FIRE - CARIBOU RELATIONSHIPS: (V) WINTER DIET OF THE BEVERLY HERD IN NORTHERN CANADA, 1980-87

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8. Thomas, D.C. 1998c. Fire-caribou relationships: (VIII) Background information. Tech. Rep. Series No. 316. Can. Wildl. Serv., Prairie & Northern Reg., Edmonton, Alberta. 104pp.

SUMMARY: I explored variability associated with the microhistological technique and with population and environmental variables in assessing diet of barren-ground caribou (*Rangifer tarandus groenlandicus*) in the 1980s on winter range in north-central Canada. Variables with little or no effect on relative densities of total lichen fragments included duplicate samples; age, sex, and physical condition of the caribou; season (December *vs.* March); and year at a given location. Delayed necropsies and expression of rumen fluids through cheesecloth reduced lichen densities in the residual rumen material. Variability was observed among three major habitat types. Decreases in lichens and increased use of shrubs and graminoids occurred in the sequence: forest, forest-tundra ecotone, and tundra. Differences in fragment densities in paired, composite rumen and fecal samples (n = 20 comparisons) were small for *Cladina*-type lichens and total lichens, which usually comprised 72 to 88% and 84 to 95% of the samples, respectively. Relationships between rumen and fecal data sources for minor and trace forages often were inconsistent and highly variable because of inadequate microscopic sampling (number of fields). *Cetraria*-type lichens were overestimated in fecal samples, whereas *Peltigera* and *Usnea* types were grossly underestimated. A review of error sources in using the macrohistological technique indicates probable gross underestimates of lichens in the diet. Microhistological analysis of feces of caribou on winter range may be the most accurate technique provided that mosses comprise a small proportion of the diet.

RÉSUMÉ : Nous avons étudié la variabilité associée à la technique microhistologique et aux variables de population et de milieu dans l'évaluation du régime alimentaire du caribou de la toundra (*Rangifer tarandus groenlandicus*) dans les années 80 dans l'aire d'hivernage du centre-nord du Canada. Les variables qui avaient peu ou pas d'effet sur la densité relative de l'ensemble des fragments de lichens comprenaient la duplication des échantillons, l'âge, le sexe et l'état physiologique du caribou, la saison (décembre ou mars) et l'année (pour chaque site). Le report de l'autopsie et la filtration du liquide de rumen à travers une gaze avaient pour effet de réduire la densité des lichens dans le liquide de rumen résiduel. Une variation a été observée dans trois principaux types d'habitat. Une diminution progressive de la consommation de lichens associée à une augmentation de celle des arbustes et des graminoïdes est apparue dans la séquence suivante : forêt, écotone forêt-toundra, toundra. L'analyse d'échantillons combinés de panse et de matières fécales appariés (n = 20 comparaisons) a révélé de faibles différences dans la densité des fragments pour les lichens du type *Cladina* et pour les lichens de toute espèce, qui constituaient environ 72 à 88 % et 84 à 95 % des échantillons, respectivement. Les relations entre les données concernant le rumen et les matières fécales pour les aliments mineurs ou à l'état de traces étaient incohérentes et hautement variables, à cause d'un nombre insuffisant de champs. Les lichens du type *Cetraria* ont été surestimés dans les matières fécales, tandis que ceux des types *Peltigera* et *Usnea* ont été fortement sous-estimés. Une analyse des sources d'erreur associées à la technique macrohistologique a indiqué que la part des lichens dans le régime alimentaire a probablement été fortement sous-estimée. L'analyse microhistologique des fèces de caribou dans l'aire d'hivernage semble être la technique la plus précise, à condition que les mousses représentent une petite fraction du régime alimentaire.

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INTRODUCTION

A study of caribou diet, forage digestibilities, and effects of forest fires on winter range of the Beverly herd of barren-ground caribou was conducted between 1980 and 1988. The study was divided into three primary phases: (1) changes in physical condition of caribou while on forested range from December to March (reports 1 and 2 in this series); (2) movements and distribution of the herd in relation to burns and snow (report 3); and (3) relationship between time since fire and biomass of caribou forages (report 4). This report is the fifth of a series of six data reports serving as a basis along with other data in the literature for a final report outlining conclusions and recommendations (report 7). Report 6 contains fire history data and maps for Saskatchewan and Manitoba north of 58°N and for the entire winter range of the Beverly herd in the NWT. Report 8 reviews literature with focus on the Beverly herd.

Preliminary data were obtained on forages used by caribou in the primary study area, forested range bounded by 104°W in the east, 112°W in the west, 60°N in the south, and "limit of trees" or "tree line" in the north. In anticipation of the fire study, rumen samples were obtained from 104 caribou at 18 locations on winter range of the herd in March 1980 and 1981. After sieving to remove particles <0.85 mm, samples were examined microscopically at low magnification (6X) to determine relative occurrence of plant fragments. The results (Thomas and Hervieux 1986), based on 300 grid points, indicated that lichens were the primary forage of caribou in winter and vegetation sampling (cover and biomass) over four summers was structured accordingly.

The second step was to obtain information on digestibility of forages. Studies were conducted in 1980 and 1981 using *in vitro* methods, whereby rumen fluids from caribou were used to digest coarsely-ground forages in an oxygen-free, buffered medium. The results (Thomas and Kroeger 1981, Thomas et al. 1984) confirmed the high digestibility of lichens, thereby increasing their importance as an energy source relative to such forages as shrubs, sedges, and mosses.

Sparkes and Malechek (1968) and Dearden et al. (1972, 1975), in laboratory tests, found high correlations between relative weights of milled mixtures of caribou forages and estimated relative densities using the microhistological technique. The technique was applied to feces of caribou to estimate diets (reviewed by Boertje et al. 1985) usually without correction for the technique's propensity to overestimate or underestimate some species, genera, or groups. Boertje (1984) and Boertje et al. (1985) suggested that the microhistological technique using fecal samples was inadequate to evaluate diet because some forages were not detected, whereas some others were either grossly overestimated or underestimated relative to diet estimated from bite counts. Boertje et al. (1985) listed studies where microhistological results deviated from other data sources. However, several studies have reported reasonably reliable results from microhistological analysis of fecal or rumen material (reviewed by Gill et al. 1983). For example, Anthony and Smith (1974) obtained similar results for volumetric analysis of deer (*Odocoileus* spp.) rumens and microhistological analysis of feces. Todd and Hansen (1973) found no significant difference in microhistological results from rumen and fecal samples of bighorn sheep (*Ovis canadensis*) but similar comparisons have not been made for caribou.

The samples consisted of 1258 caribou shot by hunters in mid March, 1980-87, and December, 1982-86, to monitor over-winter changes in fat reserves of caribou while they occupied the forested range. More information was needed on validity of the microhistological technique to assess diet (e.g., Boertje et al. 1985). My primary objective was to assess winter diet in support of range studies. Secondary objectives were to compare results from rumen and fecal samples from the same composite group of caribou, and to evaluate diet differences among sampling procedures, duplicates, sex, ages, physical condition, season, years, location, and habitat type. Testing for sex, age, and condition differences has important implications regarding use of pellets to assess diet of caribou of unknown sex, age, and condition. The results should help evaluate validity of the technique to assess diet from feces collected on winter ranges in north-central Canada (Thomas and Barry 1991).

