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2ND INTERNATIONAL ARCTIC UNGULATE CONFERENCE

The 2nd International Arctic Ungulate Conference was held 13-17 August 1995 on the University of Alaska Fairbanks campus. The Institute of Arctic Biology and the Alaska Cooperative Fish and Wildlife Research Unit were responsible for organizing the conference with assistance from biologists with state and federal agencies and commercial organizations. David R. Klein was chair of the conference organizing committee. Over 200 people attended the conference, coming from 10 different countries. The United States, Canada, and Norway had the largest representation. The conference included invited lectures; panel discussions, and about 125 contributed papers. There were five technical sessions on Physiology and Body Condition; Habitat Relationships; Population Dynamics and Management; Behavior, Genetics and Evolution; and Reindeer and Muskox Husbandry. Three panel sessions discussed Comparative caribou management strategies; Management of introduced, reestablished, and expanding muskox populations; and Health risks in translocation of arctic ungulates. Invited lectures focused on the physiology and population dynamics of arctic ungulates; contaminants in food chains of arctic ungulates and lessons learned from the Chernobyl accident; and ecosystem level relationships of the Porcupine Caribou Herd.

The Arctic Ungulate Conference incorporates the former International Reindeer/Caribou Symposium and the International Muskox Symposium. In 1972, the First International Reindeer/Caribou Symposium was held at the University of Alaska Fairbanks (UAF), organized by the Institute of Arctic Biology and the Alaska Cooperative Wildlife Research Unit. The Symposium was attended by biologists, managers, and administrators from the Circumpolar North who were involved in research and management of caribou and reindeer. Proceedings of the Symposium were published as a special issue of the Biological Papers of the University of Alaska. Following this successful symposium, subsequent Reindeer/Caribou Symposia were hosted in Norway (1979), Finland (1982), Canada (1985), and Sweden (1988). In 1983, the Institute of Arctic Biology and Cooperative Wildlife Research Unit organized the First International Muskox Symposium at UAF. A Second Muskox Symposium was organized in 1987 at the University of Saskatchewan in Canada. In 1991, the 1st International Arctic Ungulate Conference, incorporating the International Reindeer/Caribou Symposium and the International Muskox Symposium, was held in Nuuk, Gteenland, organized by the Ministry for the Environment of Greenland and the Danish Polar Center. Thus, the 2nd International Arctic Ungulate Conference brought this scientific meeting back to Fairbanks 23 years after its initiation at UAF in 1972.

The Second International Arctic Ungulate Conference,
Fairbanks, Alaska, 13-17 August, 1995.

Arctic ungulates at the northern edge of terrestrial life

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Abstract: The 2 ungulate species that occur in the High Arctic, *Rangifer tarandus* and *Ovibos moschatus*, exhibit considerable adaptive plasticity in response to habitat variability throughout their circumpolar distribution. *R. tarandus*, however, has a much wider latitudinal distribution and occurs within a wider range of both forest and tundra habitat rypes than *O. moschatus*, reflecting greater morphological, physiological, and behavioral plasticity. As a consequence, muskoxen have been less successful than caribou and reindeer in maintaining populations at their southern limits. Muskoxen, however, existed throughout Pleistocene glaciations in the cold periglacial steppes of Eurasia and North America and find the closest analog to this vegetation type in the High Arctic, where they have been more successful than *R. tarandus* in maintaining their populations.

Key words: High Arcric, *Ovibos moschatus*, *Rangifer tarandus*, insularity, adaptability.

Rangifer, 16 (2): 51-56

Introduction

A broadly acknowledged ecological paradigm states that the diversity of plant and animal species declines from rhe equator to the poles along a latitudinal gradient (Fischer, 1960). Both Wallace (1878) and Darwin (1860) in the mid-1800's were impressed by the great diversiry of species they observed in the tropics, in contrast to temperate latitudes. The paucity of plant and animal species at high latitudes has been interprered largely on the basis of the climatic extremes rhat exist there, viewed from a human bias, rather than an ecological or biogeographical perspective. For terrestrial macrophytes, the small amount of the Earth's surface rhat is not covered by the seas or glacial ice in polar regions, in contrast to lower latitudes, has placed limits on the potential for habitat diversity which has been an important constraint on their presence there. In addition, since the end of the Pleistocene, virtually all plant and animal life in the High Arctic (characterized by a growing season of 2-2.5 months; only 8 mammal species, 10-20 nesting bird species and 50-115 vascular plants; Bliss, 1981) has arrived there from only the single direction of the lower latitudes. Although dispersal of some plant and animal species has occurred longitudinally within the Arctic, those species also had a southern origin.

Further complicating the occupation of land areas in the High Arctic by planrs and animals has been the insular characreristic of the ice-free lands present there. Even Greenland, of continent size, is fractured into a multitude of "islands" of ice-free land separated from one another by broad expanses of the ice cap and glaciets extending from it to the surrounding sea.

Primary Productivity in the High Arctic

The major constraints on plant growth in the High Arctic, in addition to the limited available ice-free land area, include the brief summer season during which remperatures are warm enough and light is present for photosynthesis; the limited available moisture wherever the land is free of ice; and the limited availability of essential nutrients in the poorly developed soils. In spite of these severe constraints, plants do grow in the High Arctic and produce sufficient plant biomass to support a complex of vertebrate herbivores, a few of which, like muskoxen and caribou (reindeer), are resident there throughout the year.

Although vascular plant species are relatively few in the High Arctic (less than 150 species in northern-most Greenland; Bay, 1992), in contrast to lowet latitudes, those present are highly adapted to the extreme conditions that exist there (Savile, 1972). High arctic plants are frost tolerant during the growth period and they grow and mature rapidly, taking advantage of the 24 hours of daily solar insolation. Their prostrate or low growth form benefits from solar warming at the soil surface, and the graminoids and forbs translocate most of their accumulated photosynthates to overwintering live tissues below ground or in the moss layet at the end of the growth season.

Plants growing in the poorly developed soils of the High Arctic are often nutrient limited. Plants, such as the Leguminosae and alder (*Alnus* spp.) that support nitrogen-fixing bacteria in root nodules, although present throughout much of the Arctic, do not reach rhe High Arctic (Bay, 1992).

Ungulates in the High Arctic

Plant production in the High Arctic is low in contrast to lower latitudes, and it is reasonable that fewer herbivores occur there, both in number of species and total biomass (Kaufman, 1995; Klein & Bay, 1994). Those vettebrate herbivores that occur in the High Arctic have special adaptations to deal with the seasonal variability in weather and in quality and availability of plant material for food. Birds avoid the climatic extremes of winter and the associated decline in quality and availability of forage through migration. Because of the insular nature of the High Arctic, mammals do not have the option of migtation to lower latitudes. MacArthur (1972) proposed that in North America, species are limited in their northern distribution by physical conditions, whereas their southern distribution is limited by biotic interacrions. I think, however, that this generalization reflects an anthropocenttic bias nurtured by the human pteoccupation with the severity of the arctic climate.

Factors of the environment indirectly related to climate may play equally important roles. For example, the southern distributions of the boreal forest cervids, moose (*Alces alces*) and deer (*Odocoileus* spp.), in North America are limited in the arid West by availability of suitable habitat, which includes shrubs or trees as cover and winter forage. Thus, they are limited by the biotic charactetistics of the habitat, which in turn are products of climatic constraints on growth of trees and shrubs, a physical constraint. Similarly, muskoxen and Peary caribou (*R.t. pearyi*) are limited in their high arctic distribution by the distribution and production of plants suitable as forage, and the availability of plant biomass throughout the year (Fig. 1). Thus, it is biotic constraints as mediated by the climate of the High Arctic, that detetmines where these species may exist rather than the direct effect of climate on the animals.

Both caribou and muskoxen are morphologically, physiologically, and behaviorally well adapted to the climatic extremes of the Arctic (White *et al.*, 1981). Nevertheless, it is climatic extremes, through their effect on forage production and availability, that have primary influence on limiting population numbers of ungulates in the High Arctic. The ditect effects of these climatic exttemes on the animals are the increased energy costs associated with traveling through, and foraging through, deep snows, loss of access to fotage due to icing conditions, the added energy costs of thermoregulation, and lost foraging opportunity during extreme winter storms.

The two species of ungulates that have occupied the High Arctic have evolved different physiological, morphological, and behavioral attributes that enable them to exist there. The muskox, that during Pleistocene glaciations was ptesent throughout the semiarid periglacial steppe that extended from southern Europe across Asia into North America (Kurtén, 1968), is well adapted as a generalist grazer of graminoid vegetation (Guthrie, 1984). Its large body size and large rumen (White *et al.*, 1981) enable it to digest grasses and sedges

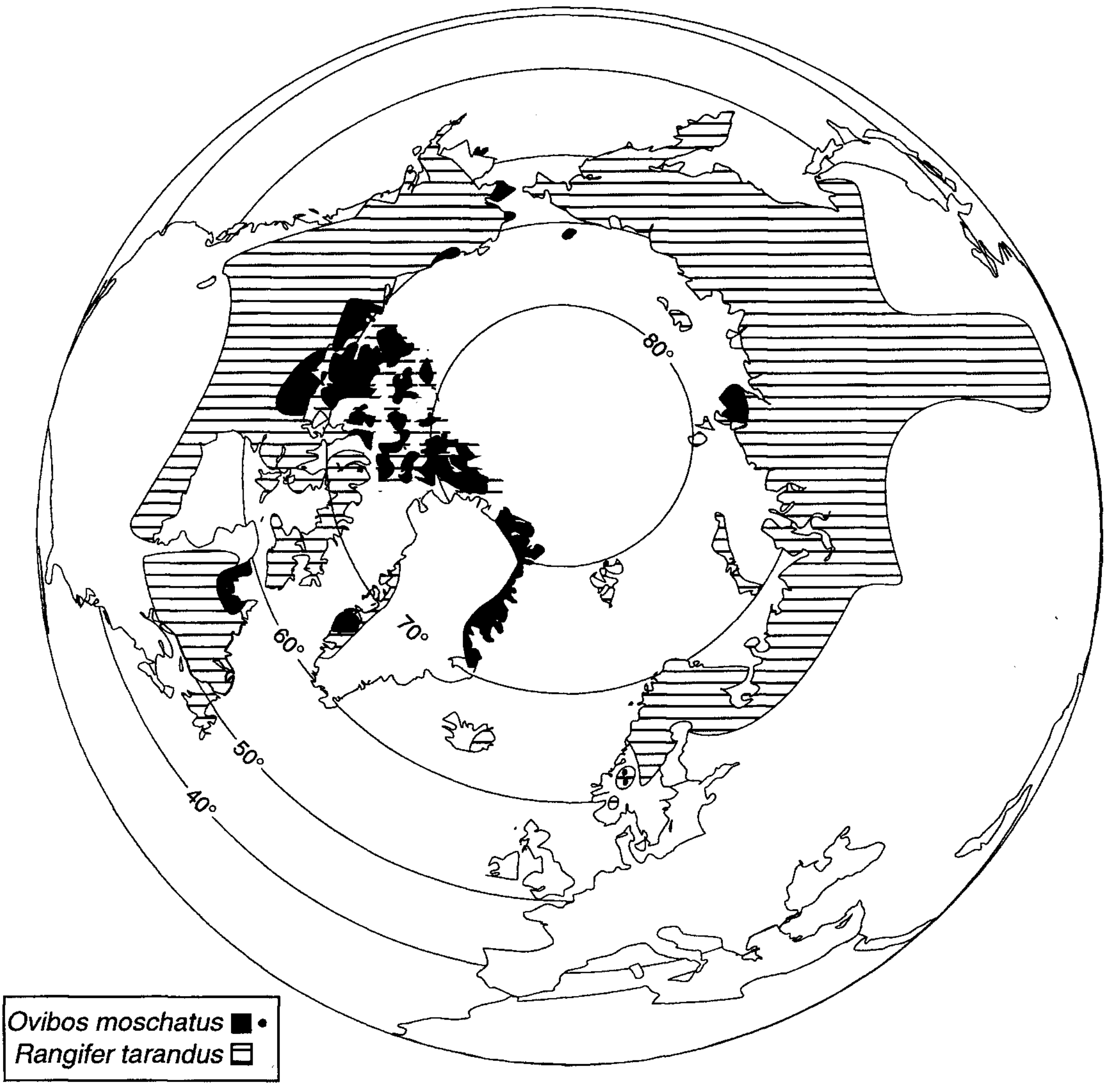

Fig. 1. Holarctic distribution of *Rangifer tarandus* (caribou and reindeer) and *Ovibos moschatus* (muskoxen), including reintroductions of muskoxen to historical range in northern Alaska, and introductions outside of historical range in western Alaska, Quebec-Labrador, western Greenland, Norway, Sweden, and the Taimyr Peninsula and Wrangel Island of Russia.

with a high fiber content, especially during winter. Muskoxen also are highly energy conservative in virtually all of their life processes, including daily activity, seasonal movements, predator avoidance, and social inreraction (Jingfors, 1980; Klein, 1992). Morphologically, their low surface to body mass ratio and extremely efficient insulative pelage equip them well to conserve body heat during the extreme cold of high arctic winters.

