

COMPARITIVE DIGESTIBILITY BY
CATTLE VERSUS SHEEP: EFFECT
OF FORAGE QUALITY

By

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Table of Contents

Chapter	Page
I. INTRODUCTION.....	1
II. REVIEW OF LITERATURE.....	3
Feed Processing Form.....	3
Site and Extent of Digestion.....	3
Ruminal Function.....	6
Post Ruminal Digestion.....	9
Relative Stomach Size.....	9
Efficiency of Energy Use for Maintenance and Gain.....	10
Summary.....	11
Literature Cited.....	12
III. COMPARITIVE DIGESTIBILITY BY CATTLE VERSUS SHEEP: EFFECT OF FORAGE QUALITY.....	16
Abstract.....	16
Introduction.....	17
Materials and Methods.....	18
General.....	18
Animals and Housing.....	18
Experimental Design and Sampling.....	19
Laboratory Methods.....	20
Calculations and Statistics.....	20

Results.....	22
Discussion.....	27
Implications.....	30
Literature Cited.....	31

List of Tables

Table	Page
1. Chemical composition of experimental forages fed to beef steers and wethers.....	34
2. Effects of ruminant specie and forage quality on intake, fecal output and total tract digestion.....	35
3. Effect of ruminant specie and forage quality on nutrient intake, fecal and digestible nutrient intake [g/(d*kg BW)].....	36
4. Effect of ruminant specie and forage quality on nutrient intake, fecal and digestible nutrient intake [g/(d*kg BW ^{0.75})].....	37
5. Effect of ruminant specie and forage quality on in situ rate and extent of ruminal DM and NDF digestion.....	38
5. Effects of ruminant specie and forage quality on ruminal fermentation.....	39

CHAPTER I

Introduction

Ruminant animals may have a diverse range of body size, but are generally anatomically and physiologically similar. Ruminant animals can be defined as even toed hooved mammals that chew their cud and have a complex four chambered stomach. Cattle and sheep are the most common ruminant animals raised in the United States. For this reason most of the ruminant nutrition research conducted to date has involved cattle and sheep. With the rising cost of maintaining research animals and the growing concerns of budgets within research institutions, a popular approach has been to use sheep as a research model for cattle. Sheep have many advantages over cattle, including: 1) they are smaller and consume less feed; 2) they cost only a fraction of a feeder calf or finishing steer; 3) they take up less space and require less day-to-day maintenance. The potential downside to using sheep as a model in scientific experiments is that results may not be the same as results from cattle. Research has shown that bovine and ovine don't always respond to diets the same. Therefore, the question is whether or not research and results conducted using sheep can be used for improving beef production. It is important that scientists fully understand the nutritional similarities and differences between sheep and cattle if they want to model cattle using sheep.

Although differences in nutrient digestibility between cattle and sheep are generally small, highly digestible foods, such as cereal grains, tend to be more efficiently digested by sheep, whereas poorly digested feedstuffs, such as low quality roughages, tend to be better digested by cattle (McDonald, 2002). It has been hypothesized that this occurs because cattle have a greater proportional ruminal fill and lower particle passage

rate than sheep. It is generally believed that sheep masticate feed more extensively than cattle, and that reduction in particle size may allow sheep to have a more rapid passage rate.

Research contrasting different ruminant species has been conducted for almost a century. During that time period, research has shown the similarities and differences among cattle and sheep. The following chapter summarizes that literature.

CHAPTER II

Review of Literature

Feed Processing Form

The form in which a concentrate or forage diet is offered to sheep and cattle has been shown to influence the way animals will perform, but generally processing effects are similar for cattle and sheep. For example, Weir et al. (1959) compared pelleted rations to meal or chopped rations. For both steers and wethers, their results showed an advantage of feeding high roughage diets as pellets versus non-pelleted rations. The diet consisted of high quality alfalfa that was chopped and mixed with ground barley. Specifically, the pelleted ration showed increased gains and improved feed conversion for both steers and wethers. This has been supported by research conducted with high-concentrate diets. Newland et al. (1962) reported an improvement in feed efficiency of steers and lambs fed pelleted corn vs. ground or shelled corn.

Site and Extent of Digestion

Forages and fibrous roughages consumed by ruminants consist mainly of β -linked polysaccharides such as cellulose, which cannot be broken down by mammalian digestive enzymes (McDonald, 2002). That is why ruminant animals have a special digestive system that involves microbial fermentation of food before it is exposed to their own digestive enzymes. Many factors which affect total digestibility of diets fed to ruminants also influence site at which digestion occurs (Church, 1998).

It has been shown that cattle and sheep vary in how long feedstuffs are retained in the digestive tract and the extent to which they are digested. Prigge et al. (1994) stated that the particulate retention time differed ($P < 0.10$) with ruminant species; cattle retained digesta approximately 50% longer than sheep. This was supported by data of Reid et al. (1990), who observed differences in DM and NDF digestibility between cattle and sheep, suggesting that increased body size resulted in increased digestibility due to longer retention times. Reid et al. (1990) also showed that dry matter intake ($\text{g/kg BW}^{0.75}$) was 26.8 grams greater for cattle than for sheep, and intake of NDF averaged across three different types of forages was 19.1 grams greater for cattle than for sheep. Prigge et al. (1994) observed significant ruminant species x forage and ruminant species x level of intake interactions for digestible dry matter. Prigge et al. (1984) fed steers and wethers switchgrass or ryegrass at two levels of intake. Total tract digestibility of ryegrass was similar in steers and wethers; however, digestibility of switchgrass was seven percentage units less in wethers than steers. At the high level of intake, wethers digested both forages six units less than steers, whereas the difference in digestibility was only one unit less when forages were fed at low intake. In support, McDonald (2002) reported that cattle digest low-quality forages better than sheep. In addition, Averts et al. (1984) suggested that the better digestion by cows compared with sheep was partly due to the longer retention time of low-quality feeds in the rumen.