METHODS

Caribou were shot on organized hunts each year from 1980 through 1987. Samples were obtained throughout the range (**Fig. 1**) in early winter (1982-86) and late winter (1980-87) (**Table 1**). In March 1980 and 1981, caribou carcasses were transported entire by aircraft to a base where rumen contents were removed for a study of forage digestibilities. Rumen fluids were expressed through four layers of cheesecloth and remaining material was frozen. Thus, 5-8 hr elapsed from caribou being shot and rumen contents being frozen. Those strained samples from delayed necropsies were all in batch 1. In 1982 and later, caribou were necropsied in the field within 1-3 hr of being shot on lakes and returned to a central location. Litre samples of rumen contents and 50-100 pellets from the colon quickly froze and were kept frozen until subsamples were obtained for microhistological examination (Sparks and Malechek 1968). For each collection site, equal volume/number subsamples of rumen and fecal material from 10 adult females were pooled into composite samples. Then duplicate samples each containing 50 ml of rumen contents and 20 pellets were coded and sent in salt (50:50) in four batches to the Composition Analysis Laboratory in Fort Collins, Colorado.

Figure 1

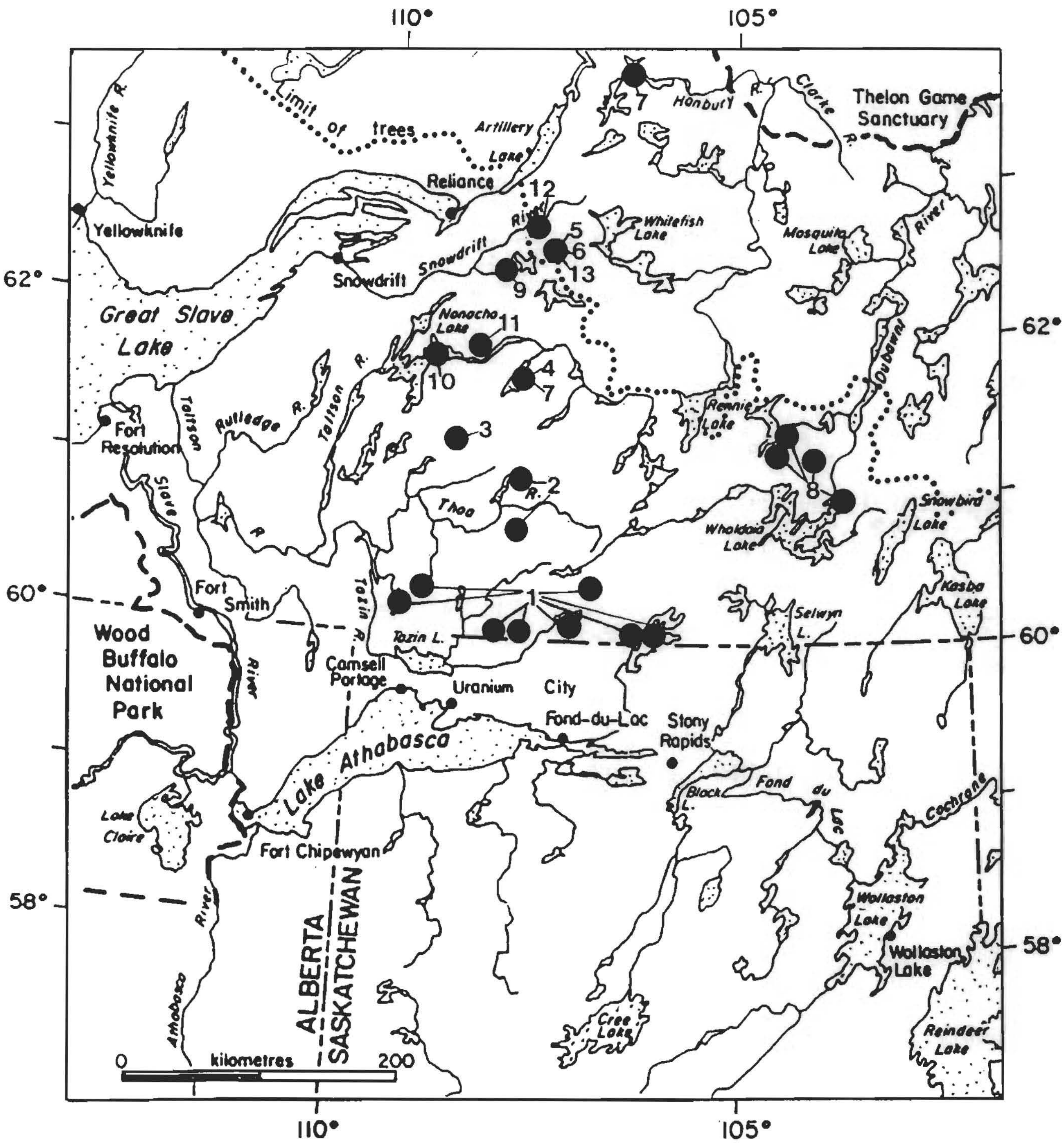

Figure 1. Locations where rumen and fecal samples were obtained on winter range of the Beverly herd of caribou, 1980 through 1987.

Table 1. Dates, locations, sex, ages, and physical condition of caribou from which composite samples of rumen and fecal material were obtained from 1980 through 1987.

Year	Month	Location[1]	Sex	Age	Physical condition
1980	Mar	Several (11)	Female	Adult	Average
1981	Mar	Several (4)	Female	Adult	Average
1982	Mar	Halliday L.	Female	Adult	Average
			Male & F	Calf	Average
1982	Nov	Porter L.	Female	Adult	Average
1983	Mar	Tent L.	Female	Adult	Average
1983	Dec	Tent L.	Female	Adult	Average
1984	Mar	Porter L.	Female	Adult	Average
		Sifton L.	Female	Adult	Average
1984	Dec	Wholdaia L.	Female	Adult	Average
		Veira L.	Female	Adult	Average
1985	Mar	Jones L.	Female	Adult	Average
1985	Dec	Nonacho L.	Female	Adult	Average
1986	Mar	Cobb L.	Female	Adult	Average
			Male	Adult	Average
			Male & F	Calf	Average
1986	Dec	Tent L.	Female	Adult	Average
			Female	2.5 yr	Good
			Female	2.5 yr	Fair
1987	Mar	Tent L.	Female	Adult	Good
			Female	Adult	Fair
			Male	Adult	Average

[1] See Thomas and Hervieux (1986) for 1980 and 1981 sample locations and Thomas and Kiliaan (1991) for 1982 and later locations. Fecal samples were not obtained at five of the 1980 locations and at three of the 1981 locations.

Composite samples were obtained from adult females in average condition for the collection period. "Composite" refers to pooling of fecal or rumen samples from several caribou, usually 10. Composite samples also were obtained from other sex, age, and physical condition classes for comparison with adult females in average condition, where adequate samples permitted us to do so. Included were adult males, calves, 2.5-year females, and mature (> 3 years old) and 2.5-year females in relatively poor condition. Physical condition was evaluated by body weight, back fat depth, and weight of kidney fat (Thomas and Kiliaan 1998a).

Analysis was based on the occurrence (present-absence data) of recognizable plant fragments of species or groups in 20 microscopic fields at 100X magnification on each of five slides. Frequency of occurrence data were converted to density values and relative density values by personnel at the Composition Analysis Laboratory. We obtained raw data for each slide from the laboratory, which normally only provides mean values and standard deviations for pooled data from five slides, i.e., 20 x 5 = 100 fields. Alternative sampling techniques are described by Williams (1987).

Differences between and among means were tested by Kruskal-Wallis and Mann-Whitney non-parametric methods (Sokal and Rohlf 1981). Equivocal variables at 95% probability (e.g., one of two cases different) were judged to be not different if differences disappeared at the 99% level. Proportions of total lichens was the criteria for decisions on whether variables affected dietary compositions. Data for minor and trace forages were believed to be unreliable (Holechek and Vavra 1981).