Caribou and reindeer, in contrast to muskoxen, have morphological constraints that are the heritage of their Cervidae origin. These are their small body size and long legs, relative to muskoxen, which limit theit tumen size and give them a relatively high sutface to body mass ratio. Their life style and its adaptation to the High Arctic have, therefore, evolved in a different direction than muskoxen. Rather than being highly energy conservative as are muskoxen, caribou must expend much more energy per unit body mass for survival (Fancy, 1986; Thing *et al.*, 1987; Klein, 1992), and with smaller rumen capacity, must be much more selective for forage of high digestibility. Although caribou are better adapted than muskoxen for foraging through deep snow, in the High Arctic suitable forage for them is most frequently found in areas with least winter snow accumulation. White *et al.* (1981) have shown that long fiber graminoids are poorly digested by caribou and reindeer. Peary caribou, as a result of work by Thomas & Edmonds (1984) and Parker & Ross (1976), are known to be highly selective foragers, focusing heavily on *Luzula* spp., mosses, and lichens in winter and willow (*Salix arctica*), *Saxifraga oppositifolia*, and other forbs in summer. Low plant species diversity and low plant biomass in the High Arctic, especially for non graminoid species, necessitates high mobility fot selective foragers. Parker & Ross (1976) found Peary caribou ro be much more mobile in their daily foraging than muskoxen in the Canadian High Arctic. A selective foraging behavior requiring high mobility in high arctic *Rangifer*, in an environmenr of low and dispersed plant biomass, with long winters without plant growth has presumably selected for small body size. This seems counrer inruitive relative to thermoregularion and Bergman's rule. Small body size, however, in the high arcric winrer in an ungulare species with moderately high enetgy requiremenrs per unir body mass (White *et al.*, 1981), can be more easily maintained in an environment of extremely low usable plant biomass. Additionally, the relatively smaller body size in *Rangifer* than in muskoxen, necessitates selection for running speed in *Rangifer* for predator avoidance. This behavior selecrs for long leg length (Klein *et al.*, 1987) with associated higher energy costs expended for locomotion and thermoregulation. Exceptions do occur, however, as in the case of the Svalbard reindeer (*R t. platyrhyncus*), that live in a predator-free environmenr with limited options for movemenr because of the insular narure of rheir habitats (Reimers, 1977). Their long isolation from competition with muskoxen may also have been a factor in their unique adaptations of short legs, larger rumen capacity, and high capability for body fat storage (Klein & Sraaland, 1984).

Limiting Factors for Ungulates in the High Arctic

The adaptations of *Rangifer* and *Ovibos* for life in the High Arctic have enabled these two ungulates to occupy available and accessible habitats there. Nevertheless, the extreme climatic conditions that exist in the High Arctic with periodic short and long term climatic fluctuations have accounted for wide fluctuations in population numbers of high arctic ungulates with localized extinctions, followed by repopulation of suitable habitats (Melgaard, 1986; Syroechkovskii, 1995).

The greater locomotive efficiency of *Rangifer* (Klein, 1992), and wide adaptability to substrates and habitats have enabled them to gain access, during the Holocene, to large areas of the Holearctic that have not been reached by muskoxen. These include Newfoundland and the Quebec-Labrador peninsula, the southeast and west coasts of Greenland (Meldgaard, 1986), Svalbard, Franz Josef Land (Zale *et al.*, 1994), Novaya Zemlya, Severnaya Zemlya, and the New Siberian Islands (Fig. 1). In a few of rhese areas, populations have subsequently declined to extinction or have periodically been reestablished through movements from adjacent continental populations (Meldgaard, 1986; Syroechkovskii, 1995). Similarly, in northern and northeastern Greenland, caribou have periodically been presenr, with intervals of absence, over at least 7000 years, presumably the returning populations derived from movements from Ellesmere Island in the Canadian High Arctic (Meldgaard, 1986). The most recent population in northeast Greenland was *R. t. eogroenlandicus*, an endemic subspecies, persisted there until atound the turn of the last century (Meldgaard, 1986).

The less mobile muskox has been much slower ro colonize areas of rhe Arctic that presumably would supporr ir, however, human assistance in recent decades has established it in western Greenland and on the Quebec-Labrador peninsula and reestablished it in former habitats in Alaska, the Yukon Territory, and on the Taimyr Peninsula of Russia (Klein, 1988) (Fig. 1).

The muskox has also been less successful than caribou and reindeer in maintaining its populations when confronted by hunting by indigenous and western cultures. In the High Arctic of Greenland (Vibe, 1967) and Canada (Barr, 1991) where humans have been absent from vast areas until recent times, the muskox has been more successful in maintaining its populations in association with climatic extremes than have caribou. This difference appears to be a function of the muskox's capability of using low quality, high fiber forage, which constitutes the greatest portion of the total available plant biomass in winter in the High Arcric (Klein

& Bay, 1990). Forage biomass in the sedge meadows used by muskoxen is more srable than the forages eaten by caribou, with the exception of lichens, which are scarce in the High Arcric. In addition, the energy conservative life style of muskoxen and their capability ofi accumulating larger fat reserves than most high arctic *Rangifer* (Thing *et al.*, 1987; Reimers *et al.*, 1982), gives them an advantage when forage is limited in winter.

Predarion by wolves is undoubredly a factor in further reducing populations ofi both muskoxen and caribou in the High Arctic that may already be suppressed by climatic exttemes affecting forage availability. Alrhough extremely low populations of ungulate prey will not likely sustain wolfi populations in the insular-like disjuncr habitats of the High Arctic, there are likely differences in how wolves affect low density populations of muskoxen versus caribou. As densities of prey populations decline so do those of wolves. Minimal pack size fot efficient predation on muskoxen, especially adults, must be greater than for predarion on the much smaller high arctic caribou. Thus, as both prey and predator densities decline, muskoxen may be less vulnerable to predation by wolves than caribou. Additionally, the disjunct nature of unirs ofi habirat for muskoxen in the High Arctic may result in less predation on that species when wolfi numbers are also low.

The periodic presence of wolves in northern and northeast Greenland in this century (Dawes *et al.*, 1985), during which muskoxen persisred as the only ungulate prey, also demonstrares that wolves were not capable of driving muskoxen to exrinction in association with the climatic extremes ofi the High Arctic. Instead, wolves died out, allowing for recovery of suppressed muskox populations. It is noteworthy that although muskox numbers in northeast Greenland declined markedly around the turn of the last century the endemic caribou (*R. t. eogroenlandicus*) declined to extinction (Vibe, 1967). Vibe postulated climatic extremes as a primary factor in the decline of muskoxen and the extirpation of caribou, however, wolves may also have been a factor.

It is apparent that proximity to the North Pole has not limited arctic ungulates in their northward disttibution. Both species have reached the northernmost land areas, although densities decline matkedly with increasing latitude. Periodic extirpation of populations has occurred regionally in the past in association with climatic extremes rhat have limired forage production and access to it. The muskox, however, has been a somewhat better survivor under the environmental constrainrs of the High Arctic than has been the caribou.

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Fire - caribou - winter range relationships in northern Canada

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Abstract: We needed data on temporal changes in caribou forages after fire and relative use of age-classes of forests by caribou to help devise a fire suppression priority strategy for caribou winter range in north-central Canada. Consequently, from 1983 through 1986, we estimated the abundance of vegetation and relative use by caribou at 197 sites in western and eastern study areas on the winter range of the Beverly herd of caribou (*Rangifer tarandus*). Species of lichens attained peak biomass at different periods after fire - as early as 40-60 years for *Cladonia* spp. to >150 years for *Cladina rangiferina* and *Cetraria nivalis*. Biomass of the primary "caribou lichen", *Cladina mitis*, increased rapidly from 21-30 years after fire to 41-50 years and attained maximum biomass at 81-90 years in the west and 41-60 years in the east. However, total lichen biomass increased wirh age of forest to 100-150 years because biomass of *Stereocaulon* spp. did not peak until after 100 years. The biomass of "caribou lichens" (*Cladina* spp. and *Cetraria nivalis*) stabilized after 61-80 years in the west and 41-60 years in the east. The biomass of terrestrial lichen species can be predicted from their cover. Caribou lichen abundance apparently was only one of several factors that caused caribou to use stands 151-250 years after fire more than other age classes.

Key words: burns, habitat, lichens, *Rangifer tarandus,* succession.

Rangifer, 16 (2): 57–67

Introduction

Large fires in 1979 burned 1.4 million ha of caribou winter range northeast of Fort Smith, Northwest Territories (NWT). Consequently, aboriginal hunters requested mote fire suppression on forested wintet range of caribou. Previous studies of the effects of natural fires on forested winter ranges of caribou (*Rangifer tarandus groenlandicus*) in this patt of Canada (e.g. Scotter, 1970; Johnson & Rowe, 1975; Johnson, 1979; Miller, 1980) had produced divergent views. Therefore, a fire review panel concluded that more information was needed on the effects of fires on caribou and their wintet range (Murphy *et al.*, 1980).

Results from studies in 1980 and 1981 on caribou diet (Thomas & Batry, 1991) and digestibility of forages (Thomas *et al.*, 1984) compelled us to focus primarily on lichens as winter forage. This report provides results of the third phase of fire-caribou studies from 1982 through 1988 - the relationship between time since fire and the quantity of caribou forage and its use by caribou.

Our objectives were: (1) To measure the abundance (cover, biomass, and frequency of occurrence) of caribou forages relative to time since fire; (2) To assess the relationship between cover and biomass of caribou forages; and (3) To obtain information on relative use of forest types and ages by caribou.

Associations among flora and their relationship to caribou use will be reported separarely.

Characteristics of the study areas were detailed by Bradley *et al.* (1982). The rerrain is Precambrian Shield overlain by various amounts of glacial till. Jack pine (*Pinus contorta*) germinates within 1-5 years of srand-replacing crown fires, whereas spruce (*Picea* spp.) arise continuously. West of about 107°30'W in the NWT, pine dominated xeric sites after fire, grading to dominance by black spruce (*P. mariana*) in lowland sites. Pine persisted to age class 150-200 years at rocky and sandy sites in the west but did not occur in forests >100 years in the east. Sptuce usually was most numerous even where pine dominated the canopy. East of about 107°30'W in the NWT pine failed to regenerates after fire except on the most-favorable sourhern exposures near 60°N. Whire spruce (*P. glauca*) occurs throughout the forested region but only in favorable locations characterized by sandy or gravelly alluvial soil.

In March 1982 through 1988, snow was deeper in the eastern block than in the west, averaging 64 cm and 56 cm, respectively (Thomas, 1991). Snow and the regional burn pattern influenced caribou distribution, though caribou readily travelled through individual burns of all ages and sizes.

Methods

Five study areas were selected in the core of the winter range, where large lakes provided access by boat. We sampled 139 sites west of 107°W ("west block") and 58 east of 107°W ("east block"). The western sites wete clustered around Porter, Nonacho, and Thekulthili lakes; the eastern ones around Beauvais and Selwyn lakes (Fig. 1).

The basic design was to sample two ages across a fire boundary and compare floral abundance and caribou use. The paired sites had the same landform, surface materials, elevation, etc. In this way, physical variables that could affect vegetative characteristics wete "controlled". Representative xeric sites were chosen on ridge tops or on gentle slopes where caribou tended to feed. Our samples were restricted to canopy openings, as the vegetation differed under the drip areas of trees.

A site was selected at the first location along a burn boundary where the terrain was relatively flat and uniform. At 100-200 m ftom the boundary, a stake was thrown >5 m over a shoulder to mark the southwest cornet of a 10 m x 10 m plot. Then quadrats (inside dimensions 25 cm x 50 cm) were tossed laterally 3-5 m while looking upward and slow-

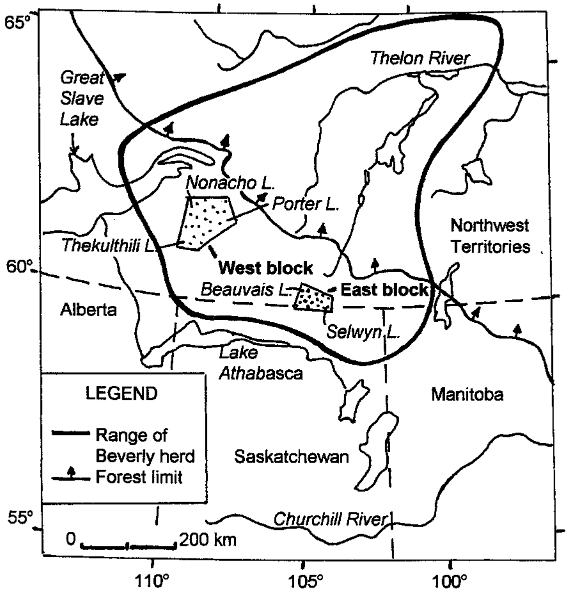

Fig. 1. Location of west (W) and east (E) block study areas within forested winter range of the Beverly herd of barren-ground caribou in northern Canada.

ly walking in and near the plot. Those landing under trees with low branches or on grazed lichen mats were tossed again until a standatd number of 10 quadrats was established. In stands <50 years old, 15 to 25 quadrats were sampled because of greater variation in lichen distribution. Arboreal lichen abundance to 2 m above ground was rared visually on an ordinal scale of 0 to 4 (1=sparse, 2=light, 3=moderarely abundant, and 4=abundant).

Diameter at breast height (DBH) of all trees in the plot was measured with a vernier caliper. A minimum of two of the tallest trees of each species were felled and measured for height and DBH. Several sections cut 25 cm above the ground were saved for counts of annulations. Fire scars were obtained from several pine and, failing that, from spruce. Lacking fire scars, we estimated forest age by adding 5 and 10 years to the maximum number of annulations in pine (preferred) and spruce, respectively. In ancient stands, the estimated time since death of the oldest fallen "mothet" spruce was added to the estimated age of the oldest spruce in the associated layeted clone. Time since death was based on subjective evaluation of the degtee of rot without benchmarks.

Peller groups of caribou and other species were counted in two belt transects 4 m x 100 m and restricted to the habitat type that was sampled. Starting points of each transect was one corner of the plot and direction was arbitrary yer remain in the habitat type. Winter-type pellets survived about 2-3 years in mesic habitats and 4½-6 years on xeric sites (Thomas & Kiliaan, 1994). About 50% of the groups would be detectible in fecal surveys at 2½ and 4½ years, respectively, after deposition of the pellets.

