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THE TROPHIC ECOLOGY OF *BISON BISON* L. ON SHORTGRASS PLAINS

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INTRODUCTION

Historically, the North American buffalo or bison (*Bison bison* L.) has been important to the ecology and activities of man, yet little is known about its ecology and especially its feeding habits and nutrition in relation to natural vegetation. This paper elucidates recent findings on this subject comparing, where possible, bison with cattle and sheep.

Bison are recognized as 'grass eaters' (Larson 1940; Longhurst 1961). Garretson (1938) suggested that bison during the last century consumed mostly 'buffalo grass', a variety of species other than *Buchloe dactyloides* (Nutt.) Engelm. Martin, Zim & Nelson (1951) reported that bison in Oklahoma consumed mostly blue grama (*Bouteloua gracilis* (H.B.K.) Lag.), sand dropseed (*Sporobolis cryptandrus* (Torr.) A. Gray), little bluestem (*Andropogon*, sp.), and windmill grass (*Chloris* sp.). The genera *Avena*, *Agropyron*, *Bromus*, *Hierchloe*, *Elymus*, *Koeleria*, *Stipa*, *Phragmites*, *Distichlis*, *Hordeum* and *Carex* are prominent in the diets of bison in the Athabasca region (Soper 1941) and in south-eastern Utah (Nelson 1965). Martin *et al.* (1951) reported an exception in which the diet of bison in Arizona contained 71% saltbush (*Atriplex* sp.). In general, North American bison diets differ from those of wisent (*Bison bonasus* L.) (Borowski, Kransinski & Milkowski 1967) where at least 20% of the diet consists of browse; grasses and sedges comprising a relatively small proportion. These studies, however, give little indication of the effects of different season and pasture conditions on dietary composition.

Forage intake rates by bison are not fully understood. Borowski *et al.* (1967) reported that an adult wisent weighing about 250 kg consumes 9–15 kg dry matter/day, equivalent to 3·5–6·0% of their live weight. This value is higher than in cattle (Agricultural Research Council 1965) and agrees with Burback (1951) who stated that two bison consume as much forage as three cattle. In contrast, Peters (1958) found that bison consumed 25% less than similar sized cattle when placed in pens with unlimited food.

There is little information on forage digestion by bison. Pearson (1967) reported that bison rumen microflora in southern Utah is similar to that in domestic cattle. This finding alone, however, is inadequate to compare forage digestibility. Sczaniawski (1960) found that cattle calves had greater digestive capacity than wisent calves when fed on four artificial foodstuffs.

MATERIALS AND METHODS

This study was conducted on the Pawnee Site in north-eastern Colorado on shortgrass vegetation in which blue grama is the dominant species. The methods used have been

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described by Peden (1972). Three treatments, representing lightly grazed and heavily grazed pasture, were stocked with zero, one and three cattle animal-units/12 ha/month between 1 May and the end of October.

After being bottle-fed from 1 to 3 months old, five yearling bison were fitted with oesophageal fistulas. Similarly managed and fistulated domestic cattle and sheep were also maintained. Diet sampling occurred within 1 week of six specified dates: 15 December 1970, 25 March, 5 May, 25 June, 25 August and 20 October 1971. The last five dates were preceded by an adjustment period of at least 10 days when the animals received no supplemental feed and were alternated daily between the lightly grazed and heavily grazed treatments.

Extrusa samples from all available and healthy, oesophageal fistulated bison, cattle and sheep were collected on alternate days over an 8-day period from both treatments. Each collection period ranged from 30 to 60 min of grazing time.

Immediately after collection, the samples were oven-dried for 24 h at 55° C. The dried samples were ground through a 1-mm-mesh screen and thoroughly mixed. Daily samples from each animal, month and treatment were bulked. Equal aliquots from daily samples were used to make the composite samples. Thus, for each sample period two composite samples were obtained from each animal; one from the lightly grazed and one from the heavily grazed treatment. These composite diet samples were used to determine forage composition and digestibility. There were three to six replicate digestion estimates for each composite diet sample.

For each composited diet sample for both bison and cattle, 48-h dry-matter nylon-bag microdigestion coefficients were determined using three rumen fistulated bison and cattle. A four-way analysis of variance was used to test for difference between the digestibility of forage collected by bison and by cattle, their digestive capacity, and forage digestibility among the six sample dates and the two treatments. Interactions of these four main effects were also considered. With the exception of the December 1970 sample period, the rumen fistulated animals were maintained for at least 10 days on native pasture prior to the digestion trials.

