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Peary caribou, muskoxen and Banks Island forage: Assessing seasonal diet similarities

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Abstract: Peary caribou (Rangifer tarandus pearyi) and muskoxen (Ovibos moschatus) on Banks Island had considerable similarity in their annual diets, with monthly similarities ranging from 17.8–73.3%. Diet similarity was more pronounced in areas of high muskox density (ca. 1.65/km²) than in areas of low muskox density (ca. 0.4/km²). Willow (Salix arctica) and sedge (Carex aquatilis and Eriophorum spp.) represented >80% of the monthly diet of muskoxen. The caribou diet was more diverse, and was dominated by sedge, willow, Dryas integrifolia, and Oxytropis maydelliana, Lichen use was rare, likely as a consequence of low availability on Banks Island. Lichen standing crop was estimated at 2.96 g/m². The differences in muskox diet between high and low density areas could not be explained by differences in forage distribution or standing crop. We discuss diet similarities of caribou and muskoxen and potential consequences for the current Peary caribou population in relation to winter weather conditions and increasing muskox density.

Key words: diet overlap, food competition, arctic, Northwest Territories, Rangifer tarandus pearyi, Ovibos moschatus.

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Introduction

Between 1972 and 1994 Peary caribou (Rangifer tarandus pearyi) numbers on Banks Island decreased from ca. 12,000 (Urquhart, 1973) to 709±128 (SE) animals, excluding calves (J. Nagy & N. Larter, unpubl. data). Contrastingly, during that same period, muskox (Ovibos moschatus) numbers, excluding calves, increased from ca. 4,000 (Urquhart, 1973) to 64,608±2,009 (J. Nagy & N. Larter, The decrease in caribou numbers unpubl. data). was attributed to a variety of factors including severe winter weather, predation, harvest, inter-island movements, and competition with muskoxen as reviewed by Nagy et al. (1996). The actual cause or causes of the decline remain unknown. However, in order to manage the recovery of the Peary caribou population on Banks Island, it is important to assess dietary overlap and the potential for food competition between the 2 species given the current animal numbers and forage abundance and distribution.

Caribou and muskoxen are the only ungulate species successfully occupying arctic tundra environments. Caribou and muskoxen have different morphological adaptations which have presumably enabled them to utilize fotage resources with little overlap (Klein, 1992). Muskoxen represent the classic grazer (Hofmann, 1989). With a large body size and gut capacity, they are capable of processing large amounts of low quality forage. Caribou are representative of a mixed feeder type, and are inter-

mediate between roughage feeders and concentrate selectors (Hofmann, 1989). Their smaller body size and smaller gut capacity, combined with a higher fasting metabolic rate than muskoxen (Tyler & Blix, 1990), require them to pursue a more selective feeding strategy. In contrast to muskoxen, caribou meet their nutritional tequirements by a relatively rapid rate of passage of highly digestible forage (Klein, 1992).

Lichen is an important winter food for barrenground caribou on the mainland, but in the high arctic islands which support low lichen biomass, caribou use other forages, usually willow and graminoids (Reimers et al., 1980; Klein, 1992). In west Greenland, where lichen biomass was apparently depleted by overgrazing (Staaland & Olesen, 1992), both muskox and caribou diets were dominated by monocots. In areas inhabited by muskoxen only, willow became an important summer diet component (Thing et al, 1987). Therefore, both animals demonstrate the ability to utilize a variety of forages when availability dictates. Muskoxen can clearly make good use of high protein, low-fibre foods (White et al., 1984; Adamczewski et al., 1994) and even though they show many attributes of classic grazers they can be quite selective in their feeding (Oakes et al, 1992). Despite their relatively wide muzzles muskoxen ate remarkably adept at finding the leafy portions of forage and rejecting larger stems (J. Adamczewski, pers. comm.).

Reconsideration of data on muskox and caribou ecology implies that competition for food may occur where muskox concentrations are high (McKendrick, 1981), and that overlapping winter diets may adversely affect caribou numbers (C. Olesen, unpubl. data).

In this paper we report pteliminary findings on the Peary caribou and muskox diers, monitored on a monthly basis, the current forage distribution and standing crop of the 4 major terrestrial habitats in areas of high and low muskox density on Banks Island, and compare our findings with previous work

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 ateas where weather stations are located, tending toward Arctic Desert inland. Winters are long and cold; summers are short and cool.

