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Comparisons of Ruminal Fermentation Characteristics and Microbial Populations in Bison and Cattle†

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Ruminal microbial populations, fermentation characteristics, digestibility, and liquid flow rates in two ruminally cannulated bison and two ruminally cannulated Hereford steers fed a prairie hay diet were compared. No significant differences in anaerobic bacterial counts, volatile fatty acid concentrations, or ruminal pHs were evident between bison and cattle. Also, no significant differences in neutral detergent fiber digestibility, indigestible fiber retention time, or intake were detected between bison and cattle, although cattle had higher levels ($P < 0.08$) of ruminal dry matter and indigestible fiber than bison. Bison had a smaller ($P = 0.02$) ruminoreticular volume, faster liquid dilution rates, and faster liquid turnover times than cattle. The average ruminal ammonia nitrogen concentration was higher ($P = 0.02$) in bison (1.17 mg/dl) than in cattle (0.79 mg/dl). Total ciliate protozoal counts and cell volume were greater ($P = 0.07$) in bison (32.8×10^4/g and 407.1×10^{-4} ml/g, respectively) than in cattle (15.7×10^4/g and 162.2×10^{-4} ml/g, respectively). Bison harbored higher ($P < 0.02$) numbers of *Dasytricha* spp., *Eudiplodinium maggii*, *Eudiplodinium bursa*, and *Epidinium* spp. than cattle and possessed a type B protozoan population. The cattle possessed a mixed type A-type B population that was characterized by *Ophryoscolex* spp. and *Polyplastron* spp. in association with low concentrations of *Epidinium* spp. and *Eudiplodinium maggii*.

Both bison and cattle are generalist herbivores that are capable of subsisting on high-fiber diets. Bison, however, are less discriminate grazers and consistently select lower-quality forages than cattle (29). Poor-quality forages apparently are digested more efficiently by bison than by cattle (22, 33). The mechanisms that are responsible for the putative differences in digestive capacity between bison and cattle have not been examined, but they may involve differences in ruminal microbial populations. Orpin et al. (27) have determined that a highly specialized ruminal microflora, which is particularly effective in fiber digestion, enables high-arctic Svalbard reindeer (*Rangifer tarandus platyrhynchus*) to survive low-quality nutritional conditions. Bison may likewise possess microbial populations that differ from those of domestic ruminants.

Relatively little is known about ruminal fermentation characteristics and microbial populations in bison. One brief report concluded that microorganisms in bison appeared to be similar to those found in domestic livestock (28). Preliminary investigations, however, indicated that ruminal protozoal populations differed both quantitatively and qualitatively between bison and cattle. The objectives of this study were to better understand the possible differences between bison and cattle by comparing ruminal fermentation characteristics, digestibility, bacterial numbers, and protozoal populations in both species.

MATERIALS AND METHODS

Animals and sampling. Two bison were obtained as 6-month-old calves from a wild bison herd and were isolated from the cattle during captivity. In the ensuing 14 months, the bison were castrated, ruminally cannulated, and familiarized with frequent handling. The two bison steers (average weight, 265 kg) and two ruminally cannulated Hereford steers (age, 30 months; average weight, 457 kg) were penned separately in late February, when the study was begun, and offered coarsely chopped prairie hay (4.5% crude protein, 69.4% neutral detergent fiber) at 12-h intervals ad libitum. No additional feed was provided. Orts were removed and weighed each morning, immediately before feed was offered. After a 14-day adjustment period, ruminal samples in one animal were collected before the morning feeding from the mid-dorsal sac, ventral sac, and reticulum with 125-ml plastic containers that were capped in situ. Orts and water were removed 2 h after feed was offered; and subsequent ruminal samples were collected at 2, 4, 6, 8, and 12 h postfeeding. During the next 3 days, the three remaining animals were sampled similarly, and the procedure was then repeated 3 weeks later.

Sample preparation. Immediately after each collection, the three ruminoreticular subsamples were transported to a laboratory and composited under oxygen-free CO_2. Approximately 20 ml of ruminal contents was pipetted with a wide-orifice pipette into tared flasks containing 10% (vol/vol) Formalin. Flasks were reweighed, and additional Formalin was added to obtain a 1:1 (wt/wt) dilution of ruminal contents. This mixture was used for protozoal enumeration.

The remaining ruminal sample was blended for 1 min under CO_2 and strained through four layers of cheesecloth. The pH of the strained ruminal fluid was recorded, fermentation products were analyzed, and bacteria were enumerated.

