



Eating a high fiber diet during pregnancy increases intake and digestibility of a high fiber diet by offspring in cattle

R.W. Wiedmeier^a, J.J. Villalba^{b,*}, A. Summers^a, F.D. Provenza^b

^a Department of Animal, Dairy and Veterinary Sciences, Utah State University, 4815 Old Main Hill, Logan, UT 84322, United States

^b Department of Wildland Resources, Utah State University, 5230 Old Main Hill, Logan, UT 84322, United States

ARTICLE INFO

Article history:

Received 13 December 2011

Received in revised form 8 August 2012

Accepted 23 August 2012

Keywords:

Fetal programming

Intake

Digestibility

Fiber

Experience *in utero*

ABSTRACT

Experiences early in life influence preferences for the forages which animals eat as adults, but little is known about how such experiences affect forage intake and digestibility. We hypothesized that experience with high fiber (HF) diets *in utero* enables cattle to better utilize HF diets by enhancing intake and digestibility of HF diets. We exposed cows to either HF or low fiber (LF) diets from October 20 until parturition on March 15. The HF diet was primarily ammoniated wheat straw (AWS), while the LF diet was mainly grass hay (700 g/kg orchardgrass and 300 g/kg meadow bromegrass). The two diets were iso-net energy (NE_m), isonitrogenous, and similar in mineral and vitamin contents, but they varied 10-fold in neutral detergent soluble carbohydrates. Following weaning, the 8 mo old calves from mothers fed HF or LF diets during pregnancy were fed AWS and a high fiber supplement, and dry matter (DM) intake and digestibility were measured during the last half of a 40 d experiment (*i.e.*, 26 d adaptation, 14 d measured DM intake, 5 d measured DM digestibility). Intake (5.6 *versus* 5.3 kg/d; P=0.04) and digestibility (545 *versus* 523 g/kg; P=0.03) of AWS were higher for calves fed HF than for those fed LF diets. As a result, digestible DM intake of AWS was higher for HF than LF (3.1 *versus* 2.8 kg/d; P<0.01). Calves fed HF diets ate more straw as a proportion of their diet than did calves fed LF (733 *versus* 723 g/kg; P=0.05). Total digestible DM intake (*i.e.*, AWS+ supplement) was higher for calves fed HF than LF diets (4.7 *versus* 4.4 kg/d; P<0.01), as was total diet DM digestibility (613 *versus* 600 g/kg; P=0.07). Calves were weighed at the conclusion of the DM intake and digestibility measurement periods, and then fed an AWS/processed wheat middlings diet for an addition 28 d to determine daily gain. Collectively, increases in intake and digestibility affected body weight gains such that HF diet fed calves numerically gained more than LF fed calves even during this short period (0.45 *versus* 0.41 kg/d; P=0.13). Higher DDM intake is likely important for pregnant cows and their offspring which winter for many months under extensive range conditions on dormant forages where their NE_m requirements are marginally satisfied. These effects on offspring, further magnified by experiences with their mothers early in life, make cows and their progeny better adapted to using dormant forages during winter.

Published by Elsevier B.V.

Abbreviations: AIA, acid insoluble ash; AWS, ammoniated wheat straw; BAR, barley grain; BCS, body condition score; BW, body weight; CP, crude protein; DM, dry matter; DMD, DM digestibility; DDM, digestible dry matter; GH, grass hay; HF, high fiber; LF, low fiber; NDF, neutral detergent fiber; NDSC, non-digestible soluble compounds; NEm, net energy for maintenance; VFA, volatile fatty acid; WM, processed wheat middlings.

* Corresponding author. Fax: +1 435 797 3796.

E-mail address: juan.villalba@usu.edu (J.J. Villalba).

1. Introduction

Natal experiences affect preferences for forages and habitat in insects, fish, birds and mammals (Davis and Stamps, 2004), and experiences *in utero* and early in life influence the foraging behavior of goats, sheep and cattle later in life (Provenza and Ralph, 1988, 1990; Provenza, 1995a, 2003). Preferences in lambs begin *in utero* through exposure to flavors (Simitzis et al., 2008). For example, onion and garlic flavors are transferred *in utero* and in milk, thereby pre-adapting young animals to eat onion and garlic (Nolte et al., 1992; Nolte and Provenza, 1992a,b). Postpartum, lambs previously exposed to saltbush *in utero* grew faster and handled a salt load better than lambs from mothers on pasture, while excreting salt more rapidly, drinking less water, and maintaining higher intake when eating saltbush (Chadwick et al., 2009a,b,c).

