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Early experience with diverse foods increases intake of nonfamiliar flavors and feeds in sheep[1,2]

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ABSTRACT: This study determined whether early experiences by sheep with monotonous or diverse diets influence intake of unfamiliar flavors and feeds later in life. Thirty 2-mo-old lambs were randomly assigned to 3 treatment diets (n = 10): diverse (DIV), diverse with plant toxins (DIV+T), and monotonous (MON). Lambs in DIV received in 9 successive periods of exposure 4-way choice combinations of 2 foods high in energy and 2 foods high in protein from an array of 6 foods: 3 high in energy [beet pulp, oat grain, and a mix of milo:grape pomace (60:40)] and 3 high in digestible protein (DP) (soybean meal, alfalfa, corn gluten meal). Lambs in DIV+T received the same exposure as DIV, but 2 plant toxins, oxalic acid (1.5%) and quebracho tannins (10%), were randomly added to 2 of the feeds in each of the choice combinations. Lambs in MON received a monotonous balanced diet, made with a mixture of all 6 feeds detailed before. All treatments received their feed in 4 separate buckets. During exposure, treatments did not differ in total daily DMI ($P = 0.31$), but daily intake of ME was less ($P < 0.02$) and daily intake of DP was greater ($P < 0.03$) for lambs in DIV and DIV+T than for lambs in MON. Treatments did not differ in ADG or G:F ($P > 0.05$). After exposure, lambs were offered a familiar feed (wheat bran) containing novel flavors (maple, garlic, or bitter) and 2-way choices of novel feeds (fescue hay vs. corn distillers grains, rice vs. calf manna, and green peas vs. rolled oats). Intake of maple-flavored wheat bran tended ($P = 0.08$) to be greater for lambs in DIV than for lambs in DIV+T and MON. Intake of bitter-flavored and garlic-flavored wheat bran were greater ($P = 0.03$ and $P = 0.04$, respectively) for lambs in DIV and DIV+T than for lambs in MON. During 2-way choice trials, lambs in DIV, but not in DIV+T, showed greater intakes of fescue hay ($P = 0.05$) and rice ($P = 0.04$) than lambs in MON. Intake of green peas was greater ($P = 0.03$) for lambs in DIV and DIV+T than for lambs in MON. At the end of testing, lambs in DIV but not in DIV+T showed greater ADG than lambs in MON ($P = 0.05$). Thus, early exposure to diverse foods enhanced acceptance of novel flavors relative to early exposure to a monotonous ration. Early experience with diverse feeds plus plant toxins led to a less diverse diet than early experience with diverse feeds. Early exposure to diverse feeds may be beneficial in production systems that require rapid acceptance and high intake of unfamiliar feeds.

Key words: dietary diversity, diet selection, early food experience, neophobia, sheep

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INTRODUCTION

Ruminants are reluctant to eat novel feeds (Provenza, 1995). This phenomenon, known as food neophobia, can reduce intake and decrease animal performance, even in animals faced with highly nutritious novel feeds (Launchbaugh, 1995; Bowman and Sowell, 1997). Food neophobia is a behavioral response elicited by animals to avoid overingesting toxins or nutrients from foods with unknown postingestive effects. Feed recognition involves at least 2 events: generalization of familiar cues (e.g., flavors, odors) in the unfamiliar feed and learning about the postingestive effects of the novel feed (Villalba and Provenza, 2000). Once the novel feed is ingested, the animal calibrates future intake according to the learned postingestive consequences associated with its consumption (Bermúdez-Rattoni, 2004). This learning process is well understood for ruminants (Provenza, 1995, 1996), but less is known about the effect of previous experiences on the acceptance of novel feeds.

Ruminants evolved in diverse feeding environments, eating a variety of nutrients and plant toxins (Freeland and Janzen, 1974; Westoby, 1978). Thus, dietary diversity should be crucial in the development of cognitive abilities related to feeding behavior. Previous exposure to varied foods was shown to reduce neophobic responses in rats (Pliner et al., 1993) and humans (Mennella et al., 2007). Moreover, experiences early in life are expected to have more pronounced effects than later in life because early development induces lifelong changes in physiology and behavior (Provenza and Villalba, 2006).

We hypothesized that sheep exposed early in life to varied diets with different concentrations of nutrients and plant toxins will show greater acceptance of novel flavors and feeds than animals exposed to a monotonous diet. Our objective was to determine the effect of exposure to feed diversity early in life in the daily pattern of consumption of novel flavors and feeds by lambs.

MATERIALS AND METHODS

The study was conducted at the Green Canyon Ecology Center, located at Utah State University in Logan, UT, according to procedures approved by the Utah State University Institutional Animal Care and Use Committee (Approval #1408). Throughout the study, lambs had free access to water and trace mineral salt blocks.

Animals and Exposure Period

Thirty 2-mo-old Finn–Columbia–Polypay–Suffolk crossbred lambs of both sexes with an average initial BW of 29 ± 4 kg (mean ± SD) were individually penned outdoors under a protective roof in individual adjacent pens, measuring 2.4 × 3.6 m. Lambs were familiar with alfalfa and barley grain, as these feeds comprised the basal diet of their mothers. Animals were weaned, placed in individual pens, and fed alfalfa pellets for ad libitum intake and 300 g/d of barley grain for 15 d.

Lambs were then randomly assigned to 3 treatments (10 lambs/treatment) with restrictions of randomization on BW and sex, such that all treatments were balanced for these variables. Treatments were structured to expose lambs to diverse (**DIV**), diverse with phytochemicals (**DVT+T**), or monotonous (**MON**) diets. Lambs in DIV were fed simultaneously an array of 4 feeds taken from a group of 6 feeds: 3 feeds high in digestible protein (**DP**)/ME ratio (soybean meal, alfalfa, corn gluten meal); 3 feeds low in DP/ME ratio [beet pulp, oat grain, and a mix of milo:grape pomace (60:40); Table 1]. Lambs from this treatment received all possible 4-way choice combinations of 2 feeds high in DP/ME ratio and 2 feeds low in DP/ME ratio (9 combinations; Table 2).