Ptecipitation is low with an annual mean of 9 cm (Zoltai *et al*, 1980). Sachs Harbour is the only permanent settlement on the Island. Zoltai *et al.* (1980) provided a general overview of the geology and glacial history.

Habitat types were adapted from Kevan (1974), Wilkinson et al. (1976), and Ferguson (1991). There are 4 major terresttial habitats: i) wet sedge meadow, ii) upland barren, iii) hummock tundra, and iv) srony barren. Wet sedge meadows (WSM) are generally level hydric and hygric lowlands characterized by Carex aquatilis, Eriophorum scheuchzeri, and Dupontia fisheri. Upland barrens (UB) are well drained sires found on the upper and middle parts of slopes. Vegetation is dominated by Dryas integriifolia and Salix arctica. Hummock tundta (HT) is found on moderately steep slopes characterized by individual hummocks which are vegetated primarily by dwarf shrubs (D. integrifolia, S. arctica, and Cassiope tetragona). Stony barrens (SB) have a coarse gravelly substrate and are sparsely vegetated. This habitat is found on wind blown areas, ridges, and gravel and sand bars. A more detailed description of the flora can be found in Porsild (1980), Wilkinson et al. (1976), and Zoltai et al. (1980).

Methods

Two field camps were established in June 1993 on southcentral Banks Island: one camp located in a high density muskox area (1.64 muskox/km²), 90 km ENE of Sachs Harbour, and the other in a low density muskox atea (0.41 muskox/km²), 130 km ENE of Sachs Harbour. Two or 3 permanent straight line transects were marked off in each of the 4 major terrestrial habitat types located in each of the high and low muskox density areas.

Fresh (< 4 hour old) Peary caribou faecal samples were collected opportunistically during all field trips. The location and habitat the samples were collected from was recorded. Additional samples were collected from huntet killed animals and from 12 animals taken during a collection in winter 1993-94. A total of 124 samples were collected from all months, range of 5–18 samples/month, except January. We present monthly diet composition pooled across sex and age classes with the individual caribou as the sample unit. June and November data are pooled across years.

Preliminary analysis of data collected during March and May, 1993 indicated that the mean sedge component of individual muskox faecal samples (n=70) collected from 22 groups of muskoxen was similar to the mean sedge component determined by lumping the individual samples across groups, 62.9 vs. 64.2% respectively. Also, the SD associated with the mean of 70 individual samples (34.31) was higher than any SD associated with one of the 22 groups (average SD = 7.98, range SD 0.042 - 32.3with 16 groups having SD < 7.98). Therefore, we assumed that composite samples of fresh (< 4 hour old) muskox faeces from a number of individuals were representative of a group of muskoxen, and that by sampling groups instead of individuals we would be able to get a better measure of the diet over a larger portion of the population. Consequently, we used the composite sample from a muskox group as the sample unit. Initially the sample unit consisted of samples pooled from 5 pellet groups. This was reduced to 3 pellet groups/muskox group. We collected muskox faecal samples from mixed sex and age groups during all months except January and September in the high density area. The number of groups sampled each month ranged from 1 - 10, representing between 5 and 152 animals. In the low density atea, samples were collected during April, June, July, August, and October. The number of groups sampled each month ranged from 1 - 7 representing between 30 and 89 animals. The location, habitat the samples were collected from, and group size was recorded. We present mean monthly diet composition of muskoxen with groups as the sample unit, weighted by the numbet of individuals in a group. June to August data are pooled across years.

Faecal samples were thawed, air dried for 24 hours, oven dried at 60°C for 48 hours, and ground through a 1 mm screen with a centrifugal mill. Subsamples (1 g) were forwarded to the Composition Analysis Laboratory, Ft. Collins, Colorado for analysis. Diet composition was determined by analyzing plant fragments (Sparkes & Malechek, 1968) according to Hansen et al. (1976). The microhistological technique has inherent limits, such as an inability to separate some species, and a limited percent of identifiable fragments in the slides (Johnson et al, 1983; Barker, 1986). We deemed this method suitable for this study, since differing proportions of forage classes, not changes in individual species composition wete of importance, and this method had been used in previous work on Banks Island. We used the following fotage classes: sedge (Cyperaceae), willow (S. arctica), grass (Gramineae), rose/saxifrage (Rosaceae and Saxifragaceae), legume

(Leguminosae), lichen (*Cetraria* spp., *Cladonia* spp., *Cladina* spp., *Peltigera* spp., and *Thamnolia subuliformis*), and other (other forbs, moss, and *Equisetum* spp.). There were traces of unidentifiable forb material in 6 samples, (4 caribou and 2 muskoxen, ranging from 0.33 – 0.89%) which were included in the other category, and traces of unidentifiable grass material in 51 muskox samples, (ranging from 0.46 – 1.93%) which were included in the grass category. We present results from samples collected prior to September, 1994. We used the Renkonen index (Renkonen, 1938; Krebs, 1989) to compare monthly percent diet similarity (PS) between Peary caribou and muskoxen in both high and low density areas.

