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Comparative digestibility by cattle versus sheep: Effect of forage quality[1,2]

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ABSTRACT: The objective was to determine the effect of forage quality on apparent total tract digestibility and ruminal fermentation in cattle versus sheep. Five yearling English crossbred (Hereford × Angus) steers (440.4 ± 35.6 kg of initial BW) and 5 yearling whiteface (Rambouillet × Columbia × Debouillet) wethers (44.4 ± 4.6 kg of initial BW), each fitted with a ruminal cannula, were randomly assigned to 1 of 3 forage sources within ruminant specie, and the study was conducted over 3 periods. For forage source, both animal and period served as the blocking factor with all forage sources represented once within each animal and all forage sources represented at least once within each period. The treatment structure was arranged in a 2 × 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 ($P \leq 0.06$) amounts of forage, and intake was more influenced by forage quality ($P < 0.001$) than ruminant species ($P = 0.35$). When expressed per unit of metabolic BW, cattle consumed more ($P < 0.001$) DM, NDF, and N than sheep. Apparent total tract digestibility was similar among steers and wethers when alfalfa or grass hay was fed, but decreased to a greater extent in wethers when low-quality lovegrass hay was fed (ruminant species × diet interaction, $P \leq 0.01$). Rate (%/h) of ruminal NDF disappearance was greater ($P = 0.02$) for alfalfa and grass hay than lovegrass, but was not influenced ($P = 0.12$) by ruminant species. In addition, ruminal DM fill was influenced more ($P < 0.01$) by forage than by ruminant species ($P = 0.07$). Steers and wethers had greater ($P < 0.01$) DM fill from grass hay and lovegrass hay than alfalfa before and 5 h after feeding. Ruminal VFA were generally not influenced ($P \geq 0.06$) by ruminant specie. Results 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 because cattle digest low-quality forages to a greater extent than sheep. Expressing digestibility as digestible intake per unit of BW allows for a wider range of forage qualities to be compared when substituting sheep for cattle.

Key words: cattle, diet quality, digestibility, forage source, sheep

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INTRODUCTION

Research in ruminant nutrition has most often used cattle or sheep. With decreasing resources available for research, cattle have become an expensive option for many scientists, and sheep are often used as a model for cattle. Cattle are nonselective grazers that have large gastrointestinal tracts in which they retain feeds for relatively long periods. These animals derive significant energy from microbial digestion of the cell wall (fiber) of plants in the reticulorumen (Welch, and Hooper, 1988).

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Sheep are intermediate between selective and nonselective ruminants, and they consume a relatively lower-fiber diet which is fermented faster than high-fiber diets (Van Soest, 1982). We hypothesized that cattle would more completely digest low-quality, high-fiber forages than sheep. Conversely, sheep would digest high-quality, low-fiber feeds to a greater extent than cattle. Replacing cattle with sheep would reduce cost, decrease the amount of space needed to conduct research, and allow an increased number of research animals.

Data obtained from sheep studies are often used to make inference to cattle nutrition (Ferrell et al., 1986; Lobley et al., 1992; Rihani et al., 1993). For example, Rihani et al. (1993) demonstrated that energy and N do not need to be synchronized in the rumen of lambs for optimal OM digestibility and microbial synthesis and efficiency. These results have been used to infer that protein supplementation in cattle does not need to be daily because the recycling of N enables the rumen microbes to overcome any short-term effects of asynchrony (Valkeners et al., 2004). This concept has been subsequently determined in sheep (Cole, 1999; Currier et al., 2004) and cattle (Cole et al., 2003; Archibeque et al., 2007). However, fewer experiments have directly compared cattle and sheep, and additional research would be beneficial to determine if sheep are a good model for cattle. Therefore, the 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 × Angus) steers (440.4 ± 35.6 kg of initial BW) and 5 yearling whiteface (Rambouillet × Columbia × Debouillet) wethers (44.4 ± 4.6 kg of initial BW), each fitted with a ruminal cannula, were randomly assigned to 1 of 3 forage sources. Steers were fitted with a 10 cm i.d. ruminal cannula and were housed in individual 10 × 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 × 3.6 m) with ad libitum access to clean fresh water.

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

	Forage type		
Item	Alfalfa	Grass hay	Lovegrass hay
DM	91.0 ± 0.57	91.7 ± 0.42	92.0 ± 0.36
OM	88.2 ± 0.53	90.4 ± 1.54	91.4 ± 4.25
NDF	34.1 ± 3.13	74.7 ± 2.68	81.9 ± 1.66
ADF	23.1 ± 2.49	41.6 ± 2.15	44.9 ± 1.35
CP	17.5 ± 2.02	7.29 ± 1.15	2.49 ± 0.57

[1]Mean ± SD is based on 10 independent samples collected once during each collection period before feeding from each animal.