The cover of plant species within each quadrat was estimated visually to the nearest 1%. Personnel were trained using paper cutouts of various shapes and percent cover. Biomass was obtained by first mist wetting the vegetation using a plastic spray "bottle". Otherwise the dry lichens fractured when handled. All live vegetation produced in previous seasons, except moss, was removed from within each quadrat. Sorting enrire samples was too time consuming (2-4 hours) so we sorted a subsample of one-third or more by weight. The initial sorting was checked in the laboratory before drying samples at 55°C fot 3 days and weighing them on a microbalance.

We expressed terrestrial lichen biomass as total biomass and as weighted biomass where *Cladonia* spp., including *Cl. uncialis*, was reduced 50% and *Stereocaulon* spp. was reduced 75% for reasons discussed later. *Cladina mitis*, *C. rangiferina*, and *Cetraria nivalis* were totalled as "caribou lichens." Reindeer lichens were defined as *Cladina* and *Cetraria* by Russell *et al.* (1993).

Forest ages generally were grouped into eight classes to describe changes in forage at the site level, with 20-year intervals to 100 years and 50 thereafter. The classes were a compromise between the need to chatacterize rapid changes in abundance up ro 100 years and maintaining reasonable sample sizes in older classes. Quadrar data were grouped in 10-year age classes to 100 years to better define vegetation dynamics and to display frequency of occurrence data.

A tree biomass index was calculated as the cumulative sum of products of the number of trees in each 5 cm DBH class and the median value of each class (e.g., 8 cm for class 6-10 cm).

Snow depth was measuted periodically, 1982 through 1988, in forest openings at several locations in each block as explained in Thomas (1991).

Frequency of occurrence of species was extracted from biomass data for each quadrat. Site means were used for most analyses of relationships. We categorized the data measures as interval (biomass, number of pellet groups, number of trees, DBH classes), ratio (cover, frequencies), and ordinal (arboreal lichen biomass) and rhen selected tests accordingly using SYSTAT (1992) and BMDP software. Data normality was checked with normal probability plots. Unaltered cover values produced results similar to percentages transformed by arcsine. Results from Pearson and Spearman correlations were almost identical. Alpha was 0.05 for all tests.

Herein, age refers to post-fire age, *C.* is *Cladina, Cl.* is *Cladonia,* and *Cet.* is *Cetraria. Cladina stellaris* was included with much more abundant *C. mitis.*

Results

Terrestrial lichen biomass in relation to time since fire

In west and east blocks, biomass of lichen species and groups varied significantly (Kruskal-Wallis 1-way ANOVA) with forest age. For most species/groups this difference was caused by significant increases in biomass between classes 21-40 and 41-60 years. Consequently, means for age classes 1-20 years did not differ from those for 21-40 years and means for age classes 41-60 years and older did

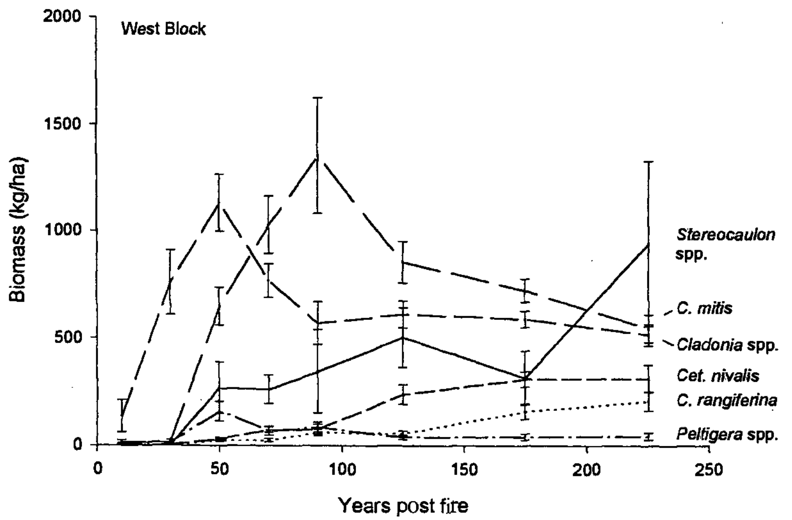

Fig. 2. Post-fire biomass of lichen species at 20-year intervals to 100 years, and 50 years thereafter, in the west block of foresred winter range of the Beverly herd of caribou. The bars are standard errors about mid-point means.

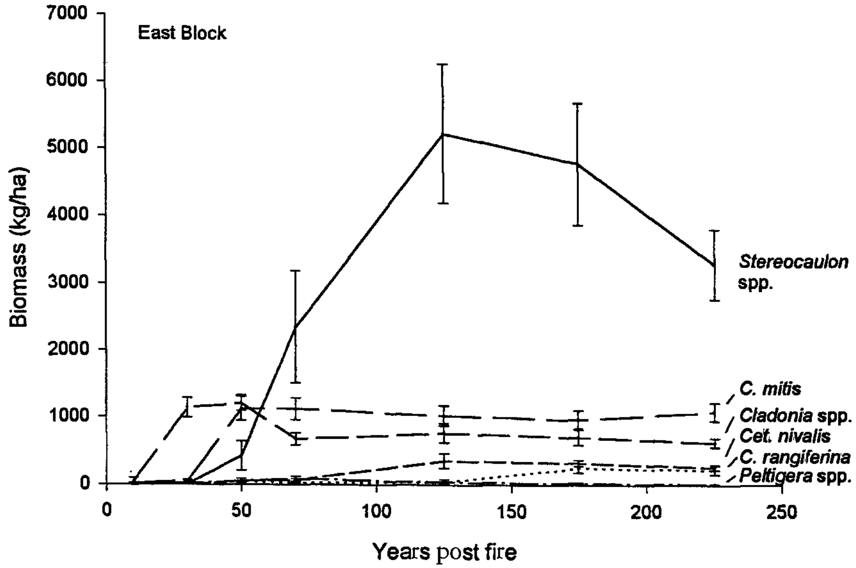

Fig. 3. Post-fire biomass of lichen species at 20-year intervals to 100 years, and 50 years thereafter, in the east block of forested winter range of the Beverly herd of caribou. The bars are srandard errors about mid-point means.

not differ. Exceptions were *Cet. nivalis*, where significant differences occurred either side of 100 years, and *Cladonia* spp. where year classes 21-40 and 41-60 did not differ.

In the west block, mean biomass of lichens based on site data was low in the 1-20 and 21-40 year classes except for *Cladonia* spp. (less *Cl. uncialis*) in the 21-40 year class (Fig. 2). The mean biomass of *Peltigera* spp. and *Cladonia* spp. peaked in class 41-60 years. The mean biomass of *C. rangiferina, Cet. nivalis,* and *Stereocaulon* spp. peaked after 150 years.

The mean biomass of *Cet. islandica/arenaria* (not shown) peaked in the 61-80 year class and *Cl. uncialis* in the 81-100 year class (Thomas & Kiliaan, 1994).

Biomass of *Stereocaulon* spp. in age group 100-200 years was over 10 fold higher in the east than in the west (Fig. 2 & 3). The biomass of *C. mitis* was maintained in older sites in the east but declined aftet 80-100 years in the west.

In the west block, there was little change in total and weighted lichen biomass after class 21-40 years (Fig. 4). The high biomass of *Stereocaulon* spp. in the east block (Fig. 5) caused total and weighted lichens to peak in classes >100 years. The biomass of caribou lichens remained about constant aftet 20-40 years in the east block and 40-60 years in the west block.

Data for decade age classes to 100 years (Table 1) in the west block indicated a rapid increase in biomass of caribou lichens from 20-30 years to 70-80 years and stability thereafter (Fig. 6). Stability was two decades earlier for weighted and caribou lichens.

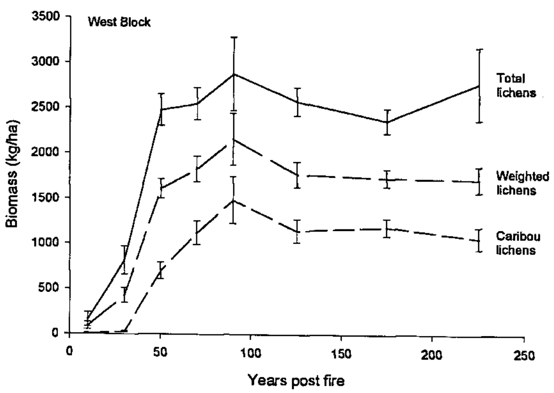

Fig. 4. Post-fire biomass of total, weighted, and "caribou lichens" at 20-year intervals to 100 years, and 50 years thereafter, in the west block of forested winter range of the Beverly herd of caribou. The bars are standard errors about mid-point means.

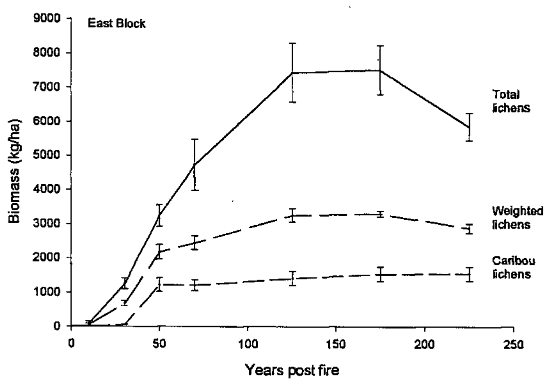

Fig. 5. Post-fire biomass of total, weighted, and "caribou lichens" at 20-year intervals to 100 years, and 50 years thereafter, in the east block of forested winter range of the Beverly herd of caribou. The bars are standard errors about mid-point means.

Table 1. Mean biomass (kg/ha) of lichen species in quadrats at 10- and 50-year intervals after fire in the west block of forested caribou winter range in northern Canada, 1983-85. Standard errors are in smaller print below each mean.

Age class (yr)	No. of sites	No. of quads	Other *Clad.*[1]	*C. mitis*	*Pelt.* spp.	*Cl. unc.*	*Cet. niv.*	*Cet. isl.*	*C. rang.*	*Stereo.* spp.
1-10	04	69	0	1	0	0	0	0	0	0
11-20	06	59	229	10	25	5	1	2	0	0
			47	5	9	3	1	1		
21-30	08	109	691	20	20	6	6	2	1	3
			65	5	7	2	3	0	0	2
41-50[2]	07	85	1128	336	202	162	14	21	12	160
			94	39	35	29	5	2	3	30
51-60	16	148	1108	811	127	225	38	34	27	335
			80	48	28	20	7	3	7	72
61-70	07	69	918	789	109	288	65	44	22	204
			68	54	35	33	13	5	6	54
71-80	11	107	668	1126	41	260	77	56	26	289
			49	75	9	21	12	6	8	60
81-90	07	67	557	1256	95	372	83	33	67	444
			71	98	20	34	18	5	12	135
91-100	02	20	585	1757	46	325	48	42	42	52
			89	328	13	36	12	7	12	18
101-150	23	227	610	853	38	236	242	43	56	503
			30	39	7	15	20	4	7	76
151-200	26	257	587	721	39	194	310	33	159	318
			25	28	10	11	19	3	20	55
201-250	19	198	497	541	41	163	352	30	220	893
			23	29	10	11	29	3	25	143

[1] Excluding *Cl. uncialis*. Abbreviations: quads=quadrats, *Clad.* = *Cladonia* spp., *C.* = *Cladina*, *Pelt.* = *Peltigera*, *Cl.* = *Cladonia*, *unc.* =*uncialis*, *Cet.* = *Cetraria*, *niv.* = *nivalis*, *isl.* = *islandica*, *rang.* = *rangiferina*, *Stereo.* = *Stereocaulon*.
[2] No sites 31–40 years.

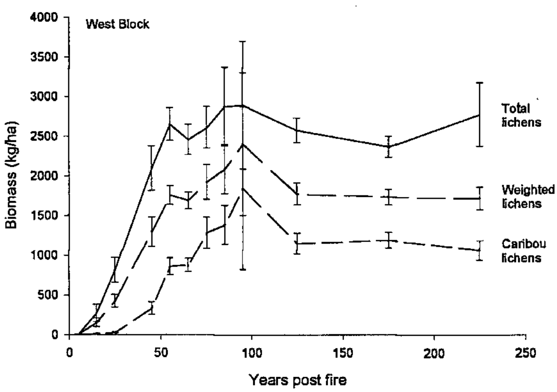

Fig. 6. Post-fire biomass of total, weighted, and "caribou lichens" ar 10-year intervals to 100 years and 50 years thereafter based on quadrat data from the west block of the forested winter range of the Beverly herd of caribou. The bars are standard errors about mid-point means.

Terrestrial lichen cover in relation to time since fire

Cover values peaked as early as 21-40 years for other *Cladonia* spp. and as late as 201-250 years for *C. rangiferina* (Table 2). Cover of *C. mitis*, the key caribou lichen species, peaked at 81-100 years.

Frequency of occurrence of plants in quadrats at sites

The frequency of occurrence of species and groups in 1415 quadrats in the west block was tabulated at 10-year and 50-year classes (Table 3). Most quadrats in forests >50 years contained *C. mitis, Cl. uncialis, Cladonia* spp., and *Cet. islandica/arenaria. Cet. nivalis* was neatly ubiquitous in quadrats in sites >100 years and *C. rangiferina* and *Stereocaulon* spp. were common. The frequency of *Peltigera* spp. decreased after class 91-100 years.

Table 2. Mean percent cover of lichens in eight age classes of forest sampled in the west block of the winter range of the Beverly herd of caribou, 1983-85. Standard errors are in smaller print below each mean.