Forage availability was assessed by 2 measures, standing crop and the presence/absence of forages in Twelve 0.125 m² plots (Wein & Rencz, 1976) were clipped along 2 or 3 permanent transects in each habitat at both camps at 3 times during the snow free period: mid-June, mid-July, and mid/late-August. Transect lengths ranged from 90 to 450 m depending upon habitat type. Plot locations were assigned systematically without replacement based upon total transect length in each habitat. We clipped the following forages at ground level: sedge, grass, legume (Oxytropis spp., Hedysarum mackenzii., and Astragalus alpinus), ericad (Cassiope tetragona), rose/saxifrage (Dryas integrifolia, Saxifraga spp.), and other forbs. Lichen was plucked from the substrate. Only current annual growth of willows was clipped. In the laboratory, sedge, grass, and Cassiope tetragona samples were separated into their live and dead components; willow was separated into leaf/bud and stem components. All samples were oven dried at 60°C for 48 hours and weighed to 0.1 mg. We used ANOVA to determine whether there were habitat, sampling time (June, July, August), area (high vs. low muskox density), and year effects on the standing crop of each forage. Because there were no year effects, we pooled data across years. Since growth rate of lichen is low, we calculated the mean standing crop from all the plots clipped in upland habitats (UB, HT, and SB) pooled across sampling time and year.

Occurrence data were collected during each clipping episode and again in early August. We lumped fotages into the same 8 classes as above. We compared the occurrence of forages in similar habitats between low and high density muskox areas using a X^2 contingency analysis.

Results

The annual diet of caribou was dominated by sedge, willow, legume, and rose/saxifrage (Fig. 1). Willow was the dominant component during June to August. Legume and rose/saxifrage were dominant components duting December to April. The sedge component remained relatively constant at *ca.* 25% each month. Lichen and grass use was negligible.

The annual diet of muskoxen was dominated by sedge and willow in both high and low density areas (Fig. 2). There was a high percent similarity (PS>89) of muskox diets between high and low density areas with the exception of a larger proportion of willow in the June and legume in the July diet in the high density area which reduced PS to 52 and 76, respectively (Table 1). From October to Match willow represented *ca.* 20–48% of the monthly diet. Willow use peaked in May at *ca.* 70%. Sedge use ranged from a low in May (*ca.* 28%) to a high in August (*ca.* 83–93% high and low density areas respectively).

Monthly PS of caribou and muskoxen (from both high and low density areas) ranged from 18 to 73. Monthly PS was generally >30.0 for most months and greatest in the high muskox density (Table 1). Sedge (*Carex* spp. and *Eriophorum* spp.) and willow made up substantial portions of the annual diet of both caribou and muskoxen (Figs. 1 and 2).

In areas of high muskox density, standing crop of legumes and *Dryas integrifolia* were significantly

Table 1. The Renkonen index of percent similarity (PS) of the monthly diets of caribou and muskoxen in high density areas (C/MH), caribou and muskoxen in low density areas (C/ML), and muskoxen in high and low density areas (MH/ML) determined from this study. The PS of the seasonal diets of caribou and muskoxen in 1972–73 (C/M of summer and winter found at the bottom of the table) is based upon analysis of the data in Shank *et al.* (1978) and Wilkinson *et al.* (1976).

Month/ Season	PS C/MH	PS C/ML	PS MH/ML	PS C/M
February	58			
March	37			
April	18	22	93	
May	38			
June	73	34	52	
July	25	28	76	
August	43	33	90	
October	45	45	99	
November	52			
December	44			
Summer				48
Winter				68

(P<0.01) greatet than in areas of low muskox density. Mean standing crop of legumes, pooled across time and all 3 upland habitats (n=228), and D. inte-

grifolia (n=312), pooled across time and all 4 habitats, were 2.15 g/m² and 4.64 g/m² vs. 0.41 g/m² and 3.53 g/m² in high and low muskox density areas respectively. No other forages showed an area effect on standing crop. The standing crop of lichen was 2.96 g/m² (n=456).