Experimental Design and Sampling

The study evaluated 3 forage sources; it was conducted using 2 ruminant species (wethers and steers) and 5 animals within ruminant species over 3 experimental periods. For forage source, both animal and period served as blocking factors with all forage sources represented once within each animal, and all forage sources were represented at least once within each period. The treatment structure was arranged in a 2 × 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*). Chemical 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) every 2 wk and stored in an enclosed barn. Old world bluestem and bermudagrass grass hays were chopped simultaneously in a 50:50 (wt/wt) ratio. Forage was fed daily at 0700 h at 115% of that consumed the previous 24 h so that each steer and wether had ad libitum access; refusals were weighed daily.

Each of the 3 periods were 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 h to facilitate estimating fecal output (Merchen, 1988). Beginning at 0600 h on d 10, fecal grab samples were collected at 6-h intervals until 0400 h 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 4 layers of cheesecloth and pH was measured using a portable pH meter and combination electrode (HI 9024; Hanna Instruments SRL, Palermo, 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, a 5.0-g sample (ground to pass a 2-mm screen; Wiley mill model 4; Thomas Scientific, Swedesboro, NJ) of the forage that each individual animal was consuming at the time was placed in nitrogen-free polyester bags (5 × 10 cm, 50 ± 15 μm pore size; Ankom, Fairport, NY) and 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 × 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 3 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 h on d 21, total ruminal contents were removed, weighed, and mixed thoroughly, after which a subsample 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 1 forage and 1 ort 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 (method 942.05, 990.02; AOAC, 1997), NDF (with heat-stable amylase addition), and ADF (ANKOM 200 Fiber Analyzer; Ankom Corp., Fairport, NY) concentrations were determined in forage, orts, and fecal samples. In addition, Cr concentrations were determined in fecal samples according to the method of Hill and Anderson (1958) using atomic absorption spectrophotometry.

Acidified samples of ruminal fluid were thawed and centrifuged at 1,500 × *g* for 15 min and analyzed for ammonia concentration by the phenol-hypochlorite method (Broderick and Kang-Meznarich, 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).

Ruminal bacteria were isolated from a 2-kg sample of rumen contents. Ruminal contents were blended on high speed in a food processor for 1 min, and the mixture was strained through 4 layers of cheesecloth. Feed particles and protozoa in ruminal samples were removed via centrifugation at 1,000 × *g* for 10 min. Bacteria were separated from supernatant by centrifugation at 27,000 × *g* for 20 min. Isolated bacteria was dried in a forced-air oven (50°C) and analyzed for DM, ash, N (as described previously), and purines (Zinn and Owens, 1986).

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, as previously described (Ankom 200 Fiber Analyzer); DM; N; and purines (as described previously).

Calculations and Statistics

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

The effective ruminal disappearance of DM, NDF, and CP was calculated as described by Ørskov and McDonald (1979) as A + B × (Kd/[Kd + Kp]), where A = soluble fraction, B = slowly degradable fraction, Kd = disappearance rate, and Kp = passage rate (0.05 h^{-1}). Protein remaining in in situ bags was adjusted for microbial protein contribution. Microbial protein was calculated using the N to purine ratio of ruminally isolated bacteria and purine content of in situ remaining material. The undegradable intake protein (**UIP**) values were calculated using an equation adapted from Broderick (1994): UIP = {[kp/(kp– kd)] × in situ slowly degradable CP fraction}– in situ insoluble CP fraction, where kp is the particle dilution rate (assumed to be 0.05 h^{-1}) and kd is the rate of protein degradation. The in situ insoluble CP fraction was calculated by subtracting CP effective degradability from 100. The calculated difference between total protein and UIP was termed degradable intake protein (**DIP**).

Data collected as single point collections were analyzed using the Mixed procedure of SAS (SAS Inst. Inc., Cary, NC). The statistical model included ruminant species, forage source, ruminant species × forage source, and period. Animal was considered a random effect. The covariance structure used was variance component. Data repeated over time (hour, ruminal pH, ammonia, and VFA concentrations) were analyzed as repeated measures using the Mixed procedure of SAS. The model included ruminant species, forage source, ruminant species × forage source, period, time, and the time × treatment interactions (Littell et al., 1998). Animal was considered a random effect and the animal × period interaction was the subject. The covariance structure used

Table 2. Effect of ruminant species and forage quality on intake and apparent total tract digestion