Major plant groups were lichens, evergreen shrubs, graminoids, conifer leaves, forbs, and mosses. Major genera discriminated by the Composition Laboratory included *Cladonia* type, *Cetraria* type, *Peltigera* spp., *Usnea* spp. (sometimes included with *Cladonia* type), *Ledum*, *Loiseularia*, *Empetrum*, and *Equisetum*. The *Cladonia* type included genera *Cladonia*, *Cladina*, *Stereocaulon*, *Alectoria*, and *Thamnolia (not present)*. *Cetraria* type included genera *Cetraria*, *Hypogymnia*, *Evernia*, *Dactylina* (not present), *Coelocaulon* (not present), and *Usnea* spp. Shrubs included Ericaceae, *Ledum*, *Loiseularia*, *Empetrum*, *Arctostaphylos*, and *Vaccinium*. Forbs included *Astragalus/Oxytropis, Cornus* (not present), *Hedysarum* (not present), *Rubus, Saxifraga, Stellaria, Equisetum*, and unknown. *Equisetum* was listed separately for some samples.

RESULTS

Rumen treatment differences

Preliminary analysis indicated differences between rumen and fecal samples in relative fragment densities of *Cladonia*-type lichens. These were in batch 1 obtained in 1980 and 1981. Differences between rumen and fecal samples disappeared in subsequent batches. Densities for *Cladonia*-type lichens were higher in fecal samples in all seven comparisons (two significant) in batch 1. In other batches, relative fragment densities were higher (n = 9) and lower (n = 11) in rumen samples compared with fecal samples. I suspect that in 1980 and 1981 samples (batch 1), digestion after death and before freezing the rumens reduced the lichens to small particles and they were expressed with fluids used in digestibility studies. Compared with results for batches 2-4, densities of fragments of other lichen genera in rumen samples of batch 1 were low relative to densities in feces. Therefore, I deleted batch 1 results from further comparisons between results for rumen and fecal samples.

Another minor batch difference was occurrence of *Empetrum* sp. and *Equisetum* spp. in batch 2 samples and not in samples from other batches. I interpret this as being a detection problem rather than a real difference among samples. Amounts were sufficiently small that batch two samples were included in further analyses.

Differences between duplicates

Differences between duplicates were significant ($P < 0.05$) for total lichens in 2 of 35 rumen samples and 4 of 27 fecal samples. Fragment densities of *Cladonia* type lichens in rumen and fecal samples differed on average by 5.5 and 5.4%, respectively, or about 7% of mean values. The results from duplicates were combined to increase number of slides per location/year from 5 to 10 and number of fields from 100 to 200.

Some differences between duplicates were attributable to clumping or incomplete mixing of samples. For example, results for one slide were bizarre: 11.8% *Cladonia vs.* 83.7-90.5% in others; 25.1% *Cetraria vs.* 2.7-7.1%; 57.4% *Loiseularia vs.* 0-3.2%. Some differences may be caused by discrimination problems. For example, *Pinus* sp. probably was confused with *Picea* sp. in one rumen sample. In the first group of slides, *Pinus* was not detected and *Picea* averaged 5.2% (range 1.7-9.4%); in the duplicate, *Picea* was detected only in one of five slides (1.7%) but *Pinus* averaged 3.1% (range 1.5-3.9%).

Differences between rumen and fecal samples

A minority of differences were significant: 7 of 27 for total lichens; 6 of 27 for each of shrubs and moss; 6 of 25 for conifers; 3 of 26 for graminoids; and 0 of 15 for forbs. Differences after 1981 were about equally numerous in both directions for fragment densities of total lichens, conifer leaves, shrubs, graminoids, forbs, *Cladonia* type, *Pinus*, *Empetrum*, and *Loiseularia* spp. (**Table 2**).

Statistics for correction factors, fecal to rumen, based on all post-1981 samples reveal a high degree of variability except for total lichens and *Cladonia*-type lichens (**Table 3**). Data for plants with density proportions less than 30% are unreliable, resulting in large variation. Fragment densities of *Cetraria*-type lichens were always higher in fecal samples after 1981 but the opposite generally was true for *Peltigera* spp. and *Usnea* spp. Fragment densities of mosses usually were higher in rumen samples, whereas the reverse was true for *Ledum* spp. and *Equisetum* spp.

The most reliable correction factors may be for samples with highest proportions of minor components. Individual correction factors, fecal to rumen, for *Cetraria* type lichens in samples obtained after 1981 and where the minimum fragment density for inclusion of either rumen or fecal samples was arbitrarily set at 10%, were 0.25, 0.32, 0.33, and 0.54; for *Peltigera* spp. 2.86; and for *Loiseularia* spp. 1.49. Additional factors, where minimum values for inclusion were 5%, were as follows: *Cetraria*-type 0.36, 0.37, 0.39, 0.46, 0.56, 0.76, 0.78, 0.94, and 0.99; *Usnea* spp. 31.41; *Peltigera* spp. 6.63; *Carex* spp. 1.32 and 2.07; *Ledum* spp. 0.61; and *Loiseularia* spp. 0.03, 0.18, and 1.15.

Minor differences allowed us to group data from rumen and fecal samples for major plant groups, thereby increasing number of slides to 20 and number of fields to 400. The influence of other potential variables could then be tested with greater confidence.

Table 2. Numbers of samples where relative fragment densities were higher in rumen samples (+), higher in fecal samples (-), or the same (0), in all comparisons (n = 27), and in post 1981 samples (n = 20) for six major plant groups and for common genera.

Plant group	Numbers in each category					
	All samples			Post-1981 samples		
	+	-	0	+	-	0
Total lichens	10	17	0	9	11	0
Conifer leaves	14	9	2	9	7	2
Shrubs	13	13	1	10	10	0
Moss	9	18	0	5	15	0
Graminoids	13	13	0	10	10	0
Forbs	9	5	1	5	4	0
Cladonia type	10	17	0	10	10	0
Cetraria type	6	21	0	0	20	0
Peltigera spp.	22	3	0	15	3	0
Usnea type	20	2	1	14	2	0
Pinus sp.	11	4	0	5	3	0
Ledum spp.	18	9	0	13	7	0
Empetrum sp.	5	5	0	5	5	0
Loiseularia sp.	11	14	0	11	7	0
Equisetum spp.	5	1	0	5	1	0

Note: Absence of plant groups reduces sample size in many cases.
Note: Differences are numerically higher or lower but not always statistically so.

Age, sex, physical condition, season, and year differences

Factors not influencing fragment densities of major plant groups in rumen and fecal samples included age, sex, physical condition of caribou, season (December vs. March) or year (e.g. **Table 4**). All comparisons for age, sex, and physical condition

Table 3. Statistics for correcting fecal relative densities of plants to rumen relative densities based on samples obtained from caribou from 1982 through 1987 on the winter range of the Beverly herd in north-central Canada.

Plant group	Correction factor, fecal to rumen			
	Mean	SD	95% CI[1]	*n*
Total lichens	0.98	0.06	0.96 - 1.01	20
Shrubs	1.11	0.55	0.86 - 1.37	20
Conifer leaves	1.38	1.27	0.67 - 2.08	15
Graminoids	1.25	0.82	0.85 - 1.66	18
Moss	0.81	0.91	0.37 - 1.25	19
Forbs	1.66[2]	0.47	-2.57 - 5.90	2
Cladina type	0.99	0.08	0.96 - 1.03	20
Cetraria type	0.51	0.24	0.40 - 0.63	20
Peltigera spp.	3.67	4.65	1.09 - 6.24	15
Usnea spp.	7.88	10.23	-0.67 -16.43	8
Pinus sp.	1.55	1.93	-0.48 - 3.57	6
Empetrum sp.	1.03	0.71	0.52 - 1.54	10
Ledum spp.	1.30	0.95	0.86 - 1.75	20
Loiseularia spp.	1.97	1.43	0.94 - 3.00	10

[1] Confidence interval.
[2] 1.78 ± 1.14 (n = 5) including 1980-81 samples.

were for samples obtained at the same location in order to eliminate confounding variables. Season comparisons were also made for the same location and also for all December versus all March samples obtained within habitat types after 1981. Comparisons among years were for adult females partitioned by season and restricted to post 1981 for rumen samples.