Table 1. Nutritional composition of feeds offered to lambs during exposure and feeding trials (DM basis)

	Nutrient composition				
Item	ME[1], Mcal/kg	CP, %	DP, %[2]	DP/ME ratio[3]	NDF, %
Exposure period					
Low DP/ME ratio					
Milo:grape pomace (60:40)	2.1	11.3	5.0	2.4	34.7
Oat grain	2.5	11.7	8.9	3.5	27.2
Beet pulp	2.6	10.7	6.4	2.5	41.9
High DP/ME ratio					
Soybean meal	2.9	47.3	43.0	14.8	12.4
Corn gluten meal	3.1	53.7	48.3	15.5	7.1
Alfalfa	2.1	17.8	12.1	5.7	45.6
Mix offered to MON group[4]	2.4	16.0	12.2	5.0	30.6
Feeding trials					
Wheat bran	2.3	16.6	12.3	5.3	39.7
Corn distillers grain	2.9	26.3	19.1	6.6	36.8
Fescue hay	1.9	12.7	8.1	4.3	60.4
Rolled oats	3.2	14.2	11.4	3.6	12.6
Green peas[5]	2.8	24.7	21.5	7.7	16.0
Calf manna[6]	2.5	26.1	25.0	10.0	13.7
Rice	2.4	11.6	6.3	2.6	6.4

[1]Metabolizable energy values from NRC (1985), except for green peas and calf manna (see footnotes [5] and [6]).

[2]Digestible protein (DP) values are from NRC (1985), except for green peas and calf manna (see footnotes [5] and [6]).

[3]The DP/ME ratio represents the relation between ME and DP.

[4]The mix was composed of 38% milo, 12% oat grain, 10% soybean meal, 22% alfalfa, 10% grape pomace, 5% beet pulp, and 3% corn gluten meal.

[5]Estimated values for ME and DP were obtained from Fundación Española para el Desarrollo de la Nutrición Animal (de Blas et al., 2003).

[6]Estimated values for ME and DP were provided by manufacturer (Manna Pro Products, LLC, Chesterfield, MO).

Table 2. Dietary preferences (intake of 1 feed/total feed intake) of lambs early exposed to diverse feeds offered on choice with or without plant toxins added (DIV+T or DIV, respectively), for each feed combination offered during exposition

		Feed[1]							
		High DP/ME ratio			Low DP/ME ratio				
Treatment	Feed combinations[2]	Soybean meal	Corn gluten	Alfalfa	Oat grain	Beet pulp	Milo:grape mix	SEM	*P*-value
DIV	abcd	0.41^{a}	0.12^{b}		0.13^{b}		0.34^{a}	0.05	<0.001
	abce	0.43^{a}	0.10^{b}		0.20^{ab}	0.27^{ab}		0.07	0.02
	abde	0.40^{a}	0.10^{c}			0.19^{bc}	0.31^{ab}	0.06	0.003
	acdf	0.41^{a}		0.30^{ab}	0.08^{c}		0.21^{b}	0.04	<0.001
	acef	0.33^{ab}		0.39^{a}	0.07^{c}	0.21^{bc}		0.05	<0.001
	adef	0.27		0.32		0.19	0.22	0.04	0.18
	bcdf		0.13^{b}	0.45^{a}	0.11^{b}		0.31^{a}	0.04	<0.001
	bcef		0.16^{b}	0.42^{a}	0.10^{b}	0.32^{a}		0.04	<0.001
	bdef		0.08^{b}	0.39^{a}		0.30^{a}	0.23^{a}	0.05	0.005
DIV+T	a(t)b(o)cd	0.47^{a}	0.05^{b}		0.13^{b}		0.35^{a}	0.05	<0.001
	a(o)b(t)ce	0.30^{ab}	0.13^{b}		0.11^{b}	0.46^{a}		0.06	0.001
	abd(t)e(o)	0.52^{a}	0.20^{b}			0.12^{b}	0.16^{b}	0.03	<0.001
	a(o)cdf(t)	0.28^{a}		0.28^{a}	0.10^{b}		0.34^{a}	0.04	0.007
	ac(t)e(o)f	0.37^{a}		0.47^{a}	0.08^{b}	0.09^{b}		0.04	<0.001
	a(t)def(o)	0.31		0.14		0.29	0.26	0.04	0.11
	bc(t)d(o)f		0.21^{a}	0.62^{a}	0.08^{b}		0.09^{b}	0.03	<0.001
	bc(o)e(t)f		0.20^{b}	0.51^{a}	0.02^{c}	0.27^{b}		0.03	<0.001
	b(t)def(o)		0.06^{b}	0.17^{b}		0.40^{a}	0.37^{a}	0.05	<0.001

[1]Digestible protein (DP) and ME ratio.

[2]Feed combinations are composed of: "a," soybean meal; "b," corn gluten meal; "c," oat grain; "d," milo:grape mix; "e," beet pulp; "f," alfalfa hay. For treatment DIV+T, the first feed preceding the letter "t" or "o" within parentheses was mixed with quebracho tannins (10%) or oxalic acid (1.5%), respectively.

[a–c]Within a row, means without a common superscript letter differ ($P < 0.05$).