	Alfalfa		Grass hay		Lovegrass hay			*P*-values[1]		
Item	Steers	Wethers	Steers	Wethers	Steers	Wethers	SEM	Species (S)	Forage (F)	S × F
Animal replicates	5	5	5	5	5	5				
DMI, g/d	11,447[a]	986[b]	9489[a]	1022[b]	3976[a]	553[b]	279.0	0.001	0.001	0.001
DMI, % of BW	2.90	2.24	2.36	2.35	0.99	1.21	0.19	0.35	0.001	0.08
DMI, g/(d·kg $BW^{0.75}$)	129.1[a]	57.5[b]	105.7[a]	60.5[b]	44.4[a]	31.3[a]	5.59	0.001	0.001	0.001
Apparent total tract digestibility, %										
OM	89.0[a]	87.6[a]	83.7[a]	82.1[a]	68.7[a]	53.1[b]	2.41	0.004	0.001	0.01
NDF	79.1[a]	75.1[a]	84.4[a]	82.1[a]	71.9[a]	51.7[b]	3.32	0.004	0.001	0.03
ADF	77.2[a]	76.7[a]	81.6[a]	81.1[a]	68.2[a]	49.6[b]	3.41	0.03	0.001	0.02
N	91.9[a]	89.3[a]	83.8[a]	75.2[a]	54.7[a]	3.2[b]	5.26	0.002	0.001	0.001

[1]Probability values associated with ruminant species (S), forage quality (F), and ruminant species × forage quality interaction (S × F).

[a,b]Row values within forage quality with different superscripts differ ($P < 0.05$).

was autoregressive 1. When the ruminant species × forage source interaction was significant ($P < 0.05$), differences (least significant difference; $P < 0.05$) among ruminant species were tested within each forage type. When ruminant species 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-quality (alfalfa), medium-quality (grass hay), and low-quality (lovegrass hay) 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 species and forage quality on DM intake and total tract digestibility are presented in Table 2. Species × 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) was greater ($P < 0.05$) for steers than wethers for each forage type. However, as the forage quality decreased, the difference in DMI was smaller. Intake of DM [g/(d·kg $BW^{0.75}$)] was greater ($P < 0.05$) for steers than wethers when consuming alfalfa hay or grass hay; however, no difference ($P = 0.11$) was detected when consuming lovegrass hay. Dry matter intake (% of BW) was not influenced ($P = 0.35$) by ruminant species 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 (%) for OM, NDF, ADF, and N responded with ruminant species × diet interactions ($P < 0.05$; Table 2). Digestibility of OM, NDF, ADF,

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

	Alfalfa		Grass hay		Lovegrass hay			*P*-values[1]		
Item	Steers	Wethers	Steers	Wethers	Steers	Wethers	SEM	Species (S)	Forage (F)	S × F
Intake, g/(d·kg BW)										
OM	28.3	21.7	23.6	23.3	9.9	12.4	1.90	0.37	0.001	0.07
NDF	11.2	8.2	19.9	18.6	9.2	10.6	1.08	0.28	0.001	0.15
ADF	7.2	6.0	10.6	0.7	4.9	6.2	0.65	0.83	0.001	0.18
N	0.9	0.6	0.3	0.3	0.1	0.1	0.07	0.06	0.001	0.06
Fecal output, g/(d·kg BW)										
OM	3.16[a]	2.46[a]	3.84[a]	4.19[a]	3.09[a]	5.86[b]	0.33	0.006	0.001	0.001
NDF	2.32[a]	1.84[a]	3.08[a]	3.35[a]	2.61[a]	5.08[b]	0.30	0.005	0.001	0.001
ADF	1.64[a]	1.28[a]	1.92[a]	2.06[a]	1.57[a]	3.08[b]	0.18	0.007	0.001	0.001
N	0.07[a]	0.6 [a]	0.05[a]	0.06[a]	0.02[a]	0.06[b]	0.006	0.009	0.002	0.001
Digestible intake, g/(d·kg BW)										
OM	25.1	19.3	19.7	19.1	6.8	6.6	1.76	0.13	0.001	0.23
NDF	8.9	6.4	16.8	15.3	6.6	5.5	0.99	0.04	0.001	0.78
ADF	5.5	4.8	8.7	8.7	3.3	3.2	0.60	0.53	0.001	0.79
N	0.89	0.59	0.26	0.22	0.03	0.001	0.063	0.03	0.001	0.08

[1]Probability values associated with ruminant species (S), forage quality (F), and ruminant species × forage quality interaction (S × F).

[a,b]Row values within forage quality with different superscripts differ ($P < 0.05$).