Table 4. Relative densities of fragments of major plant groupings in composite, paired rumen samples of caribou of different sex, age, and fat reserves.

Age/ Sex	Month/ Year	Relative fragment densities (%)					
		Lichens	Shrubs	Conifers	Graminoids	Forbs	Mosses
Adult F	Mar 86	94.8	2.3	1.4	0.0	0.0	1.6
Adult M	Mar 86	93.6	4.0	1.1	0.5	0.0	0.9
Adult F	Mar 87	80.9	14.3	0.1	0.4	0.0	0.2
Adult M	Mar 87	76.7	16.1	0.6	0.0	0.0	0.2
Adult F	Mar 82	94.6	1.8	2.0	0.7	0.0	1.3
Calf	Mar 82	87.8	4.1	4.3	0.9	0.3	2.5
Adult	Mar 86	94.8	2.3	1.4	0.0	0.0	1.6
Calf	Mar 86	94.4	2.3	1.3	1.0	0.0	1.0
Adult[1]	Dec 86	85.4	10.4	0.0	1.7	0.0	0.1
2.5 yr	Dec 86	82.6	12.0	0.4	1.9	0.0	0.1
Fat[2] 2.5 yr	Dec 86	82.6	12.0	0.4	1.9	0.0	0.1
Lean[3] 2.5 yr	Dec 86	87.2	6.5	0.7	0.9	0.0	0.3
Fat adult	Mar 87	80.9	14.3	0.1	0.4	0.0	0.2
Lean adult	Mar 87	86.6	11.7	0.2	1.3	0.0	0.2

[1] Adult is >3 years old.
[2] Fat individuals had >20 mm back fat.
[3] Lean caribou had 0-4 mm back fat.

Geographic location and habitat type differences

There was significant variability among five (fecal) and 11 (rumen) locations sampled in March 1980 but not among two and four locations sampled in March 1981 (Fig. 1). There were no differences among and within those samples based on macrohistological data (Thomas and Hervieux 1986).

March 1984 samples from forested habitat (Porter Lake) and tundra (Sifton Lake) differed in fragment densities of total lichens, shrubs, conifers, and moss. Addition of data for March 1983 from Tent Lake, which is located in the forest-tundra ecotone between Porter and Sifton lakes, revealed differences among all three habitat types (**Table 5**). Values for the ecotone were intermediate between the other two. Further comparisons between results for nine forest locations and six ecotone sites, at first partitioned for season and then grouped, indicated significant differences in all cases.

Differences between macrohistological and microhistological techniques

The comparison was pooled rumen data for 1980-81 and results for the same grouped samples reported by Thomas and Hervieux (1986) for percent composition from 300 points (grid intersections) of screened material viewed at 6X magnification (histological technique). Proportions of lichens were lower and proportions of conifer leaves, shrubs, and mosses were higher in histological results relative to those for the microhistological technique (**Table 6**).

Table 5. Plant fragment relative densities in pooled rumen and fecal samples from three habitat types on the winter range of the Beverly herd, 1982 through 1987 (number of locations in parentheses).

Plant group	Plant fragment relative densitiy (%) Forest (*n*=9) Mean	SD	Forest-tundra(*n*=10) Mean	SD	Tundra (*n*=1) Mean	SD
Lichens	91.1	5.19	86.9	7.53	78.6	8.49
Shrubs	3.2	2.52	8.8	7.02	12.4	7.19
Conifer leaves	2.1	2.37	0.5	0.99	0.0	0.00
Graminoids	1.9	3.04	2.2	2.53	6.4	5.25
Forbs	0.1	0.42	0.1	0.48	0.2	0.66
Moss	1.5	1.51	0.6	1.02	2.6	2.33
Lichens						
Cladonia type	81.2	8.55	80.8	10.01	69.8	7.96
Cetraria type	6.0	4.57	4.7	6.25	5.9	4.27
Peltigera spp.	2.8	3.22	0.9	1.92	0.7	1.22
Usnea spp.	1.2	1.93	0.5	1.42	2.0	2.66
Shrubs						
Ledum spp.	1.9	2.11	3.3	2.81	6.8	3.75
Loiseularia spp.	0.3	0.72	4.3	5.91	3.0	4.05
Empetrum spp.	0.9	1.60	0.5	1.32	2.6	2.73
Forb						
Equisetum spp.	0.1	0.30	<0.1	0.24	0.0	0.00

Table 6. Microhistological and macrohistological estimates of plant composition in rumen samples obtained in March 1980 and 1981 from caribou on winter range of the Beverly herd.

Plant group	Relative fragment densities (%)					
	Microhistological (*n*=15)[1]			Macrohistological (*n*=18)[2]		
	Mean	SD[3]	95% CI[4]	Mean	SD[3]	95% CI[4]
Total lichens	88.0	9.57	86.4-89.5	68.5	6.36	65.0-72.0
Conifer leaves	5.2	3.72	4.6- 5.8	11.9	5.09	9.1-14.7
Shrubs	3.6	2.78	3.1- 4.0	5.6	1.27	4.9- 6.3
Moss	1.0	1.24	0.8- 1.2	4.9	2.55	3.5- 6.3
Graminoids	0.5	1.07	0.4- 0.7	0.0	0.00	0.0- 0.0
Forbs	0.4	0.79	0.2- 0.5	0.0	0.00	0.0- 0.0

[1] Number of fields = 150.
[2] Data from Thomas and Hervieux (1986).
[3] Standard deviation.
[4] Confidence interval.

DISCUSSION

Practical application of the microhistological technique

Results obtained in this study (Thomas and Barry 1991) clarify some questions pertaining to use of the microhistological technique and point to efficient uses of it. There were conflicting data on differences in diet among sex, age, and condition classes of caribou. These results indicate that under winter conditions on the Taiga Shield, collections of fecal pellets from caribou of unknown sex, age, and physical compositions among sex, age, and condition variables is understandable considering the uniformity of vegetation at feeding sites and the choices present at the bottom of feeding craters. Differences in condition are largely a function of the snow-free period when differences between males and females (Helle 1980, Boertje 1984) and calves and adults (Bergerud 1972, Boertje 1984) were observed.

The relatively small differences between results for rumens and fecal pellets adds confidence to use of pellets to assess diet. Pellet collections are vastly easier to obtain than rumen samples. In parks and in studies of rare species, it is not possible to obtain adequate numbers of representative rumen samples. The results for batch differences indicate that rumen samples should be obtained from an animal as quickly as possible after death and then frozen or fixed in formalin. Although not proven, it is likely that digestion can continue in the warm rumen for several hours after death. Rather than analysing duplicates of each fecal or rumen sample, I suggest that a larger number of slides be viewed for each sample. If a bizarre result is obtained, the sample in question can be re-analysed. The subject of sample size requires careful scrutiny by anyone considering use of the microhistological technique. Sample sizes are specific to the objectives of each study and the composition of the diet.

Sample size and the microhistological technique

Free et al. (1970) suggested that 100 fields (five slides) at 125X magnification was adequate for plants comprising >5% of diet, and 400 fields yielded estimates within 5% of the mean at *P* = 90% where relative weight of a plant was 30-60% of a sample. According to Holechek and Vavra (1981), five slides per sample (100 fields) produced reasonable estimates for species comprising >20% of a diet. At 95% probability (*P*) and 10% sampling error, numbers of slides required, at 20 fields per slide, for a species with proportions of >30%, 29-20%, 19-10%, 9-5%, and 4-0% are 1, 9, 30, 60, and 156, respectively. At 90% *P* the numbers are 3, 6, 19, 41, and 100; at 80% *P* they are 1, 3, 9, 20, and 49, respectively (Holechek and Vavra 1981). By grouping duplicates; rumen and fecal samples, ages, sexes, and samples from caribou of different fat reserves; and different locations within 1980 and 1981, slide totals were increased to 10, 20, and 40-100 at some sites. Hanson and Graybill (1956) discussed sample size in food habits studies.