Each choice combination was fed for 5 consecutive d and all periods occurred in a concatenated sequence until all combinations were offered. Exposure to each choice combination was randomly assigned among animals, such that the sequence of feed combinations in the experimental design was counterbalanced. Lambs in DIV+T received the same exposure described for DIV, but 2 plant toxins, oxalic acid (1.5%) or quebracho tannins (10%), were added to both feeds with low DP/ME ratio or both feeds with high DP/ME ratio, choosing only 9 from all possible feed-plant toxin combinations (Table 2). This imposed the challenge of balancing nutrients at the cost of handling intake of toxins. The concentrations of plant toxins used in this study have been used safely in previous studies and represent concentrations sheep typically encounter in plants while grazing in rangelands (Villalba et al., 2004). At the concentrations used in the present study, tannins may reduce digestion and food intake (Robbins et al., 1991), and oxalates may inhibit respiratory enzymes, reduce blood calcium concentrations, and affect renal function (Cheeke and Shull, 1985). Finally, lambs in MON received a monotonous balanced ration throughout exposure (NRC, 1985; Table 1), constituted by a unique mixture of all 6 feeds used for the other two groups of lambs (38% milo, 12% oat grain, 10% soybean meal, 22% alfalfa, 10% grape pomace, 5% beet pulp, 3% corn gluten meal). All treatments received feeds in 4 individual plastic buckets and distributed at random inside each individual feeder every day. All lambs had ad libitum access to their respective treatment diets from 0830 to 1500 h for 45 d. Offered and refused feeds were weighed to determine daily intake. Lambs were weighed at the end of exposure.

After exposure, lambs in all treatment groups were offered the monotonous ration for ad libitum intake for 15 d, such that they had the same immediate past orosensory and postingestive experiences before testing.

Acceptance of Novel Flavors and Choice Tests with Novel Feeds

Response to novel flavors was evaluated using wheat bran flavored with maple, bitter (Lucta, S.A., Montornés del Vallés, Spain), and garlic (Pacific Seasonings, Inc., Kent, WA) flavors. To estimate intake responses to the novel flavors, lambs were familiarized with plain wheat bran, which was offered from 0800 to 0815 h for 5 consecutive days. After this period, lambs were offered from 0800 to 0815 h wheat bran flavored with maple (8%) for 3 d, then wheat bran flavored with bitter (4%) for 3 d, and finally wheat bran flavored with garlic (2%) for 4 d (1 more day was added to this flavor to reach stable consumption among treatments). The order of flavor presentation was selected at random. Flavor concentrations at the aforementioned ranges have been used in previous studies testing flavor preferences in sheep (Villalba and Provenza, 1996, 1997a,b). From 1500 to 1600 h, all the lambs were fed alfalfa pellets for ad libitum intake.

Immediately after the trials with novel flavors, all the lambs were exposed to 3 consecutive trials of 5 d each involving choices between 2 novels feeds (Table 1): trial 1, corn distillers grains and fescue hay; trial 2, calf manna and rice; and trial 3, green peas and rolled oats. All feeds were provided in individual buckets from 0800 to 0815 h. From 1500 to 1600 h, all lambs were fed alfalfa pellets for ad libitum intake. Lambs were weighed at the end of this period.

Statistical Analyses

Exposure Period. Total daily DMI, total daily macronutrient intake, and performance parameters (ADG and final BW) for lambs in MON, DIV, and DIV+T were compared using a 1-way ANOVA. Analyses were run with the General Linear Model procedure (**GLM**; SAS Inst., Inc. Cary, NC).

Daily intake of and preference (intake of 1 feed/total feed intake) for each feed from all feed combinations offered to lambs in DIV and DIV+T were compared using a split-split-plot design with the MIXED procedure of SAS. Treatment (DIV and DIV+T) was the main plot, feed combination (9 combinations) was the subplot, and feed (each of the 6 feeds) was the sub-subplot in the analysis (fixed effects). Preference values were transformed (arcsine square root transformation) to meet assumptions of normality and homogeneity of variances

Daily intake of ME and DP from all feed combinations offered to lambs in DIV and DIV+T were analyzed with a repeated measures model run with the MIXED procedure of SAS. The statistical model included treatment (DIV and DIV+T), feed combination (9 combinations), and their interaction (treatment × feed combination) as fixed effects. Macronutrient intake in each feed combination was the repeated measure.

The effect of adding quebracho tannin or oxalic acid on feed intake was compared between lambs exposed or not to these plant toxins (DIV and DIV+T, respectively). We also determined whether the effects of plant toxins on intake were modulated by the nutritional characteristics of the feeds to which they were added (high DP/ME ratio or low DP/ME ratio). Nutritional characteristics of feeds affect toxin intake by lambs (Provenza et al., 2003). Thus, we performed 2 analyses: the first evaluated either the effect of quebracho tannin or oxalate on intake, whereas the second contrasted the effect of both toxins. To evaluate the effect of plant toxins on intake, a repeated measures model run with the MIXED procedure of SAS was used, including toxin (present or not) and feed type (high DP/ME ratio or low DP/ME ratio) as fixed effects. To contrast the effect of both plant toxins, a crossover design was used, including only lambs exposed to toxins. The statistical model included plant toxin (quebracho tannin or oxalate) and feed type (high DP/ME ratio or low DP/ME ratio) as fixed effects. The analysis was run using the GLM procedure of SAS.

Finally, we computed a diversity index (Shannon's diversity index; Hutcheson, 1970) to estimate and compare the degree of dietary diversity selected by lambs in DIV and DIV+T during exposure. Diversity indexes were previously used for the study of dietary diversity in humans (Drescher et al., 2007) and Shannon's index (diversity score $= -\sum_{i=1}^{S} pi * lnpi$, where S is the number of foods and pi represents the proportional contribution of the i food to the total amount eaten) was chosen for this study because it takes into account not only the variety of foods items included in the diet but also the proportional contribution of each one to the total intake.

Testing Period. Daily intake of flavored wheat bran and daily intake of all novel feeds offered during choice trials (as-fed basis; g/kg BW) were analyzed with a repeated measures design using the MIXED procedure of SAS. The statistical model included early exposure, day, and their interaction (exposure × day) as fixed effects. Daily intake was the repeated measure. At the end of testing, BW and ADG were compared among treatments with a 1-way ANOVA using the GLM procedure of SAS.

For all cases where the MIXED procedure was used, lamb was the random factor in the model and lambs were nested within treatments. The selected within-animal covariance matrix (autoregressive order–1, compound symmetry, variance components) always provided the best fit for the data, according to the Schwarz's Bayesian criterion (Littell et al. 1998). Model diagnostics included testing for a normal distribution of the error residuals and homogeneity of variance. When the main effect was significant ($P < 0.05$), means were compared using the Tukey–Kramer honestly significant difference test (Ruxton and Beauchamp, 2008).