 X^2 analysis of the occurrence data indicated significant differences (P<0.01) in occurrence of forages between the high and low density muskox ateas in the 3 upland habitats. There were no differences in wet sedge meadows. In

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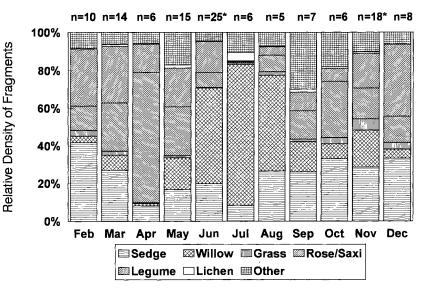


Fig. 1. Diet composition of Peary caribou, based upon the mean percent relative density of faecal plant fragments. n = number of samples (individuals). An asterix indicates data pooled over 2 years.

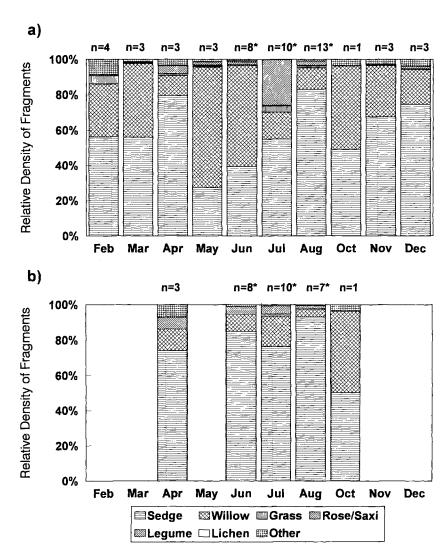


Fig. 2. Diet composition of muskoxen in high (a) and (b) low density muskox areas, based upon the mean percent relative density of faecal plant fragments. n = number of samples (groups). An asterix indicates data pooled over 2 years.

high densiry muskox areas, hummock tundra had more sedge and legume and less lichen, upland barren had more sedge, legume, grass, and willow, and stony barren had more sedge and less grass and other forbs than was found in corresponding habitats in low density muskox areas (Table 2).

Discussion

Studies various on Canadian arctic islands in the 1960's and 1970's suggested that caribou and muskoxen coexisted with little resource overlap (Tener, 1965; Kevan, 1974; Thomas Edmonds, 1984). Studies were conducted in the early 1970's to compare diet composition of the 2 ungulates on Island (Wilkinson et al., 1976; Shank et al., 1978) and the Patty Islands (Patker, 1978). Again, competition for food was generally ruled because of little dietary overlap. Muskox summer and winter diets were both dominated by graminoids, generally sedges

Table 2. The percent frequency occurrence of various forages in the 3 upland habitats located in high and low density muskox areas: hummock tundra (HT, 84 plots), upland barren (UB, 96 plots), and stony barren (SB, 84 plots). See text for forage class descriptions.

Habitat	Muskox Density	Sedge	Willow	Grass	Ericad	Lichen	Legume	Rose/Saxift.	Other
HT	High	86	45	35	4	29	31	92	36
n = 84	Low	57	48	25	0	90	11	96	33
UB	High	90	27	44	0	78	32	93	24
n = 96	Low	58	15	16	0	71	8	92	26
SB	High	66	5	7	0	85	1	88	8
n=84	Low	38	6	19	0	74	0	88	20

(*Carex* spp.) which were abundant in wet lowland habitats. Caribou summer and winter diers were both dominated by willow (*Salix* spp.), forbs, grasses and sedges which were abundant in drier upland habitats, but the proportion of willow in the winter diet was reduced.

Knowledge of forage availability is an integral requirement for documenting competition for food (Klein & Staaland, 1984; Gunn, 1990), yet data pertaining to forage availability was conspicuously absent from previous studies. Therefore, Wilkinson et al.'s (1976) conclusions about the lack of competition between muskoxen and caribou on Banks Island are not surprising. Their study was conducted in summer, when forage quality and availability are highesr.

