Preference of Sheep for Foods Varying in Flavors and Nutrients[1]

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ABSTRACT: Our objective was to better understand the importance of flavor and nutrients in food preferences of lambs. Three foods differing in flavor and nutritional quality were created by grinding and mixing grape pomace, barley, alfalfa pellets, and soybean meal in different proportions: food 1 (2.21 Mcal/kg DE, 8.1% DP), food 2 (2.42 Mcal/kg DE, 11.0% DP), and food 3 (2.68 Mcal/kg DE, 13.8% DP). Intake of each food, offered singly and together, was assessed when foods 2 and 3 were flavored with 1% onion or 1% oregano. Lambs (n = 24) preferred food 3 > 2 > 1, regardless of flavor ($P < .05$), and they continued to prefer food 3 > 2 > 1, even when they received the toxin LiCl after eating one of the three foods ($P < .05$). When offered a choice, lambs always ate substantial amounts of all three foods, even though they might have been expected to eat food 3 exclusively. We hypothesize selection of a varied diet resulted from a decrease in preference for food just eaten as a result of sensory input (taste, odor, texture, i.e., a food's flavor) and postingestive feedback (effects of nutrients and toxins on chemo-, osmo-, and mechano-receptors) unique to each food. Thus, we submit that 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 enhancing food preference and intake.

Key Words: Food Preference, Nutrition, Flavor, Diets

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Introduction

Food preferences originate from the functional interrelationship between taste and postingestive feedback, determined by an animal's physiological condition and a food's chemical characteristics (Provenza, 1995, 1996a,b). Taste (as well as smell and sight) enables animals to discriminate among foods, and feedback from nutrients and toxins calibrates taste (hedonic sensations) in accord with a food's homeostatic utility. Thus, animals acquire preferences for foods that are nutritious and they become averse to foods that are deficient in nutrients or contain excesses of toxins (Provenza, 1995, 1996a,b).

Our objective was to better understand the importance of flavor (taste plus odor) and nutrients in the food preferences of lambs. We wanted to determine whether lambs discriminated among three foods of relatively similar nutritional quality, and if they did, to determine whether they ate the most nutritious food exclusively or whether they ingested all three foods. We also determined whether added flavors affected lambs' preference for the three foods.

Materials and Methods

Thirty-four lambs (Finn-Targhee-Columbia-Polypay crossbreeds of mixed sexes) were purchased at 6 wk of age and moved to the Green Canyon Ecology Center in Logan, UT. Twenty-four lambs (42 kg) were used in Exp. 1 (July 13 to September 2, 1994) and 10 different lambs (48 kg) were used in Exp. 2 (August 17 to September 9, 1994). Lambs were put in individual pens and they had access to water and mineral blocks ad libitum.

In both experiments, lambs received three foods (Table 1) differing in flavor and nutritional quality that were created by grinding and mixing grape pomace, barley, alfalfa pellets, and soybean meal in different proportions: food 1 (2.21 Mcal/kg DE, 8.1% DP), food 2 (2.42 Mcal/kg DE, 11.0% DP), and food 3 (2.68 Mcal/kg DE, 13.8% DP). We determined intake

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Table 1. Nutritional characteristics of foods used in Experiments 1 and 2 (as-fed basis)

Component	Food 1	Food 2	Food 3
Food ingredients, %[a]			
Barley	35	40	46
Grape pomace	40	32	20
Alfalfa	22	18	19
Soybean meal	3	10	15
Digestible energy, Mcal/kg[a]	2.21	2.42	2.68
Digestible protein, %[a]	8.1	11.0	13.8
In vitro digestibility, %[b]	52.0	56.9	64.0
Crude protein, %[c]	15.9	16.9	18.1

[a]Each food was composed of four ingredients that were ground to about 1 mm and mixed (cement mixer). Calculated values for digestible energy (DE) and digestible protein (DP) for the three foods are based on the following values obtained from NRC (1985): barley, 3.26 Mcal/kg DE, 8.5% DP; grape pomace, 1.09 Mcal/kg DE, 1.6% DP; alfalfa, 2.41 Mcal/kg DE, 14% DP; soybean meal, 3.37 Mcal/kg DE, 46% DP.