Since the standard error of the mean percentage nylon-bag digestion estimate of every cell in the analysis of variance was less than 1%, the means were fitted to a Fourier series (Jackson 1957) of three harmonics with time of year as the independent variable. The values of February 1971 are linear extrapolations between the preceding and following sample dates. The means were shifted on the time axis to produce equivalent time periods. This bias is probably not serious since each sample period extended over 2–3 weeks.

Percentage dry weight plant composition of both bison and cattle composite diet samples was determined microscopically (Sparks & Malechek 1968). Each of the identified species was classified as warm-season grasses, cool-season grass, warm-season forb, cool-season forb, or shrub as described by Sims & Singh (1972). The warm-season plants grow during the summer and mature in either late summer or fall, and the cool-season species grow in spring and flower in early summer.

Seeds, unknown species and cactus were discarded from the analyses since they rarely occurred. Multivariate analyses were used to test for differences in percentage dry weight of plant groups among the diets of bison, cattle and sheep, between the diets collected from the two treatments, sample dates and digested (nylon-bag residue) and non-digested material.

Percentage composition by weight of crude protein was estimated for each composited bison and cattle diet sample. A three-way analysis of variance was used to test for differences between the two ungulates, grazing treatments and sample dates.

Movement records were kept for each sample period and involved recording the direction and location of the herd every 5 min during each diet sample collection period. Movement intervals marked on the map were each divided into twenty equal segments. At the extremes of each segment, a one point quadrat was used to record the plant species. The data for individual species were then bulked as in the diet samples. The percentage cover for each plant group was determined for each sample day and for each ungulate species, this permitted a weighting of cover to those areas which were grazed most frequently. A multivariate analysis was used to test for differences in cover between grazing species, grazing treatments and sample dates.

An index of similarity, R_0 (Horn 1966), was used to describe overall similarity of the diet composition vectors for each animal species at each sample date, to those of herbage cover. An R_0 value of 1·0 implies identical composition vectors, while one of zero a complete lack of similarity. A relatively low R_0 value indicates a greater degree of selectivity when comparing a diet with the available herbage.

RESULTS

Plant composition of the diets

A total of thirty-six plant species were identified in the bison diets. These are classified (Table 1) as warm-season grass, cool-season grass, warm-season forbs, cool-season forbs and shrubs. The percentage dry weight of plant groups are given in Table 2. Differences

Table 1. *Classification of plants observed in bison diets*

'Grasses'

Warm season

Aristida longiseta Steud.
Bouteloua gracilis (H.B.K.) Lag.
Buchloe dactyloides (Nutt.) Engelm.
Muhlenbergia sp.
Sporobolis cryptandrus (Torr.) A. Gray.

Cool season

Agropyron smithii Ryd b.
Bromus tectorum L.
Carex heliophora Mackenzie
Festuca octoflora Walt.
Oryzopsis hymenoides (Roem. & Schult.) Ricker
Stipa comata Trin. & Rup.

Forbs

Warm season

Aster tenacetifolius (H.B.K.) Nees.
Cirsium undulatum (Nutt.) Spreng.
Eriogonum sp.
Evolvulus nuttallianus R. & S.
Guara coccinea Pursh.
Iva axillaris Pursh.
Kochia scoparia (L.) Schrad.
Liatrus punctata Hook.
Mirabilis linearis (Pursh.) Heimerl.
Oenothera sp.
Psoralea tenuiflora Pursh.
Salsola kali L.
Sphaeralcea coccinea (Nutt.) Rydb.
Thelesperma sp.

Cool season

Allium textile Nels. & Macb.
Astragalus sp.
Bahia oppositifolia A. Gray
Plantago purshii R. & S.
Tradescantia occidentalis (Britton) Smyth.

Shrubs

Artemisia frigida Willd.
Chrysothamnus nauseosus (Pursh.) Britton.
Gutierrezia sarothrae (Pursh.) Britt. & Rusby
Yucca glauca Nutt.

Cactus

Opuntia polycantha Haw.