RESULTS

Exposure Period

Total Daily DMI, Daily Macronutrient Intake, and Performance Variables. Mean total daily DMI did not differ among DIV, DIV+T, and MON (41.9, 41.3, and 43.9 ± 1.2 g/kg BW, respectively; means ± SEM, $P = 0.312$). However, daily intake of ME was less for lambs in DIV and DIV+T than for lambs in MON (103.3 and 102.6 vs. 117.9 ±2.9 kcal/kg BW, respectively; means ± SEM, $P < 0.021$). In contrast, daily intake of DP was greater for lambs in DIV and DIV+T than for lambs in MON (8.2 and 8.4 vs. 7.0 ± 0.4 g/kg BW, respectively; means ± SEM, $P < 0.033$). No differences in daily intake of ME ($P = 0.851$) or DP ($P = 0.724$) was found between DIV and DIV+T. At the end of exposure, lambs from DIV, DIV+T, and MON showed similar BW (55, 53, and 57 ± 2 kg, respectively; means ± SEM, $P = 0.278$), similar ADG (230.0, 227.3, and 260.0 ± 19.5 g/d, respectively; means ± SEM, $P = 0.351$), and similar G:F (157.6, 141.2, and 152.5 ± 6.2 g/kg respectively; means ± SEM, $P = 0.723$).

Dietary Preference and Daily Feed Intake for Lambs Exposed to DIV and DIV+T. Lambs offered choices showed clear preferences for specific foods (Table 2). Dietary preferences among lambs in DIV and DIV+T differed in most of the feed combinations (treatment × combination; $P < 0.048$). The only case where both treatments showed a similar pattern of feed preferences was when they were offered soybean meal, corn gluten meal, oat grain, and milo:grape pomace mix ($P > 0.718$).

Average daily intake for each feed across all the feed combinations was similar between both free-choice treatments (treatment × feed interaction, $P > 0.683$). The greatest intake was observed for alfalfa hay and soybean meal, followed by the milo:grape pomace mix and beet pulp, with the lowest intake for corn gluten meal and oat grain (15.9 and 15.0 > 11.8 and 10.5 > 5.2 and 4.2 ± 0.5 g/kg BW, respectively; means ± SEM, $P < 0.001$). Average daily ME intake was similar among treatments ($P = 0.88$) and no treatment × feed combination interaction was observed ($P = 0.94$; Figure 1).

Average daily DP intake was similar among treatments ($P = 0.80$). However, DP intake was greater for lambs in DIV+T than for lambs in DIV when lambs in DIV and DIV+T were offered soybean meal, corn gluten meal, milo:grape pomace mix, and beet pulp, and lambs in DIV+T had quebracho tannins added to milo:grape pomace and oxalic acid added to beet pulp (13.6 vs. 10.3 ± 0.5 g/kg BW, respectively; means ± SEM, treatment × feed combination interaction; $P = 0.003$; Figure 1). In contrast, lambs in DIV showed a greater DP intake than lambs in DIV+T when offered oat grain, milo:grape pomace mix, alfalfa hay, and soybean meal, and lambs in DIV+T had quebracho tannins added to alfalfa hay and oxalic acid added to soybean meal (9.9 vs. 7.8 ± 0.5 g/kg BW, respectively; means ± SEM, $P = 0.04$). Finally, DP intake was greater in both treatments when soybean meal was present in the combination (feed combination effect, $P = 0.003$; 9.4 vs. 6.3 ± 0.5 g/kg BW for soybean meal present vs. absent, respectively; means ± SEM, $P < 0.001$).

Effects of Plant Toxins on Diet Selection. Quebracho tannins did not affect intake of feeds, either with a low or a high DP/ME ratio (31.5 vs. 43.4 and 50.5 vs. 50.1 ± 11.7