[b]In vitro dry matter digestibility was determined by the Moore modification of Tilley and Terry (1963) using ruminal fluid from a ruminally cannulated heifer fed grass hay.

[c]Nitrogen was determined by the Hach Technique. Crude protein calculated as N × 6.25.

of each food, offered singly and together, when foods 2 and 3 were flavored with 1% onion or 1% oregano. Foods were offered in separate containers, and the position of each food was changed daily. The foods were offered from 0800 to 1700 and intake was recorded at 0900, 1300, and 1700. Initially, intake was measured at hourly intervals to determine patterns of eating. Lambs ate most from 0800 to 0900, so we provided more food at 0900 to ensure ad libitum availability from 0900 to 1300.

Food preferences and aversions have been conditioned with flavors including cinnamon (Launchbaugh and Provenza, 1993); onion, garlic, and oregano (Nolte and Provenza, 1992; Villalba and Provenza, 1996a,b); orange and grape (Burritt and Provenza, 1992); and strawberry and banana (Thorhallsdottir, 1991). These flavors help animals discriminate among foods but they do not affect intake, provided concentrations are not high enough to cause postingestive malaise (Villalba and Provenza, 1996a,b). In the following experiments, we added 1% oregano and 1% onion flavors to foods 2 and 3 (Table 1).

Experiment 1: Preference for Foods. The objectives of Exp. 1 were to assess the role of flavor in the lambs' discrimination and preference for foods of different nutritional quality and to determine whether the food highest in nutrients would be eaten to the exclusion of the other foods. Further, we wished to determine whether preference for the foods could be changed by administering the toxin LiCl after lambs ate one of the three foods. First, lambs were offered 2,000 g of each food for 3 d from 0800 to 1700 in the sequence food 1, 2, and 3 to acquaint them with each food (Table 2). Food 1 was unflavored; foods 2 and 3 contained 1% oregano and 1% onion powder, respectively. Next, we offered the animals all three foods and measured intake and hence preference for each of the three foods for 8 d. On d 9, lambs (eight/treatment) were offered one of the three foods from 0700 to 0800 and then received LiCl (250 mg/kg BW) by gavage (duToit et al., 1991); 2 h later lambs were fed alfalfa pellets. On d 10 to 16, lambs again had access to all three foods. On d 17 and 18, they were fed alfalfa pellets. On d 19 to 23, they were offered all three foods without flavors.

Experiment 2: Effects of Flavor. The objective of Exp. 2 was to assess the relative importance of flavor and nutrients in food preference. First, lambs were offered 2,000 g of each food for 3 d from 0800 to 1700 in the sequence food 1, 2, and 3 (Table 2): Food 1 (no flavor added) was offered on d 1 to 3 to all lambs; food 2 was provided with either 1% onion (treatment 1, n = 5 lambs) or 1% oregano (treatment 2, n = 5 lambs) on d 4 to 6; and food 3 was given with either 1% oregano (treatment 1) or 1% onion (treatment 2) on d 7 to 9. Then, we measured preference when all three foods were offered simultaneously: Lambs in treatment 1 (n = 5) were offered foods 2 and 3 with 1% onion and 1% oregano, respectively, and lambs in treatment 2 (n = 5) were offered foods 2 and 3 with 1% oregano and 1% onion, respectively. The foods were offered from 0700 to 1700 for 3 d and intake was measured at 0900, 1300, and 1700.

Statistical Analyses. For Exp. 1, the analyses of variance had three treatments (LiCl after eating foods 1, 2, or 3), and the data were analyzed separately for d 1 to 8 (pre-LiCl), 10 to 16 (post-LiCl), and 19 to 23 (flavors removed). For Exp. 2, the statistical analysis had two treatments (onion or oregano flavor). Lambs were nested within treatments, and food (1, 2, 3) was a split plot in the analyses for both experiments. Periods within days and days were repeated measures (Winer, 1971).

