WET SEDGE MEADOW HABITAT OF SOUTHERN BANKS ISLAND EXCLUDED FROM GRAZING BY LARGE HERBIVORES FOR FIVE YEARS: EFFECTS ON ABOVE GROUND STANDING CROP

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ABSTRACT

Grazing exclosures were erected in wet sedge meadow habitat on southern Banks Island at the start of the 1993 growing season. Exclosures (n=5) were established in areas of high (1.6-1.9 muskox/km^2) and low (0.3-0.4 muskox/km^2) muskox density. In late-August (21-25), we clipped the aboveground standing crop of forages in plots (n=2) located within and adjacent to each exclosure. Late-August clipping within and adjacent to exclosures was repeated annually in 1994, 1996, and 1997. Early snow and freezing temperatures prevented clipping in late-August 1995. Exclosures in the low density muskox area were often damaged, and the experiment was ended in this area after one season; time series data were limited to the area of high muskox density. Mean aboveground standing crop (dry weight) of sedge material varied annually ($P<0.05$) in both grazed and excluded areas, *ca.* 500-1100 kg/ha, being greatest in 1997 and lowest in 1993 and 1994. The mean proportion of live sedge material (dry weight) in aboveground sedge biomass also varied annually ($P<0.05$) in both grazed and excluded areas, *ca*. 0.05-0.40, being lowest in 1996. The aboveground standing crop of sedge exposed to grazing did not differ ($P>0.9$) from that found in areas excluded from grazing, regardless of the amount of time excluded from grazing. However, the proportion of live sedge in the late-August aboveground sedge standing crop in excluded areas increased ($P<0.02$) relative to grazed areas over time implying selective herbivory of green sedge material. At current grazing levels the data are not indicative of degradation of wet sedge meadow habitat during summer.

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INTRODUCTION

Sedge-dominated wet meadows are the most productive High Arctic plant communities (Muc 1977; Henry *et al*. 1990; N. Larter unpubl. data). They represent one of the most distinctive community types (Bliss and Svoboda 1984; Ferguson 1991) and are important forage communities for a variety of resident and migratory herbivores. In the early 1970’s Wilkinson and Shank (1973) studying the range relationships of muskox and caribou on Banks Island, estimated the aboveground standing crop of a variety of plant species found in various habitats. They estimated the aboveground standing crop of wet sedge meadow habitat at 1,731 kg/ha (wet weight). This habitat was believed to be important for muskoxen. Because fewer than half of their plots (n=14) in feeding areas showed actual traces of grazing, they believed that grazing pressure was low to moderate and was not having a negative impact (Wilkinson and Shank 1973). Subsequently, there has been increased interest in the relationships between herbivory, by muskoxen in general, and its effects on these most productive habitats in the High Arctic with much of the research being conducted on Ellesmere Island (Henry *et al*. 1990; Raillard 1992; Henry and Svoboda 1994; Henry *et al*. 1994; Henry 1998; Raillard and Svoboda 1999; Tolvanen and Henry 2000)

Muskox numbers on Banks Island increased dramatically since the early 1970’s and by 1992 were estimated at over 50,000 $\geq$1 year-old animals (Nagy *et al*. 1996), with local densities being the highest reported for the species. The rapid increase in muskox numbers renewed local concern about the potential negative impacts on the range by such a large herbivore population. Increasing herbivore populations are believed to be regulated by density dependent responses which are often related to a decrease in available per capita forage (Riney 1964; Caughley 1970;

Larter *et al.* 2000). Early research projects initiated on Banks Island in the 1990's tried to directly or indirectly assess the impacts of muskox herbivory on the range. Oakes *et al*. (1992) determined which plant species found in a dicot-dominated mesic habitat of northern Banks Island were grazed by muskoxen. Mulder and Harmsen (1995) measured the impact of grazing on a legume species (*Oxytropis viscida*) found in upland habitats of northern Banks Island. Unfortunately, they believed that the plant was utilized by muskoxen only; subsequent studies indicated that both caribou and Arctic hares make substantial use of *Oxytropis* spp. (Larter and Nagy 1997; Larter 1999). Smith (1996) used exclosures to document grazing impact on *Eriophorum triste*-dominated wet sedge meadows in northern Banks Island by high densities (1.8 muskox/km^2) of muskoxen.