After birth, young livestock learn what and what not to eat and where and where not to go from their mothers (Thorhallsdottir et al., 1990; Mirza and Provenza, 1990, 1992; Howery et al., 1998). Lambs fed nutritious feeds such as wheat grain with their mothers for as little as 1 h/d for 5 d eat more wheat than lambs exposed to wheat grain without their mothers. Even 3 yrs later, with no additional exposure to wheat grain, their intake was nearly 10 times higher if the lambs were exposed to wheat grain with their mothers than if inexperienced lambs were exposed alone or not exposed at all (Green et al., 1984). After weaning, goats reared from 1 to 4 mo of age with their mothers on blackbrush dominated rangeland ate more blackbrush at 4 and 13 mo of age than did goats naive to blackbrush. Moreover, experienced goats consumed 30% more blackbrush than inexperienced goats when allowed to choose between blackbrush and alfalfa pellets (Distel and Provenza, 1991). Cross fostering studies show young goats from different breeds, one breed which prefers high tannin browse and the other which does not, eat more high tannin browse if their foster mothers eat high tannin browse (Glasser et al., 2009). Finally, young herbivores learn motor skills needed to harvest grasses, forbs and shrubs (Flores et al., 1989a,b; Ortega-Reyes and Provenza, 1993a,b), acquire preferences for forages (sheep – Nolte and Provenza, 1992a,b; Squibb et al., 1990, goats – Biquand and Biquand-Guyot, 1992), and their bodies adapt to using particular forages (Ortega Reyes et al., 1992; Distel et al., 1994, 1996). Sheep fed low quality forages early in life eat and digest low quality forages better, and they recycle N better later in life than sheep reared on higher quality diets (Distel et al., 1994, 1996). By interacting with the genome during growth and development, social and biophysical environments influence gene expression and behavioral responses (Schlichting and Pigliucci, 1998; LeDoux, 2002; Moore, 2002; Dufty et al., 2002), and create animals locally adapted to landscapes (Provenza, 2008).

Experience early in life affected cattle performance during a 3 yr study in which initially 5 yr old cows were fed ammoniated straw annually from December to May. Throughout all 3 yrs of the study, experienced cows, which had previously eaten straw for only 2 mo as calves, had higher body weight (BW) gains and body condition scores (BCS), produced more milk, and bred back sooner than cows with no exposure to straw (Wiedmeier et al., 2002). In cattle, heritability of dry matter (DM) intake and digestibility of low quality forages is only ~20% (Wiedmeier et al., 1995), which suggests that these responses are due to environmental influences early in life.

Our objective was to determine if feeding cows a high fiber (HF) diet during gestation would increase intake and digestibility of HF forages by their offspring. We hypothesized that experience with HF diets *in utero* better enables cattle to use HF forages later in life by enhancing intake and digestibility of HF forages.

2. Materials and methods

2.1. Cow management procedures

We selected 18 cows from a herd of 250 commercial beef cows managed under a four breed sire rotation system involving Angus, Hereford, Tarentaise and Gelbvieh sires. Angus bulls were used prior to the study, so that the cows selected were over 0.75 Black Angus breeding. The selected cows (5–7 yrs of age) were frame score 5–6 and 560 kg BW with an average BCS of 5–6 (Selk, 2010). Extensive production, performance and pedigree records enabled selected cows to be uniform regarding adjusted 205 d BW of their calves and postpartum intervals to rebreeding. To reduce genetic variation, all cows were at least half siblings and 6 of the cows were full sisters. To help ensure a uniform group of calves, the estrus of the cows was synchronized using the CEDR® System (InterAg, Hamilton, New Zealand). All cows were then mated to a single Black Angus bull for spring calving on March 15. The bull was average in the Angus breed regarding mature body size, growth propensity and maternal characteristics (yearling weight expected progeny difference +14.5 kg).

On October 17, calves were weaned and the cows to be used in this experiment were placed in individual pens. Cows then received any medical treatment deemed necessary by the attending veterinarian, including routine boosters of vaccinations and control of internal and external parasites. All procedures were approved by the Institutional Animal Care and Use Committee at Utah State University (Project Number 729R).

2.2. Dietary treatments

Cows were randomly assigned to two treatments (*i.e.*, 9 cows/group), such that each group was as similar as possible in BW, frame score, age and previous performance based on calf adjusted 205 d BW and postpartum interval to rebreeding. From October 20 until parturition the following March, cows were fed either HF or low fiber (LF) diets. The HF diet was primarily ammoniated wheat straw (AWS), while the LF diet was primarily grass hay (GH; 700 g/kg orchardgrass and 300 g/kg meadow

Table 1
Ingredient and nutrient composition of the high and low fiber diets fed to beef cows during gestation.