Results

Experiment 1: Preference for Foods. Consumption of foods 1, 2, and 3 was 1,907, 1,776, and 1,580 g when 2,000 g of each food was offered separately for 3 d at

Table 2. Foods offered and sequence of feeding during adaptation and preference tests in Experiments 1 and 2

Days within periods	Foods offered	Amount, g
Exp. 1		
Foods offered singly (adaptation)		
Days 1 to 3	F1[a]	2,000
Days 4 to 6	F2[a] + oregano	2,000
Days 7 to 9	F3[a] + onion	2,000
Foods offered together (preference tests)		
Pre-LiCl (d 1 to 8)	F1, F2 + oregano, F3 + onion	Ad libitum
LiCl (d 9)[c]	F1 – T1[b]; F2 – T2[b]; F3 – T3[b]	Ad libitum
Post-LiCl (d 10 to 16)	F1, F2 + oregano, F3 + onion	Ad libitum
Post-LiCl (d 17 to 18)	Alfalfa pellets	Ad libitum
Post-flavors (d 19 to 23)	F1, F2, F3	Ad libitum
Exp. 2		
Foods offered singly (adaptation)		
Days 1 to 3	F1 – (T1 and T2)	2,000
Days 4 to 6	F2 – onion (T1), oregano (T2)	2,000
Days 7 to 9	F3 – oregano (T1), onion (T2)	2,000
Foods offered together (preference test)		
Days 1 to 3	F1, F2 + onion, F3 + oregano (T1)	Ad libitum
Days 1 to 3	F1, F2 + oregano, F3 + onion (T2)	Ad libitum

[a]F1, F2, and F3 refer to foods 1, 2, and 3, respectively (see Table 1).
[b]T1, T2, and T3 refer to treatments 1, 2, and 3, respectively (see text for details).
[c]On d 9 of Exp. 1, lambs (eight/treatment) received LiCl following ingestion of foods 1 (T1), 2 (T2), or 3 (T3), and then they had ad libitum access to alfalfa pellets for the remainder of the day.

the beginning of the experiment ($P < .005$; Table 3). Lambs ingested 4.21, 4.30, and 4.23 Mcal of digestible energy (**DE**) and 154, 195, and 218 g of digestible protein (**DP**) from foods 1, 2, and 3; the DP/DE ratios were 37, 45, and 52 g of DP/Mcal of DE for foods 1, 2, and 3 (Table 3).

When all foods were offered simultaneously (Table 3), lambs preferred food 3 (936 g) > 2 (537 g) > 1 (330 g) before receiving LiCl ($P < .001$), and they preferred food 3 (843 g) > 2 (510 g) > 1 (345 g) after receiving LiCl ($P < .001$), albeit intake of food 3 decreased (936 to 843 g; $P < .05$). Lambs preferred food 3 (1,377 g) > 2 (489 g) > 1 (201 g) when oregano and onion were removed from foods 2 and 3 ($F = 146$; df = 2,42; $P < .001$), and their intake of food 3 increased (843 to 1,377; $P < .05$). For pre-LiCl, post-LiCl, and post-flavors, DE intakes were 4.54, 4.25, and 5.32 Mcal/d, DP intakes were 215, 200, and 260 g/d, and DP/DE ratios were 47, 47, and 49 g of DP/Mcal of DE, respectively. The highest levels of intake occurred pre-LiCl (4.54 Mcal of DE/d, 215 g of DP/d) and post-flavors (5.32 Mcal of DE/d, 260 g of DP/d).

Experiment 2: Effects of Flavor. Consumption of foods 1, 2, and 3 was 1,887, 1,423, and 1,462 g when each food was offered separately for 3 d at the beginning of the experiment ($P < .025$). Lambs ingested 4.17, 3.44, and 3.92 Mcal of DE and 153, 157, and 202 g of DP from foods 1, 2, and 3 (Table 3). The DP/DE ratios were 37, 46, and 51 g of DP/Mcal of DE for foods 1, 2, and 3.

