THE UNIVERSITY OF MANITOBA

ESTIMATED PRODUCTIVITY OF MUSKOX (OVIBOS MOSCHATUS) ON NORTHEASTERN DEVON ISLAND, N.W.T.

by

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A dissertation submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

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ABSTRACT

The productivity of muskox was studied on the Truelove Lowland of northeastern Devon Island, N.W.T. between May 1970 and August 1973. The number of muskox occupying the 44 km² lowland ranged from zero during the spring melt and runoff to 114 in March 1973. These muskox were part of a population totalling approximately 275 whose range extended from Sverdrup Inlet east to Sverdrup Glacier. The total range area below 200 meters is 301.4 km².

A growth curve for wild muskox based on weights of domesticated muskox and wild muskox is proposed. Energy requirements of domesticated muskox were determined and were used to estimate the energy requirements of free-living muskox. Based on the proposed body weight and estimated energy requirements of wild muskox a predicted 20.8 percent of the available forage was harvested from areas grazed during the period of snow cover. Examination of areas grazed in winter showed that an average of 23.6 percent of the forage had been removed.

The net biomass increase for the population in the year ending 30 April 1973 was 12 percent. The growth of calves contributed 53 percent of this increment.

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Calves account for only 5.1 percent of the total forage removal by muskox grazing. The significance to the productivity of this muskox population of the Truelove Lowland appears to be an abundance of forage which is readily available in the season when forage is most difficult to obtain.

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INTRODUCTION

The muskox (Ovibos moschatus Zimmerman) is native to the tundra of North America and Greenland and is the largest herbivore in these parts. Unlike the caribou, the muskox is not migratory or nomadic The muskox is the only ruminant but is sedentary. species whose natural distribution is restricted to Many features of muskox anatomy tundra regions. seem to be specialized adaptations for energy conservation in a cold tundra environment. Some of these are: short, heavily furred ears and tail, highly insulative underwool (qiviut) which is protected by long, thick guard hair, and a fully furred muzzle. The behavioral characteristic of muskox taking a defensive position rather than fleeing when threatened may also be a direct attempt to conserve energy.

Despite the growing interest in muskox domestication and the recent increase in mineral exploration in Arctic regions, only two field studies of muskox biology on native range had been conducted prior to the onset of this study in 1970. Tener (1965) began research in 1951. He synthesized the available information and added many details on muskox life history, social behavior, and habitat. He dealt extensively

with and clarified muskox taxonomy. Gray (1973) dealt specifically with social organization of muskox on Bathurst Island. Harington (1961) prepared an extensive review of the evolution, distribution and history of the muskox group.

This study was conducted on Devon Island, It is part of an integrated ecosystem research N.W.T. project sponsored by the International Biological Facilities established by the Arctic Programme. Institute of North America in 1961 served as a base of operations. I spent 668 days in the study area during the following periods: 9 May to 3 September 1970, 28 April to 31 October 1971, 5 May to 20 August 1972, 21 September 1972 to 16 May 1973, 1 August to In February and March 1972 I conducted 21 August 1973. feeding experiments with captive muskox at College, During these periods I collected data on Alaska. population dynamics, social, reproductive and maternal behavior, seasonal movement and density, seasonal habitat selection, productivity and energy requirements Only the productivity and energy of muskox. requirement aspects of this study will be discussed at this time.

Range of muskox

According to available records, muskox have never been abundant but were fairly widely distributed Prior to the introduction of firearms (Hone, 1934). muskox ranged over nearly all the tundra regions of mainland North America and the Arctic Islands as well as around the northern coastal fringes of Greenland. The notable exception to this distribution is the total lack of evidence suggesting that muskox ever inhabited Baffin Island or the tundra of the Ungava Peninsula. Firearms and fur trading drastically reduced the numbers and distribution of mainland muskox. In the half century following 1860 the Hudson's Bay Company traded more than 15,000 skins from the mainland (Tener, 1965). It is known that thousands were taken by whalers and explorers from the Arctic Islands. The American explorer Peary, for example, shot at least 600 between 1898 and 1909 to support his polar explorations (Hone, 1934). By 1865, muskox were extirpated from Alaska (Hone, 1934). To prevent a similar course of events the Government of Canada gave total protection to the beast in 1917. In 1927 the Thelon Game Sanctuary, an area of some

15,000 square miles, was established by an Order in Council of the Government of Canada, primarily to serve as a preserve for muskox (Clarke, 1940).

