

Does seasonal variation in forage quality influence the potential for resource competition between muskoxen and Peary caribou on Banks Island?

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Abstract: Inter- and intra-annual variation in forage quality may influence population dynamics of Peary caribou and muskoxen on Banks Island. From 1993 to 1998 we collected 300 composite samples of sedge (*Carex aquatilis* and *Carex* spp.), willow (*Salix arctica*), legume (*Oxytropis* spp. and *Astragalus* spp.), and avens (*Dryas integrifolia*). Samples were collected in mid-June (start of the growing season), mid-July (peak of the growing season), mid-late August (senescence), and early (November), mid- (February), and late- (April/May) winter. We analysed forages for percent digestibility (*in vitro* acid-pepsin dry matter digestibility), crude protein (CP), fibre, lignin, and energy content. There was significant inter-annual variation in levels of lignin, fibre, and energy, and significant intra-annual (seasonal) variation for all quality measures and forages, which reflected the strong difference in quality between summer and winter. We discuss the relationship between forage quality and seasonal diet composition of Peary caribou and muskoxen, and the potential implications for the reduced Peary caribou and high muskoxen populations.

Key words: arctic, digestibility, energy, fibre, lignin, nitrogen, *Ovibos moschatus*, protein, *Rangifer tarandus pearyi*.

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Introduction

Peary caribou (*Rangifer tarandus pearyi*) and muskoxen (*Ovibos moschatus*) are the two dominant resident large herbivores on Banks Island. Since 1972 caribou numbers declined from ca. 12 000 (≥ 1 year-old animals) to an estimated 436 ($s_{\bar{x}} = \pm 71$) in 1998 (J. Nagy & M. Branigan, unpubl.); most of the decline occurred by 1991. In contrast, muskox numbers increased from ca. 4000 (≥ 1 year-old animals) in 1972, to 45 833 ($s_{\bar{x}} = \pm 1938$) in 1998, reaching a peak at 64 608 ($s_{\bar{x}} = \pm 2009$) in 1994 (Larter & Nagy, 1997; J. Nagy & M. Branigan, unpubl. data). The reasons for these population

changes are unclear (Nagy *et al.*, 1996; Larter & Nagy, 2001b), but intra- and inter-annual differences in forage quality and availability may be contributing factors. Larter & Nagy's (1997) reanalysis of Wilkinson *et al.* (1976) and Shank *et al.* (1978) indicated that, historically, caribou and muskoxen on Banks Island had substantially similar diets.

Sedges (*Carex aquatilis* and *Carex* spp.), arctic willow (*Salix arctica*), legumes (*Oxytropis* spp. and *Astragalus* spp.), and avens (*Dryas integrifolia*) collectively represent $\geq 65\%$ of the monthly diet of Peary caribou and $\geq 90\%$ of the monthly diet of muskox-

en on Banks Island (Larter & Nagy 1997; unpubl. data). In this paper we report seasonal and annual (1993-1998) changes in crude protein, digestibility, lignin, fibre, and energy content of forages that are important dietary items of Peary caribou and muskoxen on Banks Island, and discuss whether patterns of forage utilization by caribou and muskoxen are consistent with Hofmann's (1989; 2000) prediction that muskoxen should use fibrous forages of relatively low quality whereas caribou should select easily digestible high quality forage. Population changes of these herbivores on Bank's Island may be related, in part, to variation in availability and quality of the main forage species.

Study area

Banks Island is the most western island in the Canadian arctic archipelago and covers approximately 70 000 km². The climate is arctic maritime along coastal areas, tending toward arctic desert conditions inland (Zoltai *et al.*, 1980). Mean monthly temperatures are below 0 °C from September through May, and mean minimum daily temperatures range from -30 to -40 °C from December to March. Snow cover persists into June. The depth of snow cover varies, being greatly affected by wind, and is deepest in low-lying areas. Larter & Nagy (2000) provide a more detailed account of snow conditions in various habitats. Summers are short and cool, with mean maximum daily temperatures ranging from 5 to 10 °C from June through August. Annual mean precipitation is 90 mm (Zoltai *et al.*, 1980). Sachs Harbour (125 inhabitants) is the only permanent settlement on the Island.