Onion and oregano did not alter preference for foods 2 or 3 ($P > .10$; Figure 1). Instead, lambs preferred food 3 (1,353 g) > 2 (330 g) > 1 (264 g), regardless of flavor ($P < .001$; Table 3). The highest intake of DE and DP occurred when lambs were offered all three foods (5.01 Mcal of DE/d, 244 g of DP/d), as opposed to when each food was offered singly (Table 3). The

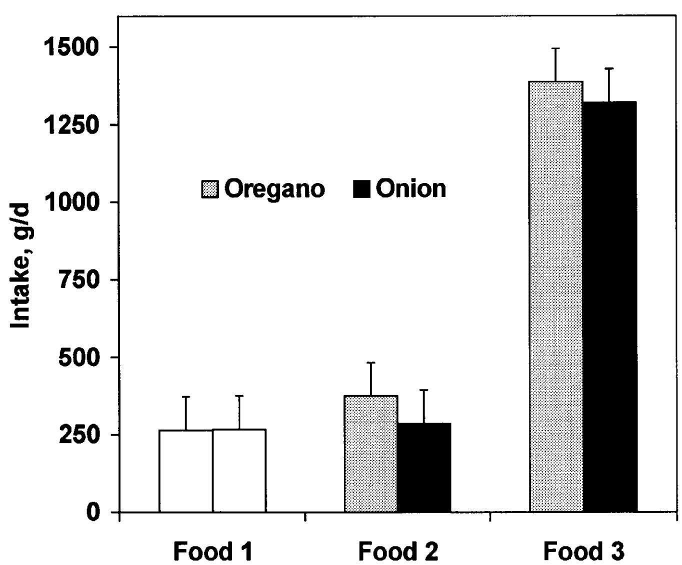

Figure 1. Intake (SEM = 108) of foods 1, 2, and 3 by lambs when all three foods were offered simultaneously in Exp. 2. Half of the lambs received foods 2 and 3 with 1% onion and 1% oregano, respectively, whereas the other half of the lambs were offered foods 2 and 3 with 1% oregano and 1% onion, respectively. Food 1 was unflavored.

Table 3. Food ingestion during adaptation and preference tests in Experiments 1 and 2

Item	Food 1	Food 2	Food 3	Total
Exp. 1				
Foods offered singly				
Intake, g/d	1,907[a]	1,776[b]	1,580[c]	—
DEI, Mcal/d	4.21	4.30	4.23	—
DPI, g/d	154	195	218	—
Ratio DPI/DEI	37	45	52	—
Foods offered together				
Pre-LiCl (d 1 to 8)				
Intake, g/d	330[a]	537[b]	936[c]	1,803[d]
DEI, Mcal/d	0.73	1.30	2.51	4.54
DPI, g/d	27	59	129	215
Ratio DPI/DEI	37	45	52	47
Post-LiCl (d 10 to 16)				
Intake, g/d	345[a]	510[b]	843[c]	1,698[e]
DEI, Mcal/d	0.76	1.23	2.26	4.25
DPI, g/d	28	56	116	200
Ratio DPI/DEI	37	45	52	47
Post-flavors (d 19 to 23)				
Intake, g/d	201[a]	489[b]	1,377[c]	2,067[f]
DEI, Mcal/d	0.44	1.18	3.70	5.32
DPI, g/d	16	54	190	260
Ratio DPI/DEI	36	46	51	49
Exp. 2				
Foods offered singly				
Intake, g/d	1,887[a]	1,423[b]	1,462[b]	—
DEI, Mcal/d	4.17	3.44	3.92	—
DPI, g/d	153	157	202	—
Ratio DPI/DEI	37	46	51	—
Foods offered together (d 1 to 3)				
Intake, g/d	264[a]	330[a]	1,353[b]	1,947
DEI, Mcal/d	0.58	0.80	3.63	5.01
DPI, g/d	21	36	187	244
Ratio DPI/DEI	36	45	52	49

[a,b,c]means in a row and [d,e,f]means in a column differ ($LSD_{.05}$). For Exp. 1, SEM = 64 when foods were offered singly and SEM = 45 for pre-LiCl, post-LiCl, and post-flavors. For Exp. 2, SEM = 108 when foods were offered singly and 77 when foods were offered together.

ratio of DP/DE was 49 g of DP/Mcal of DE when the three foods were offered simultaneously.

Discussion

Foods Offered Singly. When all three foods were offered singly during Exp. 1, lambs ingested food 1 > 2 > 3. Their intake of DE remained relatively constant (4.21, 4.30, 4.23 Mcal/d). During Exp. 2, lambs ingested food 1 > 2 = 3, which resulted in DE intakes of 4.17, 3.44, and 3.92 Mcal/d, and DP intakes of 153, 157, and 202 g for foods 1, 2, and 3. Protein:energy ratios varied from 36 to 52 g of DP/Mcal of DE when lambs were offered the three foods singly (Table 3).