	High fiber					Low fiber				
	Nov ^a	Dec ^b	Jan ^c	Feb ^d	SEM	Nov ^a	Dec ^b	Jan ^c	Feb ^d	SEM
Ingredient (kg/d as fed)										
AWS ^e	8.97	10.00	10.55	10.91	–	–	–	–	–	–
GH ^f	–	–	–	–	–	6.55	8.00	8.59	9.79	–
WM ^g	3.20	4.50	5.00	6.25	–	–	–	–	–	–
BAR ^h	–	–	–	–	–	2.13	2.27	2.34	2.32	–
Limestone	0.0366	0.0813	0.973	0.1447	–	–	–	–	–	–
Dicalcium phosphate	–	–	–	–	–	–	–	–	0.0157	–
NDSC ⁱ	–	–	–	–	–	0.0149	0.0050	0.0009	–	–
Salt	0.0281	0.0281	0.0364	0.0364	–	0.0281	0.0281	0.0364	0.0364	–
Vitamin premix ^j	0.0291	0.0291	0.0364	0.0455	–	0.0291	0.0291	0.0364	0.0455	–
Mineral premix ^k	0.0264	0.0242	0.0232	0.0227	–	0.0337	0.0278	0.0254	0.0241	–
Nutrient composition										
CP ^l kg/d	1.03	1.21	1.29	1.45	0.013	1.03	1.21	1.29	1.43	0.013
NE _m ^m MJ/d	52.3	61.1	64.9	71.1	1.870	52.3	61.1	64.9	71.1	1.674
NDF ⁿ kg/d	7.59	8.55	8.98	9.54	0.260	4.20	5.06	5.42	6.11	0.156
eNDF ^o kg/d	7.08	7.83	8.46	8.55	0.240	3.28	4.00	4.30	4.90	0.124
NDSC ^p kg/d	0.96	1.20	1.29	1.48	0.037	2.88	3.29	3.47	3.73	0.100
NDSFP ^q kg/d	0.81	0.99	1.05	1.19	0.031	0.95	1.12	1.20	1.34	0.035
NF-NDSC ^q kg/d	0.15	0.21	0.23	0.29	0.007	1.93	2.16	2.27	2.39	0.066

^a November, 165 d.

^b December, 196 d.

^c January, 227 d.

^d February, 255 d.

^e Wheat straw, ammoniated.

^f Grass hay.

^g Wheat middlings.

^h Barley grain, ground.

ⁱ Neutral detergent soluble carbohydrates.

^j Vitamin premix: vitamin A, 1102 kIU/kg; vitamin D, 110 kIU/kg; vitamin E, 6614 IU/kg.

^k Mineral premix: Zn, 6012 mg/kg; Mn, 5011 mg/kg; Cu, 2004 mg/kg; I, 201 mg/kg; Se, 61 mg/kg.

^l Crude protein.

^m Net energy for maintenance.

ⁿ Neutral detergent fiber.

^o Effective neutral detergent fiber, based on increased chewing time, increased saliva flow, and stimulation of ruminal contractions (NRC, 2000).

^p Neutral detergent soluble fiber.

^q Non-fibrous neutral detergent soluble carbohydrates.

bromegrass). The two diets were iso-net energy (NE_m), isonitrogenous, and as similar as possible in mineral and vitamin levels (Table 1). The major difference in diets was the type of carbohydrates being neutral detergent fiber (NDF) versus non-digestible soluble compounds (NDSC). Use of AWS allowed feeding of LF forage without a NE_m deficiency throughout the last trimester of gestation.

2.3. Forages and supplements

Wheat straw for the AWS diet was obtained from a single 8 ha field of spring wheat just after the wheat was harvested. The straw was baled early in the morning to incorporate as much dew as possible to enhance ammoniation (Lalman et al., 2010). Bales were removed from the field, stacked and sealed under a 6 mil black polyethylene tarp (Reef Industries, Inc. Houston, Texas, USA) anchored with gravel at the base of the stack. Anhydrous ammonia (35 g/kg of DM) was injected through a steel pipe imbedded in the stack. Ammoniation of wheat straw occurred in early August and the stack remained covered until October 1 when one face of the polyethylene sheet was removed to allow excess ammonia to dissipate. Nutritional characteristics of the wheat straw DM differed before and after ammoniation: 36 versus 85 g/kg crude protein (CP); 813 versus 782 g/kg NDF; 392 versus 553 g/kg *in vitro* DM digestibility (DMD), respectively.

Grass hay (GH) used for the study, harvested from a single 7 ha field at mid-bloom, was 118 g/kg CP, 581 g/kg NDF and 587 g/kg *in vitro* DMD (DM basis).

Enough forage to last the entire study was processed. The AWS was chopped to 10 cm average length and stored in a commodity bin. After chopping, AWS was thoroughly mixed with a front-end loader to minimize among bale variation. The GH was processed in an identical manner. Wheat middlings (WM) were purchased from a local flour mill, and barley grain (BAR), obtained from Utah State University Experiment Station stocks, was coarsely ground in a hammer mill which broke the kernels into three or four pieces.

The AWS was supplemented with WM which were 173 g/kg CP and 416 g/kg NDF (DM basis). The *in vitro* DMD of the WM supplement was 800 g/kg. The GH was supplemented with BAR which was 119 g/kg CP and 183 g/kg NDF (DM basis). Mineral and vitamin supplements and premixes were added to both diets as needed to ensure their adequacy (Table 1).

After each 30 d of gestation, diets were reformulated as the NE_m and CP requirements of the cows increased with advancing fetal development. As much as possible, the amount of diet fed was adjusted rather than making changes in the proportion of ingredients in the diets (Table 1).

Diets were offered as total mixed rations (Table 1). Enough of the diets to last 10–12 d were mixed in a vertical screw-type mixing wagon and stored in a clean and dry commodity bin. Appropriate amounts of the diets were weighed and rations fed at 0800 h daily to each cow based on calculated NE_m requirements for her BW, day of gestation, and environmental conditions (Table 1). Cows were weighed and received a visual BCS scale (1 emaciated to 9 obese; Selk, 2010) at the beginning of the study and at 28 d intervals thereafter. Back fat thickness between the 12th and 13th ribs was also measured using ultrasonography (Aloka Co., LTD, SSD 500, 6-22-1, Mure, Mitaka-SHI, Tokyo, Japan) at 28 d intervals to help ensure the cows were fed their required level of nutrients from the diets.