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

	Alfalfa		Grass hay		Lovegrass hay			*P*-values[1]		
Item	Steers	Wethers	Steers	Wethers	Steers	Wethers	SEM	Species (S)	Forage (F)	S × F
Intake, g/(d·kg $BW^{0.75}$)										
OM	125.6[a]	55.8[b]	105.6[a]	60.2[b]	44.4 [a]	32.1[a]	5.47	0.001	0.001	0.001
NDF	49.7[a]	21.8[b]	89.2[a]	48.0[b]	41.2[a]	27.3[b]	3.34	0.001	0.001	0.002
ADF	31.8[a]	15.6[b]	47.5[a]	27.7[b]	21.9 [a]	16.1[a]	2.01	0.001	0.001	0.006
N	4.24[a]	1.67[a]	1.38[a]	0.74[b]	0.24 [a]	0.15[a]	0.21	0.001	0.001	0.001
Fecal output, g/(d·kg $BW^{0.75}$)										
OM	14.1[a]	6.4[b]	17.2[a]	10.7[b]	13.7[a]	15.1[a]	1.06	0.001	0.001	0.001
NDF	10.4[a]	4.8[b]	13.8[a]	8.6[b]	11.6[a]	13.1[a]	0.92	0.001	0.001	0.001
ADF	7.35[a]	3.3[b]	8.6[a]	5.3[b]	7.0[a]	7.9[a]	0.57	0.001	0.003	0.001
N	0.30[a]	0.16	0.21[a]	0.16[b]	0.10[a]	0.15[a]	0.017	0.003	0.001	0.001
Digestible intake, g/(d·kg $BW^{0.75}$)										
OM	111.6[a]	49.4[b]	88.4[a]	49.4[b]	30.7[a]	17.0[a]	5.03	0.001	0.001	0.001
NDF	39.4[a]	16.3[b]	75.4[a]	39.4[b]	29.6[a]	14.3[b]	3.04	0.001	0.001	0.01
ADF	24.5[a]	12.2[b]	38.8[a]	22.4[b]	14.9[a]	8.1[b]	1.86	0.001	0.001	0.05
N	3.98[a]	1.51[b]	1.16[a]	0.58[b]	0.14[a]	0.01[b]	0.206	0.001	0.001	0.001

[1]Probability values associated with ruminant species (S), forage quality (F), and ruminant species × forage quality interaction (S × F).

[a,b]Row values within forage quality with different superscripts differ ($P < 0.05$).

and N was not affected ($P \geq 0.26$) by ruminant species when consuming alfalfa hay or grass hay. However, apparent digestibility of OM, NDF, ADF, and N was greater ($P = 0.001$) for steers than wethers when lovegrass hay was fed.

Effects of ruminant species and forage quality on characteristics of digestion [g/(d·kg BW)] are presented in Table 3. Intake of OM, NDF, ADF, and N [g/(d·kg BW)] were greater ($P = 0.001$) for alfalfa hay and grass hay than for lovegrass hay, but not influenced ($P \geq 0.06$) by ruminant species. Fecal output of OM, NDF, ADF, and N [g/(d·kg BW)] were influenced by a ruminant species × forage quality interaction ($P < 0.01$). When alfalfa hay or grass hay were fed, fecal output of OM, NDF, ADF, and N [g/(d·kg BW)] were similar in steers and wethers ($P \geq 0.07$). However, when lovegrass hay was fed, fecal output of OM, NDF, ADF, and N was greater ($P < 0.05$) for wethers compared with steers. Digestible intake [g/(d·kg BW)] of NDF ($P = 0.04$) and N ($P = 0.03$) was greater for steers compared with wethers, while OM ($P = 0.13$) and ADF ($P = 0.53$) were not affected by ruminant species. Digestible OM intake was greater ($P = 0.001$) for alfalfa hay and grass hay than for lovegrass hay [22.7 = 19.4 > 6.7 ± 1.24 g/(d·kg BW) for alfalfa hay, grass hay, and lovegrass hay, respectively]. Digestible NDF intake was greater ($P = 0.001$) for grass hay than for alfalfa hay and lovegrass hay [7.6 < 16.1 > 6.1 ± 0.70 g/(d·kg BW) for alfalfa hay, grass hay, and lovegrass hay, respectively]. Digestible ADF intake was greater ($P = 0.001$) for grass hay, intermediate for alfalfa hay, and lower for lovegrass hay [5.5 < 8.7 > 3.23 ± 0.42 g/(d·kg BW) for alfalfa hay, grass hay, and lovegrass hay, respectively]. Digestible N intake was greater ($P \leq 0.02$) for alfalfa hay, intermediate for grass hay, and lower for lovegrass hay [0.74 > 0.24 > 0.02 ± 0.045 g/(d·kg BW) for alfalfa hay, grass hay, and lovegrass hay, respectively].