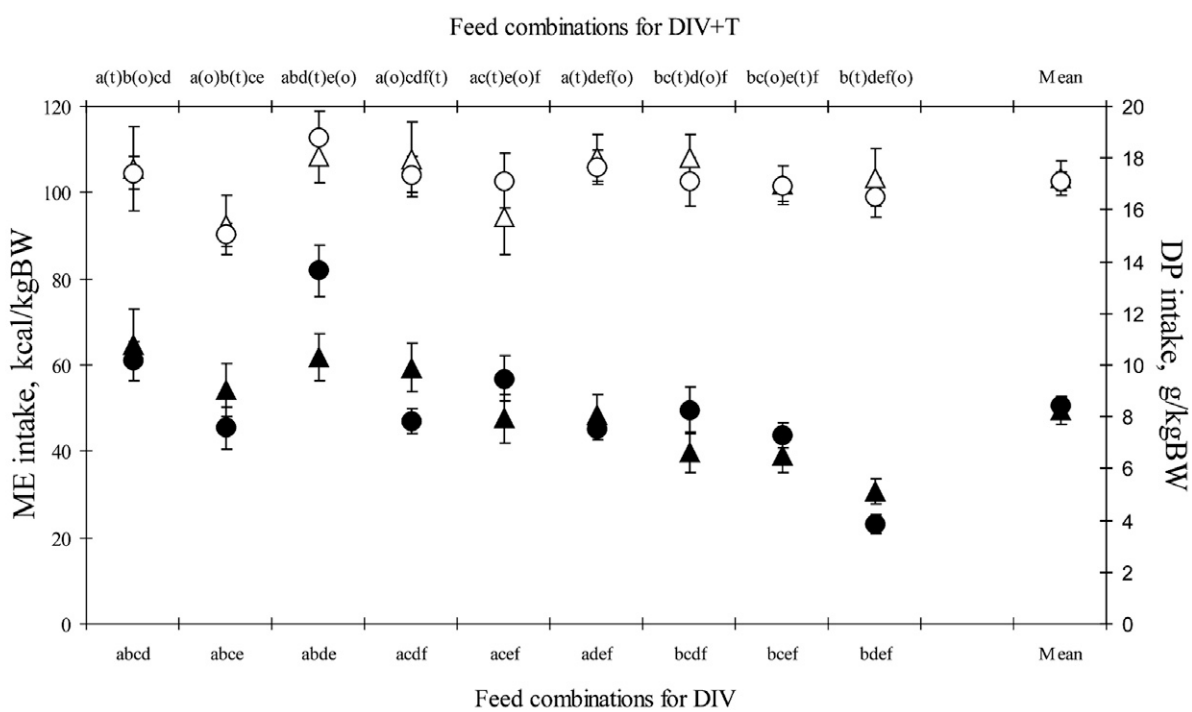

Figure 1. Average ME intake (empty symbols) and digestible protein (DP) intake (full symbols) by lambs early exposed to diverse feeds offered on choice with (circles) or without (triangles) plant toxins added (DIV+T or DIV, respectively), for each feed combination offered during exposure. Feed combinations are composed of: "a," soybean meal; "b," corn gluten meal; "c," oat grain; "d," milo:grape mix; "e," beet pulp; "f," alfalfa hay. For treatment DIV+T, the first feed preceding the letter "t" or "o" within parentheses was mixed with quebracho tannins (10%) or oxalic acid (1.5%), respectively.

Table 3. Dietary diversity scores of lambs early exposed to diverse feeds offered on choice with or without plant toxins added (DIV+T or DIV, respectively), for each feed combination offered during exposition

Feed combinations[1]		Dietary diversity scores			
DIV	DIV+T	DIV	DIV+T	SEM	*P*-value
abcd	a(t)b(o)cd	1.24	1.14	0.04	0.05
abce	a(o)b(t)ce	1.28	1.22	0.04	0.22
abde	abd(t)e(o)	1.27	1.22	0.05	0.29
acdf	a(o)cdf(t)	1.27	1.31	0.04	0.30
acef	ac(t)e(o)f	1.26	1.14	0.04	0.02
adef	a(t)def(o)	1.36	1.34	0.03	0.37
bcdf	bc(t)d(o)f	1.22	1.03	0.05	0.01
bcef	bc(o)e(t)f	1.25	1.12	0.03	0.02
bdef	b(t)def(o)	1.27	1.19	0.04	0.05

[1]Feed combinations are composed of: "a," soybean meal; "b," corn gluten meal; "c," oat grain; "d," milo:grape mix; "e," beet pulp; "f," alfalfa hay. For treatment DIV+T, the first feed preceding the letter "t" or "o" within parentheses was mixed with quebracho tannins (10%) or oxalic acid (1.5%), respectively.

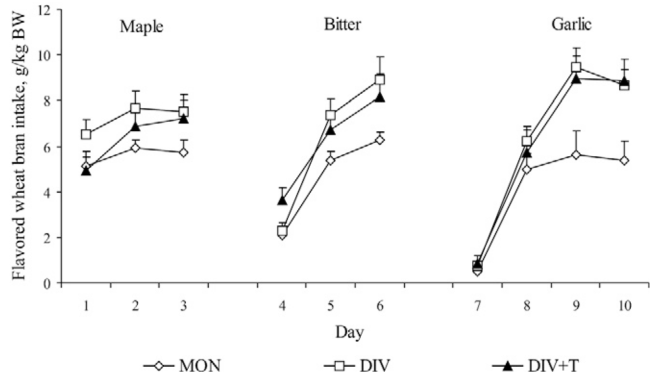

Figure 2. Intake of flavored wheat bran by lambs exposed early in life to a diverse feeding environment (DIV), diverse feeding environment where plant toxins were added (DIV+T), or dietary monotony (MON). Values are means for 10 animals/group. Vertical bars represent +1 SEM.

g/kg for each feed type, respectively, with and without quebracho tannins; means ± SEM, $P = 0.343$). Oxalic acid reduced feed intake (5.3 vs. 11.2 ± 0.3 g/kg BW for feeds with and without oxalic acid, respectively; means ±SEM, $P < 0.001$), regardless of feed type (low or high DP/ME ratio; $P = 0.785$). Oxalic acid reduced intake more than quebracho tannins did (5.3 vs. 8.2 ± 0.4 g/kg BW, respectively; means ± SEM, $P < 0.008$) and feed type did not influence this pattern ($P = 0.901$).

Dietary Diversity Scores. Lambs in DIV+T that received plant toxins in 2 of the 4 feeds offered selected a less diverse diet (in 5 of the 9 feed combinations offered) than lambs exposed to DIV (Table 3).

Flavored Wheat Bran Acceptance Trials

Intake of Maple-flavored Wheat Bran. Average intake tended to be greater ($P = 0.077$) for lambs in DIV than lambs in MON. Lambs in DIV showed greater ($P = 0.046$) intake than lambs in DIV+T only for the first day of testing (Figure 2). Lambs in DIV+T showed a greater ($P = 0.044$) intake than lambs in MON only during the last day of testing.

Intake of Bitter-flavored Wheat Bran. Lambs in DIV and DIV+T had similar ($P = 0.668$) intake but greater ($P = 0.030$) than lambs in MON. There was a treatment × day interaction ($P = 0.028$), which can be explained by the greater intake by lambs in DIV and DIV+T during the second ($P < 0.005$) and last day ($P < 0.002$) of testing (Figure 2).

Intake of Garlic-flavored Wheat Bran. Lambs in DIV and DIV+T showed a greater ($P = 0.045$) intake than lambs in MON; however, there was a treatment × day interaction ($P < 0.011$). This interaction can be explained by a greater intake by both DIV and DIV+T treatments during the third ($P < 0.001$) and last day ($P < 0.001$) of testing (Figure 2). Average intake was similar for lambs in DIV and DIV+T ($P = 0.814$).