Digestion of nutrients appears to vary between ruminant species depending on the quality of the forage. Dry matter intake by both cattle and sheep was 20 grams higher for alfalfa than for cool season (C_3) and warm season (C_4) grasses (Reid et al., 1990). In addition, dry matter turnover times for the trials conducted by Reid et al. (1990) were

faster for alfalfa than for the other two grasses. Species differences that occurred in their experiment varied. However, the authors reported that mean dry matter intake was greater for cattle than sheep. Also dry matter digestion was three percent higher for cattle than sheep, and NDF digestibility was three percent higher for cattle and goats than for sheep. Reid et al. (1990) stated that a critical factor in limiting the utilization of warm-season grasses by ruminant animals may be the availability of N at the ruminal level for effective fiber degradation. Cattle seem to have the advantage in forage digestion except for when ruminal nitrogen is limiting, where sheep have shown an advantage in energy and protein digestion (Alexander et al., 1962). Improved digestibility of low-quality grass hay by sheep compared with cows could be ascribed to the low protein content of the ration. Alexander et al. (1962) reported that yearling wethers fed low-quality coastal Bermuda grass hay had significantly greater digestibility of protein and energy than mature cows. This advantage in digestibility by sheep apparently disappears as the protein levels of feeds increase above 15% of dry matter (Averts, 1984). For example, in the work of Alexander et al. (1962), digestibility of forages with higher protein content was greater in cattle compared with sheep. Similarly, Cipolloni et al. (1951) showed a significant species x feed interaction with dry roughages which would tend to confirm these results. Specifically, Cipolloni et al. (1951) showed differences in the digestibility of organic matter, crude fiber, nitrogen-free extract, ether extract and total digestible nutrient content of dry roughages between cattle and sheep. Cipolloni et al. (1951) stated that for accurate results on digestibility data, one must use cattle for collecting cattle data, and sheep for collecting sheep data.

Jordan et al. (1951) fed three different qualities of prairie hay to steers and wethers and noted the greatest difference between species was when late maturity hay was fed. Jordan et al. (1951) suggested that sheep showed greater variation among animals for a given ration than cattle. However, in contrast to Cipolloni et al. (1951), Jordan et al. (1951) indicated that differences were less than two percent and suggested that the many advantages for testing many feeds using sheep warranted applying their digestion coefficients to cattle.

Research has been conducted comparing the utilization of silages by sheep and cattle. This work has shown digestibility and nutritive value with steers was highest for silage harvested at the medium-hard dough stage of ear development (Colovos et al., 1970). Colovos et al. (1970) reported that sheep digested and utilized the two more mature forms of silages five percent better than steers. Colovos et al. (1970) concluded from his study that the feeding value of corn silage determined by using sheep can not be applied to cattle.

Ruminal Function

A question that has been proposed is how ruminal function differs between different ruminant species. For example, rumination time is a factor that could influence results of research conducted with one ruminant species versus another. Welch et al. (1969) conducted research to evaluate the effect of forage quality on rumination time of sheep. Their results showed that with a decline in forage quality and increasing fiber digestion, rumination time increased in sheep. To compare their results with cattle, Welch et al. (1970) followed up a year later with the same research trial using cattle.

Results from Welch et al. (1970) showed that the same cell wall constituent (CWC)-rumination time relationship that existed in sheep also existed in cattle. For example, when the poorer-quality forage was consumed both sheep and cattle required more rumination time for particle size reduction. However, a difference was noted in the amount of time needed to ruminate per gram of CWC. Cattle rumination times ranged from 0.11 to 0.15 min./g CWC, whereas sheep rumination time was between 1.12 and 1.14 min./g CWC. Welch et al. (1970) stated that this difference could be attributed to many factors. One factor suggested was that cattle have a larger reticulo-omasal orifice which will accept larger sizes of course fiber particles. An additional factor was that cattle have a bigger mouth with larger tooth area which allows them to be more efficient at grinding forages.

Reid et al. (1990) reported there was no difference between C₄, C₃, and legume classes of forages in rate of passage averaged across animal species. Passage rates tended to be slower for warm-season grasses than C₃ and the legume. Reid et al. (1990) also indicated that cattle had slower particulate passage rates than either sheep or goats. Ruminal turnover times (h) were also slower for cattle than for sheep (Reid et al., 1990). In contrast to the suggestion made by Welch et al. (1970), greater rumination times might result in a greater reduction in particle size and thereby increase particulate passage rate and decrease turnover time in sheep compared with cattle.

Differences in bacteria and protozoa types and numbers have also been shown to vary among ruminant species. When fed a winter concentrate ration cattle and sheep have been shown to contain about 50 billion bacteria per gram of fresh ruminal contents (Gall et al., 1949). On lush pasture in the month of June, Gall et al. (1949) reported that

cattle had 96.1 billion bacteria and sheep had 85.4 billion bacteria per gram of ruminal contents. Gall et al. (1949) concluded that there were no differences in bacteria types between cattle and sheep when fed similar rations. Dehority (1978) reported that sheep inoculated with steer ruminal fluid developed 24 of the same types of microorganisms. Although the sheep developed the same organisms, the animal itself, by some physiological factors, determines which genera and species could become established in the rumen, suggesting a slight protozoa specificity in the domestic ruminant animal. Dehority (1978) suggested that some changes in the ruminal environment of an animal may be necessary for the establishment of some protozoa species. However, more than ruminant specie, the total number of ruminal bacteria appears to be more dependent upon the type of diet the animals are fed. Prigge et al. (1984) observed no differences between the microfora of cattle and sheep, and in their ability to degrade different forage species.

Gall et al. (1949) indicated that there was no difference in ruminal pH between ruminant species fed a similar diet. Gall et al. (1949) showed that the pH of ruminal contents that were not contaminated with saliva ranged from about 6.3 to 7.3 for both cattle and sheep. Prigge et al. (1984) reported similar results. In addition, volatile fatty acids (VFA) and the acetate:propionate ratio were not influenced by ruminant species in the work of Prigge et al. (1984).

Concentrations of VFA have been researched and compared across ruminant species. Newland et al. (1962) researched the effects of ration preparation on VFA concentrations in ruminant animals. He showed that various kinds of processed corn effected a change in the molar proportion of ruminal VFA. The most important change was the significant decrease in the molar percent of acetic acid and an increase in

propionic acid by most forms of processed corn compared with ground shelled corn. However, this narrowing of the acetate:propionate ratio was marked in both sheep and cattle. Newland et al. (1962) also showed that processed corn resulted in greater total VFA concentration than ground shelled corn, and that the change in VFA concentration was most likely related to the improved feed efficiency by sheep and cattle fed processed rations. In general, VFA concentration and molar proportions of VFA appear to be influenced more by diet than by ruminant specie.

Post-Ruminal Digestion

Ruminal digestion in ruminant animals has been extensively studied, but there has been limited work conducted on post-ruminal digestion. Warner et al. (1972) showed that one-third of the cellulose administered into the lower digestive tract of steers and wethers was digested. Since the amount of infused cellulose digested was the same when cellulose was infused into the abomasum or cecum, it was suggested that most of the post-ruminal digestion of cellulose occurred in the cecum and large intestine. Although a species difference may exist, it appears reasonable to assume based on Warner et al. (1972) results that most of the cellulose digested posterior to the rumen is digested in the cecum and large intestine, and that both steers and wethers respond the same.

Relative Stomach Size

The relative size of cattle and sheep stomach has been shown to differ. Warner et al. (1965) reported differences in the size of the compartments of the stomach using the wet stomach tissue method. They showed the mass of the reticulo-rumen of cattle was

around 56 to 60% of the total stomach mass, whereas the mass of the reticulo-rumen of sheep was 69 to 73% of the total size. The omasum of cattle was between 23 and 30% and for sheep it was between 5 and 6%. Finally, abomasal mass for cattle was 23 to 30% and for sheep it was 5 to 6% of the total stomach mass. Therefore, anatomical differences in the stomach complex between cattle and sheep appear to exist.