It is advisable to obtain results based on five slides for one sample and then estimate required number of slides to satisfy the particular question or test. Proportions of most plant groups in Table 3 were 1-5% and some were <1%. Calculation of adequate correction factors would require analysis of 100-150 slides. Correction factors are therefore crude and preliminary. They could be refined by further analysis of samples in which a critical genus was present in highest densities. It must be remembered, however, that correction factors are unique to dietary proportions for which they were obtained.

Whether the microhistological technique is adequate (Boertje et al. 1985, Vavra and Holechek 1980) depends on what the questions are and available information on diet in a study area. Non detection of mushrooms (Boertje 1981) and underestimation of forbs (Boertje et al. 1985, Samuel and Howard 1983) was not a problem in our winter samples. Mosses occurred in negligible amounts in both rumen and fecal samples. That group is overestimated by the technique (Dearden et al. 1975, Boertje 1984). Controlled experiments are needed where estimated diet, by weight, are fed to fistulated animals and rumen samples and pellets are collected at appropriate times. Evaluation of intake from bite counts (Boertje 1984, Duquette 1984) is subject to considerable error and is a questionable basis for evaluating rumen and fecal techniques. Intake data from esophageal or rumen fistulas (Staines 1976, Vavra et al. 1978) are preferred for studies using captive animals that are allowed to forage on natural range.

Interpretation of previous macrohistological results

Proportion of lichens in our samples, as estimated by microhistological techniques, are considerably higher than previous estimates based on macrohistological methods. Potential sources of error in use of rumen analysis to estimate diet by conventional methods were reviewed by Gaare et al. (1977). Histological-based results of rumen analysis of Scotter (1967), Miller (1976a, 1976b), and Thomas and Hervieux (1986) probably underestimated lichens in the diet of caribou in the study area on three counts: (1) losses from washing rumen contents through screens would be greater for lichens than for vascular tissue; (2) lichens are easily masticated, rapidly digested, and pass through the rumen more rapidly than vascular species (Bergerud 1972, Gaare et al. 1977); and (3) proportion of forage species should be adjusted by deletion of non-forage items such as mosses and conifer needles that are ingested incidentally. Consequently, reported diet based on histological or macrohistological methods probably underestimated proportional intake of lichens.

Gaare et al. (1977) found that up to 50% of rumen contents passed through screens as fine as 0.2 mm. Scotter (1967) reported 68.5% of lichens, by weight, washed through sieve sizes of 4.76, 2.83, and 2.00 mm. Proportions of lichens in samples increased as screen size decreased but an average for results from three screen sizes was reported (Scotter 1966).

Miller (1976a, 1976b) found that lichens comprised about 50% of rumen samples obtained from caribou in northern Manitoba and Saskatchewan. His technique involved use of 95% ethyl alcohol as a fixative, washing and sieving of samples through a screen of unstated size, and manual sorting to vegetation groups for a set period of 2 hours. The bleaching of lichens with alcohol, washing through what probably was a relatively coarse screen, and propensity of contract laboratory workers to preferentially sort coarse material undoubtedly resulted in a gross underestimation of lichens in the diet. Bergerud (1972) found that *Cladonia* (= *Cladina*) spp. were underestimated in screenings and fungi overestimated. Considerable amounts of fine lichen fragments would pass through a 0.85 mm screen recommended by Bergerud and Russell (1964) and employed by Thomas and Hervieux (1986). These small fragments contribute to estimates based on the microhistological technique.

Gaare et al. (1977) developed a formula to adjust rumen composition for differential turnover times of ingesta. It was the ratio of the turnover times of a component and average turnover time of all components. There are, however, few data on turnover times of caribou forages. Limited data and assumptions led Gaare et al. (1977) to believe that the lichen proportion in the diet of Norwegian reindeer should be increased from 56% to 70%. Bergerud (1972) estimated that twigs and leaves from evergreen trees accumulated in rumens after their incidental ingestion. Differential turnover times affect dietary estimates based on microhistological analysis of rumen contents but not results from feces. This factor probably accounts for slightly higher proportions of lichens in fecal samples *vs.* rumen samples. An estimate of order of turnover times, fastest to slowest was lichens, mosses, herbs, woody material, and graminoids (Gaare 1979, in Thing 1984).

There is justification in adjusting macrohistological and microhistological data to account for non-forage items such as conifer leaves and moss, which almost certainly are ingested incidentally with intertwined lichens in our study area. Such adjustments to our data increases proportion of lichens from 91% to 94%. That amount is in accordance with field observations at feeding sites where little other than lichens appeared to be consumed. The adjustment provides a more realistic picture of what forages caribou are attempting to ingest. Lichens totalled 67% and mosses 29% of fragment densities in feces from the Porcupine herd of barren-ground caribou in Yukon Territory (Thompson and McCourt 1981). Assuming that moss was ingested incidentally raises the proportion of lichens to 94% (100 x 67/71).

Bergerud (1972) and Helle (1981) concluded that mosses were ingested incidentally but others, such as Thompson et al. (1978), assumed that high proportions in feces must indicate intentional ingestion. Proportion of moss in diets appears to be a good index of inaccessibility of forages preferred by caribou. Inaccessibility can be caused by snow, compacted snow, or ice. In the High Arctic and some tundra range, only tops of hills are available for foraging in some winters and vegetation growing there is low and sparse. A relatively large proportion of moss is ingested in such cases.

The microhistological technique may produce a more-accurate representation of proportionate intake than macro techniques where mushrooms (Boertje et al. 1985), forbs (Samuel and Howard 1983), and mosses (Dearden et al. 1972) are not a problem or data are adjusted for them. The tendency has been for researchers to accept old results and view microhistological results with scepticism.

The importance of lichens in the diet is greater than their adjusted proportionate occurrence because of their higher digestibility compared with most other forages in the diet (Person et al. 1980, Thomas and Kroeger 1980, 1981; Thomas et al. 1984). The *in vitro* digestibility of terrestrial lichens in flasks with added urea probably simulates what occurs naturally in the four stomachs and caecum of a caribou. Those digestibilities averaged about double (71% *vs.* 34%) the average for common low shrubs (*Vaccinium* spp., *Ledum* spp., and *Empetrum* sp.) (**App. 1**). Data on *in* *vitro*, dry-matter disappearance obtained in Alaska was highly variable but their *in vivo*, nylon bag results are more reliable. Even they must be assessed in terms of dietary history of the fistulated animals, time of year when experiments were conducted, and other factors. Digestibilities as high as 95% were obtained for lichen species (**App. 2**). High digestibility of lichens, their lack of lignin, and their ease of mastication would facilitate their rapid passage through the rumen. Passage times of 11-23 hours were obtained for tethered reindeer on summer ranges in Alaska (White and Trudell 1980).

Forage preferences

Lichens are preferred over most other forages by caribou in winter but there are few data on preferences within the lichen group. Banfield (1954) defined palatability as the relative occurrence of plant species in stomach samples divided by relative occurrence of plant species in caribou habitats. Preference now refers to ingestion proportion *vs.* proportion available and palatability refers to plant characteristics that result in preference differences. In the study area, Banfield (1954) rated *Cladonia* (*Cladina*) and *Cetraria* as highly palatable (preferred) in winter and *Cl. rangiferina, C. alpestris, Cet. nivalis*, and *Cet. islandica* as highly preferred in summer. Scotter (1967) listed the lichen component in caribou rumens from the study area in winter as 84% *Cladina* spp., 7% *Peltigera* spp., 4% *Stereocaulon* spp., 4% *Cladonia* spp., and 1% *Cetraria* spp.