Choices between Pairs of Novel Feed Trials

Fescue Hay vs. Corn Distillers Grains. Lambs in DIV showed a greater intake ($P = 0.05$) of fescue hay than lambs in MON. No differences were observed in fescue hay intake either among lambs in DIV and DIV+T ($P = 0.726$), or among lambs in MON and DIV+T ($P = 0.192$; Figure 3). Corn distillers grain intake was similar among treatments ($P = 0.600$).

Calf Manna vs. Rice. Lambs in DIV showed a greater average intake ($P = 0.038$) of rice than lambs in MON. Rice intake differed across days (treatment × day, $P = 0.035$) and was greater for lambs in DIV than lambs in MON for the last 3 d of testing ($P = 0.021$, $P = 0.033$, and $P = 0.049$, respectively). Intake of rice also was greater for lambs in DIV than lambs in DIV+T but only for the last day of testing ($P = 0.027$; Figure 3). No differences were observed in rice intake among lambs in DIV+T and lambs in MON ($P = 0.451$). Average calf manna intake was similar among treatments ($P = 0.381$).

Rolled Oats vs. Green Peas. Intake of green peas was greater ($P = 0.035$) for lambs in DIV and DIV+T than lambs in MON. Intake differed across days (treatment × day, $P = 0.032$) and was greater for lambs in DIV and DIV+T than lambs in MON for the last 4 d of testing ($P = 0.017$, $P < 0.001$, $P < 0.001$, and $P < 0.026$, respectively; Figure 3). Intake of rolled oats was similar among treatments ($P = 0.240$).

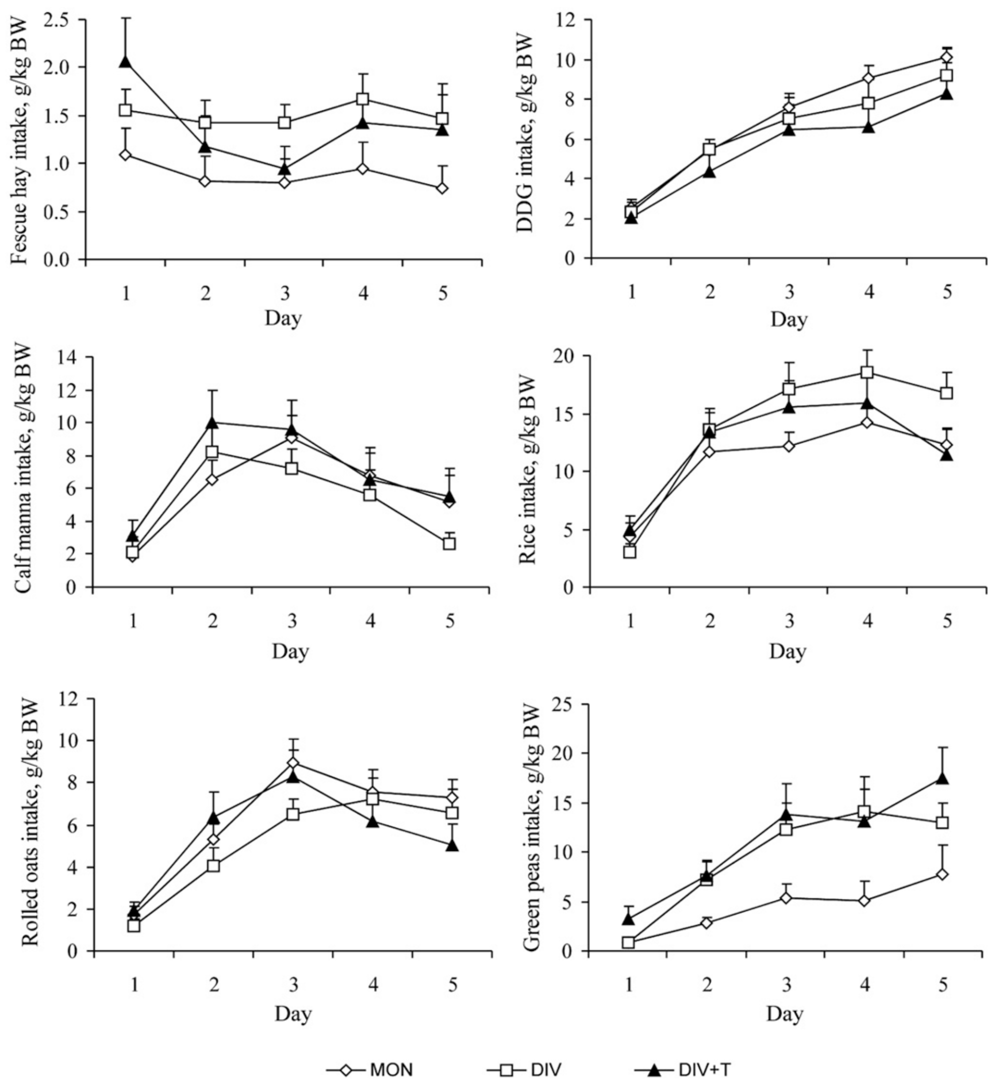

Figure 3. Intake of novel feeds offered on choice by lambs exposed early in life to a diverse feeding environment (DIV), diverse feeding environment where plant toxins were added (DIV+T), or dietary monotony (MON). Lambs were exposed to 3 consecutive feeding trials, each involving a choice between 2 novels feeds: fescue hay and corn distillers grains (DDG), calf manna and rice, and rolled oats and green peas, respectively. Values are means for 10 animals/group. Vertical bars represent +1 SEM.

Body Weight and ADG after Trials Involving Novel Flavors and Feeds

At the end of the study, lambs from DIV, DIV+T, and MON showed similar BW (59.7, 57.4, and 61.0 ± 1.9 kg, respectively; means ± SEM, $P = 0.540$). During testing with novel flavors and feeds, ADG was greater ($P = 0.050$) for lambs in DIV than lambs in MON (170.8 vs. 132.7 ± 12.0 g/d, respectively; means ± SEM), whereas no difference was observed among lambs in DIV+T and lambs in DIV ($P = 0.400$), or among lambs in DIV+T and lambs in MON ($P = 0.564$).