Efficiency of Energy use for Maintenance and Gain

The efficiency with which cattle and sheep digest various feeds is usually considered to be essentially the same. Although specific differences have been observed as previously discussed, it has generally been assumed that the differences are not very large. A comparison of the dietary energy requirements of different species, as well as different sized animals within a species, cannot be made on a weight basis alone (Garrett, 1959). Because body size of ruminant species varies greatly, it is both necessary and convenient to have some suitable unit of reference for comparing energy requirements. These values have varied over the years, but it is now generally accepted that basal metabolism varies with approximately the 0.75 power of body weight ($BW^{0.75}$; McDonald, 2002). Garrett et al. (1959) stated that the maintenance requirements of sheep and cattle are identical on the basis of $BW^{0.75}$. The estimates (coefficients) that Garrett et al. (1959) reported are: total digestible nutrients (**TDN**) = $0.036BW^{0.75}$; digestible energy (**DE**) = $76BW^{0.75}$; metabolizable energy (**ME**) = $62BW^{0.75}$; and net energy (**NE**) = $35BW^{0.75}$, where daily requirements for TDN and BW are expressed in pounds, and DE, ME, and NEg are in kilocalories. Blaxter et al. (1961) reported no differences of any magnitude were found in the percentage losses of dietary energy in feces, in urine or as

methane if comparisons were made at comparable nutritional levels in sheep versus cattle. Blaxter et al. (1961) added that the net availability of ME for maintenance was the same in both species at 80.4%.

Use of ionophores has become popular in ruminant diets to improve feed efficiency and/or rate of gain. In cattle, monensin and lasalocid increase apparent DE by an average of 2.0 percentage units (Spears, 1990). In sheep, responses in DE from feeding an ionophore have been variable, and on average have had no effect on DE (Spears, 1990). The differences observed between cattle and sheep in DE responses to ionophores may be related to species differences. Cattle consume more feed, which might explain the greater response in cattle. However, more experiments have been conducted with cattle, which might have biased the results. In addition, more experiments with cattle have been conducted with high-concentrate diets, whereas experiments with sheep have used high-roughage diets. Sheep generally had a greater response when high-concentrate diets were fed, similar to cattle.

Summary

Research comparing different ruminant animals has been conducted for more than a century. The data that has been generated over those years suggests that there is no clear cut answer as to whether or not sheep and cattle can be used interchangeably for research. However, there are several differences to consider. Site and extent of nutrient digestion appear to differ in cattle and sheep depending on quality of forages and nutrient value of the feeds. Although bacteria and protozoa numbers tend to differ, VFA concentrations appear to be similar between the species. Although data is limited,

efficiency of energy use for maintenance and gain is considered to be essentially the same. From the reviewed literature, it appears that sheep could be used as a model for cattle (or vice versa) in some but not all situations. Sheep should only be used as models when diet of high forage or medium quality forage. Differences become too large when low quality forage diets are fed. Scientists should make the decision to substitute sheep for cattle based on the previous literature and the research they propose to conduct.

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Chapter III

Comparative Digestibility by Cattle versus Sheep: Effect of Forage Quality

ABSTRACT: The objective was to determine the effect of forage quality on nutrient digestion by cattle vs. sheep. Five yearling English crossbred (Hereford x Angus) steers (initial BW = 440.4 ± 35.6 kg) and 5 yearling whiteface (Rambouillet x Columbia x Debouillet) wethers (initial BW = 44.4 ± 4.6 kg) each fitted with a ruminal cannula were randomly assigned to one of three forage sources in an incompletely replicated 6 x 6 Latin square design experiment. The treatment structure was arranged in a 2 x 3 factorial with ruminant species (2) and forage source (3) as the factors. Forage sources were: 1) alfalfa hay (*Medicago sativa*; 17.5% CP and 34.1% NDF, DM basis); 2) warm-season grass hay mix (*Bothriochloa ischaemum* and *Cynodon dactylon*; 7.3% CP and 74.7% NDF, DM basis); and 3) lovegrass hay (*Eragrostis curvula*; 2.5% CP and 81.9% NDF, DM basis). As a percent of BW, steers and wethers consumed similar ($P = 0.06$ to $P = 0.83$) amounts of forage and its nutrients, and intake was more influenced by forage quality ($P < 0.001$) than ruminant specie ($P = 0.06$ to $P = 0.83$). When expressed per unit of metabolic BW, cattle consumed more ($P < 0.001$) DM, NDF and N than sheep. Apparent total tract digestibility of nutrients was similar among steers and wethers when alfalfa or grass hay was fed, but was decreased to a greater extent in wethers when low-quality lovegrass hay was fed (ruminant specie x diet interaction, $P < 0.05$). Rate (%/h) of ruminal NDF disappearance was greater ($P = 0.02$) for alfalfa and the grass hay mix than lovegrass, but was not influenced ($P = 0.12$) by ruminant specie. In addition, ruminal DM fill was influenced more ($P < 0.01$) by forage than by ruminant specie ($P =$

0.07). Steers and wethers had greater ($P < 0.01$) DM fill from grass hay and lovegrass hay than alfalfa before and 4 h after feeding. With the exception of the branched-chain VFA, ruminal VFA were generally not influenced ($P = 0.06$ to $P = 0.59$) by ruminant specie. However, across all forage sources, wethers tended ($P = 0.06$) to have a greater proportion of propionate than steers. Total ruminal VFA concentration was greatest ($P < 0.001$) for alfalfa, intermediate for grass hay, and lowest for lovegrass hay. In contrast, the acetate:propionate ratio was highest ($P < 0.001$) for lovegrass, intermediate for grass hay, and lowest for alfalfa. Our data suggest that apparent total tract digestibilities are more similar among ruminant species when moderate- to high-quality forages are evaluated. However, sheep are not an adequate model for cattle when low-quality forages are compared. This is due to cattle better digesting the low quality forages than the sheep.

Key Words: Cattle, Diet Quality, Digestibility, Forage Source, Sheep

Introduction

Research in ruminant nutrition has most often used cattle or sheep. With decreasing resources available for research, cattle become an expensive option for many scientists, and sheep are often used as a model for cattle. Research conducted with small ruminant models has met with mixed results. For example, highly digestible feeds, such as cereal grains, tend to be more efficiently digested by sheep, whereas poorly digested feedstuffs, such as low quality roughages, tend to be better digested by cattle (McDonald, 2002). Prigge et al. (1984) showed that cattle have a greater proportional ruminal fill and lower particle passage rate compared with sheep. In addition, sheep masticate feed more

extensively than cattle, and that reduction in particle size may allow sheep to have a more rapid passage rate (McDonald, 2002). Replacing cattle with sheep would decrease cost, decrease the amount of space needed to do research, and allow the number of research animals to increase. However, more data are needed to fully understand the nutritional similarities and differences in digestion and nutrient utilization between sheep and cattle. Our objective was to determine the effect of forage quality on apparent total tract digestibility and ruminal fermentation in cattle versus sheep.

