visceral afferent nerves, second-order gustatory afferent nerves, the cardiovascular system, and cerebrospinal fluid (Borison, 1986; Davis et al., 1986; Grahame-Smith, 1986). Nevertheless, it is not known if ruminants sense the effects of toxins in the same way, and by the same mechanisms, as they sense excesses

of energy or nitrogen (Provenza et al., 1994c), amino acid imbalances (Egan and Rogers, 1978), and deficits of phosphorus (Ternouth, 1991). The question is: Do ruminants sense all diet-related maladies in the same manner and by the same physiological mechanisms (Grant, 1987; Galef, 1991), or do they differ in how they sense satiety caused by carbohydrates (Miner, 1992), amino acids (Egan and Rogers, 1978), other nutrients, and toxins?

Sensory-, Nutrient-, and Toxin-Specific Aversions

Ruminants eat a variety of foods even when a monospecific diet seemingly offers more advantages (Parsons et al., 1994). The resulting variety has several benefits (e.g., obtain a balanced diet, reduce ingestion of toxic foods, optimize foraging and rumination times, sample foods, maintain a diverse microflora). Nonetheless, the benefits are typically mistaken as the *cause* of varied diets. In other words, these explanations stress why animals seek alternatives, but they do not account for why animals *stop* eating particular foods. Aversions explain why animals stop eating a particular food and taste-feedback interactions provide a mechanism for the response.

Sensory-Specific Responses

Sensory-specific satiety is a term used to refer to the decrease in preference for the taste of food as it is consumed (Rolls et al., 1981, 1984; Rolls, 1986). The sense of taste seems to have a key role in the termination of feeding (although the subject is controversial; Blundell and Rogers, 1991; Swithers and Hall, 1994). When an animal receives oral stimulation (flavors in the mouth) and is also provided with nutrients intragastrically, subsequent intake is reduced to a greater extent than when nutrients alone are provided intragastrically. The importance of oral experience is also suggested in studies of the effects of food variety on the termination of ingestion. The influence of variety has been attributed to the sensory properties of food, because an animal that stops eating one food will often consume another food, at times ingesting as many calories as eaten with the first food. The decrease in preference occurs with foods of different nutritional values (Birch and Deysher, 1986), with nutritive or non-nutritive flavors (Wooley et al., 1972; Swithers-Mulvey et al., 1991), and with the sweetest sodas even when they are tasted and not swallowed (Drewnowski et al., 1982). Thus, there is evidence that the postingestive effects of ingestion are not independent of the gustatory experience of eating (Garcia and Rusiniak, 1977; Swithers and Hall, 1994).

The controversy over the relative importance of sensory- or feedback-specific responses is misguided because both are always involved (Blundell and

Rogers, 1991; Swithers and Hall, 1994; Provenza 1995a). Feedback begins before eating as the sights, sounds, and odors associated with foods cause the release of saliva and other digestive enzymes, gastrointestinal and pancreatic hormones, and neurotransmitters involved in eating (i.e., they are Pavlovian processes). Postingestive feedback from nutrients and toxins begins within minutes of food ingestion in ruminants (Provenza, 1995a). Flavors previously paired with calories elicit the release of peptides like CCK that moderate hedonic satisfaction and cause a decrease in intake (Fedorchak and Bolles, 1988; Mehile, 1991). When a flavor is no longer paired with calories, animals acquire an aversion to the flavor, e.g., when rats receive sweet substances no longer accompanied by calories (Tordoff and Friedman, 1989). Likewise, the decrease in intake when animals receive only oral stimulation, or oral stimulation with intragastric infusions of non-nutritive solutions, as in studies reviewed by Swithers and Hall (1994), may be based on the lack of positive postingestive feedback (Provenza, 1995c). Thus, taste and feedback (presence or absence) are inevitably in interplay any time food is taken into the mouth.

Nutrient-Specific Responses

Animals prefer foods or combinations of foods that contain a variety of nutrients in appropriate proportions, presumably because they are the most satiating. Nevertheless, postingestive feedback from nutrients can cause aversions, even when animals ingest nutritionally adequate foods. Animals are likely to become averse to nutritious foods because satiety (satisfied to the full) and surfeit (filled to nauseating excess) represent a continuum and there is a fine line between satiety and aversion. Thus, eating any food to satiety is likely to cause a mild aversion, and eating a food too frequently or in excess is likely to cause a strong aversion.