Duplicate portions of the homogenized ruminal sample were frozen following acidification with 25% (wt/vol) *meta*-phosphoric acid, for volatile fatty acid (VFA) analysis (16), or with 0.1 N HCl, for ammonia nitrogen (NH_3-N) analysis. After thawing and centrifuging, VFA samples were analyzed

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TABLE 1. Ruminal liquid and solid kinetics in bison and cattle fed a prairie hay diet[a]

Species	Rumen vol (liters)	Rumen vol (ml/kg of body wt)	Liquid outflow, (liters/h)	Liquid dilution rate (%/h)	Liquid turnover (h)	Ruminal dry matter (% of body wt)	Indigestible fiber fill (% of body wt)	Indigestible fiber retention time (h)	Indigestible fiber outflow (kg/h)	Indigestible fiber passage (%/h)	Neutral detergent fiber digestibility (%)	Intake (g of dry matter day^{-1} kg^{-1} of body wt)
Bison	16.2[b]	64[b]	1.3[b]	8.39[b]	12.3[b]	1.22[b]	0.37[b]	39.8	1.52[b]	2.6	48.1	11.3
Cattle	44.0	101	2.6	5.88	17.1	1.66	0.46	42.2	2.67	2.4	45.0	12.8
SE	1.3	3	0.1	0.73	1.1	0.11	0.03	3.7	0.18	0.2	0.5	0.2

[a] The average weights of bison and cattle were 265 and 457 kg, respectively.
[b] Different from cattle ($P < 0.10$).

in duplicate by gas chromatography, and NH_3-H concentrations were determined in duplicate on an autoanalyzer.

Microbial enumeration. For anaerobic bacterial enumeration, serial 10-fold dilutions of strained ruminal fluid were made in anaerobic dilution blanks (4). Four roll tubes containing prereduced, anaerobically sterilized medium (19) and purified agar were inoculated with 0.5 ml from each of the 10^{-6}, 10^{-7}, and 10^{-8} dilutions. Colonies were counted after a 7-day incubation period at 39°C.

A portion of the Formalin mixture sample was diluted with staining solution containing methyl green in phosphate buffer with 30% (vol/vol) glycerol for protozoal enumeration. Total numbers and the generic distribution of ciliate protozoa were counted from 20 microscopic fields in a counting chamber (Sedgwick-Rafter). Identification of protozoal species was done as described by Hungate (23). The length and width of 20 random cells from each protozoal species in both bison and cattle were measured with a calibrated ocular micrometer. Members of the genus *Entodinium* was not identified to the species level, and average cell dimensions were determined from 40 randomly selected cells. Relative cell volumes were calculated from a rotational ellipsoid formula, assuming that the thickness was in constant proportion to the width (20).

Liquid flow rate. Following the first replication of sampling for microbial enumeration, a 250-ml dose of chromium-EDTA was infused into several locations throughout the rumen in all four animals, to determine liquid dilution rates (3). Liquid samples were aspirated with a screened core sampler from different ruminal locations at seven intervals during the 24 h after dosing. Fluid samples were refrigerated and centrifuged, and the supernatant was analyzed for chromium by atomic absorption spectroscopy with air-acetylene combustion (3). Dilution rates were calculated from the regression of the natural logarithm of the chromium concentration on time postdosing (17). Fluid volume was estimated by dividing the chromium dose by the antilog of the y intercept.

Digestibility. Digestibility was estimated by determining the ratio of indigestible acid detergent fiber in feed and fecal samples. Fresh fecal grab samples were collected before the morning feeding for 7 consecutive days. Midway between feedings (1400 h) on day 7, all four animals were ruminally evacuated. After the contents were weighed, three homogenous subsamples were collected from each animal for dry matter and indigestible acid detergent fiber analyses.

Forage, fecal, and ruminal samples were dried at 55°C in a forced-air oven and ground through a 1-mm-mesh screen. Equal allotments from the fecal samples obtained on 7 consecutive days were pooled for each animal. Neutral detergent fiber was determined in duplicate for forage and fecal samples (18). Indigestible acid detergent fiber was determined in duplicate for all samples from a 6-day in vitro incubation, followed by acid detergent fiber extraction of the residue (8).

Statistical analysis. Each phase of the trial was replicated, and the combined data were statistically analyzed as a split plot design, with sampling time as the subplot. Species differences were tested with animal (species) as the whole plot error term, whereas the effects of time and time × species were tested with the residual mean square as the error term. The average animal weight was analyzed initially as a covariate but was not significant for any variable, so it was removed from the analysis to increase the degrees of freedom in the error term. Liquid and particulate flow rates and ciliate cell volume were analyzed by one-way analysis of variance with animal (species) as the error term. Protozoal measurements are given as means ± standard error.

