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FAMILIARITY AND NOVELTY IN ANIMAL DIETS: IMPLICATIONS FOR MANAGEMENT

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SUMMARY

The dichotomy between that which is familiar and that which is novel causes a dynamic interplay, one which is at the foundation of behaviour. Mother brings her offspring into the field of time and space in which everything is dual (eg, past/present) and relative to the experiences of the individual (eg, familiar/novel). Environmental experiences begin in utero and continue after birth. The consequences of these experiences shape an animal's preferences and aversions, and create an interplay between the familiar and the novel. Animals typically prefer the familiar to the novel (ie, neophobic), and they generally regard anything novel with caution. For instance, herbivores prefer familiar foods adequate in nutrients to foods that are deficient in nutrients or that contain excesses of toxins. Nevertheless, they can become averse to that which is too familiar and seek that which is novel (ie, neophyllic). For instance, preference decreases when familiar foods are eaten too frequently or in excess, which encourages the consumption of novel foods and varied diets. Thus, the variety of familiar foods is an important factor to consider in management of domestic and wild animals in confinement and under free-ranging conditions.

Keywords: food preference, familiar, novel, behaviour, nutrients, toxins

INTRODUCTION

Everything in the field of time and space is dual (eg, past/present) and relative to the experiences of each individual (familiar/novel). This duality causes an interesting interplay from the standpoint of behaviour, particularly as relates to familiarity and novelty. Familiarity suggests that which is enduring, conventional, and ordinary, whereas novelty connotes change, originality, and uniqueness. The dichotomy between that which is familiar and that which is novel causes a dynamic interplay, one which is at the foundation of food and habitat selection behaviours.

SIGNIFICANCE OF THE FAMILIAR-NOVEL DICHOTOMY

Survival in a world fraught with dangers depends on discriminating that which is familiar from that which is novel, and a young animal's experiences early in life automatically structure a dichotomy between the familiar and the novel. As a result of interactions with mother (Provenza 1994, 1995b) and peers (Biquand and Biquand-Guyot 1992; Ralphs 1996), young animals acquire preferences for foods and habitats that meet needs (Scott *et al.* 1995, 1996; Howery *et al.* 1996), and they are cautious of anything novel. Thus, familiarity controls preference, and neophobia is a manifestation of the general phenomenon of fear exhibited by animals in unfamiliar situations (Barinaga 1992; Davis, 1992; LeDoux, 1992, 1994).

Lambs are reluctant to eat novel foods or familiar foods whose flavours have changed (Gluesing and Balph 1980; Gillingham and Bunnell 1989, Provenza *et al.* 1993a, 1995). Lambs routinely fed elm from one location would not eat elm of the same species from another site because the odour and taste of elm differed in the two locations (Provenza *et al.* 1993a). A change in the flavour of a familiar food also causes an immediate reduction in food intake by lambs in confinement (Provenza *et al.* 1995). When animals become ill after eating a meal of familiar and novel foods, they avoid the novel foods (Burritt and Provenza 1989a, 1991; Provenza *et al.* 1993a), and when they become ill after a meal of novel foods, they avoid the foods whose flavours are most novel (Kalat 1974; Burritt and Provenza 1989a; Launchbaugh *et al.* 1993; Provenza *et al.* 1994a). When offered foods in sequence, animals typically avoid the food eaten just prior to illness (Provenza *et al.* 1993b), unless one of the foods is novel, in which case they avoid the novel food (Revusky and Bedarf 1967). Cautious sampling of novel foods, and associating toxicosis with novel foods, helps herbivores survive in a world where the nutrient and toxin concentrations of foods are constantly changing (Freeland and Janzen 1974; Provenza and Balph 1990; Provenza *et al.* 1992).