DISCUSSION

Dietary Monotony, Feed Diversity, and Diversity with Plant Toxins during Exposure

Lambs in the treatments with a diversity of feeds consumed substantial amounts of all feeds on offer but showed clear preferences for specific feeds, which suggested selectivity rather than random sampling. Protein and energy selection by lambs faced with diverse feeds indicated greater DP and less ME ingestion than lambs in MON. This pattern of nutrient intake was closely related to the greater preference for feeds high in protein (soybean meal and alfalfa hay) over feeds with low protein content (milo:grape pomace mix and beet pulp) by lambs exposed to food diversity. However, performance (BW, ADG, and G:F) at the end of exposure was similar among all treatments, which suggested that the diet selected by the free-choice fed lambs satisfied nutrient requirements in a similar way to the balanced ration fed to MON. Keskin et al. (2004) observed greater protein intake and decreased energy intake in free-choice fed lambs compared with lambs fed a single ration, which also was associated with a similar performance among treatments. Protein overingestion in ruminants is likely to be related to the maintenance of ruminal homeostasis when ruminants ingest diets high in grain or secondary compounds, both of which can induce acidosis (James et al., 2001; Rodriguez et al., 2007). Acidosis can be prevented by the buffer capacity of ammonia (one of the by-products of protein degradation) in the rumen (Owens et al., 1998). In our study, lambs showed a greater intake of soybean meal (high proportion of RDP) than corn gluten meal (low proportion of RDP; NRC, 1985). In addition, growing ruminants displayed clear preferences for protein-rich feeds and flavors that signal protein (e.g., umami), as their requirement for protein is high (Villalba et al., 2011). Finally, nutrient requirements were established for the "average animal" under conditions imposed by animal production systems; therefore, the biological goals of individual lambs selecting a diet may lead to a dietary balance different from that expected (Atwood et al., 2001; James et al., 2002).

Plants vary not only in nutritional but also toxicological profiles, challenging herbivores to compose a nutritionally balanced diet but reducing negative digestive or physiological effects of plant toxins (Iason and Villalba, 2006). In our study, plant toxins affected dietary preferences and the diversity of feeds selected by lambs. However, average macronutrient intake by lambs exposed to DIV+T was surprisingly similar to that achieved by lambs exposed to the same feeds but with no toxins added (DIV). This suggests that lambs exposed to feeds with plant toxins had the ability to adjust their diet selection, so nutrient intake was not compromised under the constraints imposed by a reduced ingestion of potentially toxic compounds. This is supported by the fact that lambs in DIV+T showed a similar average intake of individual feeds relative to lambs in DIV throughout the study. Animals reduced the negative postingestive impacts of plant toxins and displayed grazing times and amounts of consumption comparable with animals not exposed to these compounds, when offered choices of feeds that differ in plant toxins (Villalba et al., 2004).

Plant toxins have negative impacts on tissues and metabolic processes (Cheeke and Shull, 1985). As a result, animals develop aversions of different magnitudes to toxin-containing feeds (Provenza, 1995; 1996). A diverse diet may allow animals to adjust intake in ways that minimize the specific action of toxins (Provenza, 1996; Villalba et al., 2004). Lambs in our study reduced intake of feeds containing oxalic acid but still ate significant amounts of feeds containing quebracho tannins, such that feed intake was similar either in the presence (DIV+T) or absence (DIV) of tannins. Increased protein ingestion, as observed in the current study, reduced the negative consequences of tannins on digestion in sheep and goats, and thereby increased total amount of toxin that was ingested (Villalba et al., 2002). Oxalates are quickly absorbed into the bloodstream, affecting renal function and calcium absorption (James, 1972). Experience with oxalates improves degradation of this toxin because of adaptation of ruminal microorganisms (Duncan et al., 2000). Nevertheless, ruminal adaptation to oxalates may be less consequential than the beneficial effects of protein on tannin tolerance (Frutos et al., 1998); furthermore, preference for high quality feeds mixed with oxalic acid decreases with time of exposure to the toxin (Papachristou et al., 2007).

Finally, animals offered choices with or without plant toxins selected diets that led to a similar performance at the end of exposure to that of lambs consuming a monotonous and balanced ration or diverse feeds but with no plant toxins added. These findings support the idea that ruminants faced with complex feeding environments were able to select a diet that meets their nutrient requirements, minimizing the negative impacts of toxins (Provenza, 1995).

Effects of Diet Diversity on Neophobic Responses

Compared with lambs exposed to a monotonous diet, lambs exposed to diverse feeds showed a subsequent greater intake not only of a familiar feed containing novel flavors but of different novel feeds offered in a choice. However, differences in intake were not commonly observed on the first day of testing, suggesting a similar initial neophobic response among treatments. Thus, early exposure to food diversity affected the rate at which lambs accepted new feeds across time. To our knowledge, this is the first study showing such a pattern.

Ruminants faced for the first time with a novel feed do not have previous nutritional or toxicological information to decide how much to eat. Therefore, they probably infer nutritional properties based on previous experience with other feeds (Burritt and Provenza, 1989, 1997). Animals recognize cues in the novel feed that were previously associated to specific postingestive consequences during past experiences with familiar feeds, a phenomenon known as stimulus generalization (Launchbaugh and Provenza, 1993; 1994). Sheep generalize preferences (Villalba and Provenza, 2000) and aversions (Ginane and Dumont, 2006). Lambs exposed to DIV or DIV+T did not generalize sensorial cues to a greater extent than lambs exposed to MON, because they showed similar initial reluctance to eat novel feeds.

This finding can be explained by the fact that novel flavors and feeds offered to lambs during testing were strikingly different from those offered during exposure, so generalization by lambs exposed to varied feeds may have been reduced in this context. In addition, all lambs were exposed to the same feeds, even though their presentation (mixed in a ration or as separate ingredients) was different, which may have given lambs in all of the treatments previous experience with the sensorial aspects of all the feeds. On the other hand, lambs exposed to a monotonous diet did not increase acceptance of novel items (neophyllic reaction), as might be expected for animals exposed for a long time to the same feeds (Stasiak, 2002). Animals become satiated after consuming the same food too frequently, a phenomenon known as sensory specific satiety (Rolls, 1986; Provenza, 1996).