Muskoxen represent the classic grazer (Hofmann 1989; 2000) and studies documenting muskox diet indicated that sedge was a dominant year-round dietary component (Wilkinson *et al.* 1976; Parker 1978; Thomas and Edmonds 1984; Larter and Nagy 1997). In summer 1993, as part of a comprehensive range study of Banks Island, a 5-year exclosure experiment was initiated in wet sedge meadow habitat of southern Banks Island to assess the impact of grazing by different densities of muskox on this habitat. This report documents the differences in standing crop of wet sedge meadow habitat between areas where animals grazed and areas where animals (except lemmings) were excluded from grazing, and documents the differences in the proportion of live sedge material in the late-August standing crop of sedge in grazed and ungrazed (except for lemmings) wet sedge meadow habitat. Because of unforeseen logistical problems, the majority of the data are limited to areas of high muskox density.

There are three possible outcomes of this experiment, greater aboveground standing crop or proportion of live sedge in grazed areas, greater aboveground standing crop or proportion of live sedge in areas excluded from grazing, or similar aboveground standing crop or proportion of live sedge in grazed and excluded areas. Following (McNaughton 1983), greater aboveground standing crop in grazed areas would be consistent with the hypothesis of overcompensation by sedges in response to grazing. Greater aboveground standing crop in excluded areas would be consistent with the hypothesis of undercompensation by sedges in response to grazing. Similar amounts of aboveground standing crop in areas grazed and excluded from grazing would be consistent with the hypothesis of exact compensation under the current grazing regime. We expected the proportion of live sedge material in late-August aboveground standing crop in excluded areas to decrease relative to grazed areas over time because of an accumulation of dead material and litter (Crawley 1983; Cargill and Jefferies 1984; Bazely and Jefferies 1986).

METHODS

Habitat Description

The flora of Banks Island is well documented with four major habitats being identified (Kevan 1974; Wilkinson *et al*. 1976; Porsild and Cody 1980; Zoltai *et al*. 1980; Ferguson 1991). Wet sedge meadow (WSM) is a generally level hydric and hygric lowland often associated with drainages, lakes and ponds. *Carex aquatilis* and *Eriophorum scheuchzeri* predominate with some *Dupontia fisheri*, *Equisetum* spp. and *Pedicularis* spp. present. WSM can also be found on slopes directly below permafrost seepages and year round snow banks, which provide an abundance of meltwater. Vegetative cover is virtually 100% except for areas of standing water. In raised or drier patches *Dryas integrifolia*, *Salix arctica* and flowering plants can be found. WSM covers about 15-20% of Banks Island (Larter and Nagy unpubl. data).

Exclosure Design and Integrity

During the start of the 1993 growing season (15-17 June) five exclosures were erected in wet sedge meadow habitat near each of two newly established field camps: Coyote and Bernard (Fig. 1). Field camps were located in areas of high (1.6-1.9 muskox/km^2) and low (0.3-0.4 muskox/km^2) muskox density, respectively. Each exclosure consisted of a *ca*. 2.3m x 1.7m piece of 5cm x 5cm chainlink fencing that was pegged into the ground with 6-8 pegs made out of 1cm diameter rebar. Once pegged into the ground, the fencing created a domed exclosure of approximately 1.25m^2.

Figure 1. Banks Island and the two study sites, Camp Coyote and Bernard.

Exclosures were monitored for their integrity during June (12-20), July (16-22), and August (18-28) of 1993-97. Exlosures located near camp Coyote fared much better than those located near camp Bernard, where muskox seemed to take exception to them or use them as scratching items. Only 2 of 5 exclosures maintained their integrity during the 1993 growing season at camp Bernard. At the start of the 1994 growing season we replaced and added new exclosures to bring the total number of exclosures to 7 at both sites. Unfortunately, by August 1994 it became evident that the integrity of exclosures in the vicinity of Camp Bernard could not be maintained. The exclosures were removed and the experiment at this site was abandoned. Data were limited to a single growing season for 2 exclosures. Five exclosures maintained their integrity for the full 5 years and an additional exclosure provided data from 1 growing season at Camp Coyote (Table 1).