2.4. Digestibility of diets by cows

During the first week of January, apparent total tract DMD of the diets was measured to help ensure adequate nutrient intake and to determine if the available nutrient intake associated with the diets was similar. To estimate apparent total tract DMD, the differential concentrations of acid insoluble ash (AIA) in diet versus feces were used. The AIA was an acceptable internal marker as both diets were >30 g/kg AIA (Van Keulen and Young, 1977).

2.5. Calf management procedures and diets prior to testing

On March 1, as cows approached parturition, they were moved from individual pens and placed in two clean calving pens, where they remained on their assigned diet until they calved. The first cow calved on March 13 and the last cow calved on March 22. Immediately after calving, all cows and calves were placed in a large clean pen which allowed calves access to an isolated loafing area bedded with wood shavings. While in this pen, good quality orchardgrass alfalfa hay (146 g/kg CP [DM basis] and 643 g/kg *in vitro* DMD) was available *ad libitum*. All cow calf pairs were fed high quality alfalfa grass hay in common for 45 d prior to their being placed on pasture. Calves had no access to low quality forages, as calves exposed to low quality forages such as AWS with their mothers have greatly improved performance on such forage when they eat them later in life (Wiedmeier et al., 2002).

From May 7 until October 19, all cow calf pairs grazed the same meadow pastures where the cows had grazed the previous year. The main forages were Kentucky bluegrass (*Poa pratensis* 300 g/kg), quackgrass (*Agropyron repens* 250 g/kg), silver sedge (*Carex praegracilis* 150 g/kg), reed canarygrass (*Phalaris arundinacea* 100 g/kg), tall wheatgrass (*Agropyron elongatum* 100 g/kg), and intermediate wheatgrass (*Agropyron intermedium* 100 g/kg). Cow calf pairs from this study grazed in common with 35 other cow calf pairs not a part of the study. All cattle were rotated through the three parcels at 20–24 d intervals. To maintain forage quality after grazing, each parcel was flood irrigated using water from a free flow artesian well. Due to the unevenness of the topography of the meadow, only about 0.75 of the surface area was irrigated.

While on pasture, cows received booster vaccinations for clostridial and reproductive diseases. Calves received initial vaccinations for clostridial diseases in addition to diseases associated with bovine respiratory disease complex and they received booster vaccinations for these diseases after being on the pastures for 4 wk. Cows and calves received a broad spectrum anthelmintic for internal and external parasites after being on pasture for 4 wk. The health of all cattle was observed daily by researchers and the attending veterinarian for any signs of lethargy and disinterest in foraging and none were observed. The first week of August, about midway through the grazing season, cows and calves were weighed and assessed for general health and growth rate, and sprayed with Permethrin (KMG Chemicals, Houston, TX, USA) to control external parasites.

2.6. Calf diets, forage DM intakes and digestibilities, and calf weights during testing

On October 19, calves were weaned, placed in a common pen, and fed good quality alfalfa grass hay (152 g/kg CP [DM basis] and 672 g/kg *in vitro* DMD) *ad libitum*. Calves remained in this pen until November 2. At the end of this weaning adjustment period, calves again received booster vaccinations for clostridial and bovine respiratory disease complex plus a broad spectrum anthelmintic for control of internal and external parasites. From this group of 18 weanling calves, 12 were randomly selected, 6 each from dams who had been fed each diet. Groups were comparable regarding sex, adjusted 205 d BW, and genetic relationship, which was relatively high because all dams were at least half siblings and all calves were sired by the same bull. Three calves in each group were from cows who were full sisters.

On November 3, the 12 calves were placed in individual 4×7 m pens and fed a diet similar to the HF diet except the WM, mineral supplements, and vitamin and mineral premixes were formulated into a separate supplement (WM, 944 g/kg; limestone, 21.8 g/kg; salt, 12.1 g/kg; vitamin premix, 15.1 g/kg; and mineral premix, 7.5 g/kg). The BW of calves in the two groups did not differ (274 ± 3.5 kg). As calf BW were estimated to be 311 kg at the end of a 40 d feeding period, an estimated calf BW of 293 kg was used to determine the amount of WM supplement to feed, which was offered at 0.75 of the 311 kg BW, or 2.2 kg DM/d.

Calves were fed AWS at a 10–20 g/kg refusal rate to reduce sorting. Previous experience of our research group with feeding AWS has shown excessive sorting at higher refusal rates. Our former experiments show that DM intake is higher when AWS

is provided only once daily, as cattle wait for the next feeding rather than consume AWS when AWS is provided twice daily. The WM supplement, fed daily at 0800 h, was consumed by all calves in <30 min.