Preference for the familiar over the novel is evident in habitat selection as well. Sheep and cattle prefer familiar to unfamiliar environments (Key and MacIver 1980; Howery *et al.* 1996). Sheep also prefer to forage with companions as opposed to strangers (Scott *et al.* 1995). When introduced into unfamiliar environments, naive sheep do not necessarily forage with experienced sheep, and may stray as far as 150 km from the native herd's normal range (Warren and Mysterud 1993). Sheep seek familiar foods when placed in unfamiliar environments (Gluesing and Balph 1980), and intake declines most drastically when sheep are offered novel foods in novel environments (Burritt and Provenza 1996). Animals in an unfamiliar environment walk further, ingest less food, and suffer more from malnutrition and toxicity compared with animals familiar with the environment (Griffith *et al.* 1989; Provenza and Balph 1990).

WHY HERBIVORES PREFER FAMILIAR FOODS

Animals acquire preferences for the flavours of familiar foods that have been associated with the positive postingestive effects of nutrients (Provenza 1995a, 1996). Taste (as well as smell and sight) enables animals to discriminate among foods and provides hedonic sensations. 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 or containing toxins.

Postingestive feedback from nutrients increases preference foods by increasing liking for the flavour of the food (Provenza 1995a, 1996). Lambs acquire strong preferences for the flavour of straw (onion or oregano) eaten during intraruminal infusions of energy (starch or glucose) or nitrogen (urea, casein, gluten) (Burritt and Provenza 1992; Villalba and Provenza 1996a,b, unpublished). Preferences for flavours paired with energy (starch) persist for at least 2 months following conditioning, which suggests lambs acquire a liking for flavours paired with energy. Byproducts of microbial fermentation (ie, volatile fatty acids like propionate and acetate) are quickly absorbed from the rumen and provide an immediate indication of the nutritional value of food (Villalba and Provenza 1996a,b, unpublished). Doses of propionate equivalent to as little as 1% of lambs' daily energy intake increase preference for straw (Villalba and Provenza 1996b). In the absence of energy or nitrogen, intake of flavoured straw is low and variable, which suggests that flavour alone does not predict preference (Provenza *et al.* 1996; Wang and Provenza 1996a).

Animals also prefer substances that ameliorate illness, even when the postingestive effects of the substances do not cause an increase in liking for the flavour of the food. For example, lambs experiencing grain-induced acidosis drink aqueous solutions of sodium bicarbonate; the amount they drink is directly related to the amount of grain ingested and to the amount of bicarbonate needed to neutralize acid produced by the grain; nevertheless, they do not acquire a preference for the taste of the bicarbonate solution and they strongly prefer plain water to the sodium bicarbonate solution (Phy and Provenza 1996a,b,c). Thus, the lambs drink the sodium bicarbonate solution because of its positive postingestive effects (ie, attenuating acidosis, Provenza *et al.* 1994b), not because they like the flavour.

Conversely, excesses or deficits of nutrients and excesses of toxins cause food aversions by causing a decrease in liking for the flavour of the food (Garcia 1989; Provenza 1995a, 1996). For instance, lambs that receive a toxin dose after eating cinnamon-flavoured rice no longer prefer cinnamon-flavoured wheat (though they still show a strong preference for wheat); these results reflect the fact that the lambs have generalized an aversion from rice to wheat, based on a common flavour (cinnamon) (Launchbaugh and Provenza 1993). Excesses of energy, nitrogen, or minerals can also condition food aversions (Provenza 1995a), as can excesses of byproducts of fermentation. For instance, sheep acquire aversions to flavoured straw eaten with high doses (> 10 g) of propionate (Ralphs *et al.* 1995; Villalba and Provenza 1996b), and the same is true for acetate, combinations of propionate and acetate, and ammonia (Famingham and Whyte 1993; Mbanya *et al.* 1993; Villalba and Provenza, unpublished).