The importance of *Cladina* spp. in winter diet of the Beverly and Kaminuriak herds is confirmed by percent occurrence data of Miller (1976a). *Cladina* spp. occurred in 98% of rumen samples, followed by *Stereocaulon* spp. (59%), *Cladonia* spp. (48%), and *Cetraria* spp. (1%). Use of an alcohol fixative to preserve rumens may have led to identification errors because of its bleaching action. In a subsample of 11 rumens examined in a fresh state in the field, percent occurrence of genera classified as abundant and present (parentheses) were as follows: *Cladina* 91 (100), *Cladonia* 73 (91), *Stereocaulon* 45 (100), *Peltigera* 18 (64), and *Cetraria* 9 (36) (Miller 1976b). These results suggest that *Peltigera* spp. was under-represented in fixed rumen samples. Miller (1976a) believed that *Peltigera, Stereocaulon* spp., and, possibly, *Cetraria* spp. were selected. Elsewhere there was a statement that *Cetraria* spp. were not selected by caribou in north-central Canada.

However, *Cetraria* spp. and *Alectoria* spp. were the most common genera in rumens of caribou in the George River herd that were feeding in April on the barrens of northern Labrador (Parker 1981). In forested Labrador, Hustich (1951) rated *C. alpestris* as most important for reindeer followed by *C. mitis, C. rangiferina*, and *Stereocaulon* spp. *Peltigera* spp. and *Nephroma* spp. were not eaten.

Des Meulles and Heyland (1969) found that *Cladina* spp. were selected first and *Stereocaulon* spp. were selected last by tame caribou when offered in a "cafeteria-style" experiment. Similar tests in Alaska by Holeman and Luick (1977) indicated that the preferred species was *Cladina alpestris* and *Peltigera aphthosa* was of lowest preference (**Table 7**).

Hadwin and Palmer (1922) and Palmer (1926, 1934, in Courtright 1959) rated the forage values of lichen species to reindeer in Alaska and placed them in series and groups (**App. 3**). He placed *Stereocaulon* spp. in the second group and *Peltigera* spp. in the last group. Courtright's (1959) review of forage preferences of reindeer in Alaska and Europe suggest that *Cladina* spp. are of highest preference, followed by *Cetraria* spp., *Stereocaulon* spp., and *Peltigera* spp. Larin (1937) listed *C.*

Table 7. Order of preference of caribou for lichen species in "cafeteria-style" tests conducted in Quebec and Alaska.

Preference order	Location of test	
	Quebec[1]	Alaska[2]
1	*Cladina* spp.[3]	*Cladina alpestris*
2	*Cladina rangiferina*	*Cladina rangiferina*
3	Arboreal[4]	*Stereocaulon paschale*
4	*Cetraria islandica*	*Cetraria richardsonii*
5	*Stereocaulon* spp.	*Peltigera aphthosa*

[1] Des Meulles and Heyland 1969.
[2] Holleman and Luick 1977.
[3] *C. mitis, C. alpestris*, and *C. uncialis.*
[4] *Usnea* spp., *Evernia mesomorpha*, and *Alectoria* spp.

rangiferina, C. silvatica, and *C. alpestris* as the most useful species for reindeer in the U.S.S.R. and *Stereocaulon paschale* as "little used". Overgrazing led to loss of *Cladina* spp., then *Cetraria* and *Stereocaulon* spp., and finally loss of all lichens. Preference of lichens by reindeer was related to their content of lichen acids or "raw fats". There are some reports of *Peltigera* spp. being ignored and *Stereocaulon* spp. being little used in some areas but important in others (Courtright 1959). In Sweden, Skuncke (1969) found that reindeer grazed 24% of *Cladina* spp. and 13% of *Stereocaulon* spp. although the two groups were equally abundant. In northern Norway, reindeer grazed *Cladonia* (*Cladina*) and *Cetraria* heaths in winter and virtually ignored *Stereocaulon* heaths (Oksanen 1978). In summer, they decimated *Cladonia* ranges and depleted *Cetraria* habitats.

Cladonia spp. are difficult to place in the above list because of the many species. Undoubtedly there is a range of preferences within that group from selected to ignored. Alexandrova (1940, in Courtright 1959) stated that *Cl. crispata* was "much eaten" by reindeer. Reindeer had a "moderate appetite" for *Cl. cornuta* according to Zhuginov (1961).

Concerning preference of reindeer for lichens in Russia, Zhuginov (1968) stated that *C. rangiferina, C. sylvatica* (*mitis*), and *C. alpestris* (*stellaris*) were preferred species, *Cet. cucullata* and *Cet. nivalis* ranged in second place, and *Stereocaulon paschale, Sphaerophorus globosus, Usnea* spp., and *Bryopogon* spp. were least preferred. Reindeer lichens constituted the main winter diet of reindeer in U.S.S.R. according to Davydov (1958) and Sablina (1960).

Helle (1966) listed *C. mitis*, *C. sylvatica*, *C. rangiferina, C. alpestris,* and *Stereocaulon* spp. as main species in winter diets of reindeer in Finland. Skunke (1969) stated that *Cet. islandica* was highly preferred by reindeer.

Thing (1984) found that *Peltigera apthosa* was used little (3-4% in rumen samples) in relation to its abundance in craters and believed its use was an indication of depleted range. He cited other researchers who felt that caribou rejected the species. Thing (1984) also suggested that *Empetrum nigrum* and *Vaccinium vitis-idaea* were virtually starvation foods on Greenland. Skunke (1969) viewed those species as emergency fodder in Sweden. Of all the low shrubs, *Vaccinium vitis-idaea* was eaten least by reindeer in the U.S.S.R. (Sablina 1960).

Evidence of diet and forage preferences from crater examinations

Evidence from examination of craters in winter 1980 and 198l (Thomas and Hervieux 1986) and in subsequent years indicated that *C. mitis* was extensively grazed and was the most important lichen species. *Cladina stellaris* may be equally preferred but it was not a common lichen in mesic and xeric upland sites. Small forms of *C. stellaris* are indistinguishable from *C. mitis* in the field and they are seldom detected in craters.

Based largely on examination of craters, Kelsall (1960) rated lichens, grasses/sedges, willow, birch, and *Ledum* spp. as having high palatability in winter. In contrast, caribou of the Beverly herd appeared to ignore high and low shrubs in the 1980s (Thomas and Barry 1981). Miller (1976a) found that *Cladina* spp. occurred most frequently of all lichen species in craters (50%), followed by *Cladonia* spp. (34%), *Cetraria* spp. (30%), *Stereocaulon* spp. (26%), and arboreal lichens (14%). Kelsall (1968) collated frequency of occurrence data from several sites cratered in the NWT and Saskatchewan. Ground lichens, consisting largely of *C. alpestris* (*stellaris*), *C. mitis, C. rangiferina, Cet. islandica* and *nivalis*, and *Stereocaulon* spp. totalled 47% of all species identified. Kelsall (1968) compared data on frequencies of occurrence of plants in craters and in the same general region and suggested that lichens, sedges, *Ledum* spp., and willows (*Salix* spp.) were highly preferred by caribou, whereas *Vaccinium* spp., *Arctostaphylos* spp., *Empetrum nigrum*, and *Betula* spp. were eaten in amounts approximating their occurrence in ground cover.

Inglis (1975) found that *C. rangiferina, C. mitis*, and *Cet. nivalis* comprised over 75% of vegetation in all craters made by reindeer in a forest-tundra ecotone. Edmonds and Bloomfield (1984) found that all species of lichens except *Peltigera* spp. occurred more frequently in caribou craters than in control snowpits. Evidence of cratering was visible in the summer at some sites. Use of *C. mitis* was evident at all locations. There was obvious loss of *Stereocaulon* spp. from cratering but in all cases there were other lichen species such as *C. mitis* and *Cet. nivalis* mixed with *Stereocaulon*. There was no evidence that *Stereocaulon* was grazed where it occurred in nearly pure stands. Digestibility of *Stereocaulon paschale* was the lowest of lichen species tested in 1980, when condition of caribou was below average (Thomas and Kiliaan 1998).