Habitat descriptions were adapted from Kevan (1974), Wilkinson *et al.* (1976), and Ferguson (1991). There are 4 major terrestrial habitats: wet sedge meadow (WSM), upland barren (UB), hummock tundra (HT), and stony barren (SB). WSM are generally level hydric and hygric lowlands characterized by *Carex aquatilis*, *Eriophorum scheuchzeri*, and *Dupontia fisheri*; vegetative cover is nearly 100% except for standing water. UB are well drained sites found on the upper and middle parts of slopes. Vegetative cover is 20-50% and is dominated by *Dryas integrifolia* and *Salix arctica*. HT is found on moderately steep slopes and is characterized by individual hummocks, which are vegetated primarily by dwarf shrubs (*D. integrifolia*, *S. arctica*, and *Cassiope tetragona*); vegetative cover is 35-50%. SB has a coarse gravelly substrate and is sparsely vegetated (<10%). This habitat is found on wind blown areas, ridges, and gravel and sand bars. A

more detailed description of the flora of Banks Island can be found in Wilkinson *et al.* (1976), Porsild & Cody (1980), and Zoltai *et al.* (1980).

In addition to muskoxen and Peary caribou, other resident herbivores include arctic hares, ptarmigan and lemmings. During summer there is a substantial population of nesting snow geese (*Chen caerulescens*), estimated at 439 000 ± 51 000 (95% CI) in 1995 (Samelius & Alisauskas, 1998).

Methods

Sample collection/preparation

During summer we collected vegetation samples at the start of the growing season (13-21 June), peak of the growing season (16-22 July), and senescence (18-27 August). We collected sedge (*Carex aquatilis* and *Carex* spp.) from WSM and UB respectively, willow (*Salix arctica*) and legumes (*Oxytropis* spp. and *Astragalus* spp.) from UB and HT, and avens (*Dryas integrifolia*) from UB. Samples were collected from two different sites.

During winter we collected samples in early- (7-18 November), mid- (12-26 February), and late-winter (20 April to 2 May) from WSM (*C. aquatilis*) and UB (legumes and *Dryas*). Sedge was collected over 5 winters (1993-94 to 1997-98) whereas legumes and *Dryas* were collected for the latter 3 winters (1995-96 to 1997-98) after it became apparent that these forages were an important component of the winter diet of Peary caribou (Larter & Nagy, 1997). Samples were collected from the same general area in both sites each year.

Forage samples were composed of numerous individual plants, including flowers if present, clipped at ground level (≥25 g wet weight), except for willow samples. Willow samples were partitioned into leaf and stem components, and leaves were plucked from numerous individual plants. Current year's growth of willow stems was clipped from numerous individual plants during mid-July and late-August only because stem growth had rarely been initiated by mid-June.

Samples collected in summer were stored in brown paper bags and allowed to air dry in the field prior to being transported to the laboratory in Inuvik. Sedge samples were separated into their green live matter and dead components. All other samples were considered to be current year's live growth. Samples collected in winter remained frozen until transported to the laboratory in Inuvik where they were thawed at room temperature for 24 h. Winter samples were not separated into live and dead components. All samples were dried at 60

°C for 48 h, and ground through a 1 mm screen with a centrifugal mill.

Subsamples of all forage samples (≤ 10 g dry weight) were analyzed at the Animal Science Department, University of British Columbia to determine their dry matter, nitrogen, energy, lignin, and fibre content. We determined percent digestibility at the Inuvik laboratory.

Forage quality analyses

Dry matter content was determined for all samples. Duplicate samples ($n = 8$) were analyzed to determine the accuracy of the measurement (99.8%). All analyses were calculated on a dry weight basis. We determined percent nitrogen concentrations for all samples by micro-Kjeldahl (Nelson & Sommers, 1973). Each sample was run once, and duplicate samples were run to determine the accuracy of the measurement (96.9%; $n = 48$). We calculated percent crude protein (CP) content by the standard conversion ($6.25 \times$ percent nitrogen). We determined percent digestibility for all samples except one sample of live *Carex* spp. Percent digestibility was determined by *in vitro* acid-pepsin digestibility following Tilley & Terry (1963) and Spalinger (1980). Larter (1992; 1997) found this simple method provided an index of forage fibre content comparable to that of the more complicated acid-detergent fibre technique (Van Soest, 1967). We used the mean percent digested for the statistical analysis ($n = 4$ or 5 separate runs). High digestibility values indicate low fibre content and vice versa (Larter, 1992).

We determined percent lignin content by acid-detergent lignin (ADL) (Van Soest, 1963) and percent fibre content by acid-detergent fibre (ADF) (Van Soest, 1967). We determined lignin and fibre content for *Salix*, legume, *Dryas*, live summer *C. aquatilis*, and winter *C. aquatilis* samples only. Samples were run once through each analysis. Duplicate samples were run to determine the accuracy of the measurements for acid-detergent lignin (77.7%; $n = 29$) and acid-detergent fibre (95.1%; $n = 67$).