Forage Sampling and Analysis

During late-August (21-25), the senescent period, we clipped forage in clip plots located inside and adjacent to each intact exclosure for all years except 1995. Early snowfall and low temperatures had frozen the ground to such an extent that we were unable to raise the exclosure from the substrate in late-August 1995. We grouped forages into the following classes: sedge (predominantly *Carex aquatilis*), willow (*Salix arctica*), avens (*Dryas integrifolia*), horsetail (*Equisetum* spp.), grass (*Poaceae*), lichen, and other forbs. All new growth forage, except willow, was clipped at ground level; plant litter was not collected. We clipped leaves and current annual growth from willow; buds were included in the leaf component. Lichen was plucked

Table 1. The status of all exclosures that were erected at Camps Coyote and Bernard over the course of the experiment. Status descriptions are OK, DS (destroyed), RP (replaced), and AB (abandoned).

Coyote	**June ‘93**	**Aug. ‘93**	**June ‘94**	**Aug. ’94**	**June ’95**	**Aug. ’95**	**Jun. ’96**	**Aug. ’96**	**June ’97**	**Aug. ’97**
1	OK	OK	OK	OK	OK	OK	OK	OK	OK	OK
2	OK	OK	OK	OK	OK	OK	OK	OK	OK	OK
3	OK	OK	OK	OK	OK	OK	OK	OK	OK	OK
4	OK	OK	OK	OK	OK	OK	OK	OK	OK	OK
5	OK	OK	OK	OK	OK	OK	OK	OK	OK	OK
6			OK	DS	RP	OK	OK	DS	RP	OK
7			OK	DS	AB					
Bernard										
1	OK	OK	OK	DS	AB					
2	OK	DS	RP	DS	AB					
3	OK	OK	OK	DS	AB					
4	OK	DS	RP	DS	AB					
5	OK	DS	RP	DS	AB					
6			OK	DS	AB					
7			OK	DS	AB					

from the substrate. Two plots measuring 15cm x 25cm (0.0375m^2) were clipped inside each exclosure and two plots were clipped outside each exclosure.

The central 75cm x 120cm of each exclosure provided twenty-four 0.0375m^2 plots from which two plots per year were randomly assigned to be clipped (Fig. 2.). One side of the exclosure was raised to permit clipping and then replaced in the same position as before. An 8cm nail with an attached 2.5cm x 2.5cm square of flagging tape was placed into the substrate at the upper left corner of each clipped plot.

The two plots outside the exclosure were located 2 and 3m perpendicular above and below the centre of the widest side of the exclosure in 1993 and 1994, respectively, 2m perpendicular above and below the centre of the narrowest side of the exclosure in 1996, and at 1m right angles from the lower left corner of the exclosure in 1997. In 1996 we had to use a 25cm x 50cm (0.125m^2) plot instead of the 0.0375m^2 plot for clipping outside the exclosure. As part of a related project assessing seasonal changes in standing crop of wet sedge meadows, twelve 0.125m^2 plots randomly placed on three fixed transects running through the same habitat patches were clipped three times during the summer from 1993-97. These plots were clipped during the start of the growing season (12-20 June), during the peak of the growing season (16-22 July) and during the senescent period (18-28 August).

All clipped forage was placed in labeled paper bags and allowed to air dry in the field. At the laboratory in Inuvik sedge and grass was further separated into their green live matter and dead components. All plant material was oven dried at 60^{o}C for 48 hours and weighed on a Sartorius electronic balance to $\pm$0.0001g. We determined the standing crop of the different forages present for each plot inside and adjacent to the exclosures as well as the total standing

Figure 2. Plots ($0.0375m^2$) available for clipping inside each exclosure during the course of the 5 year study. Two plots/year were randomly chosen, without replacement, for clipping.

	0cm	15cm	30cm	45cm	60cm	75cm	90cm	105cm
25cm	1	2	3	4	5	6	7	8
Center 37.5cm 50cm	9	10	11	12	13	14	15	16
75cm	17	18	19	20	21	22	23	24

crop (kg/ha), and the proportion of live and dead sedge in the standing crop. Because sedge (live and dead material) made up *ca*. 97% of the standing crop (dry weight) of all the forage clipped in wet sedge meadow habitat during summer (Larter unpubl. data) and *ca*. 90% of the standing crop during late-August we confined our analyses to the sedge component of the standing crop. The analysis did not include data from the one exclosure at Camp Coyote that was limited to a single growing season.