Several exposures are needed to familiarize animals with a novel feed (Chapple et al., 1987), depending on the strength of postingestive consequences (Provenza et al., 1994; Villalba and Provenza 1996; 1997b) and learning abilities of animals (e.g., ability to link feed ingestion with its postingestive consequences); the latter because food characterization involves cognitive processes (Provenza, 1995; Núñez-Jaramillo et al., 2009). As a result, if the consequences of ingestion are positive, animals develop a preference, whereas if consequences are negative, an aversion to the feed takes place (Villalba and Provenza, 1997a).

Assuming that feeds, during choice trials, produced similar nutritional postingestive consequences (i.e., no differences in digestion efficiency among treatments) among the experimental groups, we suggest the increased intake of novel feeds across days of testing observed in lambs previously exposed to a diverse feeding environment could be attributed to an improvement in learning abilities. Greater capacity to make associations among sensory cues (odor, taste, sight) and postingestive consequences can explain the faster increment in consumption of feeds with unfamiliar properties. Consistent with this hypothesis, infusion of a N-methyl-*D*-aspartate receptor antagonist in the cerebral insular cortex of rats, which affects the formation of gustatory memory (Martin et al., 2000), retards attenuation but not the initial neophobic reaction to a novel feed (Figueroa-Guzmán et al., 2006; Figueroa-Guzmán and Reilly, 2008).

Greater intakes of novel flavors and feeds by lambs in DIV than lambs in MON likely led to greater ADG. Livestock in feedlots, dairies, or at weaning time are typically offered unfamiliar rations, which leads to production losses until animals are familiarized with such feeds. Early exposure to diverse feeds may reduce this negative outcome by enhancing the acceptance of new feeds during those transition periods.

Addition of Plant Toxins to Feeds: Does it make an Improvement in Dietary Diversity?

Ruminants forced to mix highly nutritious feeds with feeds that contain toxins develop an increased preference for the latter (Villalba et al., 2006), which shows that avoidance of toxins depends on previous experience and the nutritional environment where ingestion of toxins takes place (Villalba et al., 2004; Baraza et al., 2005). However, herbivores with no restrictions to choose between plants with diverse nutritional and toxicological profile (e.g., during continuous grazing at low stock densities; Provenza et al., 2003) usually select a small subset of highly nutritious plants to conform the bulk of the diet, rejecting those with low-nutrient density or high-toxin content or both (Shaw et al., 2006). Paradoxically, as a consequence of selective foraging, a more diverse feeding environment due to the addition of plant toxins to feeds can reduce diet diversity among lambs as observed for lambs in DIV+T relative to lambs in DIV.

Fescue hay and rice was accepted to a greater extent by lambs in DIV than lambs in DIV+T. This response may be related to the reduced dietary diversity during exposure, manifested by the lower diversity scores in DIV+T than DIV. Even though dietary diversity can be negatively related to the persistence of conditioned taste aversions (Gentle et al., 2006), a more parsimonious explanation comes from the fact that lambs in DIV+T received multiple experiences with toxins that may have produced negative postingestive consequences. Sheep that experience negative postingestive consequences after ingestion of a novel feed show a subsequent reduction in the acceptance of other novel feeds (Launchbaugh and Provenza, 1994).

Ecological Importance of Experience with Diverse Feeds Early in Life

In nature, ruminants are commonly faced with multiple plant species that vary not only in nutritional and toxicological composition but also on how they are distributed on space and available on time (O'Reagain and Schwartz, 1995). Sheep preferred to eat a varied array of plant species and feeds (Provenza, 1996; Villalba et al., 2011) or feeds offered in different flavors (Scott and Provenza, 1998). This is so, in part, because a diverse diet most likely satisfied multiple nutrient requirements (Simpson et al., 2004). In our study, we demonstrated that lambs exposed to a diverse feeding environment early in life show not only increased intake when exposed to novel feeds but also greater ADG during trials involving exposure to novelty than lambs exposed to a monotonous diet. Our results suggested dietary diversity is not only required to fulfill nutritional requirements in nature but also for a correct cognitive development in early life.

During early stages of life, experience-dependent neuronal networks require specific information about the environment essential for normal development (Knudsen, 2004). Multiple challenges are expected for animals in the wild when they need to adapt to the common issues of life; thus, diverse information provided by the environment and animal interaction with this information ensures correct cognitive development (Meehan and Mench, 2007). In this sense, some authors (Greenough et al., 1987; Van Praag et al., 2000) suggest exposure to an "enriched" situation does not improve learning performance per se but restores what should have been an appropriated experience for animals exposed only to monotonous information. The value of diversity has never been taken seriously by humans in animal production, especially with regard to local adaptation (Provenza, 2008). Livestock production systems have usually relied on restricted-diversity diets in confinement and pastures. Our results, and those of others (Wiedmeier et al., 2002), suggest these practices can negatively affect the abilities of animals to cope with variable environments and adversely affect performance.

Conclusions

Compared with animals exposed to a monotonous feeding environment (a single feed), lambs exposed early in life to a diverse feeding environment showed a greater intake of novel feeds and flavors. Although the initial reaction of lambs in all treatments to novel feeds was similar, neophobia was attenuated faster in the 2 diversity treatments (DIV and DIV+T) than in MON. Compared with lambs in DIV, lambs in DIV+T had lower diversity scores, perhaps because multiple experiences with tannins and oxalates produced negative postingestive consequences that limited their diet diversity. We suggest diversity of feeding challenges early in life is important for the proper development of food learning skills. Early exposure to monocultures or single diets may impair future performance and adaptability of livestock, not only in confinement and on pastures and rangelands, but in any system that requires rapid accommodation to unfamiliar feeds.

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