Effects of ruminant species and forage quality on characteristics of digestion [g/(d·kg $BW)^{0.75}$] are presented in Table 4. Species × diet interactions ($P < 0.001$) were detected for OM, NDF, ADF, and N intake expressed as g/(d·kg $BW^{0.75}$). Intake of OM, ADF, and N [g/(d·kg $BW^{0.75}$)] was greater ($P < 0.05$) for steers than wethers when consuming alfalfa hay or grass hay; however, no difference ($P \geq 0.06$) was detected when consuming lovegrass hay. Intake of NDF [g/(d·kg $BW^{0.75}$)] was greater ($P \leq 0.008$) for steers than wethers for each forage type. However, the difference in NDF intake between steers and wethers was different for each forage quality. Species × diet interactions ($P < 0.001$) were detected for OM, NDF, ADF, and N fecal output expressed as g/d and g/(d·kg $BW^{0.75}$). Fecal output of OM, NDF, ADF, and N [g/(d·kg $BW^{0.75}$)] was greater ($P \leq 0.04$) for steers than wethers when consuming alfalfa hay or grass hay; however, no difference ($P \geq 0.09$) was detected when consuming lovegrass hay. In addition, species × diet interactions ($P < 0.001$) were detected for OM, NDF, ADF, and N digestible intake expressed as g/(d·kg $BW^{0.75}$). Digestible intake of OM and N [g/(d·kg $BW^{0.75}$)] was greater ($P < 0.05$) for steers than wethers when consuming alfalfa hay or grass hay; however, no difference ($P \geq 0.07$) was detected when consuming lovegrass hay. Digestible intake of NDF and ADF [g/(d·kg $BW^{0.75}$)] was greater ($P \leq 0.02$) for steers than wethers for each forage type. However, the magnitude of difference in NDF intake between steers and wethers was different for each forage quality.

In Situ Forage Digestibility

Effects of ruminant species and forage quality on in situ rate and extent of ruminal DM and NDF digestion and

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

	Forage quality				Ruminant species			*P*-value[1]		
Item	Alfalfa	Grass hay	Lovegrass hay	SEM	Steers	Wethers	SEM	S	F	S × F
DM										
Disappearance rate, %/h	5.56[a]	3.80[b]	2.69[b]	0.43	4.20	3.84	3.53	0.48	0.007	0.19
96-h extent, %	82.6[a]	68.4[b]	46.8[c]	2.42	71.2	60.6	2.09	0.007	0.001	0.38
NDF										
Disappearance rate, %/h	4.09[a]	3.66[a]	2.26[b]	0.46	3.92	2.76	0.47	0.12	0.02	0.55
96-h extent, %	61.6a[b]	69.5[a]	53.8[b]	4.17	67.6	55.7	3.39	0.02	0.05	0.99
CP degradation[2],										
DIP, % of DM	17.05	6.38	3.40	0.33	9.23	8.66	0.29	0.20	0.001	0.05
Steers	17.05	6.23	4.41[d]	–	–	–	–	–	–	–
Wethers	17.06	6.53	2.39[e]	–	–	–	–	–	–	–
SEM	0.49	0.49	0.45	–	–	–	–	–	–	–
DIP, % of CP	97.22[a]	86.28[b]	98.09[a]	0.80	93.86	94.78	0.67	0.33	0.001	0.54
UIP, % of DM	0.48[b]	0.91[a]	0.04[c]	0.05	0.51	0.45	0.05	0.38	0.001	0.52
UIP, % of CP	2.78[b]	12.51[a]	1.75[b]	0.83	6.14	5.22	0.67	0.33	0.001	0.54

[1]Probability values associated with ruminant species (S), forage quality (F), and ruminant species × forage quality interaction (S × F).

[2]CP degradability was calculated assuming kp = 5% for both steers and wethers for all 3 forage sources.

[a–c]Row values within forage quality with different superscripts differ ($P < 0.05$).

[d,e]Column within mean effects with different superscripts differ ($P < 0.05$).