We used bomb calorimetry (LECO AC-300 Automated Bomb Calorimeter) to determine energy content (cal/g converted to kJ/g by multiplying by 4.184/1000). We determined energy content for all forage samples collected from June 1993 to April 1996, except for 2 for which we lacked adequate material. From June 1996 to May 1998 we determined energy content for *Dryas*, legume, live summer *C. aquatilis*, and winter *C. aquatilis* samples only. Each sample was analyzed once, however

duplicate samples ($n = 18$) indicated that the accuracy of the measurement was high (99.3%).

Statistical analyses

For the purposes of statistical analysis we pooled forage quality measures across both sample areas, based on the rationale provided by Larter & Nagy (2001a), and partitioned sampling time into three summer (June, July, August) and three winter (November, February, April) periods. For each quality measure (CP, digestibility, ADL, ADF, energy) we used a three-way ANOVA to test for significant main effects (forage type, sample period [season], and year), and all interaction terms (SPSS, version 10.0.7, 2000). All analyses were based on Type III Sum of Squares and all forage quality measures were log-transformed prior to analysis in order to pass Levene's test of equality of variances. A full factorial (unbalanced) model was run for CP, digestibility and energy, however we did not include *Carex* spp. in the analysis for ADL and ADF because of missing data. Scheffé's test was applied in post-hoc analyses assuming a value for $\alpha = 0.05$. The relationship between different quality measures was analyzed using correlation analysis (Pearson coefficient) and discriminant function analysis (SPSS, 2000).

Results

Inter-annual variation

There were significant differences between years for acid-detergent lignin (ADL), acid-detergent fibre (ADF) and energy, but not crude protein (CP) or digestibility (Table 1). Post-hoc tests indicated that significant year effects could be partly accounted for by differences between the earlier and later years of sampling (Table 2), although this pattern was not entirely consistent. We do not know why ADL values in 1995 were so low, but this pattern was observed for all forages except the legumes.

Intra-annual (seasonal) variation

Strong seasonal effects were apparent for all quality measures. The main effect of Season and Forage*Season interactions were significant in all cases (Table 1), and reflected a strong difference between summer and winter. Within the summer or winter sampling periods respectively there were also differences over several months for most quality measures, however the magnitude of these differences was much less than the differences between summer and winter (Figs. 1 and 2).

Table 1. Results of 3-way ANOVAs with main effects forage type, season, and year to examine differences in crude protein, percent digestibility, acid-detergent lignin, acid-detergent fibre, and energy content of six forages from Banks Island. Statistical significance was conservatively set at $\alpha=0.01$ and is indicated in bold.

Effect	Crude Protein		Digestibility		Acid-Detergent Lignin		Acid-Detergent Fibre		Energy						
	df	P	F value	P	df	F value	P	df	F value	P					
Forage (FOR)	5,186	186.319	<0.000	5,185	395.908	<0.000	4,91	123.338	<0.000	4,91	102.228	<0.000	5,146	23.849	<0.000
Season (SN)	5,186	71.397	<0.000	5,185	178.727	<0.000	5,91	8.971	<0.000	5,91	35.766	<0.000	5,146	8.458	<0.000
Year (YR)	4,186	1.091	0.363	4,185	0.981	0.419	4,91	38.027	<0.000	4,91	4.993	0.001	4,146	6.574	<0.000
FOR * SN	15,186	10.061	<0.000	15,185	11.316	<0.000	13,91	2.659	0.003	13,91	7.038	<0.000	15,146	6.179	<0.000
FOR * YR	20,186	1.632	0.049	20,185	30.55	<0.000	14,91	8.298	<0.000	14,91	2.8	0.002	14,146	1.929	0.028
SN * YR	19,186	1.558	0.071	19,185	1.72	0.036	15,91	1.979	0.025	15,91	2.273	0.009	19,146	0.779	0.728
FOR * SN * YR	45,186	0.81	0.796	45,185	1.044	0.409	30,91	2.234	0.002	30,91	0.829	0.714	36,146	1.068	0.380

Table 2. Results of Scheffé post-hoc analysis of inter-annual (year) effects of 3-way ANOVA of differences in crude protein (CP), acid-detergent lignin (ADL), acid-detergent fibre (ADF), digestibility, and energy content of six forages from Banks Island. Values are means for summer sampling periods only, and values that are not significantly different between years are marked in common (underline, bold, italics).