RESULTS

Intake and digestibility. Both voluntary hay consumption and digestibility were similar between bison and cattle (Table 1). On a body weight basis, cattle had a greater amount of ruminal dry matter ($P = 0.07$) and indigestible fiber fill ($P = 0.08$) than bison, but no difference in fiber retention time or passage rate was evident. On termination of the trial, the bison lost 28 kg (10.6% weight loss) and the cattle lost 47 kg (10.3% weight loss).

Liquid flow. Bison had smaller ($P = 0.02$) ruminal volumes than cattle, after adjusting for body weight differences (Table 1). Liquid dilution rate and turnover time were faster in bison, although liquid outflow from the rumen was greater ($P = 0.06$) in cattle.

VFAs and pH. No significant differences were found between bison and cattle in total VFA concentrations or in the molar proportions of individual VFAs (Table 2). Total VFA and molar proportions of acetate, propionate, and butyrate were significantly higher at 2 h postfeeding than at prefeeding and then declined over time (data not shown). Also, no differences in ruminal pH were observed between bison and cattle for any sampling time. The ruminal pH dropped after feeding, but there was no significant time effect ($P = 0.58$).

NH_3-N. Ruminal NH_3-N concentrations were higher ($P = 0.02$) in bison than in cattle (Table 2). Ammonia concentrations at all sampling times except 2 and 4 h postfeeding were significantly higher in bison than in cattle (Fig. 1). In both

TABLE 2. Ruminal fermentation characteristics and bacterial numbers in bison and cattle fed a prairie hay diet

Species	pH	Total VFA (mM)	mol/100 mol			NH_3-N (mg/dl)	Anaerobic bacteria (10^9 CFU/g)
			Acetate	Proprionate	Butyrate		
Bison	6.69	95.7	75.8	12.9	9.4	1.17[a]	47.0
Cattle	6.71	99.0	73.9	13.6	10.9	0.79	39.8
SE	0.02	1.1	0.2	0.1	0.1	0.06	1.1

[a] Different from cattle ($P < 0.10$).

species, the highest NH_3-N concentrations occurred at 12 h postfeeding.

Bacteria. Total counts of culturable anaerobic bacteria were similar for bison and cattle (Table 2). Although time effects were not significant ($P = 0.27$), a large decline in counts occurred in both species at 2 h postfeeding (data not shown).

Protozoa. Total ciliate protozoal numbers were higher ($P = 0.07$) in bison than in cattle (Table 3). Bison possessed significantly higher concentrations of *Epidinium* spp., *Eudiplodinium maggii*, *Eudiplodinium bursa*, and *Dasytricha* spp. Other protozoal genera were similar between bison and cattle, except that *Ophryoscolex* spp. and *Polyplastron* spp. were absent in bison.

The total ciliate cell volume in bison was more than twice that in cattle (Table 3). Members of the genus *Entodinium*, containing the most numerous but relatively small protozoal species, accounted for only 7.9 and 14.7% of the total ciliate volume in bison and cattle, respectively. Members of the genus *Eudiplodinium* represented the largest proportion of protozoal cell volume in both bison and cattle.

Holotrichs exhibited a distinct diurnal cycle in both bison and cattle; however, there was a species × time interaction ($P = 0.01$) for *Dasytricha* spp. In cattle, *Dasytricha* numbers peaked at 2 h postfeeding and then declined rapidly, but in bison numbers were significantly higher at both 2 and 4 h after feeding than at the other sampling times (Fig. 2). Numbers of other protozoal species did not differ ($P > 0.10$) with sampling time, although there was a decline in *Entodinium* concentrations immediately after feeding.

Ciliate cell size significantly differed between bison and cattle for three protozoal species. *Eudiplodinium maggii* was larger in cattle (length [L], 176.2 ± 5.0 μm; width [W], 137.6 ± 3.8 μm) than in bison (L, 128.5 ± 2.8 μm; W, 89.2 ± 1.4 μm); *Ostracodinium dentatum* was larger ($P < 0.0001$) in bison (L, 113.0 ± 3.0 μm; W, 68.3 ± 1.8 μm) than in cattle (L, 82.0 ± 2.3 μm; W, 53.6 ± 1.3 μm); and *Epidinium* varieties were longer in bison (L, 136.8 ± 3.0 μm; W, 54.6 ± 1.3 μm) than in cattle (L, 97.9 ± 3.4 μm; W, 53.8 ± 1.0 μm).