CP degradability are presented in Table 5. In situ disappearance rate of DM and NDF was similar ($P \geq 0.12$) for steers and wethers. In situ disappearance rate of DM was not affected ($P = 0.48$) by ruminant species and was greater ($P \leq 0.009$) for alfalfa hay than for grass hay and lovegrass hay, and grass hay was not different ($P = 0.10$) from lovegrass hay (5.56 > 3.80 = 2.69 ± 0.46%/h for alfalfa hay, grass hay, and lovegrass hay, respectively). In situ disappearance rate of NDF was not affected ($P = 0.12$) by ruminant species and was greater ($P \leq 0.03$) for alfalfa hay and grass hay than for lovegrass hay (4.09 = 3.66 > 2.76 ± 0.46%/h for alfalfa hay, grass hay, and lovegrass hay, respectively). Extent of DM disappearance (96 h) was greater ($P = 0.007$) for steers than wethers (71.2 and 60.6 ± 2.09% for steers and wethers, respectively). In addition, it was greater ($P = 0.001$) for alfalfa hay, intermediate for grass hay, and lower for lovegrass hay (82.6 > 68.4 > 46.8 ± 2.42% for alfalfa hay, grass hay, and lovegrass hay, respectively). Extent of NDF disappearance (96 h) was greater ($P = 0.02$) for steers than wethers (67.6 and 55.7 ± 5.92% for steers and wethers, respectively). In addition, it was greater ($P = 0.01$) for alfalfa hay and grass hay than for lovegrass hay (61.6 = 69.5 > 53.8 ± 4.17% for alfalfa hay, grass hay, and lovegrass hay, respectively).

A species × diet interaction ($P = 0.049$) was detected for digestible intake protein (DIP) expressed as % of DM. Digestible intake protein was not affected ($P = 0.99$) by ruminant species when alfalfa hay and grass hay were fed. However, when lovegrass hay was fed, DIP was greater ($P = 0.05$) for steers than for wethers. Digestible intake protein (% of CP) was greater ($P = 0.001$) for alfalfa hay and lovegrass hay than for grass hay, and no difference ($P = 0.65$) was detected between alfalfa hay and lovegrass (97.2 > 87.5 < 98.3 ± 0.83% of CP for alfalfa hay, grass hay, and lovegrass hay, respectively). Undigestible intake protein was greater ($P = 0.001$) for grass hay, intermediate for alfalfa hay, and lower for lovegrass hay when expressed in proportion of DM (0.48 < 0.91 > 0.04 ± 0.057% of DM for alfalfa hay, grass hay, and lovegrass hay, respectively). When expressed in proportion to CP, UIP was lower ($P = 0.001$) for alfalfa hay and lovegrass hay than for grass hay, and no difference ($P = 065$) was detected between alfalfa hay and lovegrass hay.

Ruminal Fill and Fermentation

Effects of ruminant species and forage quality on ruminal fermentation characteristics are presented in Table 6. Ruminal DM fill was not affected ($P = 0.07$) by ruminant species, but it was lower ($P = 0.04$; 0 h, g/kg BW) for alfalfa hay than for grass hay and lovegrass hay and similar ($P = 0.25$) for grass hay and lovegrass hay (14.7 < 22.2 = 20.4 ± 1.43 g/kg BW for alfalfa hay, grass hay, and lovegrass hay, respectively). In addition, it was lower ($P = 0.01$; 5 h, g/kg BW) for alfalfa hay than for grass hay and lovegrass hay and similar ($P = 0.37$) for grass hay and lovegrass hay (16.8 < 24.7 = 21.9 ± 1.68 g/kg BW for alfalfa hay, grass hay, and lovegrass hay, respectively). Ruminal DM fill expressed per unit of metabolic BW was greater ($P = 0.001$; 0 h, g/kg $BW^{0.75}$) for steers than wethers (93.5 and 44.3 ± 3.92 g/kg $BW^{0.75}$ for steers and wethers, respectively) and at 5 h (102.4 and 49.8 ± 4.57 g/kg $BW^{0.75}$, for steers and wethers respectively). Ruminal DM fill was smaller ($P \leq 0.02$) for alfalfa than grass hay and lovegrass hay and was not different ($P = 0.12$) between grass hay and lovegrass