	1993	1994	1995	1996	1997
CP	<u>14.7</u>	<u>16.1</u>	<u>14.4</u>	<u>14.2</u>	<u>13.5</u>
ADL	<u>8.0</u>	<u>7.4</u>	2.7	<u>8.4</u>	<u>8.4</u>
ADF	42.2	<u>41.3</u>	42.9	<u>37.4</u>	<u>36.1</u>
DIGEST	<u>0.39</u>	<u>0.39</u>	<u>0.38</u>	<u>0.37</u>	<u>0.36</u>
ENERGY	<u>18.5</u>	<u>19.4</u>	19.5	<u>18.7</u>	<u>18.6</u>

Variation among forages

Crude protein

CP of forages was highest in June, and declined over the course of the summer (Fig. 1) such that August levels were similar to winter values (Figs. 1 and 2). Post-hoc tests indicated that the highest CP values were shared by *Salix* leaves and legumes, followed by *Salix* stem and *C. aquatilis*, then *Dryas* and finally *Carex* spp. (Scheffé test, $\alpha = 0.05$). During winter legumes had the highest CP (Fig. 2), and CP of *C. aquatilis* was higher during the last two winters of the study compared to the earlier years.

Percent digestibility

Digestibility of all forages was highest during June and July and lowest during November and February (Figs. 1 and 2). Overall, the most digestible forages were *Salix* leaves and legumes (ca. 40%), followed by *Salix* stem and *C. aquatilis* (31%), then *Dryas* (26%), and *Carex* spp. (21%) (Scheffé test, $\alpha = 0.05$; Figs. 1 and 2). During winter legumes were the most digestible, and *C. aquatilis* the least digestible forages (Fig. 2).

Lignin

Lignin content was lowest during June and July and highest during August and winter (Figs. 1 and 2). The highest lignin content was found in *Dryas*, followed by *Salix* leaves and stems, then legumes, and finally *C. aquatilis* (Scheffé test, $\alpha = 0.05$; Figs. 1 and 2). Lignin levels were lowest in 1995-96. During winter lignin levels were substantially lower in legumes and *C. aquatilis* than in *Dryas* (Fig. 2).