Results from both experiments suggest lambs ate to a relatively constant energy intake, but there were two exceptions (i.e., foods 2 and 3 when offered singly in Exp. 2). The lower DE intake during d 4 to 9 may have occurred because lambs were not familiar with the flavors of onion and oregano; intake often declines when animals are offered familiar foods (e.g., grape pomace) with novel flavors (e.g., onion and oregano) (Provenza et al., 1995). The lack of familiarity with oregano and onion also may have reduced intakes of foods 2 and 3 during the adaptation phase of Exp. 1.

In addition, an excessive amount of protein (relative to energy, see below) may have limited intake of food 3 in Exp. 1 (218 g/d ingested, 202 g/d recommended) and Exp. 2 (202 g/d ingested, 181 g/d recommended) (Egan, 1977; Russell et al., 1992; Kyriazakis and Oldham, 1993; Provenza, 1995, 1996a). For maximum growth of 345 g/d, 42-kg lambs (Exp. 1) of moderate potential should ingest about 5.1 Mcal/d of DE and 202 g/d of DP; for maximum growth of 300 g/d, 48-kg lambs (Exp. 2) of moderate potential should ingest about 5.1 Mcal/d of DE and 181 g/d of DP (NRC, 1985).

Foods Offered Together. When all three foods were offered together during Exp. 1, lambs always preferred food 3 > 2 > 1, but their total intake varied among periods (post-flavors 2,067 g > pre-LiCl 1,803 g > post-LiCl 1,698 g; $LSD_{.05}$ = 90). These differences were caused by changes in intake of food 3 (post-flavors 1,377 g > pre-LiCl 936 g > post-LiCl 843 g; $LSD_{.05}$ = 90). The high dose of LiCl caused lambs to eat less of food 3 but did not affect their intake of foods 1 and 2 ($LSD_{.05}$ = 90). Lambs also preferred food 3 > 2 > 1 during Exp. 2, and their total food intake was 1,947 g.

Lambs ate all three foods, even after receiving LiCl (Table 3). The aversion to food paired with LiCl was likely diminished because the lambs had eaten the foods for several days before receiving LiCl. Animals show less aversion to familiar than to novel foods (Revusky and Bedarf, 1967; Burritt and Provenza, 1991), and the strength of an aversion is greatly diminished after a novel food has been eaten for 7 d (Burritt and Provenza, 1996).

Varied Diets. Lambs ingested all three foods when given a choice, and they achieved higher levels of intake of DE and DP when offered a choice than when each food was offered singly (Table 3). Food preferences of ruminants change within meals (Jung and Koong, 1985; Newman et al., 1994), and sheep and cattle prefer alternatives to forages they have consumed for several days (Baumont et al., 1990; Newman et al., 1992, 1994; Ramos and Tennessen, 1993) or hours (Parsons et al., 1994), even when the alternatives are less nutritious. We suggest ingestion of a varied diet results from a decrease in preference for food just eaten; the decrease in preference results from the functional integration of sensory input (taste, odor, texture, i.e., a food's flavor) and postingestive feedback (effects of nutrients and toxins on chemo-, osmo-, and mechano-receptors). In what follows, we attempt to explain the selection of varied diets by lambs on the basis of this hypothesis (Provenza, 1996a).

Nutrients. Energy and protein both play primary roles in food preferences of lambs (Villalba and Provenza 1996a,b and unpublished data). Lambs prefer food high in energy, and they acquire strong preferences even for poorly nutritious foods such as straw when straw is eaten during intraruminal infusions of energy (Villalba and Provenza, 1996a,b). Nonetheless, food preferences have been shown to decrease following food ingestion. 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 protein (alfalfa) subsequently prefer food high in energy (grain) (Wang and Provenza, 1996). Lambs' preference for grain (barley) over alfalfa declines immediately after lambs eat a small meal (400 g) of barley, and lambs acquire strong aversions after eating a large meal (1,200 g) of barley (Phy and Provenza, unpublished data).