Currently, the caribou population on Banks Island is 16-fold smaller and the muskox population 16-fold larger than in 1972, therefore previous results and conclusions are likely to differ from ours. Although Wilkinson et al. (1976) and Shank et al. (1978) tuled out competition for food between muskoxen and caribou, their results demonstrated substantial similarity (PS) in diet between the two species during borh wintet (March) and summer (August) (Table 1.). PS in the diets found in the 1970's may be inflated somewhat in relation to our findings because the diet was only partitioned into 5 components versus our 7 components. Our findings indicated: i) considerable similarity in diet between the 2 ungulates regardless of muskox density, ii) a noticeable absence of lichen in the diet of caribou, iii) a noticeable absence of grasses in the diet of both catibou and muskoxen, and iv) sedges and willows wete found throughout all habitats, but grasses were found mostly in upland habitats.

The diet of caribou was more diverse than that of muskoxen, being dominated by 4 major forage groups, sedge, willow, rose/saxifrage, and legume. There was a distinct seasonal shift in proportions of willow, rose/saxifrage, and legume. Willow use was greatest during June through August, presumably when new growth leaves and stems are high in crude protein and energy content. Rose/saxifrage and legume, as well as sedge, predominated from October to May. Sedge and rose/saxifrage occur in all three upland habitats and wet sedge meadows on Banks Island, whereas legumes occur only on the upland habitats. The gtass component of the diet reported in the eatly 1970's (Wilkinson et al., 1976; Shank et al, 1978), was noticeably absent in the 1990's. Rose/saxifrage, legumes, and other forbs

appear to have teplaced this component of the diet. The lack of lichen in the diet was consistent with previous findings (Shank et al , 1978), and is likely related to low availability. Lattet & Nagy (1996) found similar percentages of lichen in the rumen contents and faecal material of mainland barrenground caribou during wintet indicating that the proportion of lichen in the diet, determined from the analyses of faecal plant fragments, was not significantly influenced by high lichen digestibility during winter. The 2.96 g/m² we report is almost 5-fold lower than the 14 g/m² reported on Coats Island (Ouellet et al , 1996), an island considered to have a low standing crop of lichen.

The muskox diet was dominated by seasonally varying proportions of sedge and willow regardless of muskox density. Standing crop and occurrence of sedges in wet sedge meadows was similar between areas, and therefore could not explain the latger proportions of sedge in the diet of animals in the low density area. The increased occurrence of legumes in the diet of animals in the high density atea during July may be related to availability. Legume standing crop and occurrence in upland barren and hummock tundra habitats was greater in rhose habitats present in the high density area. July is the peak in available ctude protein of legumes (N. Larter & J. Nagy, unpubl. data).

The occurrence of willow in both the wintet (March) and summer (August) diets of muskoxen in the high density area was 2-3 times greater than that found by Wilkinson et al. (1976) and Shank et al. (1978) in the 1970's. This difference cannot be attributed to the difference in technique used to determine diet. The macroscopic technique used by Wilkinson et al. (1976) and Shank et al. (1978) is more likely ro overestimate willow than the microscopic technique we used, because willow patticles are generally larger than those of other forages and are easily identifiable. Whether or not increased dietary willow is related to a decrease in sedge availability or an increase in willow availability is unknown. Sedge availability would appear to be high. Standing crop of sedges in wet sedge meadows in the peak of the growing season ranged from 53-65 g/m². This is greater than the 36 g/m² found in wet sedge meadows at Svetdrup Pass, Ellesmere Island, where the diet of muskoxen is almost exclusively sedge (Raillard, 1992). Increasing competition for sedges may have resulted in an increase in rhe use of other forages, like willow. Smith (1996) demonstrated that wet meadows subjected to grazing by a

high density of muskoxen had decreased net aboveground primary productivity, and that over-compensation of plant growth did not occur.

Increasing use of willows, especially during winter, by a rapidly increasing population of muskoxen is of immediate concern. During winter, willows are dormant and many years of growth can be removed, possibly more than could be replaced during one growing season. Willow twigs of ≥4 years growth have been found in the rumen of adult muskoxen during April (N. Latter & J. Nagy, unpubl. data). Continued cropping of most previous years twigs and buds may stress willow plants beyond tecovery and increase plant mortality. Reductions in new growth of willows during June to August may have serious consequences for caribou who utilize them as a primary food source during this time of lactation and body growth.