Table 2. *Percentage dry matter of plant groups in bison, cattle, and sheep diets collected from the grazing treatments*

		Dry weight (%)											
		Lightly grazed						Heavily grazed					
	Plant group	Dec.	Mar.	May	June	Aug.	Oct.	Dec.	Mar.	May	June	Aug.	Oct.
Bison	Warm-season grass	83	70	44	78	88	82	79	56	18	80	93	78
	Cool-season grass	7	28	54	15	7	17	6	21	80	12	7	9
	Warm-season forbs	6	0	1	7	5	1	11	0	1	8	1	1
	Cool-season forbs	1	0	1	1	0	0	1	0	0	0	0	1
	Shrubs	0	0	0	0	0	0	1	21	0	0	0	12
Cattle	Warm-season grass	41	32	12	24	65	58	57	35	3	22	41	21
	Cool-season grass	57	44	67	46	8	28	19	9	94	18	12	9
	Warm-season forbs	0	4	2	22	27	9	3	7	1	31	4	22
	Cool-season forbs	2	0	1	7	0	0	15	2	1	16	1	0
	Shrubs	0	21	15	1	0	5	2	46	1	13	42	47
Sheep	Warm-season grass	–	33	13	22	28	38	–	3	8	23	64	26
	Cool-season grass	–	7	50	19	4	31	–	1	81	4	6	34
	Warm-season forbs	–	4	8	38	68	28	–	1	4	69	24	18
	Cool-season forbs	–	0	1	14	0	0	–	0	0	3	1	0
	Shrubs	–	57	27	3	0	2	–	95	6	1	5	22

($P<0{\cdot}01$) in the diets among the three herbivores, the six sample dates and between the two grazing treatments, indicate that bison consumed more warm-season grass than cattle or sheep on both grazing treatments and on all sample dates. Apart from late winter and early spring, warm-season grasses comprised about 80% of bison diet. Unlike sheep and cattle diets, those of bison consistently contained less than 13% forbs. The diets of sheep and cattle frequently had relatively high proportions of forbs, especially during June and October. The occurrence of shrubs in bison diets was of minor importance only during March and October on the heavily grazed treatment. Shrubs were also most prominent during these months in cattle and sheep diets but they were higher than in bison diets at other periods. The percentage of cool-season grass in diets of cattle was in general greater than in bison diets. Except when foraging on heavily grazed pasture in March, bison consumed at least 85% grasses and sedges.

Crude protein composition of bison and cattle diets

There were differences ($P<0{\cdot}01$) in dietary crude protein between bison and cattle, the two grazing treatments and among the sample dates. Diets of both species were highest in crude protein during May and minimal in March. For the most part diets selected from the heavily-grazed treatment were slightly higher in crude protein content (Table 3).

Table 3. *Dry weight (%) of crude protein in bison and cattle diets from lightly and heavily grazed pasture*

	Lightly grazed		Heavily grazed	
	Bison	Cattle	Bison	Cattle
December	5·3	5·3	5·7	7·0
March	4·4	7·0	4·6	6·9
May	10·6	14·3	13·4	17·8
June	7·8	9·0	8·4	9·9
August	6·9	7·2	6·8	7·5
October	7·1	8·1	7·1	9·4

Forage digestibility

Seasonal trends in forage digestion are shown in Fig. 1. All the differences in digestibility discussed were significant ($P<0{\cdot}01$). The digestive power of bison differed from that of cattle when both animal species simultaneously digested similar forage collected from grazing bison (Fig. 1) from both the lightly grazed and heavily grazed treatments. The significant interaction between the effects of season and digestive capacity can be explained by the fact that the digestive capacity of bison resulted in a 15–20% greater dry matter loss in late winter than that observed in cattle while the digestive capacity was the same, or slightly higher, for cattle in the spring and summer. There was no significant interaction between digestive capacity and forage source so that similar digestion trends were observed in forage collected by cattle (Fig. 1). The forage collected by bison, however, was in general less digestible than that collected by cattle. The forage collected from the heavily grazed treatment was generally less digestible than that from the lightly grazed one. In early spring, however, digestibility of forage removed from the heavily grazed pasture was similar to, or slightly greater than, that from the lightly grazed one.

Areas of preferred grazing

Within each grazing treatment, differences ($P<0{\cdot}01$) (Table 4) in herbage cover