Materials and Methods

General

All procedures were conducted at the New Mexico State University Campus Livestock Research Center, and were approved by and conducted in accordance with guidelines established by the Institutional Animal Care and Use Committee of New Mexico State University.

Animals and Housing

Five yearling English crossbred (Hereford x Angus) steers (initial BW = 440.4 ± 35.6 kg) and 5 yearling whiteface (Rambouillet x Columbia x Debouillet) wethers (initial BW = 44.4 ± 4.6 kg) each fitted with a ruminal cannula were randomly assigned to one of three forage sources in an incompletely replicated 6 x 6 Latin square design experiment. Steers were fitted with a 10 cm i.d. ruminal cannula, and were housed in individual 10 x 30 m semi-enclosed pens equipped with concrete feed bunks and automatic waters. Wethers were fitted with a 7.5 cm i.d. ruminal cannula, and were housed in individual shaded pens (1.4 m x 3.6 m) with ad libitum access to clean fresh water.

Experimental Design and Sampling

The treatment structure was arranged in a 2 x 3 factorial with ruminant species (2) and forage source (3) as the factors. Forage sources were: 1) alfalfa (*Medicago sativa*) hay; 2) warm-season grass hay mix; and 3) Lovegrass (*Eragrostis curvula*) hay. The warm-season grass hay mix was composed of 50% 'Ironmaster' old world bluestem (*Bothriochloa ischaemum*) and 50% 'Hardie' bermudagrass (*Cynodon dactylon*). Nutrient composition of the forages is shown in Table 1. All forages were chopped through a 4-cm screen using a Bear Cat 5A (Western Bear Cat, Hastings, NE). Old world bluestem and bermudagrass grass hays were chopped simultaneously in a 50:50 (wt/wt) ratio. Forage was fed daily at 0700 at 115% of that consumed the previous 24 h so that each steer and wether had ad libitum access; refusals were weighed daily.

Each period was 21 d and consisted of 9 d adaptation to treatments followed by 12 d of sample collection. Forage and ort samples were subsampled daily during feeding and composited by animal within period. From d 1 through 13 of each period, a gelatin capsule containing 7.5 (steers) or 3.5 (wethers) g of chromic oxide was placed directly in the rumen at 0700 and 1700 to facilitate estimating fecal output (Merchen, 1988). Beginning at 0600 on d 10, fecal grab samples were collected at 6-h intervals until 0400 on d 13 and frozen (-20°C). Sampling time was moved back 2 h each day so that every 2 h of a 24-h period was represented.

On d 14, ruminal fluid was collected at 0, 3, 6, 9, 12, 18 and 24 h. Immediately after collection, 200 mL of ruminal fluid was strained through four layers of cheesecloth

and pH was measured using a portable pH meter and combination electrode (HI 9024, Hanna Instruments SRL, Italy). A 10-mL aliquot of ruminal fluid was acidified with 0.5 mL of 6 N HCl and frozen (-20°C) for later ammonia-N analysis. Another 10 mL of ruminal fluid was frozen for VFA analysis.

On d 15 through 19 of each experimental period, 5.0 g of the current forage (ground to pass a 2-mm screen) was placed in dacron bags (5 x 10 cm, average pore size was 53 microns) were used for determination of in situ DM and NDF disappearance. Incubation times were 0, 2, 6, 10, 16, 24, 48, 72 and 96 h. In-situ bags were placed in small mesh bags (31 cm x 31 cm) and inserted into the rumen. Duplicate bags with a blank at each time were placed into the rumen in reverse order so that all bags were removed at the same time. At removal time, the 0-h bags were introduced to the mesh bag and were rinsed with the others. For washing, mesh bags containing the in situ bags were placed in a plastic 19-L bucket of tap water. The bag was gently agitated for several minutes then transferred to another bucket of clean water. This procedure was repeated until the bags went through three buckets of water in which the water remained clear. Individual in situ bags were then rinsed with low pressure and low volume tap water at a sink to work all of the contents to the bottom of the bag. Bags were frozen (-20°C) and later dried at 55°C in a forced-air oven for 48 h.

For both sheep and cattle beginning at 0700 and 1200 on d 21, total ruminal contents were removed, weighed and mixed thoroughly, after which a sub-sample was obtained, and DM analyses were completed for determination of total ruminal DM and liquid contents.

Laboratory Methods

Forage and orts samples were composited by animal within period and subsampled so there was one forage and one orts sample per steer or wether and period. Forage, orts and fecal samples were dried in a forced air oven (55°C, 72 h) and ground to pass a 1-mm screen in a Wiley mill. Ash, N (micro-Kjeldahl procedure; AOAC, 1990), NDF and ADF (Goering and Van Soest, 1970) concentrations were determined in forage, orts and fecal samples. In addition, chromium concentrations were determined in fecal samples (Galyean, 1997).

Acidified samples of ruminal fluid were thawed and centrifuged at 1,500 x g for 15 minutes and analyzed for ammonia concentration by the phenol-hypochlorite method (Broderick and Kang, 1980). Another 8 mL of ruminal fluid was thawed and added to 2 mL of ice-cold metaphosphoric acid for VFA analysis. Concentration of ruminal fluid VFA was determined by gas chromatography (Erwin et al., 1961).

In situ samples were placed on a plastic tray and dried in a forced air oven at 55°C for 48 h. Residue was weighed and analyzed for NDF (Goering and Van Soest, 1970). Rate and extent of DM and NDF digestibility were calculated according to the procedures outlined by Wilkerson (1992).

Calculations and Statistics

Total fecal OM output was determined by dilution of the daily dose of Cr in feces. Fecal output of nutrients was calculated as the concentration of each nutrient (OM basis) in fecal content times total fecal OM output.

The experiment was analyzed as an incompletely replicated 6 x 6 Latin square design with 10 animals and 6 treatments. Animal served as the experimental unit. Data collected as single point collections were analyzed using the Mixed procedure of SAS

(SAS Institute Inc., Cary, NC). The model included ruminant specie, forage source, ruminant specie x forage source and period. Animal was considered a random effect. Data repeated over time (h, ruminal pH, ammonia, and VFA concentrations) were analyzed as repeated measures using the Mixed procedure of SAS. The model included ruminant specie, forage source, ruminant specie x forage source, period, time, and the time x treatment interactions (Little et al., 1998). Animal was considered a random effect and the animal x period interaction was the subject. The covariance structure used was autoregressive 1. When the ruminant specie x forage source interaction was significant ($P < 0.05$), differences (least significant difference; $P < 0.05$) among forage sources were tested within each ruminant specie. When ruminant specie and forage type effects, but not the interaction, were significant, means were separated (least significant difference; $P < 0.05$) within each factor. Results were considered significant at $P \leq 0.05$.