Calves were fed for 40 d using these procedures. The first 26 d was an adaptation period and AWS intake was measured in the next 14 d. During the last 5 d, apparent total tract DM digestibility of the diet was measured by procedures described for cows using AIA in the diet and feces (Van Keulen and Young, 1977). Samples of the WM supplement, AWS and AWS refusals were collected daily and placed in a forced air oven at 105 °C for 8 h to determine DM.

Calves were weighed at the end of the DM intake and digestibility phases, and then fed HF diets for an addition 28 d and weighed again to determine daily BW gain. Calves were not allowed access to forage or water from 1600 to 0800 h the next morning when they were weighed.

2.7. Chemical analyses and digestibility measurement in cows and calves

Diet and fecal samples from each calf and cow were collected during the last 5 d of the experiment to measure DM digestibility. Diet sampling commenced 24 h prior to fecal sampling to account for estimated digesta passage rate. Fecal samples, collected twice daily at 0730 and 1800 h (cows) and 0800 and 1700 h (calves), were generally collected from fresh uncontaminated droppings in the pens, rather than rectal grab samples, in order to reduce animal stress. In the rare event a fecal sample could not be collected in this manner, a rectal grab sample was collected. Cattle were usually bedded and arose and defecated at our arrival for feeding and sampling.

Immediately after collection, diet, refusal and fecal samples were dried in a forced-air oven at 60 °C for 72 h to determine DM intake and AIA was determined according to Van Keulen and Young (1977). Diet and fecal samples were ground to pass a 1 mm screen in a Wiley mill and then composited by animal. Samples were analyzed for N (model FP-428, Leco Co., St. Joseph, MI; AOAC 968.06, AOAC, 2000). Fiber was analyzed (ANKOM Technology, Macedon, NY, USA) for ADF (ANKOM #12) and NDF (ANKOM #13). Neither an amylase pretreatment step nor sodium sulphite was included in the NDF procedure and NDF and ADF are expressed inclusive of residual ash. Levels of eNDF (Pitt et al., 1996), NDSC, NDSF, NF-NDSC (Ariza et al., 2001) and NE_m (NRC, 2000) were also determined.

2.8. Statistical analyses

The statistical design for the repeated measures analysis of variance had 2 treatments (HF versus LF diets) and 6 calves were nested within each treatment. Data were analyzed as a split plot design with calves (random) nested within treatments. Diet (*i.e.*, HF, LF) was the between animal factor and day was the repeated measure (fixed). The response variables for calves were DM intake, DM digestibility and BW gain. All statistical analyses used SAS (2003). Results were analyzed using PROC MIXED for repeated measures (Littell et al., 1998). Model diagnostics included testing for normal distributions of error residuals and homogeneity of variances. All data met assumptions of normality and homogeneity. Means were analyzed using pairwise differences (DIFF) of least squares means.

3. Results

3.1. Cow nutrition during pregnancy

The DM intake of cows fed HF diets in January was 12.8 kg/d and DMD was 578 g/kg. The DM intake of cows fed LF diets was 11.0 kg/d and the DMD was 676 g/kg. Crude protein intakes were nearly identical, as were soluble fiber concentrations (Table 1).

Though DDM of the diets was nearly identical, their carbohydrate profiles were very different. Cows fed HF diets ate nearly 66% more NDF and 91% more eNDF than cows fed LF diets. Cows fed LF diets ate nearly 10-fold more non-fibrous soluble carbohydrate than those fed HF diets (Table 1).

3.2. Calf responses during testing

The response of calves to straw varied by treatment (Table 2). Calves whose dams had eaten HF diets during gestation ate more AWS than calves whose dams ate the LF diet (5.6 versus 5.3 kg/d, respectively; $P=0.04$). The HF calves digested a higher proportion of AWS (545 versus 523 g/kg, respectively, $P=0.03$). Thus, HF calves ate more DDM than LF calves (3.1 versus 2.8 kg/d, respectively, $P<0.01$). Differences in DM intake and digestibility affected BW gains such that HF calves gained numerically ($P=0.13$) more BW than LF calves (*i.e.*, 0.45 versus 0.41 kg/d).

4. Discussion

4.1. Role of experience in food acceptance and intake

We hypothesized that experience eating a high fiber diet *in utero* would enhance intake and digestibility of fiber later in life. Compared with calves whose dams ate a LF diet during gestation, calves whose dams ate a HF diet had higher DM intake

Table 2

Diet and body weight responses of 8 mo old calves previously exposed *in utero* to low or high fiber diets ingested by their mothers. Twelve calves were randomly selected for the study, 6 each from dams fed either the high-fiber or low-fiber diets during late gestation.

	Maternal diet		SEM	P
	Low fiber	High fiber		
AWS ^a intake, kg/d				
DM	5.3	5.6	0.09	0.04
DDM	2.8	3.1	0.05	<0.01
AWS DM digestibility, g/kg ^b	523	545	5.9	0.03
AWS proportion of the diet, g/kg ^c	723	733	33.0	0.05
Average daily gain, kg/d	0.41	0.45	0.023	0.13

^a Ammoniated wheat straw.

^b Calculated assuming supplement *in vitro* DDM of 800 g/kg.