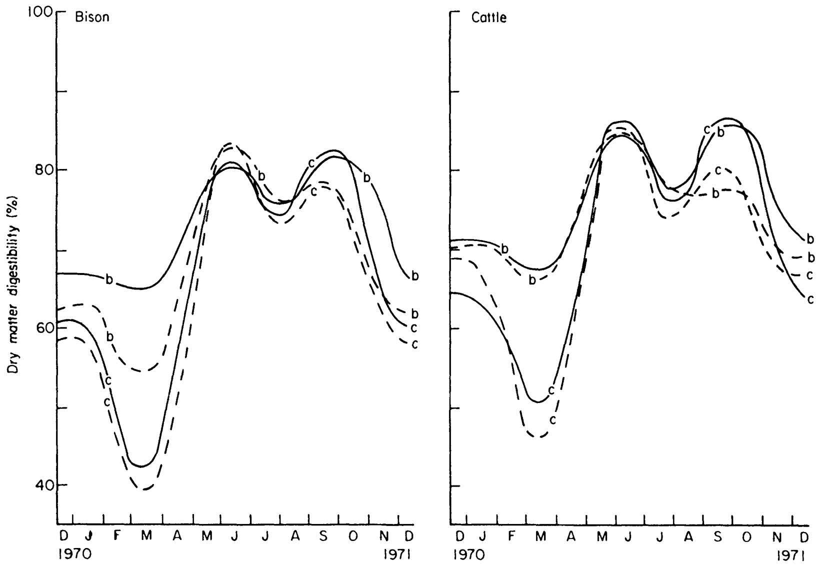

FIG. 1. Relation between digestive capacity of bison (b) and cattle (c) on forage collected by bison and cattle on both lightly grazed (continuous line) and heavily grazed (broken line) treatments.

Table 4. *Percentage cover of plant groups in preferred grazing locations*

		Cover (%)									
		Heavily grazed					Lightly grazed				
	Plant group	Mar.	May	June	Aug.	Oct.	Mar.	May	June	Aug.	Oct.
Bison	Warm-season grass	73	69	71	82	83	80	76	78	89	90
	Cool-season grass	22	22	18	8	10	13	13	8	0	1
	Warm-season forbs	2	5	7	4	1	1	4	6	3	0
	Cool-season forbs	0	2	2	1	1	0	2	2	1	0
	Shrubs	1	1	1	3	3	2	2	2	4	4
Cattle	Warm-season grass	64	60	62	73	74	72	67	70	80	82
	Cool-season grass	30	30	25	16	18	21	20	16	6	8
	Warm-season forbs	3	6	8	5	2	2	5	7	4	1
	Cool-season forbs	0	2	2	1	1	0	2	2	1	1
	Shrubs	2	2	2	3	3	3	3	3	4	4

occurred between the areas from which the bison and cattle diet samples came. The cover of warm-season grass was consistently greater where bison grazed while the cover of the other four plant groups was greater in areas selected by cattle. Maximum warm-season grass cover was observed during August and October while the relative abundance of cool-season grass was greatest in March and May. Cover of warm-season grass was greater on the heavily grazed than on the lightly grazed one.

DISCUSSION

The plant composition of the diets (Table 2) support Larson (1940), Longhurst (1961), Garretson (1938), Martin *et al.* (1951), Soper (1941) and Nelson (1965) that bison are primarily grass eaters. For shortgrass vegetation, this was more consistent during all seasons on both treatments for bison than for cattle. However, the areas within the grazing treatments selected by cattle and bison differed (Table 4) so that dietary differences may have resulted from differences in herbage between their selected areas plus differences in localized feeding behaviour, given that they both had the same choice. Areas selected by cattle for grazing were located within swales or shallow depressions, where soil moisture is higher than in the surrounding vegetation where the bison grazed. Within the localized areas, cattle were more selective than bison (Fig. 2) even though the lower warm-season grass consumption of cattle may be correlated with the smaller percentage cover of this plant group in the areas cattle selected.

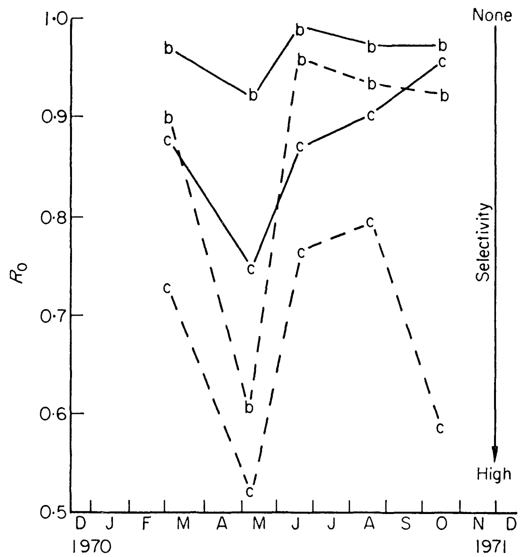

FIG. 2. R_0 similarity estimates relating percentage dry weight composition of plant groups in bison (b) and cattle (c) diets to that of herbage cover on both lightly grazed (continuous line) and heavily grazed (broken line) treatments.