Age class, yr	No. sites	*C. mitis*	*C. rang.*	*Cetr. nivalis*	Other *Cladonia*[1]	*Stereo-caulon*	*Caribou* Lichens	Total Lichens[2]
1-20	10	0.9	0.0	0.2	4.5	0.0	1.1	7.2
		0.3		0.1	2.6		0.4	3.0
21-40	8	2.3	0.0	0.1	18.9	0.0	2.4	23.1
		0.5		0.1	3.3		0.6	3.8
41-60	23	18.4	1.0	1.5	17.7	4.2	21.0	52.7
		2.1	0.2	0.4	1.8	1.5	2.3	2.7
61-80	18	30.3	1.4	3.9	14.4	4.7	35.6	64.1
		2.3	0.4	0.8	1.6	1.2	2.0	1.9
81-100	9	35.9	2.9	3.6	9.4	4.0	42.3	65.1
		4.1	1.3	1.1	1.3	1.9	4.0	2.4
101-150	23	26.0	2.7	11.0	10.7	7.1	39.6	65.6
		2.0	0.5	1.9	0.8	2.0	2.9	2.0
151-200	26	24.6	5.8	14.2	11.9	4.7	44.5	66.7
		1.2	1.3	1.3	0.8	1.8	2.1	2.0
201-250	19	19.4	6.8	12.2	9.8	12.6	38.4	67.4
		1.7	1.3	1.8	1.0	4.0	3.2	2.8

[1] Excluding *Cl. uncialis.*
[2] *C. mitis, C. rangiferina* and *Cet. nivalis.*

Table 3. Percent frequency of occurrence of terrestrial lichen species in quadrats at 10-year and 50-year intervals after fire in the west block of forested caribou winter range in norrhern Canada, 1983-85.

Age class (years)	No. of quads[1]	*C. mitis*	*Cet. nivalis*	*Cet. islandi*[2]	*Stereo-caulon*	*Peltigera* spp.	*C.rangi-ferina*
1-10	69	4	0	3	1	0	1
11-20	59	54	24	19	7	31	7
21-30	109	81	10	43	12	17	14
41-50	85	100	34	86	54	58	44
51-60	148	99	54	87	45	45	61
61-70	69	100	65	90	42	42	52
71-80	107	100	84	89	63	40	58
81-90	67	100	70	93	36	63	78
91-100	20	100	85	95	50	70	75
101-150	227	100	96	93	59	37	75
151-200	257	100	97	88	36	26	80
201-250	198	100	96	80	52	27	77

[1] Number of quadrats 25 cm x 50 cm. Number of sites is in Table 1.
[2] Included *Cetraria arenaria.*

Relationship between cover and biomass of lichens
Terresttial lichens were more robusr in the east block as indicated by comparative cover and biomass of species and groups (Table 4). Cover of most species was higher in the west and the reverse for biomass. Therefore, within block analysis was necessaty.

Biomass and cover of all species at sites were significantly correlated in both blocks (Table 5). Correlation coefficients for data from all 197 sites were intetmediate for five species and higher than west and east block coefficients for *C. mitis, C. rangiferina,* and *Cladonia* spp. Coefficients were lower for quadrat data yet still significant. In the west block,

Table 4. Mean cover and biomass of lichen species and groups at sites in forests older than 100 years in west and east blocks of caribou winter range in the Northwest Terriroties (standard errors in parentheses).

Lichen sp./group	Cover (%) West (n = 71)	Cover (%) East (n = 31)	Biomass (kg/ha) West (n = 71)	Biomass (kg/ha) East (n = 31)
C. mitis[1]	24.1 (1.0)	23.0 (1.7)	710 (43)	1026 (78)
Stereocaulon spp.	8.1 (1.5)	36.3 (3.3)	595 (134)	4149 (433)
Cetraria nivalis	12.7 (0.9)	8.1 (0.9)	294 (27)	294 (27)
Cladonia spp.[2]	10.9 (0.5)	4.8 (0.5)	577 (28)	670 (54)
C. rangiferina	5.1 (0.7)	3.6 (0.7)	148 (21)	203 (40)
Cladonia uncialis	3.6 (0.4)	2.2 (0.2)	207 (13)	241 (21)
Peltigera spp.	1.3 (0.2)	0.2 (0.1)	39 (7)	20 (6)
Cetraria islandica[3]	2.0 (0.2)	0.8 (0.1)	35 (3)	29 (4)
Caribou lichens[4]	41.9 (1.6)	34.7 (3.2)	1153 (65)	1524 (116)
Weighted lichens[5]	54.5 (1.4)	48.4 (2.6)	1767 (68)	3095 (76)
Total lichens	68.5 (1.4)	82.9 (2.1)	2606 (135)	6738 (354)

[1] Includes *C. stellaris.*
[2] Except *Cladonia uncialis.*
[3] Includes *Cetraria arenaria.*
[4] Caribou lichens=*C. mitis* + *C. rangiferina* + *Cetraria nivalis.*
[5] *Stereocaulon* reduced 75%, *Cladonia* spp. & *Cladonia uncialis* reduced 50 %.

Fig. 7. Mean arboreal abundance rating at 50 year intervals after fire in west (n=22, 35, 19, 24, & 18) and east (n=10, 16, 4, 8, & 13) blocks.

the highest cotrelations were for mat-forming *Stereocaulon* spp. and a foliose lichen (*Cet. nivalis*). The poorest fit was for sometimes misidentified *Cl. uncialis*. The second poorest correlation was for *Cet. islandica/arenaria,* species usually hidden by other species and sometimes overlooked in cover estimates.

Arboreal lichen abundance

The ttend in the west and east was an increase in arboreal lichen mean abundance ratings with age of forest to the 201-250 year class (Fig. 7). Arboreal lichens were more abundant in the east in fotests 101 to 250 years post fire (Mann-Whitney U test, P < 0.001).

Indices of past use of sites by caribou

Past use by caribou of west block sites was significantly highet than in the east (Fig. 8). For example, frequency of occurrence in forests >50 years was 64% in the west block and 29% in the east block. Mean number of pellet groups/ha was 87 in the west and 13 in the east. Excluding zeros, densities were 136±17(SE) and 44±8 in west and east blocks, respectively.

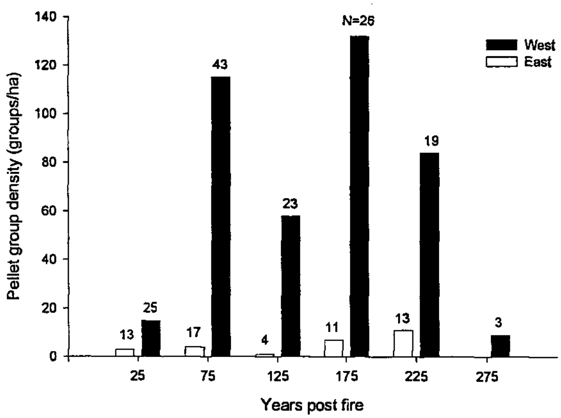

Fig. 8. Densities of caribou fecal groups in rhe west and east blocks in 50-year intervals after fire on the winter range of the Beverly herd in northern Canada.

Table 5. Regression variables used to predict biomass from cover of lichen species and groups in pine-spruce forest (west block) and spruce forest (east block). Shown are slope (*m*), intercept (*b*) and coefficent of determination(r^2). All equations are significant ($P<0.05$).

Plant species and group	West *m*	West *b*	West r^2	East *m*	East *b*	East r^2
C. mitis	36.24	-82.94	0.71	39.06	127.53	0.76
C. rangiferina	27.63	-0.40	0.78	52.14	10.85	0.90
Cl. uncialis	22.15	121.37	0.28	45.97	94.40	0.49
Cet. nivalis	24.35	-13.10	0.87	28.09	30.54	0.69
Cladonia spp.[1]	49.36	61.22	0.63	52.75	400.08	0.52
Stereocaulon spp.	82.22	-62.67	0.93	116.74	-91.55	0.89
Peltigera spp.	27.08	8.57	0.74	31.56	14.28	0.66
Cet. islandica[2]	10.85	13.38	0.49	13.53	19.84	0.35
Total lichens	45.15	-268.71	0.58	93.67	-872.58	0.57
Caribou lichens [3]	31.46	-59.48	0.73	41.91	67.46	0.79

[1] Except *Cl. uncialis.*
[2] Included *Cet. arenaria.*
[3] *Cladina mitis, C. rangiferina* and *Cet. nivalis.*

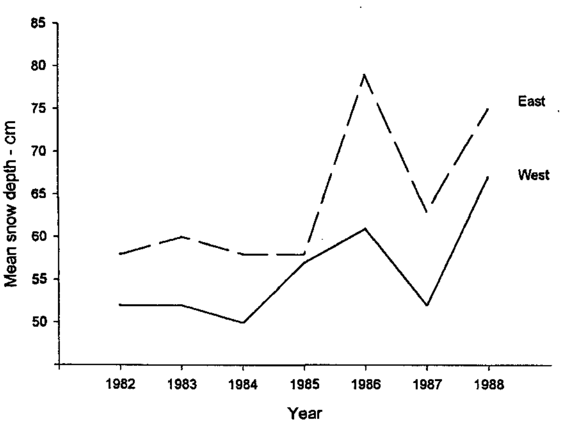

Fig. 9. Depth of snow in mid-March, 1983 through 1988, in west and east blocks of the winter range of the Beverly herd of caribou.

Use varied significantly (Kruskal-Wallis, $P<0.001$) with forest age. Peak use occurred in age class 151-200 years in the west block and at 201-250 years in the east block. We attribute higher use of west block forests in part to late-winter differences in snow depths (Fig. 9).

Caribou-pellet densities (groups/ha) in forests >50 years were 132±24 (SE) at Porter Lake, 90±11 at Nonacho Lake, 11±3 at Thekultheli Lake, 16±4 at Beauvais Lake and 12±2 at Selwyn Lake (Thomas & Kiliaan, 1994). At Nonacho Lake, where sample size was highest (n=84 sites), fecal densities at 50-year intervals were 5±3 (SE), 67±27, 53±11, 134±44, and 147±54. High densities occurred in age classes 51-200 years at Porter Lake. These significant differences in use indices means that correlations between them and vegetation components should be made within regions where use by caribou does not vary significantly.

Pellet-group densities correlared positively ($P<0.05$) with forest age, age class combinations, caribou lichens, *Stereocaulon* spp., *Cl. uncialis*, arboreal lichens, and pine density and negatively with number of trees >10 cm (DBH). Use by caribou was best predicted in the east block by age (r=0.96) and in the west block by combining the intercorrelated variables caribou lichen biomass, arboreal lichen mean rating, and number of ttees >10 cm in DBH (r=0.95). Assumptions are violated and some correlations obviously are spurious. Associations between floral species and pellet densities will be explored in more detail in the future.

Discussion

Sampling design

At a landscape scale, site selection was based on where caribou tended to feed in late winter: xeric sites near warer courses that were used as travel routes. Fot comparative purposes, selection of favorable feeding areas was deemed preferable to a completely random sampling design. Of course, biomass of lichens ar representative feeding sites differ from sites chosen at random in the same habitat type (Edmonds & Bloomfield, 1984).

At a local scale, sampling was conducted in forest openings rather than under the branches of trees. Such stratification was necessary to reduce sample variation. In particular, lichen abundance was much higher in openings of young forests than under trees. Consequently, our results for lichen abundance and use by caribou are inflated fot young (11-50 years) and early-marure (51-75 year) forests; less so for old (>150 year) forests. Bias from a completely random placement of quadrats may be as high as 50% in young age classes where trees are dense.

Adequate sampling for lichen biomass depends on the spatial variability of lichen species deemed important to caribou. Our sampling protocol was deemed adequate for abundant species and lichen groups. Previous standing crop estimates in this caribou winter range were semi-quantitative (Scotter, 1964; Miller, 1976).

Terrestrial lichen biomass

An increase from west to east in total lichen biomass and succession rate is indicated by our results combined with those of Foster (1985) and Couturier & St-Martin (1990). Total terrestrial lichen biomass at caribou feeding sites >60 years averaged 2594 and 6250 kg/ha, in west and east sites, respectively. In forests >55 years in Quebec, tetrestrial lichen biomass averaged 1540, 4463, and 8354 kg/ha in pine, mixed, and spruce forests, respectively (Couturier & St-Martin, 1990). Russell *et al.* (1993) tabulated lichen biomass fot various srudies and listed sampling differences that confound comparisons. Comparative total lichen biomass is of botanical and ecological significance but caribou ecologists must focus on lichen species most utilized by caribou.

Our weighting of terresttial lichen biomass was an attempt to reflect proportionate consumption by caribou in the study area. The weightings were arbitrary but based on preference order in cafeteria-style feeding experiments (DesMuelles & Heyland, 1969; Holleman & Luick, 1977; Norberg *et al*, 1995), rumen and fecal microhistological analyses (Thomas & Barry, 1991), and examination of feeding craters (Thomas, 1994). Some adjustment of total terrestrial lichens was necessary because *Stereocaulon* spp., of low palatability and digestibility (Thomas *et al.*, 1984), dominated terresttial lichens in old fotests, particularly in the east block. Pethaps *Peltigera* spp. should be weighted low based on lowest preference (Holleman & Luick, 1977). The higher correlarion of peller-group densities with caribou lichens than weighted lichens indicates that *Stereocaulon* spp., *Cladonia* spp., and *Peltigera* spp. may be consumed incidentally, as suggested for conifer needles and moss (Thomas & Barry, 1991).

Factors affecting use of forests by caribou

Little use was made of forests younger than 60 years, though adequate forage was present 40-60 years after fire in some locations. Deadfall was not an impediment to movement in young stands. The high biomass of *C. mitis* 50-150 years after fire corresponded to increased use by caribou in that age group. *C. rangiferina* and *Cet. nivalis* had peak biomass corresponding to highest use by caribou in forests >150 years but their biomass was low. Weighted lichens did not correlate with catibou use indicating invalid weighting. There was no indication at feeding sites that *Stereocaulon* spp., *Peltigera* spp., and "other *Cladonia*" spp. were used ro any extent by caribou. Caribou clearly were nor responding to total lichen biomass. Use by caribou was 5-11 rimes higher at Nonacho and Porter lakes than at Beauvais and Selwyn lakes yet total lichen biomass was 2.4 times higher in the east than in the west.