We used a oneway ANOVA to examine annual variation in standing crop of sedge and the proportion of live sedge material both inside and outside exclosures located in the high density muskox area (Camp Coyote). We transformed all proportion data with the arcsine square-root transformation (Zar 1999). When ANOVA indicated significant annual differences we used the Tukey test to determine where these differences were (Zar 1999). To assess the effects of the release from grazing we calculated the difference between estimates of the late-August aboveground standing crop of sedge and the transformed proportion of live sedge material between grazed and excluded areas. This was done for each year when data were available, years 1, 2, 4, and 5. We used regression analysis on the calculated differences in aboveground standing crop and proportion of live sedge versus years to see if the slopes differed significantly from zero.

For the single season of data gathered at the low density muskox area (Camp Bernard), we used a Mann-Whitney U-test to examine differences between standing crop of sedge and proportion of live sedge material.

RESULTS

There were annual differences ($P<0.05$) in late-August standing crop in grazed areas (range 529-1100 kg/ha); 1997 had significantly more standing crop than either 1993 and 1994. The difference between 1996 and 1993 standing crop was of marginal significance ($P<0.06$). Similarly, there were annual differences in aboveground late-August standing crop for excluded areas (range 520-1126 kg/ha); 1997 had significantly more standing crop than either 1993 and 1994 and 1996 standing crop was greater than that in 1994 (Fig 3a).

The proportion of live sedge standing crop found in grazed areas in late-August showed annual differences (range 0.03-0.33; $P<0.05$) being lower in 1996 than other years. The late-August proportion of live sedge standing crop in excluded areas (range 0.05-0.38) was also lower ($P<0.05$) in 1996 than in other years (Fig. 4a).

The standing crop (kg/ha, dry weight) of late-August sedge material found inside exclosures in the area of high muskox density did not differ from that found in areas exposed to grazing, regardless of the number of years of exclusion from grazing (Fig. 5a). The slope of the regression line of the differences versus time did not differ from zero. ($P>0.9$). Data from one year of exclusion from grazing in the area of low muskox density also showed no difference in standing crop between grazed and ungrazed areas ($P>0.9$; Fig. 3b).

The difference in the proportion of live sedge in the late-August sedge biomass between grazed and non-grazed areas in the area of high muskox density increased over the course of the study; the proportion of live sedge material in non-grazed areas increased relative to grazed areas over time (Fig 5b.). The slope of the regression line of the differences was different (b=-0.13; $P<0.02$) from zero. The proportion of live sedge standing crop found in excluded areas was similar to that found in grazed areas after one growing season in the low density muskox area (Camp Bernard; P>0.3; Fig. 4b).

Figure 3. Mean (±SD) above ground standing crop (kg/ha dry weight) of sedge (live and dead material combined) found in plots excluded from and available to large grazing herbivores in wet sedge meadow habitat in late-August: a) in areas of high muskox density, n=10 plots, for 4 of 5 growing seasons, b) in areas of low muskox density (Bernard), n=4 plots, for 1 growing season. Data from 1993 in the high density area are provided for comparison.