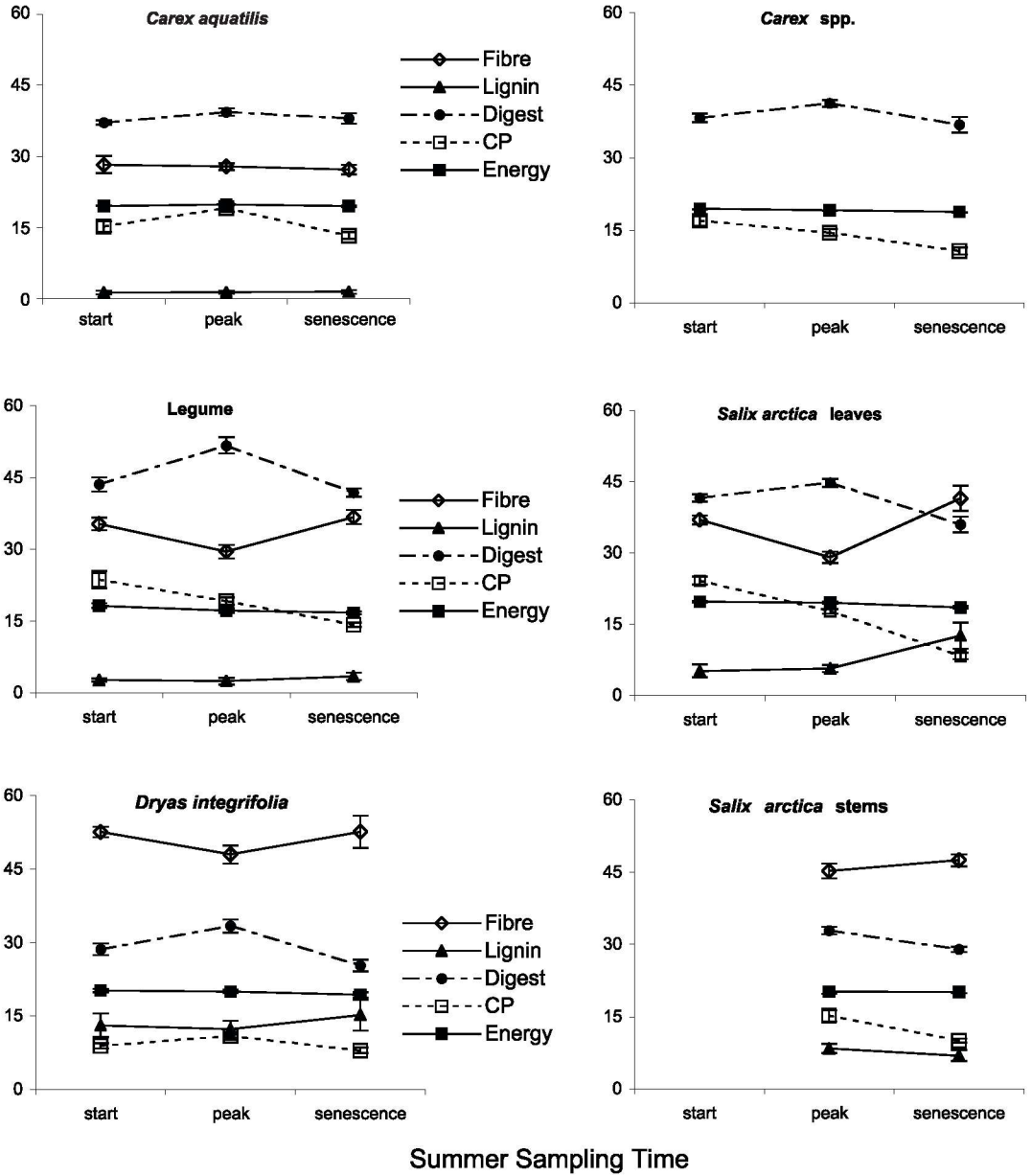


Fig. 1. Mean (s) fibre (%), lignin (%), percent digestibility, crude protein, and energy (kJ/g) content of six forages sampled during the start of, the peak of the growing season, and senescence. All values are presented on a dry weight basis and are pooled across 5 years (1993-1997).

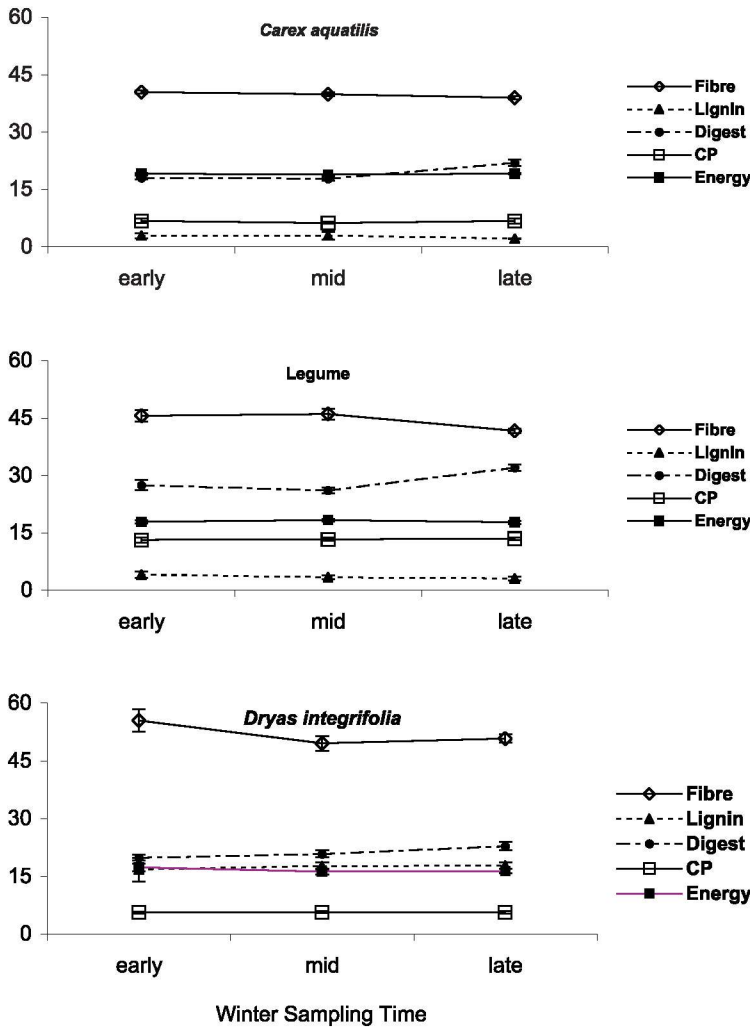


Fig. 2. Mean (\bar{s}) fibre (%), lignin (%), percent digestibility, crude protein, and energy (kJ/g) content of three forages sampled during early (November), mid (February) and late (April) winter. All values are presented on a dry weight basis and are pooled across 3 winters (1995/6-1997/8).

Fibre

Fibre content was lowest in June and July (Fig. 1). Levels increased in August but these values were similar to winter periods (Figs. 1 and 2). Post-hoc tests indicated that fibre levels were highest in *Dryas* and *Salix* stem, and then lower and very similar in all other forages (Scheffé test, $\alpha = 0.05$; Figs. 1 and 2). Fibre levels were significantly lower in 1996 and 1997, compared to 1993 - 1995. During winter fibre levels were lowest in *C. aquatilis* and highest in *Dryas* (Fig. 2).