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). Thus, we submit lambs that ate food high in energy (e.g., food 3) should subsequently have preferred foods lower in energy (e.g., foods 2 and 3). This hypothesis is consistent with the notion that the ratio of protein to energy is important in the food preferences of ruminants (Egan, 1977), and with the constant protein:energy ratios (47 to 49) when lambs were offered all three foods simultaneously (Table 3).

Flavor. Preference depends on the interrelationship between food flavor and postingestive effects of nutrients. For example, lambs fed a basal diet high in barley prefer alfalfa to barley, but when offered wheat (a differently flavored source of energy) the lambs prefer wheat to alfalfa (Wang and Provenza, 1996). These findings suggest lambs strongly prefer foods high in energy, but preference for any particular high-energy food declines after that food is eaten. Thus, offering a variety of high-energy foods (e.g., barley and wheat) encourages higher intakes, especially if the high-energy foods differ in flavor.

Lambs fed apple- or maple-flavored food one day prefer the same food in an alternate flavor the next day, and the higher the energy content of the food, the greater the change in preference (Early and Provenza, unpublished data). Rats eat more during a four-course meal when the food is flavored differently than when each course is flavored the same (Treit et al., 1983), and they eat more and gain more weight when offered high-energy foods in a variety of flavors (Naim et al., 1986). Thus, preference decreases when any food is eaten to satiety, which then encourages consumption of a variety of foods (Provenza, 1996a).

We contend lambs in Exp. 1 ate foods 1 (no flavor added) and 2 (oregano flavored) because of a decrease in preference for the flavor of food 3 (onion flavored), which was eaten repeatedly and in large amounts at every meal (Table 3). Lambs increased consumption of food 3 when its flavor changed (i.e., following removal of onion), which is consistent with the hypothesis that nutrient feedback diminished preference for food 3 because it was eaten too frequently and in excess (Provenza 1996a), not because the flavor of onion was inherently unacceptable or produced aversive postingestive effects. Indeed, lambs acquire strong preferences for onion-flavored food paired with gavage of energy (Villalba and Provenza, 1996a,b).

The high dose of LiCl likely exacerbated the aversion to the onion flavor of food 3 in Exp. 1. Lambs acquire food aversions on the basis of salient flavors. For example, lambs made averse to cinnamon-flavored rice (with a toxin dose) will not eat cinnamon-flavored wheat, though they eat plain wheat readily (Launchbaugh and Provenza, 1993). Thus, lambs' preference for onion-flavored food was likely diminished as a result of toxicosis from LiCl (Exp. 1), and from eating onion-flavored food repeatedly and in large amounts (Exp. 1 and 2). Thus, when the onion flavor was removed from food 3 in Exp. 1, intake of food 3 increased dramatically.

Variation Among Lambs. Of the 24 lambs in Exp. 1, 12 preferred food 3 > 2 > 1, three preferred food 3 > 1 > 2, six preferred food 2 > 3 > 1, and three preferred food 1 = 2 > 3. We propose most lambs preferred food 3 because it provided the greatest rate (most digestible) and amount (highest in energy and protein) of nutrient feedback. Nevertheless, the rate and amount of feedback may have been excessive for some lambs, which caused them to prefer foods 1 and 2 to food 3. This hypothesis is consistent with the fact that all lambs acquire a preference for flavored straw eaten while receiving 5 to 7.5 g of propionate, but 20% of lambs acquire an aversion when the dose is raised to 10 g (Villalba and Provenza, 1996b). Thus, we submit individual lambs differed in their metabolic responses to rates of nutrient delivery, which caused variation in their food preferences.

Implications

We suggest that offering herbivores 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., apple and maple) are all means of enhancing food preference. We also submit that intake might be increased if animals in confinement (e.g., feedlots, dairies) received a variety of foods, as opposed to monotonous diets, because offering foods in a variety of flavors and nutrients would enable each individual to select a diet to meet its nutritional needs. Intake might also be increased if pastures were seeded to mixtures of species, rather than monocultures, for the same reasons. Finally, it may even be possible to further reduce consumption of particular plants (e.g., trees in orchards, poisonous plants) by providing appropriate alternatives to animals trained with toxins like LiCl to avoid the plants (Burritt and Provenza, 1989, 1990; Lane et al., 1990).

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