Results

Chemical composition of the hays is shown in Table 1. Forages were selected to represent high (alfalfa), medium (grass hay), and low (lovegrass hay) quality forages. Neutral detergent fiber and ADF were lowest in alfalfa, intermediate for the grass hay mix and greatest for lovegrass hay. In contrast, CP was greatest for alfalfa, intermediate for the grass hay mix and lowest for lovegrass hay.

Intake, Fecal Output and Total Tract Digestibility

Effects of ruminant specie and forage quality on DM intake and total tract digestibility are presented in Table 2. Specie x diet interactions ($P < 0.001$) were detected for DM intake expressed as g/d and g/(d·kg BW^{0.75}). Intake of DM [g/d and

g/(d·kg BW^{0.75})] by steers was greatest ($P < 0.05$) for alfalfa hay, intermediate for grass hay, and lowest for lovegrass hay. DM intake (g/d) by wethers was not influenced ($P > 0.10$) by forage quality, or when expressed per unit of BW^{0.75}, intake was lower ($P < 0.05$) when lovegrass hay was fed than either alfalfa or grass hay. Dry matter intake (% of BW) was not influenced ($P = 0.35$) by ruminant specie, and was greater ($P < 0.001$) for alfalfa and grass hay mix compared to lovegrass hay for both steers and wethers.

Apparent total tract digestibility (%) responded with ruminant specie x diet interactions ($P < 0.05$) for all nutrients measured (Table 2). Digestibility of OM and N was greater for alfalfa and grass hay mix than lovegrass hay for cattle and sheep, the magnitude of the decrease in digestibility of lovegrass hay was greater in wethers than steers. In steers, apparent total tract digestibility of NDF and ADF was greatest ($P < 0.05$) for grass hay, intermediate for alfalfa, and lowest for lovegrass hay. In wethers, digestibility of alfalfa and grass hay was greater ($P < 0.05$) than lovegrass hay.

Effects of ruminant specie and forage quality on nutrient intake, fecal output, and digestible nutrient intake [g/(d·kg BW)] are presented in Table 3. Organic matter intake [g/(d·kg BW)] was greater ($P < 0.001$) for alfalfa and grass hay than lovegrass hay for both steers and wethers. For both steers and wethers, NDF and ADF intake [g/(d·kg BW)] were greater ($P < 0.05$) for grass hay than both alfalfa and lovegrass hay. A ruminant specie x forage quality interaction was found for nitrogen intake ($P = 0.05$). For both steers and wethers, N intake was greatest ($P < 0.05$) for alfalfa, intermediate for grass hay and lowest for lovegrass; however, intake of N tended ($P = 0.06$) to be greater for steers, especially when alfalfa was fed.

Ruminant specie x forage quality interactions ($P \leq 0.007$) were observed for all components of fecal output measured. Fecal output of OM, NDF and ADF by wethers was greatest ($P < 0.05$) for lovegrass, intermediate for grass hay, and lowest for alfalfa. Within steers, fecal output of OM, NDF and ADF was not influenced ($P > 0.10$) by forage quality. In contrast, fecal output of N by steers was greatest ($P < 0.05$) for alfalfa, intermediate for grass hay, and lowest for lovegrass hay, whereas within wethers, fecal output of N was not influenced ($P > 0.10$) by forage quality.

Digestible nutrient intake expressed per unit of BW generally responded similar to intake, and there were no ruminant specie x forage quality interactions ($P = 0.08$ to $P = 0.79$). Digestible OM intake [$\text{g}/(\text{d} \cdot \text{kg BW})$] was greater ($P < 0.05$) for alfalfa and grass hay than lovegrass hay for both steers and wethers. Intake of digestible NDF from the grass hay mix was greater ($P < 0.05$) than alfalfa and lovegrass hay for both steers and wethers. For both steers and wethers, digestible ADF intake was greatest ($P < 0.05$) for grass hay, intermediate for alfalfa, and the lowest for lovegrass hay. Digestible N intake was greatest ($P < 0.05$) for alfalfa, intermediate for grass hay and lowest for lovegrass hay for both ruminant species. Intake of digestible NDF ($P = 0.04$) and N ($P = 0.03$) was greater for steers than for wethers.

Data showing the effects of ruminant specie and forage quality on nutrient intake, fecal output, and digestible nutrient intake expressed per unit of metabolic BW [$\text{g}/(\text{d} \cdot \text{kg BW}^{0.75})$] are presented in Table 4. Ruminant specie x forage quality interactions ($P \leq 0.006$) were observed for intake of all nutrients measured. For steers, OM and N intake ranked alfalfa > grass hay > lovegrass hay ($P < 0.05$). Organic matter intake by wethers was lower ($P < 0.05$) when lovegrass hay was consumed than either alfalfa or grass hay.

Wethers consuming alfalfa had greater ($P < 0.05$) N intake than when consuming either grass hay or lovegrass hay. Acid detergent fiber intake for steers was greatest ($P < 0.05$) for grass hay, intermediate was alfalfa, and lowest was lovegrass. Intake of ADF by wethers was greater ($P < 0.05$) when grass hay compared with the other two forages was consumed. For steers and wethers grazing grass hay mix, NDF intake was greater ($P < 0.05$) compared with alfalfa or lovegrass.

Ruminant specie x forage quality interactions were detected for fecal output [$\text{g}/(\text{d} \cdot \text{kg BW}^{0.75})$] of all nutrients measured (Table 4). Fecal output of OM, NDF, and ADF ($P < 0.05$) by wethers was greatest for lovegrass, intermediate for grass hay, and lowest for alfalfa. Fecal output of OM by steers was greater ($P < 0.05$) when steers were consuming grass hay compared with the other two forages. Fecal output of NDF by steers was greatest ($P < 0.05$) for grass hay, intermediate for lovegrass hay, and lowest for alfalfa. Fecal output of ADF by steers was not affected ($P > 0.10$) by forage quality. Fecal output of N by steers was greatest ($P < 0.05$) for alfalfa, intermediate for grass hay and lowest for lovegrass hay, whereas fecal output of N by wethers was not influenced ($P > 0.10$) by forage quality.