Table 6. Effect of ruminant species and forage quality on ruminal fermentation

	Alfalfa		Grass hay		Lovegrass hay			*P*-value[1]		
Item	Steers	Wethers	Steers	Wethers	Steers	Wethers	SEM	Species (S)	Forage (F)	S × F
Ruminal DM fill										
0 h, g/kg BW	18.7	10.7	25.5	19.8	19.6	21.2	2.03	0.07	0.005	0.08
4 h, g/kg BW	21.9	11.7	26.0	23.4	20.9	22.9	2.38	0.07	0.01	0.06
0 h. g/kg $BW^{0.75}$	82.9	28.0	110.3	50.9	87.3	54.1	6.23	0.001	0.003	0.10
4 h, g/kg $BW^{0.75}$	97.2	30.3	116.8	60.3	93.1	58.8	7.24	0.001	0.01	0.09
Ruminal liquid fill										
0 h, g/kg BW	121.8	93.3	143.4	134.0	104.6	122.2	9.46	0.43	0.01	0.07
4 h, g/kg BW	138.2	106.6	159.3	147.0	120.5	129.7	12.51	0.27	0.04	0.29
0 h, g/kg $BW^{0.75}$	541.6[a]	242.8[b]	643.2[a]	342.8[b]	465.7[a]	314.7[b]	30.66	0.001	0.002	0.02
4 h, g/kg $BW^{0.75}$	612.9	276.5	715.1	378.4	536.7	333.3	40.07	0.001	0.02	0.18
Ruminal pH	5.96[a]	6.53[b]	6.16[a]	6.30[a]	6.68[a]	6.44[a]	0.09	0.09	0.001	0.001
Total VFA, m*M*	216.9	149.7	160.8	113.3	88.7	64.8	20.13	0.08	0.001	0.35
	mol/100 mol									
Acetate	66.3	66.0	71.2	73.0	78.8	76.2	0.91	0.40	0.001	0.51
Propionate	17.8	19.7	16.8	17.1	15.9	16.9	0.59	0.06	0.001	0.37
Isobutyrate	1.58	1.45	1.46	1.07	0.94	0.77	0.13	0.04	0.001	0.55
Butyrate	10.7	10.0	8.2	7.4	5.9	5.0	0.62	0.30	0.001	0.98
Isovalerate	1.71	1.30	1.40	0.70	0.89	0.58	0.14	0.01	0.001	0.25
Valerate	1.94[a]	1.59[b]	0.93[a]	0.80[a]	0.52[a]	0.48[a]	0.08	0.08	0.001	0.02
Ace:Prop	3.76	3.50	4.24	4.34	4.81	4.57	0.16	0.32	0.001	0.47
Ammonia N, m*M*	9.20	9.25	3.62	4.72	0.00	3.17	1.12	0.19	0.001	0.23

[1]Probability values associated with ruminant species (S), forage quality (F), and ruminant species × forage quality interaction (S × F).

[a,b]Row values within forage quality with different superscripts differ ($P < 0.05$).

hay at 0 h (55.5 < 80.6 = 70.7 ± 4.39 g/kg $BW^{0.75}$ for alfalfa hay, grass hay, and lovegrass hay, respectively), and at 5 h (63.8 < 88.5 > 75.9 ± 5.10 g/kg $BW^{0.75}$ for alfalfa hay, grass hay, and lovegrass hay, respectively).

Ruminal liquid fill at 0 h was not affected ($P = 0.43$) by ruminant species, but it was smaller ($P \leq 0.02$) for alfalfa hay and lovegrass hay than for grass hay and similar ($P = 0.53$) for alfalfa hay and lovegrass hay (107.5 < 138.7 > 113.4 ± 6.67 g/kg BW for alfalfa hay, grass hay, and lovegrass hay, respectively). At 5 h, ruminal liquid fill was not affected ($P = 0.27$) by ruminant species, but it was smaller ($P \leq 0.03$) for alfalfa hay and lovegrass hay than for grass hay and similar ($P = 0.83$) for alfalfa hay and lovegrass hay (122.4 < 153.2 > 125.1 ± 8.82 g/kg BW for alfalfa hay, grass hay, and lovegrass hay, respectively). When ruminal liquid fill was expressed per unit of metabolic BW, a ruminant specie × forage quality interaction was present ($P = 0.02$) at 0 h. Ruminal liquid fill was greater ($P \leq 0.02$) for steers than wethers for each forage type. However, the difference in ruminal liquid fill was different for each forage quality. At 5 h, ruminal liquid fill was greater ($P = 0.001$) for steers than for wethers (621.6 and 329.4 ± 24.38 g/kg $BW^{0.75}$ for steers and wethers, respectively). Also, alfalfa hay and lovegrass hay were lower ($P \leq 0.02$) than grass hay, and alfalfa hay did not differ ($P = 0.81$) from lovegrass hay (447.7 < 546.7 > 435.0 ± 28.25 g/kg $BW^{0.75}$ for alfalfa hay, grass hay, and lovegrass hay, respectively).

Ruminal pH was influenced by a ruminant species × forage quality interaction ($P = 0.001$). When alfalfa hay was fed, ruminal pH was greater ($P = 0.001$) for wethers than for steers, but when grass hay or lovegrass hay were fed, ruminal pH did not differ ($P \geq 0.07$) between species.