^c Calculated based on a constant supplement intake of 2.2 kg DM/d.

and digestibility of AWS and they gained numerically more BW. As the base ingredients in the HF and LF diets differed, and the former was ammoniated, we cannot attribute all differences in performance of the calves to fiber alone, but to the overall characteristics of the diets. While the mechanisms which caused HF and LF calves to differ were not assessed, many factors associated with consuming, digesting, absorbing and metabolizing the two diets could have prepared fetuses to use HF or LF postpartum. For example, experiences *in utero* and early in life alter morphological structures and physiological processes which affect behavior (Provenza and Villalba, 2006).

The fetal taste system is fully functional during the last trimester of gestation, and flavors in the mother's diet influence the forage preferences of her offspring. We assume that familiarity with the flavor of AWS eaten by HF dams, and passed to their fetuses during gestation, increased intake of AWS by offspring, as observed by others (Nolte et al., 1992; Nolte and Provenza, 1992a,b; Simitzis et al., 2008). However, as DM digestibility of AWS also increased, intake alone cannot account for the improved use of AWS by calves whose dams consumed HF diets during gestation.

Energetic precursors entering the gut during foraging markedly increases preferences for flavors of forages by sheep (Villalba and Provenza, 1997a), and ruminal volatile fatty acid (VFA) profiles influence the strength of those responses (Villalba and Provenza, 1997b) which, in turn, changes digestion and metabolism (Provenza, 1995b). Because rumen fermentation would be slower in cows fed HF versus LF diets, the flow of VFA from the rumen into the portal blood, and ultimately to the fetus, would likely have been slower, and perhaps more sustained, with HF diets. In addition, the VFA profile likely differed. Development of rumen epithelium depends on stimulation by VFA, which influences epithelial surface area (Van Soest, 1994). Cell proliferation in the epithelium is enhanced by acetate and propionate (Sakata and Tamate, 1979), and papillae from steers fed hay used more VFA than papillae from steers fed concentrate (Weighand et al., 1975). Thus, changes in VFA profiles and rates of their production likely influenced preferences for flavor and the later ability to digest HF diets by the fetus, which manifest in calves after birth.

Straw and other low quality forages are mainly insoluble fibrous carbohydrates (>700 g/kg NDF) which can be used by fibrolytic bacteria, protozoa and fungi in the gastro-intestinal tracts of ruminants. In our study, the profiles of these microorganisms likely did not differ because cows and calves were co-mingled after gestation. However, the demographics and metabolic activity of the fibrolytic microorganisms inhabiting the rumen and colon of HF fed calves was likely enhanced compared to LF fed calves. The number of fibrolytic microorganisms and their metabolic activities determine rate and extent of fermentation of fiber in the rumen. Morphological and physiological characteristics affect microbiological factors, including salivation rate, saliva composition, rumen volume, rate and amplitude of rumen contractions, rumen fluid dilution rate, rate of ruminal passage of digesta, rumination patterns, efficiency of rumen nutrient recycling, and interactions between VFA produced *via* fermentation and the gut epithelium and other body tissues. Alterations in any of these could have improved fibrolysis in HF fed calves.

The diets which the cows ate during gestation could have changed their grazing behavior on pasture during summer, which could have been transmitted to their calves, resulting in the differences in AWS utilization. However, this was unlikely for three reasons. First, during gestation measures were made to insure that nutrient intakes of the two diets were similar and adequate to meet the cow's nutrients requirements. While nutrient deficiencies during gestation would likely change grazing behavior on pasture, the NE_m, CP, vitamin, and mineral intakes of the two groups of cows were nearly identical throughout pregnancy, which is reflected in the nearly identical weights of their calves at birth. Second, as all cow calf pairs were fed high quality alfalfa grass hay in common for several weeks prior to being placed on pasture, any nutrient deficiencies developed during gestation would likely have been attenuated during this period. Third, cows and calves grazed in common on irrigated pastures composed primarily of cool season grasses under a rotational grazing system. Thus, the opportunity for differences in diet selection or nutrient intake was limited. If there had been differences in grazing behavior between the two groups, differences in cow and calf performance would have been expected. However, there were no differences in cow BW or BCS by the end of the summer grazing period, nor were there difference in calf 205 d BW.

5. Conclusions

Calves exposed *in utero* to high fiber diets (mostly ammoniated wheat straw) ate and digested more ammoniated wheat straw than calves exposed *in utero* to low fiber diets (mostly a mixed grass hay of 700 g/kg orchardgrass and 300 g/kg meadow bromegrass). Higher digestible dry matter intake is likely important when pregnant cows and their offspring overwinter under extensive range conditions on fibrous dormant forages which only marginally satisfy their NE_m requirements. These effects on offspring, further amplified by experiences with their mothers early in life (Wiedmeier et al., 2002), make cows and their progeny better adapted to using dormant forages during winter.

Acknowledgements

This work was supported by the Utah Agricultural Experiment Station and is published with the approval of the Director, Utah Agricultural Experiment Station, and Utah State University, as journal paper number 8382.