Digestible nutrient intake [$\text{g}/(\text{d} \cdot \text{kg BW}^{0.75})$] resulted in ruminant specie x forage quality interactions ($P \leq 0.05$) for all nutrients measured. Digestible OM and N intake by steers was greatest ($P < 0.05$) for alfalfa, intermediate for grass hay and lowest for lovegrass hay. Digestible OM intake by wethers was greater ($P < 0.05$) for alfalfa and grass hay than lovegrass, whereas digestible N intake for wethers was greater ($P < 0.05$) for alfalfa than the other hays. Digestible fiber (NDF and ADF) intake ($P < 0.05$) for steers was greatest for grass hay, intermediate for alfalfa, and lowest for lovegrass. For

wethers, digestible NDF and ADF intake were greater ($P < 0.05$) for grass hay than the other two forage sources.

In Situ Forage Digestibility

There were no ruminant specie x forage quality interactions ($P = 0.19$ to $P = 0.99$) for in situ rate and extent of ruminal DM and NDF digestion (Table 5). Dry matter disappearance rate for both steers and wethers was greater ($P < 0.05$) for alfalfa than the other two forages. Extent (96 h) of DM digestion for both steers and wethers was greatest ($P < 0.05$) for alfalfa, intermediate for grass hay mix, and lowest for lovegrass hay. Rate of disappearance of NDF for both wethers and steers was greater ($P < 0.05$) for both alfalfa and grass hay than for lovegrass. For steers and wethers, 96-h extent of NDF digestion was greatest ($P < 0.05$) for grass hay, intermediate for alfalfa, and lowest for lovegrass hay.

Ruminal Fill and Fermentation

Effects of ruminant specie and forage quality on ruminal fill and fermentation are presented in Table 6. In steers and wethers, ruminal DM fill at 0 and 4 h expressed as g/kg of BW and g/kg of BW^{0.75} was lower ($P < 0.05$) when alfalfa was consumed than the other two forages. For ruminal liquid fill at 0 h (g/kg BW^{0.75}), there was a ruminant specie x forage quality interaction ($P = 0.02$). For steers, liquid fill was greater ($P < 0.05$) when grass hay was fed than alfalfa or lovegrass. In wethers, ruminal fill was greatest for grass hay, intermediate for lovegrass, and lowest for alfalfa. Ruminal liquid fill for 0 and 4 hours expressed as g/kg BW and 4 h expressed as g/kg of BW^{0.75} was greater ($P < 0.05$) for both steers and wethers when grass hay compared with the other two forages was fed. When expressed as g/kg BW, wethers and steers had similar

ruminal liquid fill ($P = 0.27$ to $P = 0.43$) and tended ($P = 0.07$) to have similar ruminal DM fill. In contrast, when expressed as g/kg of BW^{0.75}, steers had greater ($P < 0.001$) ruminal DM and liquid fill than wethers.

A specie x diet interaction ($P < 0.001$) was observed for ruminal pH (Table 6). In steers, pH was higher ($P < 0.05$) for lovegrass than for the other two hays, whereas ruminal pH was similar among wethers. In steers and wethers, total VFA concentrations were greatest ($P < 0.05$) for alfalfa, intermediate for grass hay, and lowest for lovegrass hay. Total VFA concentrations did not differ among species, but tended ($P = 0.08$) to be greater in steers. For both steers and wethers the proportion of acetate, and the acetate:propionate ratio was greatest ($P < 0.05$) for lovegrass, intermediate for grass hay and lowest for alfalfa. In steers and wethers, proportions of propionate, isobutyrate, butyrate, and isovalerate, and concentration of ammonia N were greatest ($P < 0.05$) for alfalfa, intermediate for grass hay, and lowest for lovegrass. Ruminal proportion of valerate responded with a ruminant specie x diet interaction ($P = 0.02$). Proportion of valerate was greatest for alfalfa, intermediate for grass hay and lowest for lovegrass hay for both cattle and sheep, but the magnitude of the increase in alfalfa hay was greater in steers than wethers. Molar proportions of isobutyrate ($P = 0.04$) and isovalerate ($P = 0.01$) were greater in steers than wethers.

Discussion

Intake

Expressed per unit of BW, steers and wethers consumed similar amounts of forage and its components, and intake was more influenced by forage quality than

ruminant specie in the present experiment. However, when expressed per unit of $BW^{0.75}$, cattle consumed more DM, NDF, ADF and CP than sheep. Reid et al. (1990) reported greater intakes for cattle than sheep, consistent with the present results. In a retrospective study comparing relationships among forage quality and ruminant specie, Reid et al. (1988) reported that daily DMI, expressed as g/kg of $BW^{0.75}$, were higher for cattle than for sheep, and that differences in intake of C_4 grasses between cattle and sheep were greater than for C_3 grasses, which were greater than differences in intake of legumes. The authors concluded that determination of forage intake by sheep would have limited usefulness for the prediction of intake of the same forages by cattle. However, the question was raised regarding what power of BW should be used in making interspecies comparisons. Vona et al. (1984) reported no difference in DMI between cattle and sheep fed C_4 grass hays when intakes were calculated as g/kg of $BW^{0.90}$. This is similar to the present experiment when intake was expressed as g/kg of $BW^{1.0}$. However, in the present experiment, the significant ruminant specie x forage type interaction suggests that, on a $BW^{0.75}$ basis, it would not be meaningful to relate intake of forages by sheep to intake of cattle. A similar conclusion can be drawn when comparing digestible nutrient intake.

Apparent Total Tract Digestibility

Digestion coefficients of feeds from experiments conducted with sheep are often assumed to be applicable to cattle and vice versa. Reid et al. (1988) reported higher apparent digestibility coefficients for cattle than sheep fed legumes and C3 and C4 grasses. Differences in apparent digestibility between cattle and sheep were not as great for legumes as for the grasses. Reid et al. (1990) cited data which suggested that OM digestibility by both temperate and tropical forages fed *ab libitum* as hays was greater in cattle than sheep. For a number of C3 grasses and legumes fed fresh and in *ad libitum* amounts, OM and crude fiber digestibility was lower for sheep than for cattle, and the difference increased as digestibility decreased, similar to the present experiment. Similarly, McDonald (2002) reported that cattle digest low-quality forages better than sheep, and Averts et al. (1984) suggested that the better digestion by cows compared with sheep was partly due to the longer retention time of low-quality feeds in the rumen. Demment and Van Soest (1985) suggested that a higher digestibility of forages by cattle should result from increased body size due to longer retention time in the reticulorumen. Retention time has also been associated with decreased digestibility resulting from increased intake. Ruminal retention times of forages fed to cattle and sheep were not determined in the present experiment.

In Situ Rate and Extent of Ruminal Digestibility

In the present experiment, rate and extent of ruminal digestion by steers and wethers was similar, and digestion was influenced more by forage than by ruminant specie. Playne (1978) suggested that greater digestion of forages by cattle compared with sheep might result in part from greater recycling of nutrients to the rumen. Although

calculated rate of digestion of forages was not different among species, extent of digestion was greater in steers compared with wethers in the present experiment, supporting the hypothesis of Playne (1978). The in situ technique estimates only the ability of the rumen microflora to degrade forages, and does not account for differences in rumination, mastication, rate of passage, or other physical factors that would influence digestion in vivo.