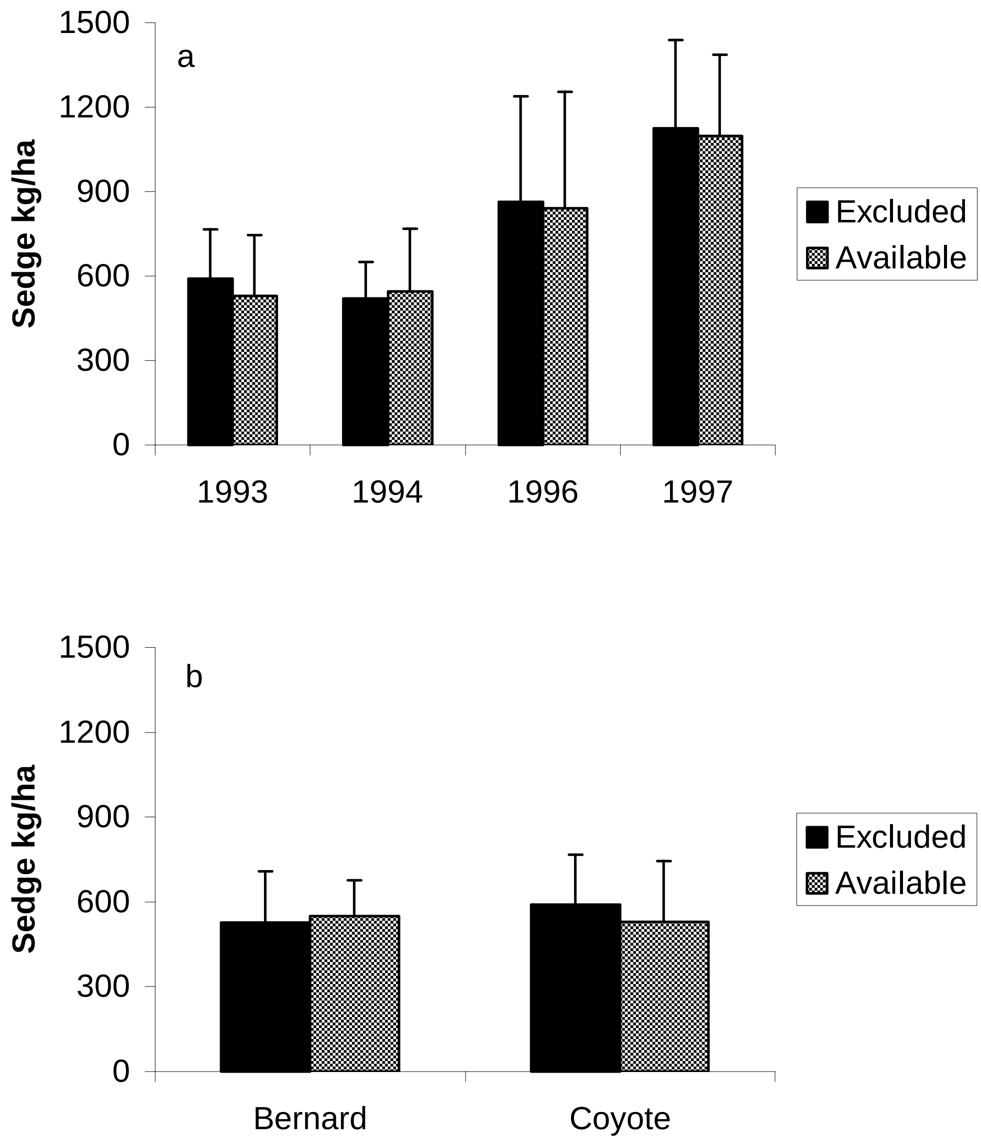


Figure 4. Mean (±SD) proportion of live sedge material found in plots excluded from and available to large grazing herbivores in wet sedge meadow habitat in late-August: a) in areas of high muskox density, n=10 plots, for 4 of 5 growing seasons, b) in areas of low muskox density (Bernard), n=4 plots, for 1 growing season. Data from 1993 in the high density area are provided for comparison.