The elevated winter use of willows may be somewhat highet than normal for our March and May data because the high density muskox area dara were collected in 1993. During winter 1992-1993, Banks Island had more snowfall than in subsequent winters, resulting in a deeper and denser snow cover of wet sedge meadows and upland battens during late winter. Muskox crater sites wete rare in wet sedge meadows, with the majority in upland habitats (N. Larter & J. Nagy, unpubl. data). These snow conditions may have forced muskoxen to feed more in uplands, where there is a higher proportion of willow forage, and therefore may have biased our Regardless, data collected in November, December, February and April of the following wintet showed much higher willow use than that found in the 1970's. Snow depth and density in wet sedge meadows and upland barrens was lower and nearer normal during the 1993-1994 winter (N. Larter & J. Nagy, unpubl. data).

Much of the traditional wintering area of caribou overlaps the high density muskox area. Any dietary overlap with muskoxen may be magnified should harsh snow conditions occur. Similar habitats provide relatively similar standing crops of eight major forage classes with the possible exception of legumes and *Dryas integrifolia* which are more prominent, both in occurrence and standing crop measures, in the high density muskox areas. However, because we have not completed habitat mapping in these areas, these data must be treated with caution tegarding an absolute measure of forage availability. Higher frequency occurrence of forages does not necessarily indicate increased standing crop.

Although caribou and muskoxen have different morphological and physiological adaptations which enable them to utilize forage resources with little overlap, our interpretation of data reported by Wilkinson et al. (1976), and Shank et al. (1978) suggests dietary overlap of forage classes occurred in the early 1970's on Banks Island. Dietary overlap between caribou and muskoxen has since become evident during 11 months of the year, is greater in areas of high muskox density, and may increase during winters with elevated snow depth and density. Currently, data cannot disprove or prove that forage competition has occurred or is occurring. However, given: i) increased willow utilization by a rapidly increasing muskox population, which may increase during harsh winters, and ii) the four-fold increase in density of a relatively sedentary potential competitor for food in traditional caribou wintering areas berween 1985 and 1994, the potential impact of muskoxen on the caribou winter range and availability of willows may well be a factor limiting the recovery of the Peary caribou population.

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References

Adamczewski, J. Z.. Chaplin, R. K., Schaefer, J. A. & Flood, P. 1994. Seasonal variation in intake and digestion of a high-roughage diet by muskoxen. – *Can. J. Anim. Sci.* 74: 305–313.

Barker, R. D. 1986. An investigation into the accuracy of herbivore diet analysis. – *Aust. Wildl. Res.* 13: 559–568.

Ferguson, R. S. 1991. Detection and classification of muskox habitat on Banks Island, Northwest Terrirories, Canada, using landsar rhematic mapper dara. – *Arctic* 44: 66–74.

Gunn, A. 1990. Status of muskox populations in Canada. – In: Holst, B. (ed.). International Studbook for muskox (Ovibos moschatus). Copenhagen Zoo, Copenhagen, 49–72.

- Hansen, R. M., Foppe, T. M., Gilbert, M. B., Clark, R. C. & Reynolds, H. W. 1976. The microhistological analyses of feces as an estimator of herbivore diet. Unpubl. Rep., Dept. Range Science, Colorado State Univ., Ft. Collins.
- Hofmann, R. R. 1989. Evolutionary steps of ecophysical adaption and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78: 443–457.
- Johnson, M. K., Wofford, H. & Pearson, H. A. 1983.
 Digestion and fragmentation: influence on herbivore diet analysis. J. Wildl. Manage. 47: 877–879.
- Kevan, P. G. 1974. Peary caribou and muskoxen on Banks Island. *Arctic* 27: 256–264.
- Klein, D. R. 1992. Comparative ecological and behavioral adaptions of *Ovibos moschatus* and *Rangifer tarandus*. *Rangifer* 12: 47–55.
- Klein, D. R. & Staaland, H. 1984. Extinction of Svalbard muskoxen through comperitive exclusion: An hypothesis. – Biol. Pap. Univ. Alaska Spec. Rep. 4: 26–31.
- Krebs, C. J. 1989. Ecological Methodology. Harper & Row Publishers, New York, 654pp.
- Larter, N. C. & Nagy, J. A. 1996. Bluenose caribou community harvest Eskimo Lakes area, February 1995. Manuscript Rep. No. 88. Dept. Ren. Res., Yellow-knife, 30pp.
- McKendrick, J. D. 1981. Responses of arctic tundra to intensive muskox grazing. *Agroboreal*. 12: 49–55.
- Nagy, J. A., Larter, N. C. & Fraser, V. P. 1996. Population demography of Peary caribou and muskox on Banks Island, N.W.T., 1982-1992. Proceedings 6th North American Caribou Conference. – Rangifer Special Issue 9: 213–222.
- Oakes, E. J., Harmsen, R. & Eberl, C. 1992. Sex, age, and seasonal differences in the diets and activity budgets of muskoxen (*Ovibos moschatus*). *Can. J. Zool.* 70: 605–616.
- Ouellet, J-P., Heard, D. & Mulders, R. 1996. Population ecology of caribou populations without predators: Southampton and Coats Island herds. Proceedings 6th North American Caribou Conference. Rangifer Special Issue 9: 17–25.
- Parker, G. R. 1978. The diets of muskoxen and Peary caribou on some islands in the Canadian High Arctic. – Can. Wildl. Serv. Occas. Pap. 35.
- Porsild, A. E. 1980. The vascular plants of continental Northwest Territories, Canada. Nat. Mus. Canada. Ottawa, 667 pp.
- Raillard, M. 1992. Influence of muskox grazing on plant communities of Sverdrup Pass (79°N), Ellesmere Island, N.W.T., Canada. Ph.D. thesis, Univ. of Toronto, 262 pp.