Growth forms of lichens provides clues to their relative importance to caribou in winter. Relatively short, spiky forms that are anchored to the substrate are not as accessible as branching fruticose forms or loose foliose forms. In terms of cratering, *C. stellaris* is most accessible followed by *C. mitis, C. rangiferina, Cet. nivalis*, and *Cet. islandica*. Those forms would tend to roll up when pawed and be easily eaten. In contrast, many *Cladonia* spp. are anchored and likely would fracture when pawed by a hoof with sharp edges.

Stereocaulon is mat forming but it should be accessible to caribou unless fall rains froze the mat. *Peltigera* spp. often adhere to the substrate by their fungal hyphae but their large size makes them accessible in winter. Caribou may have a problem separating live portions from dead parts of *Peltigera* spp.

Nutritional content of forages

Nutritional content of lichens (**App. 4 & 5**) should play a role in their preference by caribou. *Peltigera* spp. and *Stereocaulon* spp. have relatively high protein contents at about 16-20% and 6-8%, respectively (Scotter 1964, Tener 1965, Kelsall 1968, Klein 1970, Bergerud 1972, Parker 1975, Miller 1976a, Bergerud 1977, Luick 1977, Boertje 1981, Nieminen and Heiskara 1989). Results for most plant constituents are so variable that only general trends are evident. For example, crude protein content of *C. rangiferina* varies from 1.7 to 4.4%; the calcium content from 0.5 to 3.1 g/kg

(Nieminen and Heiskari 1989). Protein content of *Cladina* and *Cladonia* spp. is in the order of 2-4%. Caribou obtain additional protein from winter-green parts of sedges, horsetails, and shrubs and from *Peltigera* spp. and *Stereocaulon* spp. Those two lichen genera, though relatively high in protein content, are ingested in small proportions. They may be poorly digested and even toxic to rumen bacteria and ciliates in large proportions. Caribou are efficient at recycling urea and they may utilize protein from dead protozoa. Caribou catabolize body muscle as a protein source if necessary.

There was no indication that caribou actively sought *Peltigera* spp., *Stereocaulon* spp., green sedges, or evergreen shrubs to improve their nitrogen balance. Caribou seem to be less concerned about their nitrogen balance than biologists!

Lichens are often listed as an incomplete forage source for caribou, or worse, as a poor forage source. Palmer (1944) found that caribou lost weight in October or late winter when fed only "tall growth or moist site" (*Cladina* and *Cetraria* spp.) lichens. They gained weight in January, however, when fed "short growth/dry site" lichens (including *Alectoria, Cladonia, Cetraria, Peltigera,* and *Stereocaulon*). At first, he attributed the difference in performance to higher vitamin A in short forms but later he also implicated protein. Caribou gained weight on a mix of tall growth forms and herbaceous vegetation (Palmer 1944). Loss of weight in late winter may be normal in most age classes of caribou. It occurs to at least 4 years of age in male and female captive caribou with free access to high protein rations (McEwan 1968).

The best data on levels of trace elements, including heavy metals, in lichens and other forages is in Puckett and Finegan (1980). Organic composition of mosses in the Canadian High Arctic was obtained by Parkarinen and Vitt (1974).

Researchers have difficulty relating differences in nutrients and trace elements among forages to “performance” (measured by weight changes), forage preferences, and feeding behavior of caribou. For example, results for short and long forms of lichens goes against reindeer's preferences for those forms. There is need for more research on nutrition and feeding ecology of caribou.

Diet changes during winter

Diet of the Beverly herd in November/December and March was almost identical. Proportion by weight of lichens in rumens of Kaminuriak herd caribou was as follows: September 17%; November 53%; February 49%; April 53%; and June 18% (Miller 1976a, Fig. 5). Proportions of lichens in fecal pellets sampled from various locations in southern Keewatin District were similar in winter (61%), summer (56%), and intermediate seasons (74%) (Thompson et al. 1978). Uniforrnity of surface vegetation on forested winter range and a need to crater in snow precludes much variation in diet once caribou are on that range.

Diet changes from forest to tundra

Observed progressive decrease in lichen proportions in the diet from forest through a forest-tundra ecotone to tundra is in agreement with published data on winter diets of caribou in Canada based on the microhistological technique (Fischer and Duncan 1976, Fischer et al. 1977, Parker 1978, Thompson et al. 1978) (**App. 6**). There was a progressive decrease in proportion of lichens in the diet and a corresponding increase in the moss component. Lichens are replaced by graminoids in the winter diet of High Arctic caribou.

CONCLUSIONS

1. The microhistological technique, based on rumen and fecal material, yielded useful data on winter diet of barren-ground caribou in north-central Canada. The only comparative data were from macrohistological analyses of some of the same rumen samples (Thomas and Hervieux 1986).

2. The microhistological method may produce better estimates of proportionate ingestion of lichens by caribou than macrohistological analyses of rumen samples. Some severe biases probably are introduced to rumen analyses by macrohistological techniques from losses of material through washing screens, bias in tallying coarse material, by differential turnover times of fragment size and species, and over estimation of poorly digested material ingested incidentally with lichens.

3. Microhistological data for paired composite samples of rumen contents and feces from 5-10 caribou in winter revealed some significant differences but for most plant groups the differences were in both directions.

4. The major component in winter diet of the Beverly herd was lichens at 87-90% relative density based on both rumen and fecal samples.

5. *Cladina*-type lichens, including the *Cladina, Cladonia, Stereocaulon*, and *Alectoria*, dominated the lichen component and usually comprised 60-85% of fragments. Their proportions in rumen and fecal samples were similar.

6. Results from rumen and fecal samples for minor species (0-10% relative densities) were erratic and equivocal because of inadequate microhistological sampling intensity. However, *Cetraria* types (including *Evernia* spp., *Hypogymnia*, and some

Usnea spp.) appeared to be overestimated in fecal samples, whereas *Peltigera* spp. and *Usnea* spp. appeared to be grossly underestimated in fecal samples compared with rumen samples.

7. Conifer leaves, *Ledum* spp., *Loiseularia* spp., and graminoids were under-represented in feces relative to rumen samples.

8. Variables that did not affect fragment composition in rumen and fecal samples included age, sex, and physical condition of caribou, season (early *vs.* late winter), and year.

9. There were minor dietary differences among the habitats classified as forest, forest-tundra ecotone, and tundra. There were decreases in relative proportions of lichens and increases in proportions of graminoids and shrubs in the sequence from forest to tundra.

10. Improved estimates of diet could be obtained by establishing a series of correction factors relating relative forage weights, in the range of estimated diet, to relative fragment densities derived from the microhistological technique.

11. Correction factors are specific to the composition of each sample and therefore mean correction factors, which should be based on a large number of fields, will improve estimates but will not be specific for, and accurately correct, each sample.

12. Absence of significant differences among locations within year and habitat types means that the location of the herd at the time of sampling is of little consequence.

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Appendix 1. Apparent digestibilities (dry matter disappearance) of plant species eaten by caribou as estimated in several *in vitro* trials using test tubes and flasks with and without urea.

