August 1995

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8

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ABSTRACT

Food preference is best understood as the interaction between taste and postingestive feedback, determined by an animal's physiological condition and to a food's chemical characteristics. Taste (as well as smell and sight) enables animals to discriminate among foods and provides hedonic sensations associated with eating. Postingestive feedback calibrates taste in accord with a food's homeostatic utility: preference increases when foods are adequate in nutrients; conversely, preference decreases when foods are deficient in nutrients, when they contain excesses of toxins, and when they are too high in rapidly digestible nutrients. Preference also decreases when familiar foods are eaten too frequently or in excess, which causes animals to eat varied diets. Experiences early in life affect preference. Young animals acquire dietary habits as a result of eating particular foods, and they are reluctant to eat novel foods or familiar foods whose flavors have changed. These findings suggest: (1) deterrents based merely on offensive flavors are not likely to be effective in the absence of aversive postingestive effects, (2) many repellents are ineffective because they merely change the flavors of familiar foods (i.e., novelty effects), and (3) management to deter herbivores from eating foods must provide nutritious alternatives.

KEY WORDS

aversion, feedback, mother, novel, nutrient, preference, toxin, varied diets

INTRODUCTION

Herbivores live in a world that is constantly changing. Thus, they face challenges in meeting nutritional needs because a plant's chemical makeup (i.e., nutrient and toxin content) changes continually throughout the year, as does an animal's physiological condition (Provenza and Balph 1990). Any individual, if it is to survive, must be able to cope with such change. In this paper, I discuss how change has structured preference by addressing three questions: (1) What is preference? (2) What causes preference to change? and (3) What causes animals to prefer variety? I also suggest implications for use of repellents in mitigating animal damage. More detailed discussions of preference can be found in reviews by Provenza (1995*a*,*b*, 1996*a*,*b*).

WHAT IS 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 the dynamic interplay between nature and nurture throughout the lifetime of the individual and the existence of the species. At conception, nature (i.e., natural selection) provides each individual with a set of genetic instructions for its development, morphologically and physiologically. Thenceforth, that morpho-physiology must conform to certain needs if the animal is to survive. To facilitate survival, nature has constructed genotypes in ways that enable nurture (i.e., 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). In that sense, one can argue that the brain determines the structure of experience, but it is equally true also that experience determines the structure of the brain. In like manner, learning about foods involves neurological, morphological, and physiological changes (Provenza and Balph 1990).

Origins of Food Preference

The dynamic interplay between nature and nurture is illustrated by food preference. Preference is best understood as the result of the interaction between taste and postingestive feedback. The outcome of this feedback is determined by an animal's current physiological condition relative to a food's chemical characteristics (Provenza 1995*a*, 1996*a,b*). Taste (as well as smell and sight) enables animals to discriminate among foods and provides hedonic sensations associated with eating. Postingestive feedback calibrates taste in accord with a food's homeostatic utility (Garcia 1989). Preference decreases when foods are deficient in nutrients, when they contain excesses of toxins, and when they are too high in rapidly digestible nutrients (Provenza 1995*a*). Conversely, preference increases when foods are adequate in nutrients.

Preference is Not Cognitive or Rational

Taste-feedback interactions occur automatically anytime food is eaten, even in the absence of any cognitive association or memory of the feedback event. That is why preference changes, even though the feedback event occurs when an animal is anesthetized (Roll and Smith 1972, Bermudez-Rattoni et al. 1988, Provenza et al. 1994*b*), deeply tranquilized and unresponsive to pinches and probes (Forthman Quick 1984), or when its electrocortical activity is depressed (Davis and Bures 1972, Buresova and Bures 1973). That is also 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 and not the food caused the postingestive malaise. Thus, food preference depends on the automatic processing of taste-feedback interactions, which is mediated primarily by the brain stem and limbic system. On the other hand, food selection has to do with choice among alternatives, which involves the cortex. The cortex responds to, but typically does not cause, changes in preference (Kihlstrom 1987).

Role of Experience in Preference

An animal's experiences early in life exert a profound influence on preference (Provenza 1994, 1995*b*). Young ruminants (and humans) acquire dietary habits as a result of eating particular foods, and they are reluctant to eat novel foods or familiar foods whose flavors have changed (Birch and Marlin 1982; Provenza et al. 1993, 1995). For instance, when lambs eat a meal of novel and familiar foods and experience malaise, they avoid the novel foods (Burritt and Provenza 1989*a*, 1991). Moreover, when lambs (or rats) eat a meal of only novel foods and experience malaise, they avoid the foods that are most novel (Kalat 1974, Launchbaugh et al. 1993, Provenza et al. 1994*a*). For example, lambs fed rolled barley (familiar food), with a low and a high concentration of a novel flavor, consumed small amounts of both foods, regardless of flavor concentration. But after they eaten a meal of both foods and then received a mild toxin dose, they avoided the barley with the highest concentration of the flavor [i.e., the barley that was most different (novel) from plain barley]. Conversely, when animals become ill after eating a meal of familiar foods, they avoid the foods eaten most frequently or in excess (Provenza et al. 1994*a*, Phy and Provenza 1996*a*-In Press) and the foods that made them ill in the past (Burritt and Provenza 1996).