Ruminal Fill and Fermentation

Newland et al. (1962) showed a narrowing of the acetate to propionate ratio as digestibility increased. Similar results were observed in the present experiment, as acetate:propionate decreased as the forage changed from the poorly digested lovegrass to the highly digestible alfalfa. Volatile fatty acids and acetate:propionate were not influenced by ruminant species in the work of Prigge et al. (1984), similar to the present experiment. In general, VFA concentration and molar proportions of VFA appear to be influenced more by diet than by ruminant specie.

Implications

Digestion coefficients of feedstuffs are often used interchangeably for cattle and sheep. However, our data suggest that differences exist among ruminant species. Whereas apparent total tract digestibilities are generally similar among ruminant species when moderate- to high-quality forages are evaluated, sheep are not an adequate model for cattle when low-quality forages are compared. Therefore, scientists should not substitute sheep for cattle based when low quality forage is being considered. Scientist should make the decision to use sheep instead of cattle based on diet quality and questions wanting to be answered.

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Table 1. Chemical composition of experimental forages fed to beef steers and wethers

Item	Forage type		
	Alfalfa	Grass hay	Lovegrass hay
DM	91.0	91.7	92.0
OM	88.2	90.4	91.4
NDF	34.1	74.7	81.9
ADF	23.1	41.6	44.9
CP	17.50	7.29	2.49

Table 2. Effects of ruminant specie and forage quality on intake, fecal output and apparent total tract digestion (g/d)

Item	Steers			Wethers			SEM	P > F		
	Alfalfa	Grass hay	Lovegrass hay	Alfalfa	Grass hay	Lovegrass hay		Specie (S)	Diet (D)	S x D
DMI, g/d	11,447 ^a	9,489 ^b	3,976 ^c	986	1,022	553	279	0.001	0.001	0.001
DMI, % of BW	2.90 ^d	2.36 ^d	0.99 ^e	2.24 ^d	2.35 ^d	1.21 ^e	0.19	0.35	0.001	0.08
DMI, g/(d·kg BW ^{0.75})	129.1 ^a	105.7 ^b	44.4 ^c	57.5 ^a	60.5 ^a	31.3 ^b	5.6	0.001	0.001	0.001
Apparent total tract digestibility, %										
OM	89.0 ^a	83.7 ^a	68.7 ^b	87.6 ^a	82.1 ^a	53.1 ^b	2.41	0.004	0.001	0.01
NDF	79.1 ^{ab}	84.4 ^a	71.9 ^b	75.1 ^a	82.1 ^a	51.7 ^b	3.32	0.004	0.001	0.03
ADF	77.2 ^{ab}	81.6 ^a	68.2 ^b	76.7 ^a	81.1 ^a	49.6 ^b	3.41	0.03	0.001	0.02
N	91.9 ^a	83.8 ^a	54.7 ^b	89.3 ^a	75.2 ^a	3.2 ^b	5.26	0.002	0.001	0.001

^{a,b,c} Within ruminant specie, unlike superscripts within row indicate difference ($P < 0.05$).

^{d,e} Across ruminant specie, unlike superscripts within row indicate difference ($P < 0.05$).

Table 3. Effects of ruminant specie and forage quality on nutrient intake, fecal output and digestible nutrient intake [g/(d·kg BW)]

Item	Steers			Wethers			SEM	P > F		
	Alfalfa	Grass hay	Lovegrass hay	Alfalfa	Grass hay	Lovegrass hay		Specie (S)	Diet (D)	S x D

Intake, g/(d·kg BW)										
OM	28.3 ^a	23.6 ^a	9.9 ^b	21.7 ^a	23.3 ^a	12.4 ^b	1.90	0.37	0.001	0.07
NDF	11.19 ^a	19.92 ^b	9.23 ^a	8.21 ^a	18.61 ^b	10.59 ^a	1.08	0.28	0.001	0.15
ADF	7.18 ^a	10.60 ^b	4.88 ^a	6.04 ^a	10.74 ^b	6.23 ^a	0.65	0.83	0.001	0.18
N	0.953 ^d	0.307 ^e	0.052 ^f	0.649 ^d	0.287 ^e	0.060 ^f	0.066	0.06	0.001	0.05
Fecal output, g/(d·kg BW)										
OM	3.16	3.84	3.08	2.46 ^d	4.19 ^e	5.86 ^f	0.33	0.006	0.001	0.001
NDF	2.32	3.08	2.61	1.84 ^d	3.35 ^e	5.07 ^f	0.30	0.005	0.001	0.001
ADF	1.64	1.92	1.57	1.28 ^d	2.06 ^e	3.08 ^f	0.18	0.007	0.001	0.001
N	0.068 ^e	0.048 ^d	0.021 ^f	0.063	0.063	0.059	0.006	0.009	0.002	0.007
Digestible nutrient intake, g/(d·kg BW)										
OM	25.1 ^a	19.7 ^a	6.8 ^b	19.3 ^a	19.1 ^a	6.6 ^b	1.76	0.13	0.001	0.24
NDF	8.87 ^a	16.84 ^b	6.61 ^a	6.37 ^a	15.26 ^b	5.52 ^a	0.99	0.04	0.001	0.78
ADF	5.54 ^a	8.67 ^b	3.31 ^c	4.76 ^a	8.67 ^b	3.15 ^c	0.60	0.53	0.001	0.79
N	0.885 ^a	0.260 ^b	0.030 ^c	0.586 ^a	0.224 ^b	0.001 ^c	0.064	0.03	0.001	0.08

^{a,b,c} Across ruminant specie, unlike superscripts within row indicate difference ($P < 0.05$).

^{d,e,f} Within ruminant specie, unlike superscripts within row indicate difference ($P < 0.05$).