Perhaps there are threshold values for cover and biomass of certain lichen species or groups that caribou respond to. From age class 41-60 to 61-80 years, indices of caribou use in the west block increased from 21 ro 107. Concurrently, mean biomass of *Cet. nivalis* increased from 30 to 72 kg/ha; that of *C. mitis* incteased from 547 to 1029 kg/ha, while changes were less or reversed in other lichen species. Thus, in terms of food, the caribou seemed to be responding most to these lichen species. If caribou key to threshold amounts of species or species groups, linear analyses may produce poor correlations.

How we partitioned age and floral components is critical yet artificial. Fot example, some high correlations between caribou use indices and plant species/groups resulted for sites 50-150 years. Caribou may have a more holistic view of habitat!

Predator avoidance behavior may be a factor in habitat use by caribou. Caribou seemed to prefer open forests 150 to 250 years post-fire. Open forests facilitate visual contact with othet members of the group and wolves.

Caribou in the Beverly herd seem to have adapted their movement pattern to differences in late-wintet snow depths at a landscape scale (Thomas, 1991). Movement to parts of the range with shallower snow in late winter generally occurred early in winter when snow cover was shallow and uniform across the range. Average snow depths were slightly lower in openings of marure and old forests compared with young ones but snow depth was not a problem in most winters (Thomas, 1991).

Most feeding by caribou was in forests along and adjacent to travel routes. These are lakes and lowland connections between lakes where rravel is easy and visibility is high. Some routes are traditional. Because of numerous environmental and behavioral factors, that vary annually, prediction of habitat suitability or caribou use by any one factor will have low probabiliries. Food is important but confounding factors include distance from travel routes, escape habitat, and snow conditions.

Management implications

Our results for lichen cover and biomass defined the sequence of lichen succession after fire in the study area. Previous results were semi-quantitative and not in the core of currenr winter range (Scotter, 1964, 1965; Miller, 1976). Our data on relative use by catibou of forests of different ages is rhe first available for a wide range of age classes. These resulrs were used, in part, to develop a fire suppression straregy for the wintet tanges of two herds of caribou (Beverly & Qamanirjuaq Caribou Managemenr Board, 1994). The strategy is based on current proportions of productive caribou range (>50 years) relative to goals for such habitat in zones mapped by local hunters.

The significant correlations between lichen cover and biomass (Bergerud, 1971; this study) means that ocular cover estimates can be used to assess the abundance of terrestrial lichens. This is important for future studies where staff, funds, and time are constrained. Cover estimates could be restricted to *Cladina* and *Cetraria* spp. if sites were sampled quickly using aircraft for access.

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A test of the herbivore optimization hypothesis using muskoxen and a graminoid meadow plant community

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Abstract: A prediction from the herbivore optimization hypothesis is that grazing by herbivores ar moderate intensities will increase net above-ground primary producrivity more than at lower or higher intensities. I tested this hypothesis in an area of high muskox (*Ovibos moschatus*) density on north-central Banks Island, Northwest Territories, Canada (73°50'N, 119°53'W). Plots (1 m^2) in graminoid meadows dominated by cottongrass (*Eriophorum triste*) were either clipped, exposed to muskoxen, protected for part of one growing season, or permanently protected. This resulted in the removal of 22-44%, 10-39%, 0-39% or 0%, respectively, of shoor tissue during each growing season. Contrary to the predictions of the herbivore optimization hypothesis, productivity did not increase across this range of tissue removal. Productivity of plants clipped at 1.5 cm above ground once or twice per growing season, declined by 60±5% in 64% of the tests. The productivity of plants grazed by muskoxen declined by 56±7% in 25% of the tests. No significant change in producrivity was observed in 36% and 75% of the tests in clipped and grazed treatments, respecrively. Clipping and grazing reduced below-ground standing crop except where removals were small. Grazing and clipping did not stimulate productivity of north-central Banks Island graminoid meadows.

Key words: grazing, arctic, biomass, planr community, roots.

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Introduction

The herbivore optimization hypothesis is a prediction that grazing by herbivores at moderate intensities increases net above-ground primary productivity above ungrazed, lightly grazed and heavily grazed levels (McNaughton, 1979). Its validity is equivocal (Painter & Belsky, 1993) because of the confounding problems of scale (Brown & Allen, 1989), methodology (see Belsky, 1986) and spatial and temporal variation among studies. Subarctic graminoids increased in productivity after being grazed by wood bison (*Bison bison athabascae*) at more productive sites, but not at less productive sites because plants at ungrazed sires smothered in a thick litter layer (Smith, 1990). Productivity of nutrient-limited meadows increased in response to snow goose (*Anser caerulescens caerulescens*) grazing and increased rates of nutrient cycling (Bazely & Jefferies, 1989; Hik & Jefferies, 1990). In contrast, carbon-limited plant species often decline in productivity after being grazed (Lacey & Van Poollen, 1981) because of reduced photosynthetic leaf area.

Since the 1950s, the population of muskoxen on Banks Island grew exponentially (Vincent & Gunn, 1981; McLean *et al.*, 1989). Muskox densities are particularly high (1.52/km^2) in the Thomsen River Valley of north-central Banks Island (McLean *et al.* 1989). Despite the eruption of muskox populations across North America (Smith, 1984; Thing *et al.*, 1984; Henry *et al.*, 1994), little is known about the summer range of muskoxen in northern Canada (Parker & Ross, 1976).

Muskoxen at Sverdrup Pass on Ellesmere Island feed in sparsely vegetated uplands with shallow snow cover during winter and on more productive lowland meadows during summer (Raillard, 1992). However, if snow cover is soft and shallow in meadows during winter, muskoxen will graze meadows all year (Hubert, 1977).

Consistent with the herbivore-optimization hypothesis, I predicted that: (1) Graminoid meadows would increase producrion in response to moderate clipping or herbivory by muskoxen; (2) Removal of shoot tissue by clipping or by muskoxen would have no effect on the standing ctop of live roots.

Methods

Study Area

The study area was located neat the confluence of the Thomsen and Muskox Rivets on north central Banks Island (73°50'N, 119°53'W). The climate is Arctic Desert with long cold winters, with mean January temperatures of -30°C, and short cold summers with mean July tempetatures of 4°C. Average precipiration is only about 9 cm annually (Zoltai *et al.*, 1980). The topography is gently rolling with the hilltops rarely exceeding 250 m in elevation a.s.l..

Wilkinson *et al.* (1976) described 5 habitat types including sedge meadows and Ferguson (1991) further divided the sedge meadows into: (1) wet sedge meadows (hygric), and (2) graminoid tundra (subhygric).

Eriophorum triste and *Carex aquatilis* var. *stans* are rhizomatous sedge species that overwinter with a small amount of basal green tissue. During summer, plants are composed of 1-2 potentially fertile culms surrounded by 2-8 sterile, leafy shoots (Porsild and Cody, 1980). The 2 species were abundant in northern Banks Island graminoid meadows (Smith, 1996). Muskoxen on northern Banks Island grazed graminoid meadows where *Eriophorum triste* was dominant more often than less productive wet sedge meadows where *Carex aquatilis* var. *stans* was dominant (pets. obs.).

Experimental design

Biomass data were gathered from 3 study sites within the graminoid plant community. Two study sites, Muskox River (MR) and Thomsen River (TR) each contained a 10 m x 10 m permanent exclosure erected in mid-August 1988. Ten 1 m X 1 m plots per treatment wete clipped 1.5 cm above the ground. Ar Muskox River, a group of plots was clipped once in 1991 and twice in 1992; another group served as a control in 1991 and was clipped once in 1992. At Thomsen River, a group of plots was clipped twice in both 1991 and 1992; another group was clipped once in both 1991 and 1992; Controls were not clipped. Plots were not clipped in 1993. Clipping intensity was the proportion of standing crop removed by clipping at one time. Cumulative green biomass was green shoot tissue removed by previous clipping added to the standing crop of green tissue. Standing crop was rhe weight of green tissue and standing dead tissue. Productivity was the change in standing crop, usually green tissue, over time.

Four 25 cm x 25 cm sub-plots were randomly located in each of 5 randomly-chosen plots per tteatment in 1992 and in the other 5 plots per treatment in 1993. A different sub-plot was clipped to ground level inside each plot 4 times during each of the 1992 and 1993 growing seasons.

Study areas of about 2 ha and 4 ha, adjacent to the permanent exclosures at MR and TR, respectively, were exposed to muskox grazing. A third meadow area of abour 1 ha was Umingmuk Hill (UH). Ten transects were laid out at 10-15 m intervals, with the first transect located randomly. Disrance between ttansects was dependent on study site size. Temporary exclosures ("exclusions") were also randomly located using a random numbers table along the transects in late June 1992 and 1993 (2 pet transect at MR and TR and 1 per transect at UH). These exclosures, 1.5 m in diameter, were made from aluminum fencing wire, which allowed the passage of small mammals and birds. At the end of each growing season, I counted all new fecal groups (i.e., < 3 months old) in a 3 m-wide belt along each transect.

To measure grazing intensity, a different sub-plot (25 cm x 25 cm) was clipped to ground level inside and out of each temporary exclosure 4 times during each of the 1992 and 1993 growing seasons. Grazing intensity was the proportion of standing crop consumed by muskoxen during a rime period (McNaughton, 1985a): $G = 1 - S_g/S_e$, where, G, S_g

and S_e were the grazing intensity, standing crop in grazed areas and standing crop in temporary exclosures, respectively.

All herbage samples were dried at 40-60°C for 24 hours and later dried for 48 hours at 60°C. Each sample was thoroughly mixed and a sub-sample of about one-third of the total was divided into live and dead tissue and extrapolated to the whole sample. Ten samples per year were separated entirely to determine if sub-samples were representative of the whole.

In 1992, I estimated the proportion of live tissue in each sample. Estimates were corrected by a regression equation developed after comparing actual and estimated proportions of live tissue in 166 samples. The equation was: $y = 4.21 + 0.84x$ ($r^2 = 0.86$), where, y and x were the actual and estimated percentage of live tissue, respectively. In 1993 all samples were separated.

Below-ground biomass

Ten soil cores (10 cm x 10 cm) were removed from each treatment at each site in late August 1993. The soil cores were frozen in the field and transported to the laboratory. The cores were dried at 70°C for 72 hours, broken apart, and crushed with a rolling pin. The marerial was sifted through 0.5 mm and 0.25 mm sieves. A sub-sample of about one-third was removed from each coarse and fine root sample. Live roots were weighed in all 120 sub-samples of coarse material and 15 randomly chosen sub-samples of fine material.

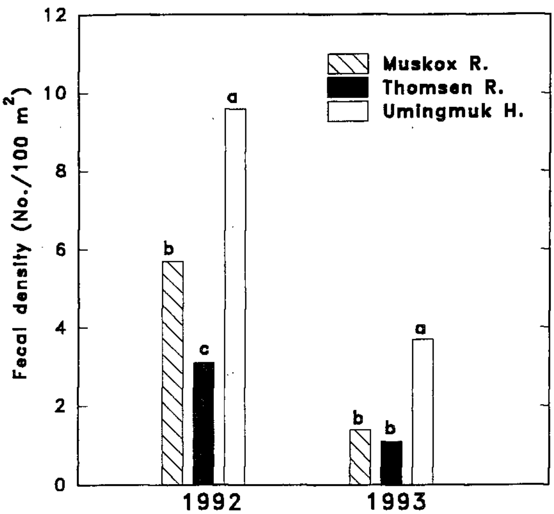

Fig.1. Fecal densities (no./100m²) (mean) in transects (n=10) at 3 study sites during the 1992 and 1993 growing seasons on northern Banks Island, Canada. Means with the same subscript within years are not significantly different at $P \leq 0.10$.

Table 1. Proportions of the standing crop removed by muskoxen at 4 dates in summers 1992 and 1993 at 3 study sites on Banks Island, NWT.[1]

Time Period	Study Sites		
	Muskox R.	Thomsen R.	Umingmuk H.
Jun 25 – Jul 9 1992	0.16a	0.27a	0.13a
Jun 25 – Jul 21	0.32a	0.26a	0.00b
Jun 25 – Jul 31	0.29a	0.23a	0.29a
Jun 25 – Aug 9	0.10b	0.12b	0.39a
Jun 25 – Jul 6 1993	0.09a	0.17a	0.30a
Jun 25 – Jul 22	0.26a	0.10a	0.22a
Jun 25 – Aug 3	0.25a	0.28a	0.23a
Jun 25 – Aug 17	0.18a	0.19a	0.29a

[1] Means with the same subscript within rows are not significantly different at $P \leq 0.10$.

The volume of each core was used to calculate the weight of toots for each 1 m x 1 m plot. Because few roots grew below 10 cm in 6 soil profiles, I concluded that root biomass estimates were slightly low. In another arctic meadow community, Muc (1977) found that 65% of below-ground standing crop was above 10 cm in soil profiles.

Data analysis

All data wete tested for normality using the Shiparo Wilks W test (SAS, 1988) and variances were tested for homogeneity using the F_{max} test (Sokal & Rohlf, 1981). If necessary, data were transformed by log + 1 or square root + 0.5 in order to satisfy the assumptions of parametric statistics. One-way analysis of variance was conducted on the results for all treatments. Means were compared with the LSD test (Sokal & Rohlf, 1981). Statistical significance was assumed to be at $P \leq 0.10$.

Results

Grazing and clipping intensities

Umingmuk Hill had the highest fecal density among the 3 study sites in both years (Fig. 1). Proportions of the standing crop removed by muskoxen ranged from 0-39% of the available fotage over 4 periods during a growing season (Table 1).