The idea of nutrient-specific satiety is based on the premise that preference depends on an animal's physiological condition relative to a food's chemical characteristics (Provenza, 1995a, 1996). Once an animal's requirement for a particular nutrient is met, preference declines for foods with high concentrations of that nutrient. For instance, lambs fed a diet high in energy (grain) subsequently prefer food lower in energy and higher in protein (alfalfa); those fed a diet high in alfalfa subsequently prefer food high in grain (Wang and Provenza, 1996a). Satiated people prefer the flavor of low-carbohydrate snacks, but food-deprived people prefer the flavor of high-carbohydrate foods (Booth and Toase, 1983; Blundell and Rogers, 1991). Sucrose or glucose tastes pleasant to fasting humans but tastes unpleasant after consumption (Cabanac, 1971). Protein (Gibson and Booth, 1986; Baker et al., 1987; Kyriazakis and Oldham, 1993; Kyriazakis et al., 1994, 1995) and carbohydrate

(Gibson and Booth, 1989) preferences also depend on an animal's nutritional state and on the proportions of energy and protein (Villalba and Provenza, unpublished data), and various neural mechanisms have been proposed to account for these responses. For instance, energy deprivation causes release of norepinephrine in the paraventricular nucleus (**PVN**), which causes an increase in preference for foods high in carbohydrates in rats; in turn, ingestion of foods high in carbohydrates causes release of serotonin in the PVN, which results in a decrease in preference for foods high in carbohydrates and an increase in preference for foods high in protein (Wurtman and Wurtman, 1986; Leibowitz, 1988; Gietzen, 1993; Noach, 1994). According to this hypothesis, lambs fed a basal ration high in energy (e.g., grain) should prefer foods high in protein (e.g., alfalfa), whereas lambs fed a basal ration high in protein should prefer foods high in energy. This hypothesis in consistent with the notion that the ratio of protein to energy is important in the food preferences of ruminants (Egan, 1977). The role of nutritional needs is also apparent when lambs are fed flavored straw with intraruminal infusions of NaCl; when lambs' needs for NaCl are met, they reject the flavored straw (Villalba and Provenza, 1996b). Thus, preference is high before ingestion of food high in a particular nutrient, but preference declines when nutrients are eaten to satiety. The specificity of these responses suggests the intake of different nutrients is regulated separately by different mechanisms (Mook, 1988).

Animals prefer highly digestible foods, but if rates of fermentation are too high, animals become ill (Provenza et al., 1994c; Cooper et al., 1995, 1996) and begin eating other foods (Provenza et al., 1995b; Wang and Provenza, 1996a; Phy and Provenza, 1996; Provenza et al., 1996). When the positive effects of nutrients are followed by illness, the pattern of intake becomes cyclic: gradual increases followed by sharp declines. This response is characteristic of nutritious foods that contain toxins (e.g., larkspur) (Pfister et al., 1994), and rapidly fermentable foods (e.g., grain) (Britton and Stock, 1987). The more familiar the food and the greater the positive feedback from nutrients, the less likely animals are to acquire lasting aversions (Burritt and Provenza, 1991, 1992), which might explain why sheep overeat clover (Parsons et al., 1994). Sheep acquire a mild aversion to clover as a result of rapid release of nutrients (i.e., soluble carbohydrates and protein) and toxins (i.e., cyanogenic compounds) in the morning. They then seek the less nutritious grass (slowly digested, lower in protein) in the afternoon, at which time the recuperative process counter-conditions the aversion to clover (Solomon and Corbit, 1974; Garcia, 1989).

By-products of fermentation (e.g., propionate, acetate, ammonia) and neuropeptides (e.g., cholecystokinin, [**CCK**]) provide an immediate indication of the nutritional value of food, and they also condition food

preferences or aversions, depending on their rate and amount of release. For instance, sheep prefer flavored straw eaten with low doses (5 to 7.5 g) of propionate intraruminally, but they acquire aversions at higher (>10 g) doses (Ralphs et al., 1995; Villalba and Provenza, 1996b); the same is true for acetate, combinations of propionate and acetate, and ammonia (Villalba and Provenza, unpublished data). Likewise, sheep consume fewer pellets during 24 h as the dose of propionate and acetate, or combinations of the two, increases (Farningham and Whyte, 1993; Mbanya et al., 1993). Neuropeptides such as CCK also condition food preferences or aversions in a dose-dependent fashion (Deutsch and Gonzalez, 1978; Stricker and Verbalis, 1990; Perez and Sclafani, 1991; Mehile, 1991), and they decrease intake in a dose-dependent fashion (Della-Fera and Baile, 1979, 1981; Grovum, 1981). In sheep, low doses of either propionate or CCK do not decrease intake, but in combination they depress intake by 44% over a 2-h period (Farningham, 1991; Farningham et al., 1993).