WHAT CAUSES PREFERENCE TO CHANGE?

Decreases in Preference

Excesses of toxins or nutrients cause food aversions, which are manifest by a decrease in intake of a particular food (Provenza 1995*a*). Food aversions occur because animals no longer prefer the flavor of the food (Provenza et al. 1994*c*). For instance, when lambs eat cinnamon-flavored rice and then receive a toxin dose, they no longer prefer cinnamon-flavored rice nor will they eat cinnamon-flavored wheat (Launchbaugh and Provenza 1993). Thus, the lambs have generalized an aversion from rice to wheat, based on a common flavor, cinnamon. Excessive rates of nutrient release also condition food aversions. For instance, sheep prefer flavored straw eaten with low doses of energy (starch, glucose) or nitrogen (urea, casein, gluten) provided intraruminally, but they acquire aversions at higher doses (Ralphs et al. 1995; Villalba and Provenza 1996*a*,*b*,*d*). Byproducts of fermentation from energy (e.g., propionate, acetate) and nitrogen (e.g., ammonia) 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 1996*b*); the same is true for acetate, combinations of propionate and acetate, and ammonia (Villalba and Provenza, 1996*b*,*c*,*d*). Thus, postingestive feedback operates on taste to decrease preference when animals ingest toxins or nutrients in excess.

Animals do not necessarily show consistent preferences for flavors in the absence of postingestive effects, as illustrated with the shrub blackbrush (*Coleogyne ramosissima*). Goats fed the current season's (CSG) and older (OG) growth twigs from blackbrush acquired a preference for OG because CSG contains much higher levels of a condensed tannin that are necessary to induce a learned food aversion (Provenza et al. 1994*a*). When CSG and OG are offered to goats naive to blackbrush, some goats originally prefer CSG, whereas others initially prefer OG. When goats finally consume more CSG than OG within a meal (averaged 44 g and 16 g, respectively) and eat enough CSG to acquire an aversion (averaged 44 g), they all ingest less CSG than OG from then onward. For nearly 10 years, we mistakenly assumed goats naive to blackbrush rejected CSG immediately on the basis of taste alone because we had never seen goats eat CSG. Instead, goats' avoidance of CSG reflects their ability to learn quickly (goats limit intake of CSG in 1 to 4 hr) based on aversive postingestive effects. The lack of a consistent response to flavor, in the absence of postingestive effects, may help explain why feeding deterrents based merely on offensive flavors are generally ineffective (Conover 1984, Andelt et al. 1992, Nolte et al. 1994). If the flavor of a deterrent is not followed by aversive postingestive effects, then any positive postingestive feedback from nutrients is likely to cause preference to increase.

Increases in Preference

Animals acquire preferences for foods that meet nutritional needs (Provenza 1995*a*). For example, lambs' intake of flavored straw increases dramatically when they receive intraruminal infusions of energy (starch or propionate) or nitrogen while eating onion- or oregano-flavored straw (Villalba and Provenza *1996a,b,c,d*). Preferences for straw are acquired with doses of starch or propionate equivalent to as little as 2.5% and 1.0% of lambs' daily energy intake, respectively. In the absence of energy, intake of flavored straw is low and variable, which again suggests flavor without postingestive effects is a poor predictor of preference. Likewise, lambs offered three foods, differing in flavor and nutrients, preferred high-(2.68 Mcal/kg DE, 13.8% DP) > medium-(2.42 Mcal/kg DE, 11.0% DP) > low-(2.21 Mcal/kg DE, 8.1% DP) quality, regardless of flavor, which suggests feedback from nutrients causes animals to like particular foods (Provenza et al. 1996). Likewise, lambs offered foods differing in flavors, nutrients, and toxins preferred foods high in nutrients and low in toxins, regardless of flavor, which suggests feedback from nutrients and toxins causes animals to prefer particular foods (Wang and Provenza 1996*a*).