Table 2. Proportion of plant tissue removed in 1992 by clipping 1 m x 1 m plots (mean±SE) (*n*=5) inside permanent exclosures at 2 study sites.

Location	Date clipped	Total no. of clippings in 1992	No. of previous clippings 1991	1992	Proportion removed
Muskox R.	July 2	1	0	0	0.22±0.05
Muskox R.	July 1	2	1	0	0.08±0.02
Muskox R.	July 16	2	1	1	0.26±0.02
Thomsen R.	July 8	1	1	0	0.25±0.05
Thomsen R.	July 8	2	2	0	0.30±0.04
Thomsen R.	July 22	2	2	1	0.14±0.02

Table 3. Standing crop estimates (g/m²) (mean±SE) (*n*=5 per treatment) obtained in 1992 and 1993 for plots with variable clipping histories inside permanent exclosures in 1992 and 1993, northern Banks Island, Canada.

		Standing crop (Mean±SE, g/m²)[1]						
		Previous clippings			Previous clippings			
Location	Date clipped	'91	'92	Standing crop	'91	'92	Standing crop	Control[2]
Muskox R.	July 27/92	1	2	45± 6b	0	1	59± 7b	111±16a
Muskox R.	July 29/93	1	2	121±13a	0	1	125±11a	151±14a
Thomsen R.	July 31/92	2	2	106±12b	1	1	129± 7b	392±30a
Thomsen R.	Aug. 3/93	2	2	148±12b	1	1	157±13b	316±57a

[1] Means with the same subscript within rows are not significantly different at $P \leq .10$.
[2] The control had a high proportion of standing dead material, whereasrhe clipped plots contained mostly green material.

Table 4. Standing crop in late July-early August, 1992 and 1993 where grazed, where muskoxen were excluded after June 25 rhat season, and in control (permanent exclosures) plots onnorthern Banks Island, NWT. (Number of plots are in parentheses).[1]

Location	Date Clipped	Mean Standing Crop (g/m²)(±SE) Grazed	Exclusion[2]	Conttol
Muskox R.	Jul. 28/92	99±12b (20)	140± 9a (20)	111±16ab (5)
Muskox R.	Jul. 30/93	116± 9b (20)	155±11a (20)	151±14a (5)
Thomsen R.	Jul. 31/92	206±20c (20)	268±16b (18)	392±30a (5)
Thomsen R.	Aug. 3/93	165±16c (20)	228±17b (20)	316±57a (5)
Umingmuk H.	Aug. 4/92	217±20b (10)	305±44a (7)	NA
Umingmuk H.	Aug. 7/93	240±24b (10)	311±30a (10)	NA

[1] Means with the same subscript within rows are not significantly different at $P \leq 0.10$.
[2] Muskoxen excluded after June 25 for that season only.

Plots clipped once in early 1992 had 22-25% of tissue removed but plots clipped twice had 34-44% of tissue removed per growing season (Table 2).

Above ground standing crop

Clipping of plots in permanent exclosures at Muskox River (MR) and Thomsen River (TR) reduced standing crop 17 to 73% below the controls in 1992 and 1993 (Table 3). By late July 1993, however, standing crop was similar in clipped and unclipped plots at MR, averaging 132±13 g/m².

Standing crop was 23-29% lower when grazed by muskoxen than in exclusions. Standing crop was 23% and 48% lower in the grazed plots than in

Table 5. Cumulative production of green biomass at 2-5 clippings over 1 and 2 growing seasons and in controls at 2 areas of northern Banks Island, NWT.

		Green biomass (Mean±SE, g/m^2)[1]						
		Previous clippings			Previous clippings			
Location	Date clipped	'91	'92	Cumulative biomass	'91	'92	Cumulative biomass	Control
Muskox R.	July 27/92	1	2	38.7±3.9b	0	1	40.5±5.6b	70.6± 9.6a
Thomsen R.	July 31/92	2	2	57.5±3.4c	1	1	86.5±6.8b	136.3±10.2a

[1] Cumulative green biomass includes green shoot tissue removed through clipping added to green standing crop on date indicated. Means with the same subscript within rows are not significantly different at $P \leq 0.10$.

Table 6. Mean (±SE) green, total and absolute productivity estimates[1] ($g\ m^{-2}\ d^{-1}$) among treatments in 1992 and 1993 1m x 1m plots (n=5) inside permanent exclosures.

			Biomass Production (Mean±SE, g/m^2/day)						
			Previous clippings			Previous clippings			
Location	Production period	Productivity component	'91	'92	Biomass production	'91	'92	Biomass production	Control
Muskox R.	Jul 3 – Jul 27/92	Green	1	2	0.8±0.2b	0	1	1.2±0.2b	2.3±0.4a
Muskox R.	Jun 27 – Jul 29/93	Green	1	2	2.6±0.4a	0	1	2.7±0.4a	3.4±0.6a
Muskox R.	Jul 3 – Jul 27/92	Total	1	2	-0.3±0.3b	0	1	1.4±0.3a	2.7±0.7a
Muskox R.	Jun 27 – Jul 29/93	Total	1	2	2.5±0.4ab	0	1	2.4±0.3b	3.5±0.6a
Muskox R.	Jul 3 – Jul 27/92	Absolute	1	2	0.8±0.2b	0	1	1.4±0.3ab	2.7±0.6a
Muskox R.	Jun 27 – Jul 29/93	Absolute	1	2	2.6±0.4a	0	1	2.7±0.4a	3.6±0.5a
Thomsen R.	Jul 8 – Jul 31/92	Green	2	2	1.4±0.1b	1	1	1.4±0.3b	4.4±0.4a
Thomsen R.	Jul 4 – Aug 3/93	Green	2	2	2.5±0.6a	1	1	1.6±0.2a	1.6±0.2a
Thomsen R.	Jul 8 – Jul 31/92	Total	2	2	2.5±0.5a	1	1	0.2±0.4b	4.5±1.3a
Thomsen R.	Jul 4 – Aug 3/93	Total	2	2	4.2±0.7b	1	1	2.5±0.7b	7.8±1.8a
Thomsen R.	Jul 8 – Jul 31/92	Absolute	2	2	2.5±0.5b	1	1	1.4±0.3c	5.2±0.7a
Thomsen R.	Jul 4 – Aug 3/93	Absolute	2	2	4.2±0.7b	1	1	2.6±0.6b	7.8±1.8a

[1] "Green productivity" is live (green) plant tissue. "Total productivity" is live (green) and dead plant tissue. "Absolute productivity" is live (green) plant rissue plus the transfer of live to dead tissue. Means with the same subscript within rows are not significantly different at $P \leq 0.10$.

control plots at MR in 1993 and at TR in both yeats, respectively (Table 4).

Herbage biomass and productivity

Productivity did not increase aftet removing 0% to 44%. The Cumulative Green Biomass in 1992 was greatest in the control and lowest when clipped twice. The 2 clippings had no additional effect over the single clipping at MR (Table 5). Estimates of green, total and absolute productivity were higher in the control than in clipped plots in 1992 and 1993; however by 1993 no change in production occurred in over one-half the cases (Table 6). There were fewer decreases in production in 1993 (42% of cases) than in 1992 (81% of cases).

Productivity declined in 25% of the grazed plots compared with 64% of the clipped plots. Production of clipped and grazed plants declined by 60±5% and 56±7%, respectively. Productivity in grazed areas was lower than production in temporary exclosures in 28% of the cases (Table 7).

Root biomass

Clipping reduced the weight of roots at TR by 10% to 32%, but moderately clipped plots had 18% more below-ground biomass than the control at MR

Table 7. Green, total and absolute productivity (g m^{-2} d^{-1}) estimates (Mean±SE) among treatments in 1992 and 1993 1m x 1m plots. (Sample sizes in parentheses).[1]

			Biomass production (Mean±SE)(g/m²/day)		
Location	Production Period	Producrivity Component	Grazed	Exclusion[2]	Control
Muskox R.	Jul 4 – Jul 28/92	Green	1.6±0.3b (20)	2.3±0.2a (20)	2.3±0.4ab (5)
Muskox R.	Jun 30 – Jul 30/93	Green	1.6±0.3b (20)	2.1±0.3b (20)	3.4±0.6a (5)
Muskox R.	Jul 4 – Jul 28/92	Total	2.2±0.6b (20)	3.5±0.4a (20)	2.7±0.7ab (5)
Muskox R.	Jun 30 – Jul 30/93	Total	1.5±0.4b (20)	2.6±0.4a (20)	3.5±0.6a (5)
Muskox R.	Jul 4 – Jul 28/92	Absolute	2.6±0.5a (20)	3.6±0.4a (20)	2.7±0.6a (5)
Muskox R.	Jun 30 – Jul 30/93	Absolute	1.9±0.3b (20)	2.9±0.4a (20)	3.6±0.5a (5)
Thomsen R.	Jul 10 – Aug 1/92	Green	2.7±0.4b (20)	3.8±0.5ab (19)	4.4±0.4a (5)
Thomsen R.	Jul 7 – Aug 3/93	Green	0.3±0.4b (20)	2.3±0.4a (20)	1.6±0.2ab (5)
Thomsen R.	Jul 10 – Aug 1/92	Total	3.7±1.0a (20)	4.1±0.9a (19)	4.5±1.3a (5)
Thomsen R.	Jul 7 – Aug 3/93	Total	1.6±3.1b (20)	3.0±0.6b (20)	7.8±1.8a (5)
Thomsen R.	Jul 10 – Aug 1/92	Absolute	4.4±0.9a (20)	5.4±0.6a (19)	5.2±0.7a (5)
Thomsen R.	Jul 7 – Aug 3/93	Absolute	2.2±0.5b (20)	3.3±0.5b (20)	7.8±1.8a (5)
Umingmuk	Jul 14 – Aug 4/92	Green	3.7±0.6a (10)	4.4±0.7a (7)	NA
Umingmuk	Jul 13 – Aug 7/93	Green	1.2±1.2a (10)	1.0±0.5a (10)	NA
Umingmuk	Jul 14 – Aug 4/92	Total	3.5±0.9a (10)	6.8±1.9a (7)	NA
Umingmuk	Jul 13 – Aug 7/93	Total	1.9±1.5a (10)	1.2±0.8a (10)	NA
Umingmuk	Jul 14 – Aug 4/92	Absolute	4.4±0.8a (10)	7.5±1.7a (7)	NA
Umingmuk	Jul 13 – Aug 7/93	Absolute	2.9±1.1a (10)	2.0±0.6a (10)	NA

[1] Means with the same subscript within rows are nor significantly different at $P \leq 0.10$.
[2] Muskoxen excluded after June 25 for that season only.

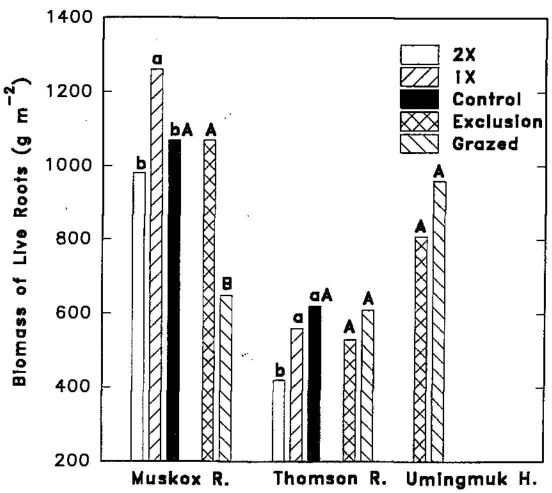

Fig. 2. Mean root biomass (g/m²) in clipped (twice=2X and once=1X) and unclipped plots (lower case subscript) and in exclusions, grazed and unclipped plots (upper case subscript) in August 1993 on northern Banks Island, Canada. Means with the same subscripts within study sites are not significantly different at $P \leq 0.10$. Clipping schedule in text.

(Fig. 2). Root weights were stable in temporarily protected plots (exclusions) at MR and TR, however grazed plots had reduced root weights by 39% compared to controls and exclusions at MR.

Discussion

The absence of increased productivity above- and below-ground, across a broad range of shoot tissue removal suggests that increased productivity aftet grazing is nor an important ecological phenomenon on northern Banks Island. Lower aerial productivity and root biomass in clipped and grazed than in controls in this study reflect high grazing and clipping intensities, latge clipped plots in the clipping experiment and severe climate. The hypothesis that graminoid meadows become more productive in response to moderate clipping and gtazing by muskoxen is rejected.

Given the ability of these plants to recover after removal of shoot tissue and the predominance of stable productivity after gtazing, current grazing intensities ate not likely to cause prolonged damage to the graminoid meadows. Muskox densities would have to be much higher to inflict damage to graminoid meadows. The decreased productivity in grazed areas is presently of little consequence to Banks Island muskoxen because the current population cannot graze all the forage produced during the summer. Meadows were intensively grazed compared with the values reported from othet tetrestrial ecosystems (Crawley, 1983; Pimentel, 1988; Raillard, 1992). However, muskoxen clearly were not food-testricted during the summer because over two-thitds of the forage remained ungrazed.

Productivity declined mote after clipping than after grazing. Clipping was concenttated early in the season, while grazing was spread more evenly throughout the growing season. In 1992, 2 clippings removed more shoot tissue than gtazing and a single clipping. Deposition of feces and urine (Putman, 1984), saliva (McNaughton, 1985b), trampling (Belsky, 1986), and selective herbivory (Bryant *et al.*, 1983) were present only in grazed areas. Plants are most vulnerable to damage from grazing early in the growing season (Bedard *et al.*, 1986). Mattheis et al. (1976) also found that intensive clipping of arctic graminoids resulted in reduced productivity. Howevet, on Ellesmere Island, Canada, intensively clipped and unclipped plots had similar above-ground productivity (Raillard, 1992).