Energy

Energy content ranged from 17-20 kJ/g for all for-

ages, and tended to be lower in the last two years of the study compared to the first three years (Scheffé test, $\alpha = 0.05$). *Salix* leaves and stems, *C. aquatilis* and *Carex* spp. had the highest energy levels, followed by *Dryas* and finally legumes (Scheffé test, $\alpha = 0.05$; Figs. 1 and 2). However, there were significant seasonal differences as well (Table 1). During winter *C. aquatilis* had the highest and *Dryas* the lowest energy content (Fig. 2).

Correlation between quality measures and classification of forages

A pairwise correlation matrix between quality measures in summer and winter was calculated in

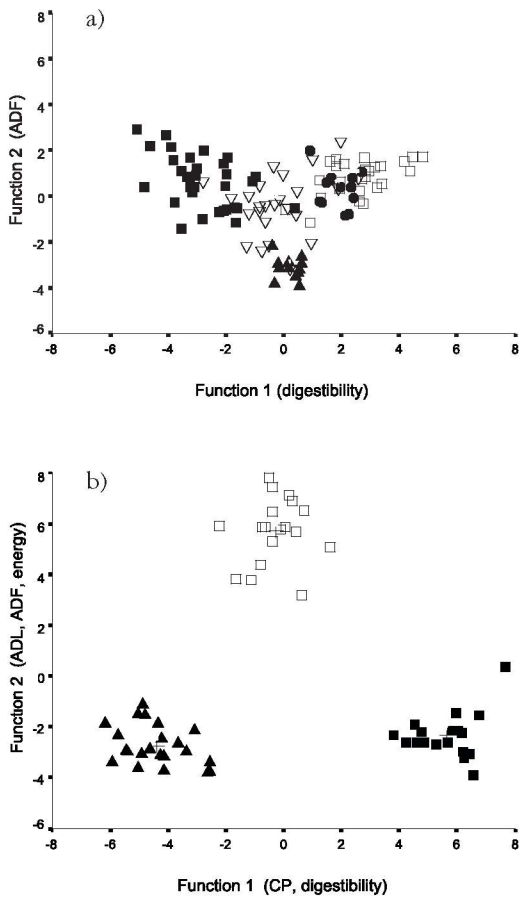


Fig. 3. Discriminant analysis classification of summer (a) and winter (b) forages, based on the five quality measures. *Carex* closed triangles (\blacktriangle), legume closed squares (\blacksquare), *Dryas* open squares (\square), *Salix* leaves open inverted triangles (∇), *Salix* stem closed circles (\bullet).

order to determine the general relationship between quality measures for all forages (Table 3). During summer, most measures were significantly correlated (negative or positive), but there were fewer significant correlations during winter. Patterns of correlations were consistent between seasons, with the exception of the relationship between ADL and energy, which was positive in summer and negative in winter. Differences between forage species contributed to the overall correlation between measures, but these correlation relationships were also consistent within forage species.

Discriminant function analysis was used to build a predictive model of forage classification based on

the five quality measures for five forages. This procedure generated a set of discriminant functions based on linear combinations of the predictor variables (quality measures) that provided the best discrimination between the forages. The canonical correlation for a discriminant function is the square root of the ratio of the between-groups sum of squares to the total sum of squares, and is the proportion of the total variability explained by differences between groups. All five quality measures were entered simultaneously, and the pooled within-groups covariance matrix was used to classify each case.

In winter, all three forage species were clearly discriminated (Fig. 3a). Function 1 explained 54.1% of the variance (canonical correlation 0.910), while Function 2 explained 45.9% of the variance (canonical correlation 0.969). The strongest correlations with Function 1 were CP (0.657) and digestibility (0.340), while the strongest correlations with Function 2 were ADL (0.617), ADF (0.308) and energy (-0.210). The relationship between quality measures on each axis is consistent with the results of the pair-wise correlation matrix (Table 3).

In summer there was more overlap among the five forages (Fig. 3b). Function 1 explained 72.8% of the variance (canonical correlation 0.910), and was most strongly correlated with digestibility (-0.652). Function 2 explained 23.5% of the variance (canonical correlation 0.780), and was most strongly correlated with ADF (0.737). The remaining quality measures (ADL, energy and CP) explained little of the variation (< 4%). *C. aquatilis* and legumes were most clearly discriminated, while *Dryas* and *Salix* stem had the greatest overlap.