WHAT CAUSES HERBIVORES TO PREFER NOVEL FOODS

Ruminants select diets from an array of plant species that vary in nutrients and toxins. Some suggest this reduces overingesting toxins (Freeland and Janzen 1974), whereas others theorize it meets nutritional needs (Westoby 1978). Both of these theories are inconsistent with the preference for a varied diet when toxins are not a concern and nutritional needs are met (eg, Wilmshurst *et al.* 1995; Provenza *et al.* 1996). I offer another explanation for this behaviour, one which encompasses the avoidance of toxins and the acquisition of nutrients (Provenza 1996). A key concept in this theory is aversion, the decrease in preference for food as a result of sensory (taste, odour, texture, ie, flavour) and postingestive (effects of nutrients and toxins on chemo-, osmo-, and mechano-receptors) feedback unique to each food.

Aversions cause animals to sample novel foods and eat varied diets. 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) are a continuum. For instance, lambs fed nutritionally balanced apple- or maple-flavoured food one day prefer the alternate flavour the next day, 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). 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. The benefits of aversions (eg, obtain a balanced diet, reduce ingestion of toxic foods, optimize foraging and rumination times, sample foods, maintain a diverse microflora) are mistaken as the cause of varied diets.

Aversions caused by nutrient imbalances cause animals to sample novel foods (Provenza 1996). For instance, lambs fed a basal ration of barley (high energy) readily eat rabbit pellets (a novel food higher in protein) but not wheat (a novel food high in energy), whereas lambs fed a basal ration of alfalfa pellets (high in protein) readily eat wheat (a novel food high in energy) but not rabbit pellets (a novel food high in protein) (Wang and Provenza 1996b). If the imbalance is sufficiently strong, aversions can cause animals to eat highly unusual foods (reviewed in Provenza 1996). For instance, cattle with mineral deficiencies eat rabbit legs and bones. Nutrient-deficient deer and other ungulates eat antlers. Goats foraging on nitrogen-deficient blackbrush pastures ingest woodrat houses high in nitrogen, and bighorn sheep use rodent middens as mineral licks. Wild ungulates and sheep with deficiencies eat lemmings, rabbits, birds, ptarmigan eggs, arctic terns, and fish. 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 like plastic, feathers, cinders, sacks, and tins.

MANAGEMENT IMPLICATIONS

Many of the principles discussed above have been employed in pastoral grazing systems and may influence grazing patterns of herbivores on rangelands. For instance, sheep herders in France offer animals a variety of foods to stimulate intake during grazing circuits (Hubert 1993; Meuret *et al.* 1994). Providing animals with a diverse mix of nutritious plants is one of the most important means of reducing toxicosis on rangelands and in pastures (Fusco *et al.* 1995). Providing alternative foods (or supplements) is also likely to enhance the persistence of an aversion when attempting to train animals to avoid poisonous plants or trees in plantations (Burritt and Provenza 1989b, 1990; Lane *et al.* 1990). Losses to wildlife exceed $3 billion annually in the U.S., much of it involving agricultural crops (Conover *et al.* 1995). Providing the proper alternate foods or nutritious supplements in different flavours may decrease depredation.

Intake might be increased if pastures contained several species (Parsons *et al.* 1994). Planting species with different kinds of secondary metabolites might also increase livestock production and stabilize plant mixes. Many shrubs and forbs contain tannins, whereas legumes like alfalfa contain saponins. Planting these species together may reduce the aversive effects of both compounds because tannins and saponins chelate in the intestinal tract (Freeland *et al.* 1985). Tall fescue infected with ascomycete fungi produces alkaloids that adversely affect food intake and livestock performance (Aldrich *et al.* 1993). The selective preference for uninfected fescue eventually leads to dominance of infected plants. Forages like 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.

Finally, the importance of varied diets may be useful in enhancing intake of animals in confinement. Improvements in the nutritional quality of diets in dairies and feedlots have led to uniform rations, which may inadvertently create aversions. Offering different foods of similar nutritional value (eg, barley and wheat), offering foods of different nutritional value (eg, barley and alfalfa), and offering the same food in different flavours (eg, maple and apple) may increase intake (Wang and Provenza 1996b).

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