The plants had adequate reserves to largely recover from clipping in only 1 summer. Factors that could have played a role in the recovery in 1993 were more active uptake of nutrients after defoliation (Chapin & Slack, 1979; Shaver *et al.*, 1986), reliance on extensive below-ground reserves (Muc, 1977), resource sharing among tillers (Jonsdottir & Callaghan, 1989), increased availability of nutrients from feces and urine (Henry & Svoboda, 1989), and the ability of tundra graminoids to occupy disturbed and undisturbed sites (Shaver & Billings, 1975).

The apparent depression of root biomass after grazing or clipping is consistent with decreased above-ground productivity. Such decreases can occur after short-term clipping (Richards, 1984), however, root weights more accurately teflect long-term perturbation than above-ground production. There is a time lag after herbivoty before changes in root biomass become appatent (Stoddart *et al.*, 1975). Higher root weights when clipped once at MR were unrelated to clipping *per se*, given the constraints on these plants imposed by lemming herbivory (pers. obs.). The MR exclosure was used as a lemming (*Lemmus* spp., *Dicrostonyx* spp.) nest during the winter of 1990-91 (pers. obs.). Lemmings can remove 90% of available forage (Schultz, 1969).

The inadvertent inclusion of mineral material on roots and subjectivity in determining live roors from dead ones both contributed to inconsistencies observed in the MR exclosure data. Root standing crop dynamics would become clearer if treatment effects were imposed over many years. Other studies examining the effects of grazers on root biomass in high latitude meadows have demonstrated neuttal or positive responses (Cargill & Jefferies, 1984; Henry & Svoboda, 1989).

Graminoid meadows showed decreased above-ground productivity after clipping and grazing treatments, large standing crops in grazed areas and the ability to largely recover from severe clipping tteatments in only 1 growing season. This decreased productivity is unlikely to adversely affect muskoxen in the short-term. Future research should be directed at determining the long-term consequences of high grazing intensities and at protecting this critical muskox habitat.

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Canadian Muskoxen in Central Europe – A Zoo Veterinary Review

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Abstract: This paper summarizes 29 years of veterinary experience maintaining a herd of muskoxen at the Tierpark Berlin-Friedrichsfelde, Berlin, Germany. The transplanted muskoxen acclimated to the zoo enviroment without faralities. However, a few srriking changes were seen. They exhibit a high sensitivity to sudden changes in weather conditions (especially falling atmospheric pressure); there is a tendency for their qiviut to become sparser with time; rutting and subsequent calving occur larer than in their native habitat. Details of medical conditions in both calves and adults are given along with information on hematology and immobilization.

Key words: *Ovibos moschatus,* disease, parasitology, pediattics, zoo medicine, review.

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Introduction

Muskoxen once roamed Northern Europe, but became extinct during the Pleistocene, presumably due to climatic changes as the glaciers retreated. To this day, climate requirements are the main limitation to successful breeding and maintenance of this species in continental Europe. The first teintroduction to Europe was in 1899, when two calves were captured from Greenland for the Duke of Bedford's zoological park at Woburn Abbey, England. From 1899 to 1969 about 300 calves were translocated from NE Greenland to Norway, Iceland and, unintentionally, to Sweden for display in zoos, domestication experiments, or for release into the wild (Alendal, 1980; Klein, 1988). Because the calf captures involved shooting all the adults within a group, the Association of European Zoo Directors banned purchase of muskox calves in 1926. In the early 60s, this situation began to change with the introduction of tranquilizer guns, faster transport and better zoo veterinary care. For recent information on maintaining muskoxen in Europe see Holst (1990).

The Tierpark Berlin-Friedrichsfelde, which was opened in 1955, covers an area of about 160 hectares, is located at 52'05°N., 13'04°E., at an elevation of 36m. In addition to a broad collection of wild ruminants, our first muskoxen (1.1 calves of the subspecies *Ovibos m. moschatus*) arrived in 1966 from the Alberta Game Farm, Edmonton, Alberta, Canada. Since then, the species has acclimated to our Central European conditions. This paper summarizes 29 years of experience maintaining captive muskoxen in a zoo environment.

Animal Maintenance

Table 1 provides a synopsis of muskox numbers, births and deaths at Tierpark Berlin-Friedrichsfelde betweem 1966–1995.

Table 1. Muskox stock development at Tierpark Berlin-Friedrichsfelde, 1966–1995.

	Total (males.females)	Source
Founding stock	2(1.1)	Canadian born, arrived in 1966
Additions	8(4.4)	Calves, Canada and European Zoo born
Birrhs	31(14.17)	including abortions and stillbirths
Losses	35(18.17)	Table 2
Moved	1(0.1)	
Present	5(1.4)	

Housing

The muskox are kept in an 850 m² enclosure with metal fencing (1.6 m high with 6 horizontal steel tubes, 72 mm in diameter. The vertical tubes are 100 mm in diameter and 2.4 m apart). A 3 x 5 m² separate pen is available for bulls and/or any sick animals. The ground is a sandy soil wirh ballast-stones. A 2m-wide concrete slab along the fence provides an abrasion surface for hooves while a few oak trees and a wooden shelter provide shade. There is no mixing of muskoxen with other species.

Feeding

Nutrition of zoo kept muskoxen has not presented serious problems. The base in our zoo is a mixtute of concentrates with a crude protein level of 23.9 % and metabolizable energy of 11.3 MJ/kg. This mixture ('pellets for herbivores' 50 %; kibbled oats 30 %; wheat bran 10 %; crushed barley 10%) is fed at the rate of 1.0 kg/animal/day, with the occasional addition of rolled oats, linseed or soya bean meal. In cases of diarrhea a special diet of crisp bread toast and ripe, dry oak are given. Vegetables in season are always provided (carrots and elder berries are favorites), as are green feed lucerne, grass, maize, rye, fresh leaves and branches of oak, willow, poplar, maple, plan-tree, and rowan. During the winter mixed hay from local grass is fed, (alfalfa being most preferred by the animals) and dried branches of oak and willow are provided. Reindeer lichen *Cladina rangiferina* is not often fed. Mineral supplements and multivitamins are added to the feed and salt licks and drinking water are available *ad. libitum* (Seidel, 1979).

Seasonal Responses

Climate change

Muskoxen are affected by sudden changes in weather conditions (especially falling atmospheric pressure and hear-waves): We typically see reduced appetite, diarrhea, and a dull attitude in response to sudden climate change. Changing the food, adding anti-diarrhea agents, and cooling the enclosure by lawn- sprinkler has overcome such phases.

Qiviut Shedding

Under Central European conditions, shedding of the underhair occurs earlier in the spring than in Canada (Tener, 1965; Pohle, 1981). Yearlings begin shedding in early March and adults in early April, although periods of cold weather will slow this process. Pregnancy will also delay shedding, which is finished shortly after calving. Most of the animals finish shedding by the end of July and growth of the winter pelage is evident in August. In calves, shedding begins in late July and is finished by late October. The outer hair is continually shed and replaced in all muskoxen. Generally, our 3 Canadian born animals, exhibit the fine underhair described by Wilkinson (1975), but females (between 12–16 years old) develop sparser, paler hair, possibly an adaptation to our mild climate. From the outset, the animals born here, and in the Munich zoo, have a thinner, shorter underhair (reduced by approximately 20 %). In these latter animals the shedding process begins about 3 weeks later and extends into late October.

Rutting/calving season

Our original Canadian bull showed signs of sexual maturity (protrusion of the penis during erection) at 12-months-old, with his first successful copulation at 2.5-years-old. The Berlin born calf, Alf, matured at 6-months-old and bred at 3.5-years-old. The typical rutting odor, caused by the bull urinating on the caudal abdominal region, begins at the end of June. Highly aggressive male rutting behavior is first evident at the age of 3–4 yeats, with a seasonal peak of rutting activity in the third week of September. Structures within the enclosure (trees, stones, fences) ate attacked and often demolished. The aggressive displays and attacking of female muskoxen can be provoked by the sight of zoo personnel. The mean rutting season is finished by the end of October, with the exception of young bulls (2-years-old) who have an extended rutting season to the end of December. This has been related to calving in late July/early August.

In general, calves are born between 1 to 22 of June (with a concenttation between 1–9 June). Birth weights range between 7.5–12.3 kg (7.5–8.9 kg in first deliveries). The age of cows at first calving was 3–4 years with calving in consecutive years (Pohle, 1981).

Pediatric Medicine

Infectious diseases

The highest mortality is among calves (Table 2). Acute cases of pneumonia, catatrhal enreritis and colisepticemia occurred with the clinical signs of dullness, inappetence, fever (>39,5°C), tachycardia, dyspnea/tachypnea, initially moderate to high leukocytosis, while in the final stages leukopenia, anemia, and cardiovascular (infection-related) collapse occurred. With the exception of *E. coli* 086:K61, no bacterial pathogens could be identified due to antibiotic treatment. The suspected initiating factor for this problem is extremely high ambient temperatures (June–Septembet, often more than 28°C). The calves become very inactive recumbent with no food intake. Pneumonia at the beginning was unilateral (under-sided) by hypostasis. Routine pteventative programs, used in orher zoo ruminants (multivitamins including Selenium; gamma globulin, from cattle; and an iron supplement – all given at birth and 14 days later, plus vaccinations against tetanus at weeks 8 and 12) wete ineffective against this condition.

Table 2. Cause of death in young and adult muskoxen kept at Tierpark Berlin-Friedrichsfelde, 1966–1995.

Condition	Calves		Adult		
	(n)	%	(n)	Age range	%
Infectious Diseases	10	43.6	6	6.5–15.5	54.5
Stillbirths	5	21.8			
Abortions	3	13.0			
Ileus/intussusception	3	13.0			
Metabolic Disorder	1	4.3			
Heart Failure	1	4.3	1	3.1	9.1
Toxins			2	7.5, 8.8	18.2
Accident			1	2.6	9.1
Old Age			1	21.5	9.1

Abortions and stillbirth

Three abortions occurred in two multipara cows of 6, 8 and 13 years old. No pathogenic agents could be isolated and the causes of the abortions ate unclear. Five cases of stillborn calves (3.2) from 3 cows have occurred; one of them had an abortion at 8 years-old and for the next two consecutive years produced stillborn calves (2.0). The calves were fully developed and no pathogens identified. As with the abortions, the causes remain unknown.

Ileus/intussusception

Three cases of acute, fatal ileus occurred in two female, mother-raised calves at 4 and 6 weeks old, and on day 4 in bottle-fed male. These all occurred during an exrreme weather phase (July, 28–32°C) with symptoms of pneumonia and colic. Symptomatic therapy, including antibiotics, was not effective.

Other

An unidentified metabolic disorder in a male calf led to lethal nephrosis (after prerenal dysproteinemia) over a 5 week course following severe trauma. Another male (14 months old) died of heart failure after a second chemical immobilization for treatment of a metacarpal fracture.

Susceptibility to Stress

For about the first 8 months, calves are very susceptible to stress. Social interactions or catching by hand resulted in immediate hyperventilation and a body temperature increase of 1–2°C within 4–7 minutes. Althougt apocrine sweat glans are associated with hait follicles (Flood *et al.*, 1989), body cooling is done mainly through the muzzle. To minimize risks of hyperthermia, all handlings are done as quickly as possible during cool times of the day. Body temperature can be reduced by cooling with a lawn-sprinkler. These dramatic reactions have never been seen in hand-reared calves. Mechanisms for regulating core body temperature in newborn calves have been described in detail by Blix *et al.* (1984).

Diarrhea and Parasites

Diatthea is always seen in calves following a sudden change of wearher or with massive coccidial infections. Treatment is based on the identification of the etiologic agent (Table 3). Of importance in bouts of diarrhea is the constant control and cleaning of the calves' analogenital region and use of an insecticide powder for protection from *Lucilia sericata*-caused

Table 3. Parasitological findings and treatment in muskoxen at Tierpark Berlin-Friedrichsfelde, 1966–1995.

Parasites	Intensity	Drug	Dosage mg/kg bw	Route
Nematodes	(+) – ++	Fenbendazole, Panacur® (HOECHST)	8	p.o.
Strongyloididae		Ivermectin, Ivomec® (MSD-Agvet)	0.2	s.c.
Stongyloides sp.		Mebendazole, Mebenver® (JANSSEN)	20	p.o.
Strongylidae		Thiabendazole, Thibenzol® (MSD-Agvet)	50	p.o.
Oesophagostomum sp.				
Trichostrongylidae				
Haemonchus sp.				
Haemonchus contortus				
Trichostrongylus sp.				
Ostertagia sp.				
Cooperia sp.				
Metastrongylidae				
Dictyocaulus viviparus				
Ascarididae				
Ascaris sp.				
Trichuridae				
Trichuris ovis				
Capillaria longipes				
Tapeworms		Praziquantel, Droncit®	8	p.o.
Echinococcus granulosus	(+)*	(BAYER)		
Moniezia sp.	+			
Coccidia**	(+) – ++			
E. arloingi, E. crandallis		Sulfadimidine (various products)	100	i.m.,p.o.
E. faurei, E. intricata,		Sulfathiazole Socatyl® (ASID)	200	p.o.
E. ninakohlyakimovae,				
E. parva				
Sarcocystis sp.	(+)			
Flies				
Lucilia sericata	+ – ++	Bromocyclen, Alugan® (HOECHST)	Local	Powder

(+) = trace burden, + = moderate burden, ++ = heavy burden, * = post mortem finding, ** = Tscherner (1973).

myiasis, a potentially serious ectoparasite problem under zoo conditions.

Two parasite groups have proved troublesome in calves; Coccidia and Trichuridae: High intensity coccidia burdens are seen particularly from the 4th month of life (when the forestomach system begins to work) and result in reduced growing rate, emaciation, and diarrhea. Adults seem to be resistant to these coccidia (Tscherner, 1973). Ova of two species of Trichuridae (Table 3) are regularly identified in cases of diarrhea and treatment is needed, even in minimal, small intensity burdens.