Total VFA production was not affected ($P = 0.08$) by ruminant species and was greater ($P = 0.001$) for alfalfa hay, intermediate for grass hay, and smaller for lovegrass hay (183.3 > 136.1 > 76.7 ± 14.23 m*M* for alfalfa hay, grass hay, and lovegrass hay, respectively). Ruminal proportion of acetate was smaller ($P = 0.001$) for alfalfa hay, intermediate for grass hay, and greater for lovegrass hay (66.1 < 72.1 < 76.0 ± 0.65 mol/100 mol for alfalfa hay, grass hay, and lovegrass hay, respectively). Ruminal propionate proportion was greater ($P = 0.001$) for alfalfa hay than for grass hay and lovegrass hay (18.8 > 17.0 = 16.4 ± 0.43 mol/100 mol for alfalfa hay, grass hay, and lovegrass hay, respectively). Acetate to propionate ratio was smaller ($P = 0.001$) for alfalfa hay, intermediate for grass hay, and greater for lovegrass hay (3.63 < 4.29 < 4.69 ± 0.11 for alfalfa hay, grass hay, and lovegrass hay, respectively).

Ruminal ammonia N was greater ($P \leq 0.009$) for alfalfa hay, intermediate for grass hay, and smaller for lovegrass hay (9.22 > 4.17 > 1.58 ± 0.85 mM for alfalfa hay, grass hay, and lovegrass hay, respectively).

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 species 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 species, Reid et al. (1988) reported that daily DMI, expressed as g/kg of $BW^{0.75}$, was greater 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 species × 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. Therefore, the most appropriate way to predict forage intake by cattle using sheep as a model would be by expressing sheep intake per unit of BW (g/kg BW).

Apparent Total Tract Digestibility

Digestibility expressed as digestible intake per unit of BW was the only measurement of digestibility that did not present a ruminant species × forage quality interaction. Therefore, using sheep to predict forage digestibility of cattle is more accurate when digestibility is measured as digestible intake per unit of BW. Although digestible OM and ADF intake per unit of BW was similar for cattle and sheep, digestible NDF and N were greater for steers than wethers. Therefore, the prediction of cattle NDF and N digestible intake using sheep will be less accurate than the prediction of OM and ADF digestible intake. 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 greater apparent digestibility coefficients for cattle than sheep fed legumes and C_3 and C_4 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 ad libitum as hays was greater in cattle than sheep. For a number of C_3 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 et al. (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 greater 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 of ruminal digestion by steers and wethers was similar, and it was influenced more by forage than by ruminant species. 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. The meaning of the greater in situ disappearance at a fixed time (96 h) for steers than wethers is that microorganisms in the rumen of sheep have less ability than microorganisms in the rumen of cattle to degrade the slower digestible fraction that is feed fiber. Therefore, although sheep have less retention time than cattle, increasing the retention time of sheep would likely result in only a marginal increase of fiber degradation. In situ studies in sheep would be a good predictor of cattle in situ degradation rate, but not of cattle extent of digestion.

Calculation of DIP and UIP is a function of CP degradation rate and passage rate (Broderick, 1994). Degradation rate of CP was estimated in the present study; however, passage rate was not estimated. Because ruminal passage rate of sheep has been shown to be faster than that of cattle (Averts et al., 1984; Demment and Van Soest, 1985), calculations of DIP and UIP with CP degradation rate and passage rate from sheep would not be accurate for cattle. A possible approach could be to use a CP degradation rate estimated with sheep and assume a passage rate for cattle.

Ruminal Fill and Fermentation

Ruminal DM and liquid fill were greater for steers than wethers when expressed per unit of metabolic BW. However, ruminant species did not affect ruminal DM and liquid fill when expressed per unit of BW. Forage quality affected ruminal DM and liquid fill both ways of expressing it, per unit of BW and per unit of metabolic BW. Therefore, ruminal DM and liquid fill of cattle can be estimated from ruminal DM and liquid fill of sheep expressed per unit of BW.

Ruminal pH was not affected by ruminant species when grass hay and lovegrass hay were fed. However, pH was greater for wethers than steers when alfalfa hay was fed. Therefore, ruminal pH of cattle can be predicted from sheep pH when moderate- or low-quality forages are fed, but it cannot be predicted as accurately when high-quality forages are fed. Ruminal ammonia and VFA concentrations were affected by forage type, but not ruminant species. Therefore, ruminal ammonia and VFA concentrations of cattle could be predicted from ruminal ammonia and VFA concentrations of sheep.

In summary, 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. The hypothesis that cattle digest low-quality forages more completely than sheep was confirmed. However, digestibility of moderate- to high-quality forages seems to be similar for sheep and cattle. Therefore, sheep should not be substituted for cattle in research settings when low-quality forage is being considered. It appears that expressing digestibility as digestible intake per unit of BW allows for a wider range of forage qualities to be compared when substituting sheep for cattle.

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