	Dry matter disappearance (%)[1] in:		
Plant species	Flasks + urea	Flasks	Test tubes
Cladina mitis	77	66	56, 53, 48, 44, 43
C. rangiferina	49	52	45, 37, 35
Cladonia spp.[2]	76, 74, 67	62, 54, 48	55, 47, 44, 44, 41, 41, 39 36, 30
Cetraria nivalis	91	87	55, 38, 34, 20
Stereocaulon spp.	66	67	48, 47, 45, 30, 24
Peltigera spp.			44, 38, 33, 32
Arboreal lichens[3]	94, 89	72, 67, 65	76, 65, 59, 52, 52, 47, 43 42, 42, 39, 32
Ledum spp.			31, 31, 19
Empetrum sp.			54, 30
Vaccinium vitis-idaea			43, 33, 25
Carex rostrata[4]			67, 63, 57
Moss species			30, 29, 29, 26, 25, 24, 24 22, 19, 18, 17, 16, 16, 15 14, 12, 7

[1] Data from Thomas et al. 1984.
[2] *C. uncialis, Cl. amaurocraea, Cl. cornuta*, and several grouped species.
[3] *Usnea hirta, Evernia mesomorpha, Alectoria americana, and Hypogymnia physoides.*
[4] Winter-green part.

Appendix 2. Apparent dry-matter digestibilities of forage species collected in Alaska and tested in fistulated reindeer and caribou (Inst. Arctic Biol. 1974).

	Dry-matter disappearance (%)			
	In vitro		Nylon bag	
Forage species	Mean	SD[1]	Mean	SD[1]
Alectoria nigricans	41.9	4.0	94.8	4.1
Cetraria cucullata	78.5	2.9	90.0	3.4
Cet. cucullata (no. 2)	82.4	6.1		
Cet. islandica	28.6	0.6	61.6	2.5
Cladina alpestris	18.2	8.7	42.8	2.3
C. rangiferina	37.4	1.0	40.9	2.5
Cladonia uncialis	33.4	14.1	35.3	2.5
Peltigera aphthosa	40.6	1.9	49.2	6.5
Stereocaulon alpinum	13.9	0.3	39.5	13.8
S. rivulorum			44.3	2.1
Betula nana	30.9	8.8	57.2	1.5
Ledum decumbens	18.5	1.3	47.6	4.2
Salix pulchra	20.1	1.5	66.6	9.5
Vaccinium vitis-idaea	19.8	4.4	64.4	1.3
Calamagrostis spp.			36.2	1.3
Carex aquatilis, green			53.1	2.2
Carex aquatilis, dead			31.7	1.4
Eriophorum vaginatum	35.2	2.8	31.0	4.0
E. angustifolium	40.5	4.2	35.3	3.7
Festuca altarca	53.0	5.4	43.4	2.5
Hierochloe alpina	56.1	3.2	63.7	7.8
Hylocomium splendens	16.1	5.4	5.9	2.3
Polytrichum juniperinum	13.6	1.7	13.2	0.4
Sphagnum magellanicum	4.4	3.0	3.4	1.7

[1] Standard deviation.

Appendix 3. Relative forage values of lichen species to reindeer and caribou according to Palmer (1926, in Courtright 1959).

Value/Species
1. **High: abundant and high palatibility**:
Cladonia sylvatica (= *mitis*-like), *C. rangiferina, C. alpestris, C. amaurocraea, C. uncialis, C. gracilis, Cetraria cucullata, Cet. islandica*
2. **Medium, lower palatability/local abundance or medium palatability**:
Cet. nivalis, Cet. richardsonii, Alectoria ochroleuca, Dactylina arctica, Nephroma arctica, Stereocaulon alpinum, S. coralloides, S. tomentosum, C. gracilis, C. amaurocraea, et al.
3. **Low: rare**:
Alectoria nigricans, Sphaerophorus coralloides, Thamnolia vermicularis, Parmelia spp., *C. crispata, C. deformis, C. gracilis, C. subsquamosa, C. cenotea, C. bellidiflora*, et al.
4. **Little or no value: small, rare, poor growth form, or unpalatible**:
Peltigera spp., *Alectoria jubata* (*americana*), *Lecidea* spp., *Cet. juniperina, C. coccifera, C. pixidata, Ochrelechia* spp., *Pertusaria* spp., *Psoroma* spp., *Physcia* spp., et al.

Appendix 4. Chemical composition (%) of caribou and reindeer forages (Kelsall 1968).

Plant species	No. of samples	Protein	Crude fat	Fibre	Ash	N-free extract
Cladina mitis	1	2.5	1.7	23.0	2.2	65.6
C. sylvatica[1]	2	1.9	1.2	44.0	2.2	50.8
C. rangiferina	5	2.2	1.6	42.3	1.5	51.4
C. alpestris	3	2.8	1.5	44.5	1.9	49.1
Cetraria nivalis	4	2.5	4.0	5.1	2.2	86.3
Cetr. cucullata	3	3.8	3.8	11.2	2.1	80.0
Cetr. islandica	5	4.6	3.4	7.9	1.5	82.7
Stereocaulon spp.	4	8.0	1.8	24.6	2.6	63.1
Peltigera spp.	1	19.8	1.3	25.3	9.1	44.5
Vac. vitis-idaea	2	5.8	3.1	20.2	2.7	68.2
Vac. uliginosum	2	6.8	3.1	31.4	3.1	55.6
Ledum decumbens	3	6.5	6.5	27.3	2.2	57.5
Empetrum nigrum	4	4.6	10.0	23.1	3.3	59.0
Arctostaphylos spp.	1	8.6	2.5	9.5	5.4	74.1
Salix spp.	15	21.0	3.1	16.7	6.5	52.7
Betula spp.	15	16.0	7.2	16.2	3.3	57.7
Equisetum spp.	6	11.4	3.3	18.8	13.6	53.0
Carex aquatilis	3	10.6	3.2	35.4	6.0	44.8
Fungi	2	34.8	4.8	20.8	8.1	31.6
Musci	2	4.8	3.4	28.3	6.9	56.6

[1] Similar to/or *C. mitis*.

Appendix 5. Mean values for lichen constituents based on values from several studies (adapted from Nieminen and Heiskari 1989).

Lichen species	% crude: Protein	Fiber	Fat	N-free extract	Element (g/kg) Ca	P	Mg	K	Na
Cladina mitis	2.2	37.0	1.6	53.5	0.9	0.4	0.3	1.0	
C. stellaris	2.5	39.4	2.5	50.8	0.8	0.5	0.3	1.2	0.2
C. arbuscula	2.5	28.0	2.2	63.6	0.8	0.6	0.4	1.4	0.2
C. rangiferina	2.8	39.8	1.5	52.6	1.2	0.8	0.4	1.3	0.2
Cladina spp.	2.9	36.7	2.6	57.0	1.0	0.5	0.5	2.5	0.8
Cetraria nivalis	2.1	7.4	2.9	84.9	1.8	0.5	0.5	2.0	0.2
Stereocaulon spp.	7.3	22.4	2.4	64.0	0.8	0.8	0.3	2.5	
Arboreal spp.[1]	5.3	6.5[2]	4.4	79.9	1.4	0.8	0.3	2.7	0.5

[1] A mixture of *Alectoria* spp., *A. sarmentosa*, and *Bryoria fuscescens*.
[2] One extreme value omitted.
Note: mid-value used where only a range was given.

Appendix 6. Percent relative density of lichen and moss fragments in rumen and fecal samples of caribou obtained on a latitudinal and ecological gradient from taiga forest to the High Arctic, based on the microhistological technique.

Location (N latitude)	Fragment source	Percent lichens	Percent mosses	Source
Taiga forest (60 - 62°)	Rumen	91	2	This study
Forest-tundra (62°)	Rumen	87	1	This study
Near tundra (64°)	Rumen	79	3	This study
S. Keewatin (60 - 65°)	Fecal	61	23	Thompson et al. 1978
N. Keewatin (65 - 70°)	Fecal	41	46	Fischer et al. 1977
Boothia Pen. (70 - 72°)	Fecal	41	51	Fischer et al. 1977
Prince of Wales Isl. (72-74°)	Fecal	22	56	Fischer & Duncan 1976
Prince of Wales Isl. (72-74°)	Rumen	0[1]	39	Parker 1978
High Arctic (74 - 76°)	Rumen	0[1]	60	Parker 1978

[1] Lichen undetected with technique used.