An interesting observation is that both maternal and hand reared eat great quanrities of sand from the enclosure (visible about 30 hours later in their feces). If prevented from eating sand to protect them from coccidia-oocysts, 1.5 days later a profuse diarrhea occurs. To stop and prevent this we provide heat sterilized humus soil (about 100 g twice/day, which is accepted).

Medical problems in adult moskoxen

Infectious diseases

Genetalized infections have been cause of death in 3.3 adult muskoxen (Table 2). Generally, no specific clinical symptoms occurred, activity and appetite wete reduced, with occasional signs of pneumonia and nasal mucus. No pathognomonic changes in hematology, blood biochemistry or serologic tests were evident and fecal floats were negative for parasites. As a rule, animals are treated symptomatically with broad spectrum antibiotics, cardiovascular drugs, and antiparasitics. Various pathogenic agents were found *post mortem* (different cocci, *Pseudomonas aeruginosa, Pasteurella multocida*, rickettsia). In addition, a variety of lesions were found: purulent pericarditis, and in a case of *Pasteurella* infection, cachexia. There was 1 positive identification of Q-fever (Wisser *et al.*, 1993). All these diseases occurred during or shortly after the rutting season (mid September to late December) – possibly from immunosupression.

Toxins

One of our adult males died from renal failure caused by *ad. lib.* ingestion of green oaks (Wundersee *et al.*, 1979). Following this incident management changed to ensure that muskoxen do not have access to large volumes of freshly fallen oaks. Very occasionally, oak-related diatrhea is seen.

In cases of unintentional overfeeding with high energy ptotein feed, laminitis has occurred, with prolapsed penis in the male. This was successfully treated by withholding protein feed fot a few days.

One 9-yeat-old cow died following a 7 hour course of incoordination and cardiogenic convulsions. Post mortem examination found epicardial and myocardial hemorrhage, hepatomegaly, tubulonephrosis, and generalized congestion. No pathogenic agents were identified, but the lesions and clinical symptoms indicate a peracute toxemia.

Trauma

The most frequent injuries among adults were wounds (often infected), contusions, scratches, hematomas and lameness caused by the rutting bull during the months August to October. Medical intervention followed general surgical procedures, involving treatment under anesthesia, local and general broad spectrum antibiotics, tetanus-prophylaxis and contact insecticides against myiasis. Tteatment was often complicated by dangerous, stress-related hyperthermia.

Reproductive disorders

Abortions and stillbirths, the most serious reproductive problem, were reported under pediatrics. Other problems, chronic lochial discharge in a primapara cow and placental retention following an abortion, were successfully treated using standard protocols. For basic information of the reproductive biology and endocrinology in muskoxen see Rowell (1991, 1993), for clinical details see Seidel (1995).

Parasites

In general the intensity of parasity of burdens in our adult muskoxen remained subclinical. Fecal examinations for parasites were performed at the parasitological laboratory (head: Dr. W. Tscherner) of the zoo. Moderate intensity burdens of *Strongyloides sp.*, *Dictyocaulus sp.* and *Moniezia sp.* were seen during the first two years after the muskoxen arrived here. Treatments followed standard procedures (Table 3).

A severe infestation with *Lucilia sericata* can result in serious clinical symptoms, e.g. a 10-year-old rurting bull with purulent secretion between and around the horn bases, had a serious infestation of maggots of this fly. After unsuccessful local treatment, the left horn was amputated at its base. Continued antibiotic treatment was again unsuccessful and the bull died of a generalized infection. At necropsy a purulent pleuropneumonia and pericarditis due to *Pasteurella* infection, were identified. In addition, old tuberculosis in intestinal lymph nodes were found. This is the first identification of TB in muskoxen at this zoo and to date no further cases have been identified.

Geriatrics

One female, shipped to us as calf, teached the age of 21.5 years-old. She produced 7 living calves, had 3 stillbirts and 2 abortions. She had her last calf at 17 years-old. After a healthy life she died of heart failure while sleeping.

Immobilization

Detailed reports on chemical immobilization fot managing free-living muskoxen have been given by (among others) Jonkel *et al.* (1975), Patenaude (1982), and Dieterich (1984); information from captive herds and zoo kept muskoxen, using injectable and inhalant agents are provided by Jones (1971), White *et al.* (1985), and Seidel (1979, 1985). Since all painful treatments in muskoxen require full chemical immobilization, we have tested a number of agents, the results of which are listed in Table 4.

Hematology/Blood Biochemistry

There are numerous publications tegarding physiological blood value in free-living captive Canadian and Alaskan muskoxen (Dieterich, 1970; White *et al.*, 1985; Dieterich & Fowler, 1986; Tedesco *et al.*, 1991; Groves, 1992), but less is known about zoo

Table 4. Immobilizing/narcotic agents used in muskoxen at Tierpark Berlin-Friedrichsfelde, 1966–1995.

Compounds	n	Trade Names (SOURCE)	Dose mg/kg i.m./i.v./p.o.	Antagonist	Trade Name (SOURCE)	Dose mg/kg i.m./i.v.	Induction Time	Recovery Time
Acepromazine Maleate	1	Vetranquil® (ALBRECHT)	–/–/0.6	– –	– –	– –	2-3 hrs	8-10 hrs
Propiopromazine Hydrochloride	3	Combelen® (BAYER)	0.1/–/–	– –	– –	– –	20-40 min	5 hrs (max)
Xylazine &	9	Rompun® (BAYER)	0.5-1.5/–/–	Yohimbine	various	–/0.1-0.3	3-6 min	30-70 min
Ketamine		various	1.0-2.0	– –	– –			
Etorphine	4	Large Animal Inmobilon® (C-Vet)	0.016-/–/– 0.018	Diprenorphine	Large Animal Revivon (C-Vet)	twice the etorphine dose - i.v. & i.m.	1-4 min	2-4 min

Table 5. Blood chemistry values from 11 healthy muskoxen raised at Tierpark Berlin-Friedrichsfelde, 1966–1995.

Parameter	Units	Value	Parameter	Units	Value
RBC	T/l	5.4-9.9	Na	mmol/l	138-142
Hb	g/l	88-144	K	mmol/l	4.1-5.6
PCV	g/l	0.25-0.50	Ca	mmol/l	2.2-2.6
WBC	G/l	4.9-12	Cl	mmol/l	74-129
Ly	%	40-65	P	mmol/l	1.7-2.6
Mo	%	2-5	Glucose	mmol/l	3.3-6.4
Eos	%	3-10	Bili	mmol/l	3.5-17.1
Bas	%	0-3	Protein	g/l	60-76
Neutro	%	45-60	Albumin	g/l	22-38
ALAT (GPT)	IU/L	18-34	Creat	mmol/l	159.1-300.5
ASAT (GOT)	IU/L				

kept muskoxen (Jones, 1971; Seidel, 1979; Hawkey, 1983). During the last 26 years most of our blood collections have been made for diagnostic purposes. The results from 11 samples, collected from healthy animals, are presented in Table 5 (Seidel, 1995).

We generally found hematological reflections of disease similar to other bovids: leukocytosis (with relative lymphocytoses) in inflammations and respiratory diseases, neutrophilia in general septicemia; reduced erythrocyre count, hematrocrit and Hb under etorphine-xylazine narcosis, and hypochromemia in Q-fever infection (Seidel, 1979; Hawkey, 1983; Wissel *et al.*, 1993).

Conclusions

- Canadian born muskoxen adapted to central European climatic and zoo conditions without serious medical or technical problems. The animals survived an average of 8.5 years, with one cow reaching 21.5 years-old.
- Breeding success is poor and a calf mortality of 84 % is extremely high (only 5 calves reached adulthood).
- Mote veterinary research is needed to reduce calf losses, especially trough prevention of infectious diseases and thermoregulatory disorders.

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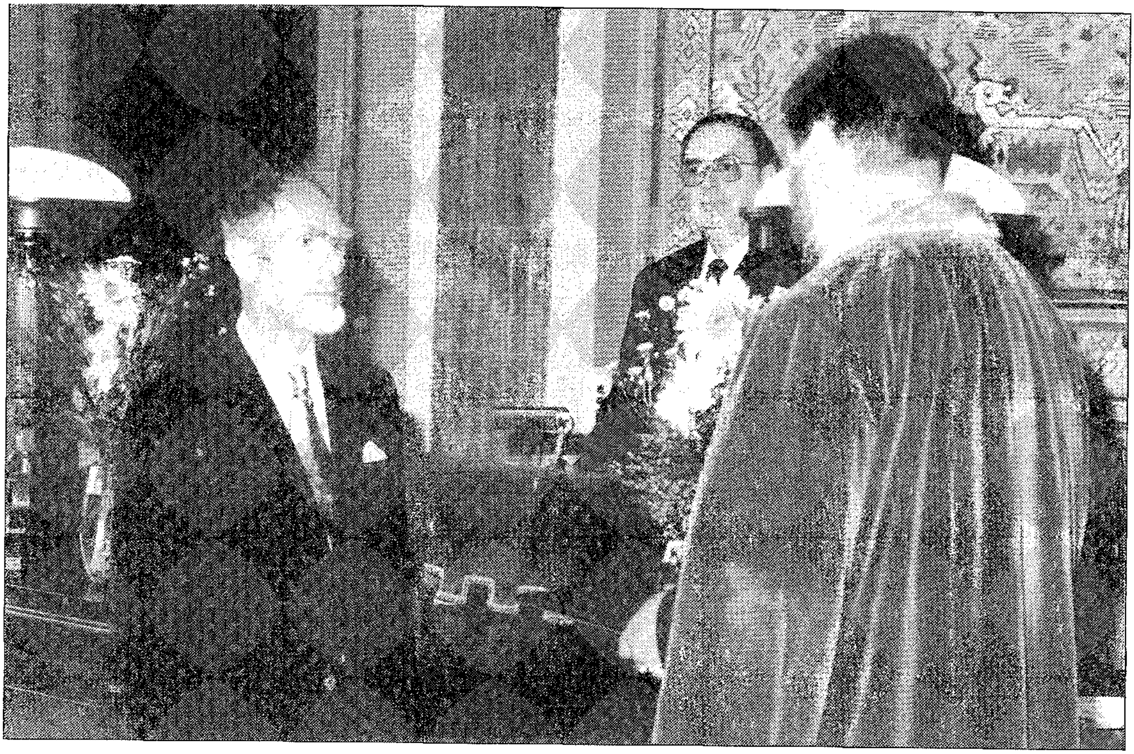

Sven Skjenneberg congratulated by dean of the Norwegian College of Veterinary Medicine Hallstein Grønstøl during the doctorial ceremony.

Photo: Inger Catrinius

On August 30, 1996, the Norwegian College of Veterinary Medicine, Oslo, granted veterinarian Sven Skjenneberg doctor h.c. during a ceremony in his honor. For the occasion, the Ceremoniarius (master of the cetemony), former dean Knut Karlberg, held this speech;

Sven Skjenneberg was born in 1923. He has worked with reindeer husbandry and reindeer diseases nearly his entire working carrier as the director of research in reindeer husbandry for the Norwegian Ministry of Agriculture and as the director of Norway's National Reindeer Research, an organization with an office in Hatstad and a research station in Lødingen. From 1981 and until his retirement in 1994, Sven Skjenneberg was the sectetary of the Nordic Council for Reindeer Research and editor of the international, scientific journal **Rangifer**. Skjenneberg is well known for both independent reindeer research and the influence he has had on the reindeer research community through the years. Skjenneberg has earned the reputation as the pioneet in modern research concerning reindeer husbandry and reindeer diseases. Together with David R. Klein from the Univetsity of Alaska, Fairbanks, Skjenneberg took the initiative in establishing "The First International Reindeer/Caribou Symposium". This has now grown ro become the "International Arctic Ungulate Conference", which includes all the important arctic ruminants.

It was also Skjenneberg who took the initiative for establishing the scientific journal **Rangifer**, for which he was editot the first 13 yeats. Skjenneberg has participated in a number of legal actions in which reindeer husbrandry has been involved, either as a member of the coutt or as an expert adviser appointed by the court. Respect for Sven Skjenneberg's expansive international activities, the scientific work he has accomplished and the cooperative work efforts he has initiated is acknowledged by, among many things, becoming an honorary doctor at the Swedish University of Agricultural Sciences in 1993. The following year, he received the Norwegian Royal Medal of Honor.

Through his important work, Skjenneberg has become highly respected in the scientific community, reindeer husbandry management and among reindeer herdsmen. "The veterinarian and artist" was a common expression used to describe Skjenneberg. His many individual exhibitions including both paintings and drawings has contributed to this title. The artist has certainly inspired the professional scientist, but today, it is the scientist which is honored.

A word from the editor:

A review of Skjenneberg's publications was presented in **Rangifer** (Vol. 13 (4), 229–232) after becoming an honorary docror in Uppsala in 1993. In addition to his professional (scientific) and artistic work mentioned by Ceremoniarius, it must also be mentioned that Sven Skjenneberg has a medal of merir for participation in the World War II. He has also been a boyscout troop leader for many years. In the area of gardening, he has held a number of talks in the planting of roses and clematis in Northern Norway. Together with his wife Ragnhild, Skjenneberg has at his home in Harstad a fabulous garden widely known for its many roses.

After almost 40 years in Northern Norway, Skjenneberg is now moving from this part of the country to join close relatives in Southern Norway. For the occasion, the county veterinarian for Troms and Finnmark has taken the initiative of arranging a dinner in honor of Ragnhild and Sven Skjenneberg. In rhe invitation it is written: "For reindeer husbandry, reindeer husbandry management and rhe vererinarians in this region, Sven has been an important cooperative partner and source of information during rhis entire period. Sven's contribution in reindeer husbandry has also gained extensive recognition outside Norway."

The Nordic Council for Reindeer Research would like to extend a congratulation, and wish both of you all the best in your new home.

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