The higher levels of crude protein (Table 3) in cattle diets may have resulted from differences in the crude protein content within individual spatially variable plant groups or species as well as from differences between the proportion of plant groups in cattle and bison diets. The higher crude protein in cattle diets may partly reflect characteristics of plants growing in the swales.

As with crude protein, the forage selected by cattle was more digestible (Fig. 1) than that eaten by bison and may reflect both the differences in plant groups or species between selected feeding areas and in the composition of plant groups in the diets.

Similarity (Fig. 2) between percentage dry weight of plant groups in the diet and their percentage cover on the ground within the areas grazed by the bison and cattle, suggests that bison are less selective than cattle and are able to more fully utilize the available herbage. Two feeding strategies would permit such differences. Firstly, bison would need to consume greater quantities of forage in a given time period, as observed by Burback (1951). Secondly a given quantity of forage would be digested to a greater degree by bison than by cattle. Our observations suggest that this may be the case (Fig. 1) during the autumn and winter. Either or both of these strategies would more readily permit bison to extract their requirements from poor quality range and thus enable greater use of the total available herbage than cattle.

During late winter crude protein (Table 3) in diets of both herbivores dropped to less than 7% and was lowest for bison. However, the drop in digestive capacity was much greater in cattle during this period. Perhaps there exist in bison a mechanism by which nitrogen-recycling is much more efficient than that in cattle as demonstrated for caribou in comparison with cattle (Wales 1972).

When the mean percentage plant composition of both the diet and the digested nylon-bag residue, and the digestibility of the diet as a whole are considered, the digestibility of the component plant groups can be calculated as follows:

Let D_i be the percent digestibility of the ith plant group. Thus

$$D_i = \left[100 \; \frac{A_i - (1-C)(A_i + B_i)}{A_i} \right]$$

where A_i is the fractional proportion of the ith plant group, B_i is the difference between the percent composition of the ith plant group in the original diet and in the residue, and C is the overall fractional dry matter digestibility.

Table 5. *Digestibility estimates for individual plant groups in bison and cattle diets*

		Digestibility (%) (nylon bag)				
	Period	Warm-season grasses	Cool-season grasses	Warm-season forbs	Cool-season forbs	Shrubs
Bison	December	70	63	20	–	–
	March	71	39	–	–	–
	May	82	79	72	62	–
	June	77	83	94	73	–
	August	79	79	86	–	–
	October	81	77	90	–	–
Cattle	December	60	68	–	–	–
	March	58	40	73	–	72
	May	83	87	–	–	86
	June	67	85	88	85	88
	August	80	97	86	–	–
	October	82	86	89	–	80

The digestibility coefficients obtained from this equation are shown in Table 5. The main point of interest is that bison, at least during winter, appear to digest the warm-season grass component better than cattle, while cattle demonstrate this same phenomenon throughout the year on the cool-season grasses. Thus, each herbivore selected a higher proportion of the plant groups which it could best digest. It is, therefore, possible that some chemo-physical characteristic of the warm-season grass component of the diet is the target of the proposed digestive efficiency mechanism. Alternatively, it is possible that each forage group selected from the different vegetative areas grazed by cattle and bison varies in its susceptibility to digestion or that the different herbivore species select different combinations of plant parts, each of which has a different susceptibility to digestion.

Eventual perfection of efficient grazing systems must consider the benefit derived from mixed herbivore species use. Cattle, bison and sheep have different seasonal diets. The former two species appear to select their diets from different areas and to choose plant species within their respective areas with different levels of selectivity. Sheep may or may not exhibit similar differences to these species. There is a need for a framework of synthesis, perhaps through operations research, to find optimal range use strategies based on a highly variable and interactive range of herbivore species.

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SUMMARY

(1) Seasonal information on dietary composition, forage digestibility and selectivity was collected for bison, cattle and sheep from two treatments representing lightly grazed and heavily grazed pasture.

(2) Bison have a greater preference for warm-season grasses and appear to feed less selectively than cattle and in different areas within shortgrass vegetation.

(3) Sheep consume fewer grasses than either species.

(4) Bison appear to have a greater digestive power than cattle when consuming low protein, poor quality forage, and may also consume greater quantities of forage as compared to cattle.

(5) These two mechanisms of feeding strategies may permit bison to exploit more fully than cattle the herbage resources on shortgrass plains.

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