Although the present distribution on the Canadian mainland is still disjunct, muskox are repopulating areas from which they were extirpated in the last century. The present Alaska muskox are originally from East Greenland stock. Tener (1965) reviewed the most recent population estimates and distribution for muskox in Canada.

History of muskox on northeastern Devon Island

The muskox range of northeastern Devon Island was submerged during the Wisconsin glaciation. The present lowlands are the result of post glacial uplift. Barr (1971) determined the ages of raised beaches on the lowlands to be from 3,000 to 9,500 years. Total uplift was 107 meters and the rate of uplift during the first 1,000 years following deglaciation averaged 4.05 meters per 100 years. The area is now considered to be in a eustatic period (Barr, 1971).

Archaelogical investigations of pre-Dorset, Dorset, and Thule Eskimo campsites at Cape Sparbo (Lethbridge, 1939; Lowther, 1960) showed no remains

of muskox but many of caribou. Harington (1964) briefly discussed this phenomenon and suggested that muskox invaded or possibly reinvaded this area in the past "few hundred years". It is only in the last two decades that caribou have either emigrated or have been extirpated.

Although Jones Sound was discovered and named by Baffin in 1616, Inglefield in 1852 was the first European to penetrate the Sound to 84° Inglefield's was an expedition West (Taylor, 1955). taking part in the search for Capt. John Franklin and Although Inglefield mapped his missing expedition. parts of the shores along Jones Sound he did not land (Baird, 1949). It is not known how many whalers hunted the waters of Jones Sound but the next known exploration in Jones Sound was by Capt. Otto Sverdrup who mapped this region from 1899 to 1902. His narrative (Sverdrup, 1904) did not detail any extensive inland expedition onto eastern Devon Island, nor did he report taking any muskox from the areas along the southern shores of Jones Sound. Dr. Frederick Cook, on his return from the North Pole, overwintered at Cape Hardy in 1908-1909 and killed six muskox there in September

1908 (Cook, 1911). Although he may have killed more, it seems doubtful that he and his two native guides would have killed more than necessary since they were equipped only with Stone Age weapons. I conclude therefore that the muskox population on northeastern Devon Island has not suffered the decimation and near extirpation that was so common to many high Arctic muskox populations during this period. Munn (1922, in Hone, 1934) reported that muskox were numerous on North Devon but had been considerably reduced by There is no evidence to support this natives. statement, for the only natives present in the Jones Sound region since 1917 were those acting as guides The R.C.M.P. to the Royal Canadian Mounted Police. did not establish posts in the High Arctic until after the Government of Canada passed laws protecting the muskox.

Harington (1964) discussed and reviewed the reports on muskox from North Devon supplied by the R.C.M.P. and others from 1908 to 1960. The minimum reported was 20, for 1929, and the maximum was 100, for 1937. It is interesting that the highest count was reported by Lethbridge, the individual who probably spent the most time there. I do not believe the

numbers reported and discussed by Harington (1964) represent the entire population as I define it. Theyprobably represent local herds within the population. Freeman (1971) reported 230 muskox for the area of northeastern Devon which I think the population occupies. The significance of Freeman's report will be discussed more fully later.