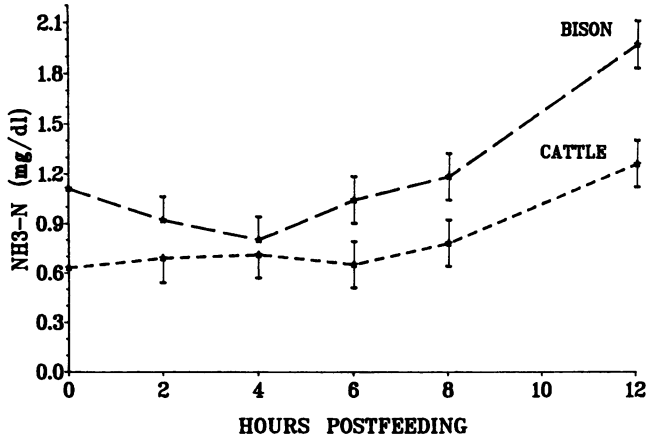

FIG. 1. Changes in ruminal ammonia concentrations in bison and cattle on a prairie hay diet. Vertical lines represent the standard error.

DISCUSSION

In contrast to data from other comparative studies of ruminants on low-quality diets (21, 22, 29, 33), our data did not confirm a putative digestive superiority of bison over cattle. However, because only two animals of each species were used in this study, any differences between bison and cattle would have to be substantial to be detected statistically.

In agreement with other reports (22, 33), we found no differences in forage intake between bison and cattle. During winter stress, however, cattle increase feed consumption and have comparatively higher intake levels than bison (6, 22). That may account for speculation that higher digestibility in bison is due to reduced feed intake and the concomitant longer retention time within the gastrointestinal tract. Schaefer et al. (35) have observed that the digesta retention time is 18% longer in bison than in three breeds of cattle. We found no differences in retention time, however, between bison and cattle, although cattle paradoxically accommodated higher levels of ruminal fill.

High ruminal ammonia concentrations tend to be associated with large protozoal numbers (38), presumably because of increased proteolysis. However, increased ruminal NH_3-N concentrations in bison also could be due to higher amounts of urea being recycled to the rumen. Peden et al. (29) have hypothesized that recycled nitrogen could account for the observed digestive differences between bison and cattle by providing a more favorable ruminal environment for microbial activity. Many herbivore species are seasonally adapted to subsist on nutritionally deficient diets and can increase the nitrogen concentration in sites of microbial fermentation (24, 34, 36). On low-quality diets, ruminal nitrogen can become limiting, and bacteria that utilize energy sources that are more readily available than cellulose may assimilate most of the NH_3-N (5). Increasing ruminal NH_3-N concentrations via the recycling of urea would enable cellulolytic bacteria to compete for nitrogen more effectively, which potentially could enhance cellulose digestion.

Differences in protozoal concentrations between bison and cattle can be correlated with variations in ruminal physiological characteristics. Animals with small ruminoreticular volumes generally have higher protozoal numbers compared with animals with larger rumens (26, 32). An increased liquid dilution rate, however, is also associated with a smaller ruminal volume (31). The ability of bison to maintain high concentrations of protozoa suggests that they are not washed out of the rumen under conditions of high liquid dilution, agreeing with reports that protozoal outflow

TABLE 3. Numbers and volume of ciliate protozoa in bison and cattle fed a prairie hay diet

Species	10^3 cells/g of ruminal fluid													
	Isotricha spp.	*Dasytricha* spp.	*Entodinium* spp.	*Diplodinium* spp.	*Eudiplodinium* spp.	*Eudiplodinium bursa*	*Eudiplodinium maggii*	*Metadinium* spp.	*Ostracodinium* spp.	*Epidinium* spp.	*Ophryoscolex* spp.	*Polyplastron* spp.	Total no.	Total vol (10^6 μm^3/g)
Bison	7.4	73.2[a]	150.7	37.3	32.4	19.9[a]	9.5[a]	2.2	9.9	15.1[a]	0	0	328.3[a]	407.1[a]
Cattle	5.4	19.6	97.5	3.1	15.4	0	1.3	2.3	12.2	1.4	0.09	<0.02	156.9	162.2
SE	0.6	3.1	4.8	2.1	1.6	1.1	0.6	0.3	1.0	0.9	0.03		6.5	27.5

[a] Different from cattle ($P < 0.10$).

more closely follows the solid rather than the liquid phase (39).

In both bison and cattle, holotrich numbers increased after feed was offered. Cyclic fluctuations in holotrich concentrations over time are caused by their behavior of sequestrating on the reticular wall and migrating into the rumen for a few hours after feed intake by the host (1, 25).