References

- AOAC, 2000. Official Method of Analysis 968.06, vol. I., 17th edition Association of Official Analytical Chemists, Inc., Gaithersburg, MD, USA.
- Ariza, P., Bach, A., Stern, M.D., Hall, M.B., 2001. Effects of carbohydrates from citrus pulp and hominy feed on microbial fermentation in continuous culture. *J. Anim. Sci.* 79, 2713–2718.
- Biquand, S., Biquand-Guyot, V., 1992. The influence of peers, lineage and environment on food selection of the criollo goat (*Capra hircus*). *Appl. Anim. Behav. Sci.* 34, 231–245.
- Chadwick, M.A., Vercoe, P.V., Williams, I.H., Revell, D.K., 2009a. Programming sheep production on saltbrush: adaptations of offspring from ewes that consumed high amounts of salt during pregnancy and early lactation. *Anim. Prod. Sci.* 49, 311–317.
- Chadwick, M.A., Vercoe, P.V., Williams, I.H., Revell, D.K., 2009b. Dietary exposure of pregnant ewes to salt dictates how their offspring respond to salt. *Physiol. Behav.* 97, 437–445.
- Chadwick, M.A., Vercoe, P.V., Williams, I.H., Revell, D.K., 2009c. Feeding pregnant ewes a high-salt diet or saltbrush suppresses their offspring's postnatal rennin activity. *Animal* 3, 972–979.
- Davis, J.M., Stamps, J.A., 2004. The effect of natal experience on habitat preferences. *Trends Ecol. Evol.* 19, 411–416.
- Distel, R.A., Provenza, F.D., 1991. Experience early in life affects voluntary intake of blackbrush by goats. *J. Chem. Ecol.* 17, 431–450.
- Distel, R.A., Villalba, J.J., Laborde, H.E., 1994. Effects of early experience on voluntary intake of low-quality roughage by sheep. *J. Anim. Sci.* 72, 1191–1195.
- Distel, R.A., Villalba, J.J., Laborde, H.E., Burgos, M.A., 1996. Persistence of the effects of early experience on consumption of low-quality roughage by sheep. *J. Anim. Sci.* 74, 965–968.
- Duffy Jr., A.M., Clobert, J., Moller, A.P., 2002. Hormones, developmental plasticity and adaptation. *Trends Ecol. Evol.* 17, 190–196.
- Flores, E.R., Provenza, F.D., Balph, D.F., 1989a. Role of experience in the development of foraging skills of lambs browsing the shrub serviceberry. *Appl. Anim. Behav. Sci.* 23, 271–278.
- Flores, E.R., Provenza, F.D., Balph, D.F., 1989b. The effect of experience on the foraging skill of lambs: importance of plant form. *Appl. Anim. Behav. Sci.* 23, 285–291.
- Glasser, T.A., Ungar, E.D., Landau, S.Y., Perevolotsky, A., Muklada, H., Walker, J.W., 2009. Breed and maternal effects on the intake of tannin-rich browse by juvenile goats (*Capra hircus*). *Appl. Anim. Behav. Sci.* 119, 71–77.
- Green, G.C., Elwin, R.L., Mottershead, B.E., Lynch, J.J., 1984. Long-term effects of early experience to supplementary feeding in sheep. *Proc. Aust. Soc. Anim. Prod.* 15, 373–375.
- Howerly, L.D., Provenza, F.D., Banner, R.E., Scott, C.B., 1998. Social and environmental factors influence cattle distribution on rangeland. *Appl. Anim. Behav. Sci.* 55, 231–244.
- Lalman, D., Horn, G., Huhnke, R., Redmon, L.A., 2010. Ammoniation of Low Quality Roughages. Oklahoma Cooperative Extension Service PSS-2243, Stillwater, OK, USA.
- LeDoux, J., 2002. *Synaptic Self: How Our Brains Become Who We Are*. Viking Penguin, New York, NY, USA.
- Littell, R.C., Henry, P.R., Ammerman, C.B., 1998. Statistical analysis of repeated measures data using SAS procedures. *J. Anim. Sci.* 76, 1216–1231.
- Mirza, S.N., Provenza, F.D., 1990. Preference of the mother affects selection and avoidance of foods by lambs differing in age. *Appl. Anim. Behav. Sci.* 28, 255–263.
- Mirza, S.N., Provenza, F.D., 1992. Effects of age and conditions of exposure on maternally mediated food selection in lambs. *Appl. Anim. Behav. Sci.* 33, 35–42.
- Moore, D.S., 2002. *The Dependent Gene: The Fallacy of "Nature vs. Nurture"*. Henry Holt and Company, New York, NY, USA.
- Nolte, D.L., Provenza, F.D., Callan, R., Panter, K.E., 1992. Garlic in the ovine fetal environment. *Physiol. Behav.* 52, 1091–1093.
- Nolte, D.L., Provenza, F.D., 1992a. Food preferences in lambs after exposure to flavors in milk. *Appl. Anim. Behav. Sci.* 32, 381–389.
- Nolte, D.L., Provenza, F.D., 1992b. Food preferences in lambs after exposure to flavors in solid foods. *Appl. Anim. Behav. Sci.* 32, 337–347.
- NRC, 2000. *Nutrient Requirements of Beef Cattle*. National Academies Press, Washington, DC, USA.
- Ortega-Reyes, L., Provenza, F.D., 1993a. Amount of experience and age affect the development of foraging skills of goats browsing blackbrush (*Coleogyne ramosissima*). *Appl. Anim. Behav. Sci.* 36, 169–183.
- Ortega-Reyes, L., Provenza, F.D., 1993b. Experience with blackbrush affects ingestion of shrub live oak by goats. *J. Anim. Sci.* 71, 380–383.
- Ortega Reyes, L., Provenza, F.D., Parker, C.F., Hatfield, P.G., 1992. Drylot performance and ruminal papillae development of lambs exposed to a high concentrate diet while nursing. *Small Rum. Res.* 7, 101–112.
- Pitt, R., van Kessel, J., Fox, D., Pell, A., Barry, M., van Soest, P., 1996. Prediction of the ruminal volatile fatty acids and pH within the net carbohydrate and protein system. *J. Anim. Sci.* 74, 226–244.
- Provenza, F.D., 1995a. Tracking variable environments: there is more than one kind of memory. *J. Chem. Ecol.* 21, 911–923.
- Provenza, F.D., 1995b. Postingestive feedback as an elementary determinant of food preference and intake in ruminants. *J. Range Manage.* 48, 2–17.
- Provenza, F.D., 2003. *Foraging Behavior: Managing to Survive in a World of Change*. Utah State University Press, Logan, UT, USA.
- Provenza, F.D., 2008. What does it mean to be locally adapted and who cares anyway? *J. Anim. Sci.* 86, E271–E284.
- Provenza, F.D., Balph, D.F., 1988. The development of dietary choice in livestock on rangelands and its implications for management. *J. Anim. Sci.* 66, 2356–2368.
- Provenza, F.D., Balph, D.F., 1990. Applicability of five diet-selection models to various foraging challenges ruminants encounters. In: Hughes, R.N. (Ed.), *Behavioural Mechanisms of Food Selection*. NATO ASI Series G: Ecological Sciences, vol. 20. Springer-Verlag, Berlin, Heidelberg, Germany, pp. 423–459.
- Provenza, F.D., Villalba, J.J., 2006. Foraging in domestic vertebrates: linking the internal and external milieu. In: Bels, V.L. (Ed.), *Feeding in Domestic Vertebrates: From Structure to Function*. CABI Publ., Wallingford, Oxfordshire, UK, pp. 210–240.
- Sakata, T., Tamate, H., 1979. Rumen epithelium cell proliferation accelerated by propionate and acetate. *J. Dairy Sci.* 62, 49–52.
- SAS®, 2003. *Statistical Analysis System, Version 9.1*. SAS Institute, Cary, NC, USA.