STUDY AREA

The northeastern coast of Devon Island, Northwest Territories has a series of five lowlands from Sverdrup Inlet east to Sverdrup Glacier. All five lowland units are separated from each other by coastal cliffs of dolomite-capped granite which rise to 300 meters. These cliffs also delimit the inland extent of the lowlands, bounding them on all sides except for occasional stream channels and gullies which drain the barren interior plateau and carry summer melt waters from the ice cap. A permanent ice cap covers most of eastern Devon Island above 600 meters. The ice cap summit is 1,800 meters.

I have delimited the muskox range to consist of all land area below 200 meters. Between Sverdrup Inlet and Sverdrup Glacier a total of 301.4 square kilometers lies below this elevation. A large portion of this area is rarely utilized by muskox due to its dry, barren, calcareous and unvegetated surface characteristics. The most westerly lowland, Newman Smith, is predominantly of this type. Only in granite rock outcrop areas there did I find areas of continuous meadow vegetation (see Figure 1).

Figure 1. Muskox range on northeastern Devon Island, N.W.T.



These meadows as well as most meadows of the muskox range of northeastern Devon are dominated by the moss-sedge association, the most abundant sedges of which are *Carex stans*, *C. membranacea*, and *C. misandra.* Salix arctica is present in most vegetation types but is not dominant or abundant in any. Meadows cover less than 10 percent of the Newman Smith Lowland, which has a total area of 139.4 square kilometers.

Truelove Lowland covers 44.4 square kilometers. Approximately 41 percent of its area is of the meadow type. Lakes, ponds, and salt lagoons make up 22.2 percent of the lowland surface. The remainder is made up of granite rock outcrops, calcareous raised beach ridges and calcareous pavement. Since Truelove Lowland was the site for the Devon Island I.B.P. Project, I will describe it in greater detail later.

Skogn Lowland covers 15.2 square kilometers. Below the southern cliffs this unit has a large continuous wet moss-sedge meadow which makes up about 30 percent of the total lowland. Skogn Lowland has no lakes or ponds on it. The coastal outcrops make up another 30 percent of the lowland. Except for a small proportion of Dryas-Heath the rest of the lowland is calcareous pavement and raised beach ridges.

Sparbo-Hardy Lowland is 66.2 square kilometers. About 5.6 percent of its surface is covered by shallow ponds. A belt of meadows about two to three kilometers wide borders the coastal areas, while the remainder of the lowland is raised beach ridges and calcareous pavement.

The Sverdrup Lowland, the most easterly of the group, is 22.6 square kilometers. It has few ponds or lakes and is generally well vegetated. It seems to be free of snow earlier than the other lowlands, probably because of its easterly exposure and proximity to the polynya ("North Water") near Coburg Island (Nutt, The agents responsible for the year round open 1969). water as well as the polynya itself may have a profound effect on all the lands bordering North Water. Soils and drainage of Sverdrup Lowland are generally more developed than those of the lowlands to the west. For this reason meadows dominated by Ardtagrostis latifolia Salix arctica also seems more are not uncommon. abundant on Sverdrup Lowland than on the others. Due to its well-developed vegetation and early melt, high muskox concentrations were observed in this area in June and early July, 1970 and 1971.

TABLE I

Lowland Areas below 200 meters on a contract of the second s

Northeastern Devon Island

Lowland	Area (km ²)	% Water	<u>% Total</u>
Newman Smith	139.4	9.4	46.3
Truelove	44.4	22.2	14.7
Truelove Valley	13.6	9.1	4.5
Skogn	15.2	0.0	5.0
Sparbo-Hardy	66.2	5.6	22.0
Sverdrup	22.6	5.5	7.5
Total	301.4		

The Truelove Lowland is bounded on the north and west by Jones Sound. The Truelove Inlet and Truelove River form its southern border. The eastern boundary is formed by a granite and limestone escarpment rising to 250 meters (see Figure 2). The Truelove Valley is an extension of the southeastern corner of the lowland. It is bounded by the same limestone escarpment on its northern wall and by a fault line in the granite on its southern wall. Melt water from the ice cap is the source of the Truelove River which flows down the valley to Truelove Inlet.