Animals also learn to ingest substances that ameliorate malaise. For instance, lambs drink more of solutions that contain sodium bicarbonate when eating a high- as opposed to a low-grain diet (Phy and Provenza 1996*b*-In Press). Otherwise, they strongly prefer plain water to sodium bicarbonate. Lambs apparently drink the sodium bicarbonate solution because it attenuates malaise caused by acidosis (Provenza et al. 1994*c*), not because they prefer the flavor. Likewise, rats prefer flavors associated with recovery from threonine deficiency, but only when they are deficient in threonine (Gietzen 1993). Thus, preferences of lambs and rats for substances that can rectify certain maladies depend on their experiences with those maladies, and they are state dependent.

Preference Depends on Need

An animal's preference for food depends on its nutritional needs. Animals prefer foods that meet nutritional needs and preference declines when needs are met. Sucrose or glucose tastes pleasant to fasted humans but tastes unpleasant after it has been consumed (Cabanac 1971). People prefer the flavor of low-carbohydrate snacks when satiated, but they prefer the flavor of high carbohydrate foods when deprived (Booth and Toase 1983). Protein (Gibson and Booth 1986) and carbohydrate (Gibson and Booth 1989) preferences also depend on an animal's nutritional state (Villalba and Provenza 1996*a*,*b*,*c*,*d*). For instance, lambs fed a basal ration high in energy (grain) preferred food lower in energy (alfalfa) when offered a choice; those fed a basal ration high in alfalfa preferred foods high in grain (Wang and Provenza 1996*b*). Lambs' relative preference for rolled barley declined immediately after eating a small meal (400 g) of barley; their aversion to barley was more persistent after eating several small meals or a large meal (1,200 g) of barley (Phy and Provenza 1996*a*). The role of nutritional needs is also apparent in the aversion of lambs to flavored straw eaten during intraruminal infusions of NaCl; when their mineral needs are met, lambs show low preference for the flavored straw paired with NaCl (Villalba and Provenza 1996*b*). Thus, preference depends on nutritional needs, and preference declines when foods are eaten to satiety (Provenza 1996*a*).

WHAT CAUSES ANIMALS TO PREFER A VARIETY OF FOODS?

Ruminants select diets from an array of plant species that vary in nutrients and toxins. Some authors 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 will eat three different 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 for this behavior—one which encompasses the avoidance of toxins and the acquisition of nutrients (Provenza 1996*a*). 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 flavor) and postingestive feedback (nutritional and toxicological effects on chemo-, osmo-, and mechanoreceptors) unique to each food. Aversions are pronounced when foods contain toxins or high levels of rapidly digestible nutrients. Aversions also occur when foods are deficient in specific nutrients. Aversions can occur even when animals eat nutritionally adequate foods in excess or too frequently because satiety (satisfied to the full) and surfeit (filled to nauseating or disgusting excess) are a continuum and there is a fine line between satiety and aversion. Thus, several types of diet-related factors can result in aversions. Moreover, these 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, sample foods, maintain a diverse microflora in the rumen) that are often mistaken as the cause of varied diets.

Understanding why animals eat varied diets can aid efforts to control wildlife depredation and to seed pastures and rangelands. Losses by wildlife exceed $3 billion annually in the United States, much of it involving agricultural crops (Conover et al. 1995). Deer and bears often eat trees in plantations and fruit orchards, especially when alternate foods are scarce. Providing an alternate food may alleviate depredation, and offering a nutritious supplement in different flavors is an inexpensive option that may further decrease depredation. Likewise, pastures and rangelands are often seeded to monocultures of nutritious species (e.g., crested wheatgrass in the West and tall fescue in the Midwest and South), but intake might increase if pastures contained several species. Sheep and cattle prefer an alternate food to one consumed for as little as half a day (Baumont et al. 1990; Newman et al. 1992, 1994; Ramos and Tennessen 1993), as illustrated by the fact that sheep prefer clover early in the day and grass later in the day (Parsons et al. 1994). The kinds and numbers of foods offered to ruminants are also important considerations in attempts to train animals to avoid foods, such as poisonous plants or trees in orchards or plantations (Burritt and Provenza 1989*b*, 1990; Lane et al. 1990). In addition to creating an aversion to a target plant, providing a desirable mix of alternative foods (or supplements) should enhance the persistence of an aversion to the plant.

IMPLICATIONS

Foraging involves a dynamic interplay between a food's flavor and its postingestive effects (i.e., nutrients and toxins) relative to the current physiological condition of the animal and the animal's past experiences. The dynamic nature of foraging has implications for the development and use of feeding deterrents. This dynamic suggests: (1) deterrents based merely on offensive flavors are not likely to be effective in the absence of aversive postingestive effects, (2) the reason many repellents are effective only temporarily is because they merely change the flavors of familiar foods (i.e., novelty effects), and (3) any management program designed to deter herbivores from eating a particular food must provide a variety of nutritious alternatives.

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