Discussion

We observed significant inter-annual variation in the quality of key forages in the diet of caribou and muskoxen on Banks Island, similar to patterns reported by Larter & Nagy (2001a). Although there are relatively consistent inter-seasonal changes in quality measures for fibre, energy, and lignin content, the absolute levels vary substantially, thereby affecting the quality of forages available for herbivores in different years. Specific inter-annual differences are likely related to variability in precipitation. For example, the lower fibre content in forages during summer 1996 and 1997 is likely related to moisture, as these summers were wetter than previous ones. Summer 1994 was drier than other years and if drier conditions cause increases in energy content this might explain higher levels in

Table 3. Pearson correlation coefficients, significance (2-tailed tests) and sample size (n) among quality measures (crude protein, acid-detergent lignin, acid-detergent fibre, digestibility, and energy content) for *Dryas*, legumes, *C. aquatilis* and *Salix* leaves and stems in summer (above diagonal), and *Dryas*, legumes, and *C. aquatilis* in winter (below diagonal). Significant correlations ($P < 0.01$) are highlighted in bold.

		CP	ADL	ADF	DIGEST	ENERGY
CP	Pearson Correlation		-0.494	-0.579	.644	-0.072
	P		.000	.000	.000	.395
	n		121	121	173	143
ADL	Pearson Correlation	-0.393		.572	-0.542	.198
	P	.002		.000	.000	.045
	n	58		121	121	103
ADF	Pearson Correlation	-0.166	.663		-0.773	.382
	P	.214	.000		.000	.000
	n	58	58		121	103
DIGEST	Pearson Correlation	.809	-0.155	-0.116		-0.412
	P	.000	.245	.386		.000
	n	62	58	58		143
EN KJ	Pearson Correlation	.093	-0.645	-0.232	-0.204	
	P	.471	.000	.080	.112	
	n	62	58	58	62	

1994 (Larter & Nagy, 2001a). We have no explanation for why lignin content was lower in 1995-96 than other years.

As anticipated all measures of forage quality also had strong seasonal components in both summer and winter. While the quality of individual forages clearly changed seasonally, a focus on one measure of forage quality at a time may not provide a complete picture of the overall quality of a particular type of forage. When we examined the correlation between forage quality measures on the most important forages for caribou and muskoxen strong patterns were observed (Table 3). In general, forage species are discriminated by digestibility in summer, while crude protein and lignin were most important in winter (Fig. 3). An understanding of variation in forage quality among species is important because the basis for forage selection is different for caribou and muskoxen.

The quality of forages consumed by large northern herbivores has been examined for caribou and reindeer (*Rangifer tarandus*) (Scotter, 1972; Person, 1975; Kuropat & Bryant, 1983; Thomas *et al.*, 1984; Klein, 1990; Côté, 1998; Mathiesen & Utsi, 2000), Svalbard reindeer (*Rangifer tarandus platyrhynchus*) (Sørmo *et al.*, 1999), muskoxen (*Ovibos moschatatus*) (Murray, 1991), and wood bison (*Bison*

bison athabasca) (Larter, 1988; Larter & Gates, 1991). Some of these studies have attempted to relate seasonal changes in animal diet with seasonal changes in the quality of various forages, while others have focused on assessing the relationship between feeding preferences and the quality of food using cafeteria-style experiments (*e.g.* deer: *Odocoileus virginianus*, Pekins & Mautz, 1988; semi-domestic reindeer, Danell *et al.*, 1994). In general, the diet of ruminant species can be predicted on the basis of their digestive anatomy, along a grazer (GR) – intermediate feeder (IM) – concentrate selector (CS) continuum, as defined by Hofmann (1989; 2000).

On Banks Island, both caribou and muskoxen forage extensively on willow leaves during June and July when willow leaves are highly digestible, have a high CP and are low in fibre and lignin content. For intermediate feeders (IM) like caribou this is expected, however this would not be expected for grazers (GR) like muskoxen. Staaland & Thing (1991) reported that muskoxen in Greenland utilized *Salix arctica* in May and July; *S. arctica* was rich in hemicellulose during this time. This selectivity for *S. arctica* was believed to be in response to ruminal mucosal enlargement, which occurs dramatically between May and June and permits rapid

and maximal absorption of nutrients (Staal and Thing 1991). In July, legumes make up a substantial portion of the diet of muskoxen on Banks Island (Oakes *et al.*, 1992; Larter & Nagy, 1997). Crude protein content has declined in legumes somewhat since June, but legume biomass (N. Larter, unpubl.) and digestibility are greatest in July. Hofmann (2000) acknowledges that muskoxen are seasonally selective and possibly their heavy use of high quality legume and *Salix* on Banks Island during summer is in response to ruminal mucosal enlargement.