There is considerable biological diversity on the lowland compared to the plateau. Barret and Teeri (1973) reported 93 species of vascular plants for the lowland, while Bliss (1972) reported 12 for The rock outcrop flora is the most the plateau. diverse, and the raised beach flora the most The meadows were classified by Muc depauperate. (1974) into three categories: hummocky sedge, frøst-boil sedge and wet sedge. In all cases Carex spp. were most dominant with Eriophorum spp. next (Muc, 1972). See Muc (1972, 1974) for a more complete discussion of the meadow composition.

The vertebrate fauna is also quite varied. Landlocked arctic char (Salvelinus alpinus) occur in the lakes. Eighteen species of birds breed on the lowland (Pattie, 1972). The mammalian fauna includes both herbivores and carnivores. Besides the muskox, herbivores are represented by the collared lemming (Dicrostonyx groenlandicus) and the arctic hare (Lepus arcticus). Peary's caribou (Rangifer tarandus pearyi) at one time ranged over northern Devon Island but none were encountered during the study. The carnivores are represented by the short-tailed weasel (Mustela erminea), the white fox (Alopex lagopus) and the polar bear (Thalarctos maritimus). No arctic wolf (Canis lupus) was seen after May 1970. I fear that this carnivore no longer occurs on northeastern Devon.

The climate of this region is that typical of high latitudes. The period of "total day" begins around 26 April and lasts until 17 August, whereas "total night" lasts from 26 October to 18 February (ca. 115 days). The lowland is usually snow free from the last week of June to the last week of August. Snow falling during July and August usually melts prior to freeze-up. Maximum weekly temperatures

occur around mid-July with a mean of near +8°C. The maximum temperature during the study was +17°C, while the minimum was -50°C. February, the coldest month during the winter of 1972-73, had a mean of -39.5°C. Precipitation during the snow free period can be either rain or snow. Summer (July and August) precipitation for 1971 was 49.3 mm. Between 20 June and 17 October 1971 the total precipitation was 65.1 mm (Courtin, 1972). Between 5 October 1972 and 16 May 1973, 56 cm of precipitation fell in the form of snow and ice crystals. Annual precipitation in the High Arctic is highly variable but rarely exceeds 200 mm (Rae, 1951). Prevailing winds are westerly and rarely exceed 10 m/sec. (22 m.p.h.). Winds greater than this velocity are usually associated with the Foehn (Courtin, 1972). Mean summer wind velocity is 3 m/sec. (Courtin, 1972). See Courtin (1972) for a more detailed discussion of micro-meteorology of the Truelove Lowland.

Figure 2.

The Truelove Lowland showing its physiographic features. The "recent deposits" are meadow.



METHODS

Determining population size and distribution

I used aerial and ground surveys to census the muskox population. See Table II for dates, areas covered and method of transportation used for population surveys.

When on foot or snowmobile, the lack of time due to difficult access to the entire range prevented complete population counts. In a fixed wing aircraft excessive speed and total lack of required manoeuverability sometimes resulted in incomplete observations although the entire area may have been covered. Only from a helicopter can an experienced observer accurately segregate muskox by sex and age. The habit of muskox herds crowding and bunching up when alarmed hinders such segregation when surveying the population on foot or by snowmobile. On all aerial surveys at least three observers recorded observations simultaneously.

Determining muskox presence and distribution on Truelove Lowland

Muskox usually enter or leave the lowland by one of four routes. In winter they usually enter from the northeast along the coast. Muskox could also enter by

TABLE II

Dates and coverage of muskox surveys on North Devon, May 1970 - August 1973

Date	Area*	Method
22 May 1970	2,3,4	Single Otter
10 June 1970	4	on foot
18 June 1970	2,3,4,5	Single Otter
19 June 1970	2,3,4,5	snowmobile
15 July 1970	1,2,3,4,5	Single Otter
10 August 1970	2,3,4,5	on foot
19 August 1970	1,2,3,4,5	Single Otter
27 May 1971	1,2,3,4,5	helicopter
12 June 1971	4,5	on foot and snowmobile
2 July 1971	1,2,3,4,5	helicopter
8 May 1972	1,2,3,4,5	helicopter
22 March 1973	1,2,3,4,5	Single Otter
25 April 1973	2,3,4,5	snowmobile
11 May 1973	1,2,3,4,5	helicopter
16 August 1973	1,2,3,4,5	helicopter