Animals acquire aversions to nutrient-deficient foods (Richter, 1943; Rozin, 1976). Aversions are most likely when the diet is grossly deficient in essential nutrients (Provenza 1995c), because animals can often increase intake to meet nutritional needs (Provenza et al., 1996). Deficits or imbalances of amino acids cause decreases in intake and food aversions in liquid-fed (Rogers and Egan, 1975) and solid-fed (Egan and Rogers, 1978) lambs. Cattle, sheep, and goats become averse to phosphorus-deficient diets, and the reduction in food intake depends on the severity of the deficiency (Ternouth, 1991).

Thus, several nutrient-related factors result in aversions, which cause animals to eat different foods, even novel foods they are typically unwilling to ingest (Provenza et al., 1995a), provided the novel foods complement their basal diet. For instance, lambs fed a basal ration of barley (high energy) will eat meal of rabbit pellets (a novel food high in protein) but not of wheat (a novel food high in energy), whereas lambs fed a basal diet of alfalfa pellets (high in protein) will eat wheat (a novel food high in energy) but not rabbit pellets (a novel food high in protein) (Wang and Provenza, 1996a).

The power of aversions to compel animals to ingest novel foods is epitomized by observations of the perverse kinds of "foods" animals ingest when they experience nutrient deficiencies. Cattle with mineral deficiencies eat rabbit legs and bones (Wallis de Vries 1992, 1994). Nutrient-deficient deer and other ungulates eat antlers (Sutcliffe, 1977). Goats foraging on nitrogen-deficient blackbrush pastures ingest woodrat houses high in nitrogen (Provenza, 1977), and bighorn sheep use rodent middens as mineral licks (Coates et al., 1991). Wild ungulates and sheep with deficiencies eat lemmings, rabbits, birds, ptarmigan eggs, arctic terns, and fish (Kelsall, 1968; Bazely, 1989; Furness, 1988; J. P. Bryant and D. Swanson, personal communication). Cattle ingesting mineral-deficient forages lick urine patches of rabbits and man, chew wood, consume soil, eat fecal pellets of rabbits, and ingest non-food items such as plastic, feathers, cinders, sacks, and tins (Green, 1925; Wallis de Vries, 1992, 1994).

Toxin-Specific Responses

Toxins cause a decrease in preference for food, but toxins do not necessarily prevent ruminants from eating a food, especially if the food contains needed nutrients (Wang and Provenza, 1996b,c). There are numerous examples where toxins cause cattle, sheep, and goats to limit intake of foods such as larkspur (Olson and Ralphs, 1986; Pfister et al., 1990, 1994) and tall fescue (Aldrich et al., 1993; Thompson and Stuedemann, 1993) that contain alkaloids, shrubs such as blackbrush (Provenza et al., 1990) that contain condensed tannins, brassica crops (Duncan and Milne, 1992, 1993) that contain glucosinolates, plants such as sacahuiste (Rankins et al., 1993) that contain saponins, coumarins, furocoumarins, and anthraquinones, and foods to which LiCl has been added (Lane et al., 1990; Provenza et al., 1990, 1993a; duToit et al., 1991; Ralphs and Cheney, 1993). Aversive feedback from toxins also causes a decrease in intake of leafy spurge (Kronberg et al., 1993), ponderosa pine (Pfister et al., 1992), bitterweed (Calhoun et al., 1981), and sagebrush (Johnson et al., 1976; Ngugi et al. 1995).

Toxins may encourage animals to eat a variety of foods containing needed nutrients, provided toxins in the foods differ in their physiological effects and are detoxified by different mechanisms. Different toxins often differ in their effects on herbivores (Cheeke and Shull, 1985), and herbivores have assorted physiological mechanisms to counter the effects of various toxins (McArthur et al., 1991). If the capacity of different detoxification systems is not exceeded, a mixed diet may enhance an animal's ability to meet its nutritional needs: animals can ingest low levels of potentially toxic compounds so none becomes lethal (Freeland and Janzen, 1974). Interactions between toxins can also affect a herbivore's susceptibility to toxins and can enhance dietary diversity. Rats eat more of a combination of foods containing tannins and saponins because tannins and saponins chelate in the intestinal tract, thereby reducing the aversive effects of both components (Freeland et al., 1985). Nutritional status can also affect a herbivore's susceptibility to toxins and enhance dietary diversity (Foley et al., 1995; Illius and Jessop, 1995). For instance, lambs eat a greater variety of foods containing the toxin LiCl as the energy content of their diet increases (Wang and Provenza, 1996c).