Sedge makes up a substantial portion of the muskox diet during August (~85%) and the winter months November to April (mean 68%, range 34-83%) (Larter & Nagy, 1997; unpubl.). During winter, sedge was the least fibrous of the three forages we examined, however, it was also the least digestible and had low CP (Fig. 2). The biomass of sedge is far greater than legumes and *Dryas* (N. Larter & J. Nagy, unpubl.), which make it an ideal forage for GR species such as muskoxen. Interestingly, willow also makes up a substantial part of the muskox diet in September (51%), October (75%), January (51%), March (36%) and May (48%) (Larter & Nagy, 1997; unpubl.). There is no leaf growth at these times of the year therefore we assume willow stem is being consumed. Visual analysis of rumen contents confirm the presence of willow stems (N. Larter & J. Nagy, unpubl.). While we lack data on the quality of willow stems during winter, it is probable that we can assume high lignin, high fibre, and higher energy content. Whether the high energy content of willow stems mitigates the high lignin content for GR-type herbivores is unknown. Increased willow in the muskox diet in late winter may be a response to high animal density and reduced per capita sedge availability during this period. Differences in the proportion of sedge in the summer diet of muskoxen may also have been density related (Larter & Nagy, 2001b). Deciduous shrubs are often an important part of caribou summer diet, so a reduction in their abundance from browsing prior to the growing season (by muskoxen) may have important consequences for caribou population dynamics (Ouellet *et al.*, 1994).

Peary caribou on Banks Island generally selected forages with similarly low lignin, moderate crude protein, and high digestibility during summer, as predicted for IM-type herbivores. Surprisingly, legumes only made up small proportions of their diet in June and August (<15%), and were virtually absent in their July diet when digestibility of legumes was the highest of all forages (Fig. 1).

Reindeer on South Georgia have a limited number of grasses available during summer and they generally selected grass species with low lignin, moderate protein, and high digestibility (Mathiesen & Utsi, 2000).

Unlike most caribou/reindeer populations, the winter diet of Banks Island Peary caribou includes negligible lichen because of extremely low biomass (Larter & Nagy, 1997). During winter, legumes and *Dryas* make up a substantial portion of the caribou diet (50-80%). Legumes are the most digestible and have the highest CP in winter while *Dryas* have the highest fibre and lignin content (Fig. 2); available biomass of *Dryas* is greater than legumes (N. Larter, unpubl.). Caribou, as an IM, would be expected to select legumes. During winter, metabolizable energy becomes a more dominant component sought in forage than crude protein (White *et al.*, 1981; Klein, 1990) and legumes have a higher energy content and are more digestible than *Dryas*. In winters with noticeably less snow cover the proportion of legume in the winter diet was higher and the proportion of *Dryas* lower (N. Larter & J. Nagy, unpubl.). Reindeer are better adapted to surviving periods of starvation (Aagnes, 1998) and although they cannot adjust to roughage with high fibre content they can better adjust to fibrous forage (Hofmann, 2000; Mathiesen *et al.*, 2000a). This might explain the dynamics of legumes and *Dryas* in the winter diet of Banks Island caribou.

The high degree of diet overlap observed on Banks Island (Larter & Nagy, 1997) is not entirely consistent with results from studies on other nearby islands in the western Canadian arctic. On southeastern Victoria Island, Staal *et al.* (1997) concluded that although caribou and muskoxen coexist in close proximity, they appear primarily adapted to different diets and foraging strategies. The predominantly graminoid diet of muskoxen and more varied, browse-dominated diet of caribou should reduce the likelihood of competition. A similar conclusion was reached by Thomas & Edmonds (1984) for caribou and muskoxen on Melville Island. These observations are also consistent with Hofmann's (1989; 2000) characterization of muskoxen as grazers, and caribou as intermediate feeders, however the lower level of diet overlap on these islands may reflect differences in densities of animals and relative availability of forage compared to the situation on Banks Island.

Overall, our analysis of forage quality, combined with earlier studies of caribou and muskoxen diets on Banks Island (Larter & Nagy, 1997; 2001b), suggest that large muskoxen populations could be

competing for the preferred forage of caribou during critical times of the year. While both species have some flexibility in their abilities to utilize a range of forages, there are distinct anatomical constraints, particularly for caribou (Hofmann, 2000). Although a number of studies have been critical of Hofmann's classification scheme (e.g. Robbins *et al.*, 1995; Van Soest, 1996), the available data appears to be supportive and indicate that this scheme is useful in assessing requirements of various species (Staaland *et al.*, 1997; Hofmann, 2000; Mathiesen *et al.*, 2000b). On Banks Island, the potential for caribou numbers to increase may be constrained by the availability of suitable forage in the presence of muskoxen.

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