Quantitative and qualitative differences in some protozoal species between bison and cattle reflect different population types rather than host specificity. Eadie (13, 15) has designated two separate ruminal protozoal populations: type A, which is characterized by the presence of *Polyplastron* spp. and *Ophryoscolex* spp.; and type B, which is characterized by *Epidinium* spp., *Eudiplodinium maggii*, and *Eudiplodinium* (*Eremoplastron*) *bursa*. Other protozoal species apparently coexist satisfactorily in either population type; but *Polyplastron* spp. is antagonistic to type B populations and selectively feeds on *Epidinium* spp., *Eudiplodinium maggii*, and *Eudiplodinium bursa*. Both bison possessed a type B population, but both cattle harbored *Polyplastron* spp. and *Ophryoscolex* spp. in association with type B protozoa, thus possessing a mixed type A-type B population.

Although Eadie (15) contended that *Polyplastron* spp. would not form a stable, mixed community with type B species, the coexistence of both types in cattle may be due to developmental polymorphism in the prey protozoa. The *Epidinium* sp. in cattle was the five-spined variety, *Epidinium cattanei*, which apparently is resistant to predation from *Polyplastron* spp. In bison, other *Epidinium* varieties prevailed and the *Epidinium cattanei* variety was undetected. *Eudiplodinium maggii* in cattle was significantly larger than that in bison. Enlarged *Eudiplodinium maggii* cells were not detected in bison, suggesting that the polymorphic plasticity of *Eudiplodinium maggii* is an inducible defense to evade ingestion by *Polyplastron* spp. *Eudiplodinium bursa* was absent in the cattle, indicating that it cannot coexist in a mixed population. Eadie (15) has observed that on intermixing, *Polyplastron* spp. preferentially engulfs the smaller type B protozoa (*Eudiplodinium bursa*) first, followed by *Epidinium* spp. and then *Eudiplodinium maggii*.

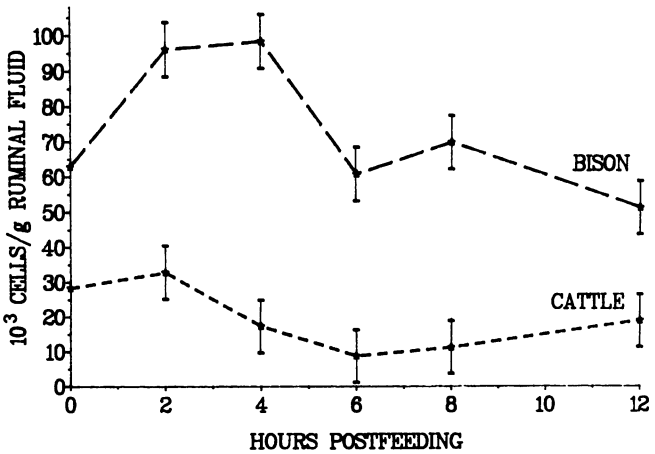

FIG. 2. Diurnal variation of *Dasytricha* numbers in bison and cattle fed prairie hay at 12-h intervals. Vertical lines represent the standard error.

The type B population found in bison epitomizes the protozoal populations that are observed in other wild ruminants. Brazilian water buffalo (*Bubalus bubalis*) (11), musk oxen (*Ovibos moschatus*) (9, 12), red deer (*Cervus elaphus*) (30), and African antelopes (*Redunca* spp.) (37) are all characterized by type B protozoal populations. In contrast, domestic ruminants commonly possess either type A or mixed type A-type B populations (2, 10, 14).

Different protozoal population types are partially responsible for the large differences in total protozoal cell volume between bison and cattle. The three type B protozoal species accounted for 47.1% of the total ciliate volume in bison, but contributed only 24.3% in cattle, primarily because of enlarged *Eudiplodinium maggii*. *Polyplastron* spp. and *Ophryoscolex* spp. concentrations were suppressed when cattle were on this diet, so despite their massive size, contributions to the ciliate cell volume were negligible. The total ciliate cell volume represents both numbers and size of individual cells and is important in enzymatic activity and the capacity to ingest bacteria and plant fragments (7). However, despite the higher protozoal cell volume in bison than in cattle, no differences in fermentation products between ruminant species were detected.

Our data for bison and cattle that were fed poor-quality hay and sampled under similar conditions indicate that there are large differences between species in ruminal NH_3 concentrations, protozoal numbers, and protozoal population types. Other differences between bison and cattle could exist, but they could not be detected statistically because of the experimental constraints of using only two animals of each species.

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