Conversely, dietary diversity will probably decrease if the same toxin occurs in a variety of foods, as happens when lambs are offered different foods containing the toxin LiCl (Wang and Provenza, 1996b). Lambs offered different foods containing LiCl

eat only the most nutritious of those foods (Wang and Provenza, 1996b), and ingest no more than 40 to 60 mg/kg BW of LiCl in a meal (duToit et al., 1991; Lauchbaugh et al., 1993). Likewise, classes of compounds such as cyanogenic glycosides act on the same sites in the body and are detoxified by the same mechanisms (Cheeke and Shull 1985), which should lead to a less diverse diet. Thus, even though at least 21 different cyanogenic glycosides are found in over 1,000 plant species (including amygdalin found in chokecherries, wild cherries, mountain mahogany, serviceberry and dhurrin found in forage and grain sorghum, Sudan and Johnson grasses) (Cheeke and Shull 1985), herbivores are likely to eat only the most nutritious plants containing cyanogenic glycosides, which will lead to a less diverse diet. Finally, detoxification processes associated with many toxins (e.g., terpenes, phenolics) also cause acidosis (Foley et al., 1995), which may result in a less diverse diet (Illius and Jessop, 1995).

Sensory-, Nutrient-, and Toxin-Specific Aversions Depend on Frequency and Amount of Stimulation

The taste of food (sensory-specific responses) and its postingestive effects (nutrient- and toxin-specific responses) both affect preference, and they interact so it is difficult to isolate the independent effects of either. Nevertheless, when the nutrient or toxin content of a food is held constant, and the frequency or amount of food ingested is varied, changes in flavor cause increases in preference. Conversely, when the flavor of the food remains constant, changes in nutrient and toxin content alter (increase or decrease) preference. In both cases, eating a food too frequently or in excess causes a decrease in preference for that food.

Flavor-Frequency of Eating

Preference for the flavor of a food declines when the food is eaten repeatedly, presumably because the taste of food consumed to satiety becomes less pleasurable (Rolls, 1986; Swithers and Hall, 1994). For instance, lambs fed nutritionally balanced apple- or maple-flavored food one day prefer the alternate flavor the next day (Early and Provenza, unpublished data). Rats offered a four-course meal consisting of the same food consume more when each course has a different flavor (Treit et al., 1983). Moreover, lambs eat more high-energy food when meals contain a variety of foods (Wang and Provenza 1996a). Consumption and weight gain in rats also increase when high-energy foods are offered in a variety of flavors (Naim et al., 1986). Thus, eating the same food too frequently causes a decrease in preference for the flavor of the food, and changing the flavor of the food causes preference to increase.

Flavor-Amount Ingested

The more of any particular food an animal eats, the greater the aversion to the food. For instance, when goats become mildly ill after eating blackbrush, they acquire the greatest aversion to the twig type (current season's growth or older twigs) consumed in the largest amount (Provenza et al., 1994a). Likewise, when rats become ill after drinking solutions of different flavors, they acquire the greatest aversion to the solution consumed in the largest amount (Bond and DiGuisto, 1975). Thus, following eating, the decrease in preference for a food is in proportion to the relative amount of the food that was consumed.

Feedback-Frequency

Animals become averse to foods eaten too frequently. For instance, the more days cattle and sheep are conditioned with toxins to avoid plants, the greater the decrease in preference (Burritt and Provenza, 1989b; Ralphs and Olsen, 1990; Provenza and Burritt, 1991; Ralphs and Cheney, 1993). This also occurs when animals are repeatedly offered nutritious foods. Lambs' relative preference for food high in energy (e.g., barley) declines immediately after eating a small meal (400 g) of barley; their aversion to barley is more persistent after eating several small meals or a large meal (1,200 g) of barley (Phy and Provenza, 1996). Exposure to food for as little as 1 d significantly decreases preference, even for a nutritionally balanced food (Early and Provenza, unpublished data). Sheep and cattle repeatedly offered a nutritious food choose to eat an alternative food (Baumont et al., 1990; Newman et al., 1992, 1994; Ramos and Tennessen, 1993; Parsons et al., 1994), and the decrease in preference is more pronounced when sheep must ingest a single food for days or weeks (Ramos and Tennessen, 1993). Thus, following eating, the decrease in preference for a food is in proportion to the number of feedback events.