- Reimers, E., Villmo, L., Gaare, E., Holthe V. & Skogland T. 1980. Status of Rangifer in Norway including Svalbard. In: Reimers, E., Gaare, E. & Skjenneberg, S. (eds.) Proc. 2nd. Int. Reindeer/Caribou Symp. Direktoratet for vilt og ferskvannskisk, Trondheim, pp. 774–785.
- Renkonen, O. 1938. Statisch-okologische Untersuchungen uber die terrestiche kaferwelt der finnischen bruchmore. – Ann. Zool Soc. Bot. Fenn. Vanamo 6: 1–231.
- Shank, C. C., Wilkinson, P. F. & Penner, D. F. 1978. Diet of Peary caribou, Banks Island, N.W.T. – *Arctic* 31: 125–132.
- Smith, D. L. 1996. Muskoxen/sedge meadow interactions, North-Central Banks Island, Northwest Territories, Canada. Ph.D. thesis, Univ. of Saskatchewan, 238 pp.
- Sparkes, D. R. & Malechek, J. C. 1968. Estimating percentage dry weight diets using a microscopic technique. – J. Range Manage. 21: 264–265.
- Staaland, H. & Olesen, C. R. 1992. Muskox and caribou adaption to grazing on the Angujaartorfiup Nunna range in west Greenland. Rangifer 12: 105–113.
- Tener, J. S. 1965. Muskoxen in Canada, a biological and taxonomic review. CWS Monograph No. 2, 166 pp.
- Thing, H., Klein, D. R., Jingfors, K. & Holt, S. 1987. Ecology of muskoxen in Jameson Land, northeast Greenland. – *Holarctic Ecol.* 10: 95–103.
- Thomas, D. C. & Edmonds, J. E. 1984. Competition between caribou and muskoxen, Melville Island, NWT, Canada. *Biol. Pap. Univ. Alaska Spec. Rep.* 4: 93–100.
- Tyler, N. J. C. & Blix, A. S. 1990. Survival strategies in arctic ungulates. *Rangifer* Special Issue 3: 211–230.
- Urquhart, D. R. 1973. Oil exploration and Banks Island. wildlife. Unpubl. Rep. N.W.T. Wildlife Serv., 105 pp.
- Wein, R. W. & Rencz, A. N. 1976. Plant cover and standing crop sampling procedures for the Canadian high arctic. *Arctic and Alp. Res.* 8: 139–150.
- White, R. G., Holleman, D. F., Wheat, P., Tallas, P. G., Jourdan, M. & Henrichsen, P. 1984. Seasonal changes in voluntary intake and digestibility of diets by captive muskoxen. *Biol. Pap. Univ. Alaska Special Rep.* 4: 203–204.
- Wilkinson, P. F., Shank, C. C. & Penner, D. F. 1976. Muskox-caribou summer range relations on Banks Island, N.W.T. – J. Wildl. Manage. 40: 151–162.
- Zoltai, S. C., Karasiuk, D. J. & Scotter, G. W. 1980. A natural resource survey of the Thomsen River area, Banks Island, Northwest Territories. Unpubl. Rep. Can. Parks Serv. Ottawa., 153 pp.

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