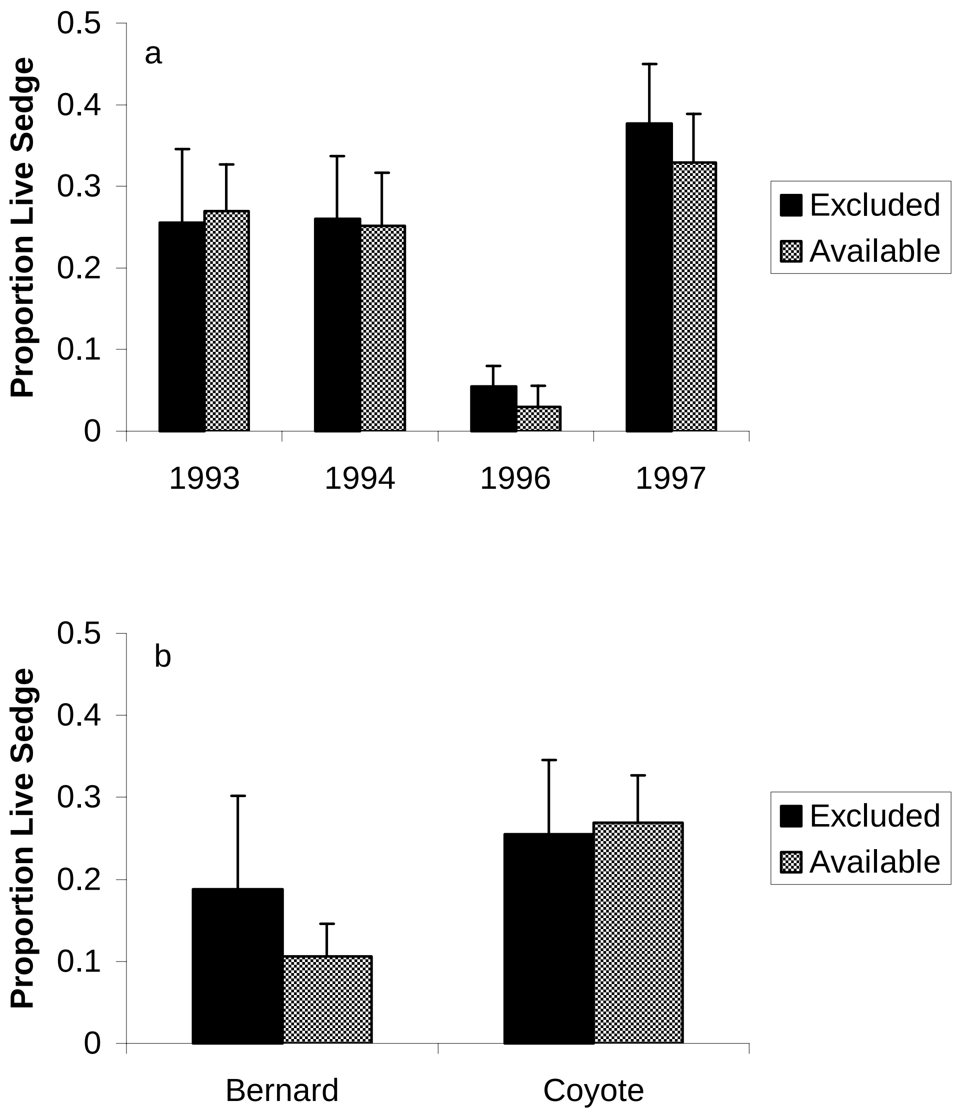
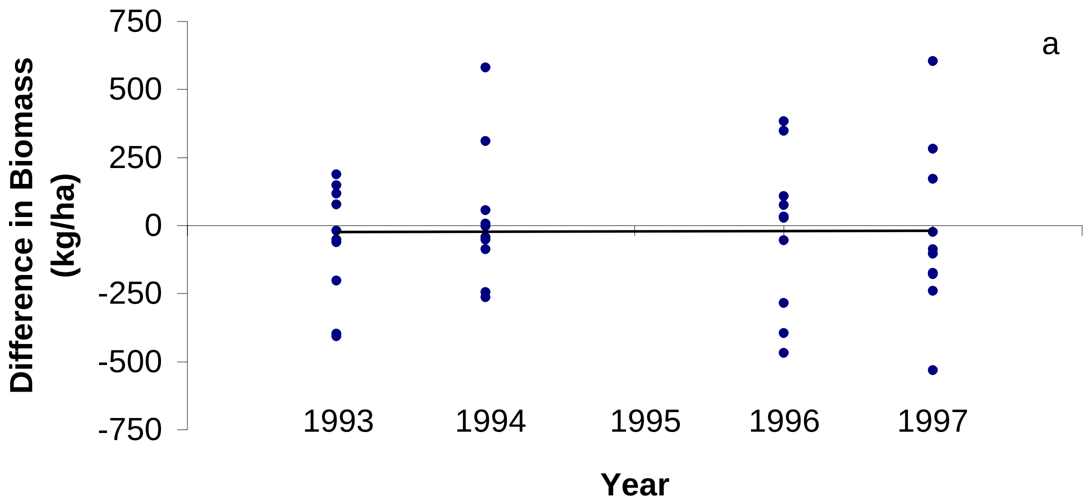
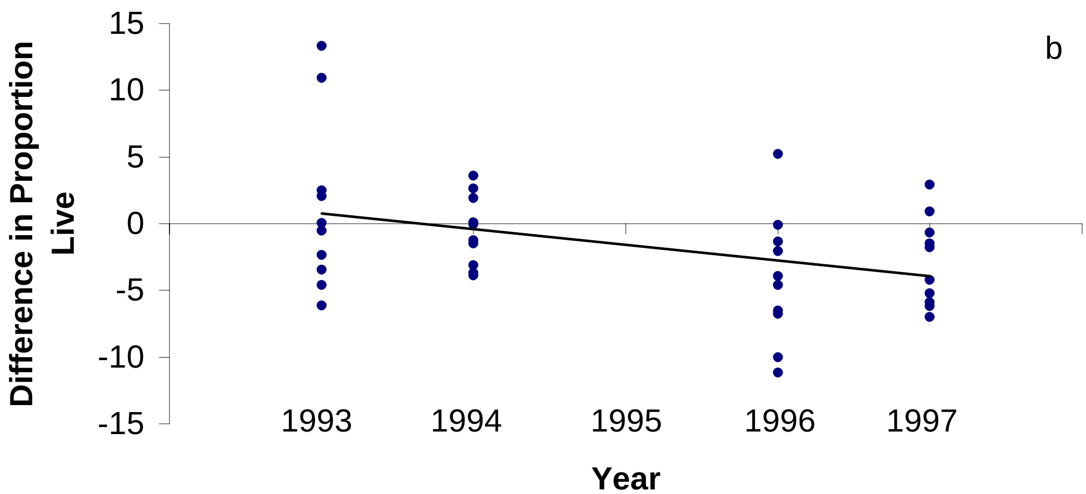