Table 4. Effects of ruminant specie and forage quality on nutrient intake, fecal output and digestible nutrient intake [g/(d·kg BW^{0.75})]

Item	Steers			Wethers			SEM	P > F		
	Alfalfa	Grass hay	Lovegrass hay	Alfalfa	Grass hay	Lovegrass hay		Specie (S)	Diet (D)	S x D
Intake, g/(d·kg BW ^{0.75})										
OM	125.6 ^a	105.6 ^b	44.4 ^c	55.8 ^a	60.2 ^a	32.1 ^b	5.47	0.001	0.001	0.001
NDF	49.7 ^a	89.2 ^b	41.2 ^a	21.1 ^a	48.0 ^b	27.3 ^a	3.34	0.001	0.001	0.002
ADF	31.8 ^a	47.5 ^b	21.9 ^c	15.6 ^a	27.7 ^b	16.1 ^a	2.01	0.001	0.001	0.006
N	4.24 ^a	1.38 ^b	0.24 ^c	1.67 ^a	0.74 ^b	0.15 ^b	0.21	0.001	0.001	0.001
Fecal output, g/(d·kg BW ^{0.75})										

OM	14.1 ^a	17.2 ^b	13.7 ^a	6.4 ^a	10.7 ^b	15.1 ^c	1.06	0.001	0.001	0.001
NDF	10.4 ^a	13.8 ^b	11.6 ^{ab}	4.8 ^a	8.6 ^b	13.1 ^c	0.92	0.001	0.001	0.001
ADF	7.3	8.6	7.0	3.3 ^a	5.3 ^b	7.9 ^c	0.57	0.001	0.003	0.001
N	0.300 ^a	0.213 ^b	0.095 ^c	0.163	0.162	0.149	0.017	0.003	0.001	0.001
Digestible nutrient intake, g/(d·kg BW ^{0.75})										
OM	111.6 ^a	88.4 ^b	30.7 ^c	49.4 ^a	49.4 ^a	17.0 ^b	5.03	0.001	0.001	0.001
NDF	39.4 ^a	75.4 ^b	29.6 ^c	16.3 ^a	39.4 ^b	14.3 ^a	3.04	0.001	0.001	0.009
ADF	24.5 ^a	38.8 ^b	14.9 ^c	12.2 ^a	22.4 ^b	8.1 ^a	1.86	0.001	0.001	0.05
N	3.94 ^a	1.16 ^b	0.14 ^c	1.51 ^a	0.58 ^b	0.00 ^b	0.20	0.001	0.001	0.001

^{a,b,c}Within ruminant specie, unlike superscripts within row indicate difference ($P < 0.05$).

Table 5. Effects of ruminant specie and forage quality on in situ rate and extent of ruminal DM and NDF digestion

Item	Steers			Wethers			SEM	P > F		
	Alfalfa	Grass hay	Lovegrass hay	Alfalfa	Grass hay	Lovegrass hay		Specie (S)	Diet (D)	S x D
DM										
Disappearance rate, %/h	5.22 ^a	4.63 ^b	2.75 ^b	5.90 ^a	2.98 ^b	2.63 ^b	0.69	0.48	0.001	0.19
96-h extent, %	85.6 ^a	73.4 ^b	54.7 ^c	79.5 ^a	63.5 ^b	38.9 ^c	3.43	0.007	0.001	0.38
NDF										
Disappearance rate, %/h	4.80 ^a	4.49 ^a	2.48 ^b	3.39 ^a	2.83 ^a	2.05 ^b	0.72	0.12	0.02	0.55
96-h extent, %	67.7 ^{ab}	75.6 ^a	59.4 ^b	55.5 ^{ab}	63.4 ^a	48.2 ^b	5.92	0.02	0.05	0.99

^{a,b,c}Across ruminant specie, unlike superscripts within row indicate difference ($P < 0.05$).

Table 6. Effects of ruminant specie and forage quality on ruminal fermentation.

Item	Steers			Wethers			SEM	P > F		
	Alfalfa	Grass hay	Lovegrass hay	Alfalfa	Grass hay	Lovegrass hay		Specie (S)	Diet (D)	S x D
Ruminal DM fill										
0 h, g/kg BW	18.7 ^a	24.5 ^b	19.6 ^b	10.7 ^a	19.8 ^b	21.2 ^b	2.03	0.07	0.004	0.08
4 h, g/kg BW	21.9 ^a	26.0 ^b	20.9 ^b	11.7 ^a	23.4 ^b	22.9 ^b	2.38	0.07	0.01	0.06
0 h, g/kg BW ^{0.75}	82.9 ^a	110.3 ^b	87.3 ^b	28.0 ^a	50.9 ^b	54.1 ^b	6.23	0.001	0.003	0.10
4 h, g/kg BW ^{0.75}	97.2 ^a	116.8 ^b	93.1 ^{ab}	30.3 ^a	60.3 ^b	58.8 ^{ab}	7.24	0.001	0.01	0.09
Ruminal liquid fill										
0 h, g/kg BW	121.8 ^a	143.4 ^b	104.6 ^a	93.3 ^a	134.0 ^b	122.2 ^a	9.46	0.43	0.01	0.07
4 h, g/kg BW	138.2 ^a	159.3 ^b	120.5 ^a	106.6 ^a	147.0 ^b	129.7 ^a	12.5	0.27	0.04	0.29
0 h, g/kg BW ^{0.75}	541.6 ^d	643.2 ^e	465.7 ^d	242.8 ^d	342.8 ^e	314.7 ^{de}	30.7	0.001	0.002	0.02
4 h, g/kg BW ^{0.75}	612.9 ^a	715.1 ^b	536.7 ^a	276.5 ^a	378.4 ^b	333.3 ^a	40.1	0.001	0.02	0.18
Ruminal pH	5.96 ^d	6.16 ^d	6.70 ^e	6.53	6.30	6.47	0.09	0.09	0.001	0.001
Total VFA, mM	216.9 ^a	160.8 ^b	88.7 ^c	149.7 ^a	113.3 ^b	64.8 ^c	20.1	0.08	0.001	0.35
----- mol/100 mol -----										
Acetate	66.3 ^a	71.2 ^b	75.8 ^c	66.0 ^a	72.9 ^b	76.3 ^c	1.02	0.59	0.001	0.43
Propionate	17.8 ^a	16.8 ^b	15.9 ^b	19.7 ^a	17.1 ^b	16.9 ^b	0.59	0.06	0.001	0.37
Isobutyrate	1.58 ^a	1.46 ^a	0.94 ^b	1.45 ^a	1.07 ^a	0.77 ^b	0.13	0.04	0.001	0.55
Butyrate	10.68 ^a	8.19 ^b	5.94 ^c	9.95 ^a	7.38 ^b	5.03 ^c	0.62	0.30	0.001	0.98
Isovalerate	1.71 ^a	1.40 ^b	0.89 ^c	1.30 ^a	0.70 ^b	0.58 ^c	0.14	0.01	0.001	0.25
Valerate	1.94 ^d	0.93 ^e	0.52 ^f	1.59 ^d	0.80 ^e	0.48 ^f	0.08	0.08	0.001	0.02
Ace:Prop	3.76 ^a	4.24 ^b	4.81 ^c	3.50 ^a	4.34 ^b	4.57 ^c	0.16	0.32	0.001	0.47
Ammonia N, mM	9.20 ^a	3.62 ^b	0.00 ^c	9.25 ^a	4.72 ^b	3.17 ^c	1.13	0.19	0.001	0.23

^{a,b,c} Across ruminant specie, unlike superscripts within row indicate difference ($P < 0.05$).
^{d,e,f} Within ruminant specie, unlike superscripts within row indicate difference ($P < 0.05$).

VITA

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Master of Science

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OF FORAGE QUALITY

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