Feedback-Amount

The degree to which a food is avoided following a meal depends on the dose of the toxin (Garcia et al., 1974; Cannon et al., 1985; duToit et al., 1991; Ralphs and Cheney, 1993), and the same is true for nutrients. For instance, lambs prefer flavored straw paired with gavage of low to moderate doses of energy (i.e., propionate, acetate) or nitrogen (i.e., urea, casein, gluten), but at higher levels of energy or nitrogen, they become averse to flavored straw (Villalba and Provenza, 1996a,b, and unpublished data). Exposure to a nutritionally balanced food for as little as 1 d decreases preference, and the decrease in preference is even more pronounced when the food is either low (90% NRC) or high (110% NRC) in energy (Early and Provenza, unpublished data). Foods that are low in energy are likely to cause deficits that cause

aversions, whereas foods that are rapidly digestible are likely to cause aversions because they quickly produce too much feedback from by-products of fermentation such as propionate, lactate, and ammonia (Provenza, 1995a). The more barley lambs consume, the more persistent the resulting aversion to this rapidly fermentable food (Phy and Provenza, 1996). Thus, the strength of an aversion also depends on the amount of feedback.

Conclusions

Many of the principles discussed have been employed in pastoral grazing systems and may be important in understanding grazing patterns of herbivores on rangelands. The reasons may not have been known, but the effects were evident. For instance, herders in France use these principles in ways that may stimulate intake during grazing trips (Hubert, 1993; Meuret et al., 1994). The grazing circuit includes 1) a *moderation* phase to calm a hungry flock (abundant but not highly preferred plants), 2) a *main course* for the bulk of the meal (medium plant abundance and preference), 3) a *booster* phase for added diversity (highly preferred plants different from the main course), and 4) a *dessert* phase to complement previously eaten forages (high plant abundance and preference). It is important to learn if grazing circuits stimulate an animal's appetite in a manner consistent with the hypothesized role of aversions in diet selection (Meuret et al., 1994).

Pastures are often seeded to monocultures of nutritious species (e.g., crested wheatgrass and tall fescue). On the basis of importance of variety, intake might be increased dramatically if pastures contained several species (Parsons et al., 1994). Planting species with different kinds of secondary metabolites might also increase livestock production and result in more stable plant mixes. Tall fescue infected with ascomycete fungi produces alkaloids that adversely affect food intake and livestock performance (Aldrich et al., 1993; Thompson and Stuedemann, 1993). The selective preference for uninfected fescue eventually leads to dominance of infected plants. Forages such as white clover contain cyanogenic compounds, which also deter herbivores. However, a combination of fescue and clover may enhance intake because they contain different kinds of toxins. Moreover, planting shrubs and forbs that contain tannins with legumes such as alfalfa that contain saponins may also be beneficial because tannins and saponins chelate in the intestinal tract, thereby reducing the aversive effects of both compounds (Freeland et al., 1985). Unfortunately, little is known about how ruminants might mix their diets to increase intake and reduce toxicosis.

Understanding why animals eat varied diets might also help us to enhance intake of animals in confinement. Remarkable advances have been made in improving the nutrition of animals in dairies and feedlots, but the emphasis has been on uniformity of diets, which may inadvertently depress intake. Offering different foods of similar nutritional value (e.g., barley and wheat), offering foods of different nutritional value (e.g., barley and alfalfa), and offering the same food in different flavors (e.g., maple and apple) may increase intake and performance in feedlots and dairies (Wang and Provenza, 1996a).

Finally, understanding why animals eat varied diets might help us to control depredation by livestock and wildlife. Variety may be an important consideration in attempts to train animals to avoid foods, such as trees in orchards or plantations or poisonous plants (Burritt and Provenza, 1989b; Lane et al., 1990); providing a desirable mix of alternative foods could enhance the persistence of aversions. Losses to wildlife exceed \$3 billion annually in the United States, much of it involving agricultural crops (Conover et al., 1995). Providing the proper alternate foods could also help alleviate wildlife depredation. Offering nutritious supplements in different flavors is an inexpensive option that may further decrease depredation.

Implications

The variety of familiar foods offered to ruminants is likely to be an important concern in efforts to increase intake and performance in confinement, on pastures, and on rangelands. Offering different foods of similar nutritional value, offering foods of different nutritional value, and offering the same food in different flavors are all means of changing preference and potentially increasing intake. Offering a variety of foods is also a way to enable each individual to select the diet that best meets its needs.

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