Figure 5. The relationships of: a) the differences in late-August aboveground standing crop (kg/ha) between grazed and excluded areas of the high density muskox area over the course of the study, and b) the differences in the live sedge proportion of the late-August aboveground standing crop of sedge between grazed and excluded areas over the course of the study.





DISCUSSION

In arctic sedge meadows, graminoids like sedges are tolerant of disturbance and grow well on undisturbed sites (Wein and Bliss 1973; 1974; Chapin and Chapin 1980; Chapin and Shaver 1981; Fetcher and Shaver 1983). Because of low herbivore densities and severe climatic conditions it was believed that herbivores played a minor role in arctic ecosystems (Bliss 1986; Pimental 1998) and that because of low species richness grazing-tolerant forbs were simply not present (Klein and Bay 1990). More recently these beliefs have been challenged as densities of muskoxen worldwide have increased dramatically (Smith 1989), with local densities of 1.5-8.4 muskox/km^2 being reported (Raillard 1992; Nagy *et al*. 1996; Smith 1996).

Henry (1998) found grazing intensity of muskoxen was an important factor determining the structure of arctic sedge meadows. Dwarf shrubs (*Salix arctica* and *Dryas integrifolia*) were more prominent in ungrazed than grazed wet sedge meadows (Henry and Svoboda 1994). Tolvanen and Henry (2000) found that grazing provided a competitive advantage for *Carex spans* over *C. membranacea* and *Eriphorum triste*, which could potentially affect the plant population structure of sedge meadows. Smith (1996) reported up to a 40% removal of shoot tissue by grazing muskoxen during a single growing season in *Eriophorum triste*-dominated wet sedge meadows.

The meadows where our study was conducted on southern Banks Island were *Carex aquatilis*-dominated which could indicate that previous grazing has provided a competitive advantage to *C. aquatilis* over *Eriphorum triste* as described by Tolvanen and Henry (2000). Historic data to confirm this are lacking. We found no difference in the amount of aboveground standing crop in wet sedge meadows between areas exposed to and excluded from herbivory (except for lemmings). Thus implying exact compensation by sedges in response to grazing. Smith (1996) generally found exact compensation by the plant community in *E. triste*-dominated wet sedge meadows in response to grazing by muskox over a two-year exclosure study on northern Banks Island. He also reported that the grazed plant community tended to be more prostrate, but no different in species composition from the ungrazed plant community. We lack comparative data. However, on Ellesmere Island Henry and Svoboda (1994) found over-compensation by *C. aquatilis* but exact compensation by *E. angustifolium triste*.

It could be argued that the lack of differences between grazed and excluded areas we report was because animal densities were not high enough to make a measurable impact on the sedge meadows. Animal density was 1.6-1.9 muskox/km^2 over all habitats, and although not all foraging by muskox occurred in the wet sedge meadows which make up about 15-20% of the area, local short-term densities of foraging muskox in wet sedge meadows could reach levels similar to the 8.4 muskox/km^2 estimated for meadows on Ellesmere Island (Tolvanen and Henry 2000). Also this study was conducted over 5 years unlike most others which were generally 2 years.