- Schlichting, C.D., Pigliucci, M., 1998. *Phenotypic Evolution: A Reaction Norm Perspective*. Sinauer Publications, Sinauer, MA, USA.
- Selk, G., 2010. *Body Condition Scoring Beef Cows*. Oklahoma Cooperative Extension Service ANSI-3283, Stillwater, OK, USA.
- Simitzis, P.E., Deligeorgis, S.G., Bizelis, J.A., Fegeros, K., 2008. Feeding preferences in lambs influenced by prenatal flavour exposure. *Physiol. Behav.* 93, 529–536.
- Squibb, R.C., Provenza, F.D., Balph, D.F., 1990. Effect of age of exposure on consumption of a shrub by sheep. *J. Anim. Sci.* 68, 987–997.
- Thorhallsdottir, A.G., Provenza, F.D., Balph, D.F., 1990. Ability of lambs to learn about novel foods while observing or participating with social models. *Appl. Anim. Behav. Sci.* 25, 25–33.
- Van Keulen, J., Young, B.A., 1977. Evaluation of acid-insoluble ash as a natural marker in ruminant digestibility studies. *J. Anim. Sci.* 44, 282–288.
- Van Soest, P., 1994. *Nutritional Ecology of the Ruminant*, 2nd edition. Cornell University Press, Ithaca, NY, USA.
- Villalba, J.J., Provenza, F.D., 1997a. Preference for wheat straw by lambs conditioned with intraruminal infusions of starch. *Br. J. Nutr.* 77, 287–297.
- Villalba, J.J., Provenza, F.D., 1997b. Preference for flavored wheat straw by lambs conditioned with intraruminal infusions of acetate and propionate. *J. Anim. Sci.* 75, 2905–2914.
- Weighand, E., Young, J.W., McGilliard, A.D., 1975. Volatile fatty acid metabolism by rumen mucosa from cattle fed hay or grain. *J. Dairy Sci.* 58, 1294–1300.
- Wiedmeier, R.D., Walters, J.L., Cockett, N.E., 1995. Heritability of low-quality forage utilization in beef cattle. *Proc. West. Sect. Am. Soc. Anim. Sci.* 46, 404–406.
- Wiedmeier, R.D., Provenza, F.D., Burritt, E.A., 2002. Exposure to ammoniated wheat straw as suckling calves improves performance of mature beef cows wintered on ammoniated wheat straw. *J. Anim. Sci.* 80, 2340–2348.