Smith (1996) reported an under-compensation response of *E. triste*-dominated wet sedge meadows, but only when a high intensity clipping regime was undertaken in addition to the natural grazing. Under natural grazing he found at least 67% of the aboveground standing crop remained ungrazed during summer, heavily grazed patches were uncommon, and even at estimated densities of 1.8 muskox /km^2, animals left a significant amount of green plant tissue. He maintained that the intense burst of primary productivity during summer exceeded the forage requirement of current herbivore numbers and concluded that *E. triste*-dominated wet sedge meadows had a limited ability to withstand intense herbivory, but those levels had not been reached by current natural grazing intensity. Our results would support the conclusion sedge meadows on southern Banks Island can support current levels of herbivory without a negative impact on summer standing crop.

Belowground biomass far exceeds aboveground biomass in wet sedge meadows (Henry *et al*. 1994; Smith 1996). Belowground biomass has been shown to be greater in grazed versus ungrazed meadows (Henry and Svoboda 1994; Smith 1996). We did not measure this. Increased belowground reserves may be in response to grazing and may be required in order to maintain adequate nutrient absorption for regrowth (Chapin 1980).

Significant annual differences in late-August aboveground standing crop could result from annual differences in grazing pressure affecting plant removal and/or different environmental conditions affecting plant growth. Larter and Nagy (2001a) documented annual differences in the quality of Banks Island forages from 1993-1998. Most of the differences were attributed to variation in environmental conditions, particularly water. Moister late-summer conditions in 1996 and 1997 were believed to be responsible for significantly higher crude protein in sedges in the following winters, which was detected in the urine chemistry of muskoxen during those winters (Larter and Nagy 2001b). Comparative data on late-August standing crop of sedge are limited but the levels reported by Smith (1996) and Wilkinson and Shank (1973) are similar to those we report in 1996 and 1997. Although we cannot dismiss annual differences in grazing pressure, annual variation in environmental conditions is likely the main factor affecting late-August aboveground standing crop.

We did not expect to find an increase in the proportion of late-August live sedge material in ungrazed areas over time. However, most other studies reported conditions at the peak of the growing season and include dead litter in their estimates of standing crop, whereas ours did not. Smith (1996) found no difference in the proportion of live green material in the mid-August aboveground standing crop between grazed and ungrazed areas over 2 years. He did not include litter in his calculation of aboveground standing crop.

We chose measures of late-August standing crop, less dead litter, because we wanted to assess conditions at the end of the growing season which would provide an estimate of the maximum quantity and quality of forages available for herbivores over the winter. Access to winter forage is believed to have more of a direct impact on herbivore populations in the High Arctic than access to summer forage. Raillard (1992) estimated only a 3.9% removal of aboveground standing crop by grazing muskoxen from sedge meadows during summer at Sverdrup Pass, Ellesmere Island, but reported that 43.7% of shoots were grazed in sedge meadows during the 10 month non-growing season. Because muskoxen forage heavily in wet sedge meadows during winter, the condition of forages in these meadows at the end of summer directly influences winter foraging conditions. The high removal of shoots by overwinter foraging may have a positive influence on the sedge community by removing material which could accumulate as litter, thereby permitting increased solar radiation and earlier plant production in the following growing season.

Our results indicate that by late-August the grazers have removed a greater proportion of live than dead aboveground standing crop thus implying selection for the greener and more nutritious sedge material over the course of the summer. Although considered a classic grazer

(Hofmann 1989; 2000), muskoxen have been shown to forage quite selectively (Oakes *et al*. 1992). Our findings support selective foraging by muskoxen during summer.

CONCLUSIONS

1) There is significant annual variation in late-August standing crop of sedge material in *Carex aquatilis*-dominated wet sedge meadows on southern Banks Island.

2) The current intensity of herbivory, primarily muskoxen, on wet sedge meadows has not been at levels that cause a measurable negative impact on growth in this plant community; no evidence of undercompensation by the plant community was measured.

3) Grazers, specifically muskoxen, selectively forage on the greener proportions of the aboveground standing crop of sedge during summer.

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APPENDIX 1

The individual plots clipped inside each exclosure at Camp Coyote for each year of the study.

	Exclosure 1	Exclosure 2	Exclosure 3	Exclosure 4	Exclosure 5
1993	7	9	23	6	14
	13	21	17	20	10
1994	19	17	11	16	12
	11	1	6	18	22
1996	17	15	20	3	1
	4	11	2	14	18
1997	8	2	8	10	6
	21	7	14	13	17