* Areas referred to by numbers are as follows:

1. Newman Smith Lowlands

2. Truelove Lowland and Truelove Valley

3. Skogn Lowland

4. Sparbo-Hardy Lowland

5. Sverdrup Lowland

crossing the ice of Truelove Inlet in the southwest but this has not been observed. I have observed muskox leaving by both of the above routes. In summer the route across the inlet is not available but they still use the northeastern coastal route. Muskox also move onto the plateau via the Gully or via Truelove Valley.

We surveyed the entire lowland and valley at least once a week during the time we were in the field to determine number and distribution of muskox on the lowland. In winter this was done on snowmobile or cross-country skiis, in summer on foot. All muskox observed on these surveys, as well as all our daily observations were recorded with sex and age noted whenever possible. I also recorded all observations reported by colleagues. I prepared daily maps on which I recorded all observations for the previous twenty-four hours. During the study, I recorded 1096 such observations for the Truelove Lowland and Valley.

We marked muskox by first immobilizing them with succinyl-choline-chloride and then attaching ear tags (Jonkel, <u>et al</u>. in prep.). I also marked free ranging muskox with a paint pistol either from a helicopter or from the ground. By these methods we marked 43 animals. Combining the age and sex structure with presence or absence of marked muskox I could reconstruct movement patterns of individual herds seen intermittently. Using these observations I have determined utilization patterns for the Truelove Lowland for the period spent in the field. This aspect will be discussed later.

Determining the age of individual muskox

Allen (1913) described the horn development in muskox. Since horns occur on both sexes and develop at different rates, immature animals can be sexed and aged fairly accurately using these criteria. Tener (1965) reviewed the horn development. I used these characters to age and sex individuals in the field. I could satisfactorily age males to four and one-half years, and females to three and one-half years. Sexes could rarely be differentiated before eighteen months of age.

Guard hair forms a skirt on the body of muskox and with increasing age this skirt becomes more prominent. I used skirt length to differentiate yearlings from two year olds where a comparison of horn development was inconclusive.

Determining live weight of wild muskox

Field weights of wild muskox are very rare. Weights reported by exploration expeditions are unreliable since they report the amount of meat removed from a carcass. Tener (1965) reported weights from several animals collected for research purposes.

Wilkinson (1973) reported weights from accidental deaths on Nunivak Island, Alaska. Wilkinson (1971, 1973) also reported weights and growth rates of muskox from the Muskox Farm at College, Alaska. Tener (1965) reported weights for captive muskox raised in Vermont, U.S.A. The N.W.T. Government Game Branch also has weights of eight yearlings and one of unknown age collected on Banks Island in March 1973. Miller (1974, unpublished) reported weights of two muskox collected for scientific purposes on Melville Island, N.W.T. In May 1972, we, with the assistance and supervision of Dr. C. Jonkel of the Canadian Wildlife Service, were the first to weigh live immobilized muskox (Jonkel, et al., in In February 1973, I also weighed three prep.). males shot by Inuit hunters. Table VII gives the weights of wild muskox from the above sources. Figure 8 shows the growth reported by Wilkinson (1973) for domestic muskox at Fairbanks.

Using these data and the following assumptions I have constructed an estimated growth curve (Figure 9) for wild muskox. If the assumptions are valid, then the estimated growth of wild muskox should approach reality:
- That calves in the wild are as heavy at birth as calves born in captivity.
- 2. That the growth rate of calves in the wild is the same as calves in captivity and that this rate of increase is not interrupted in the wild by weaning as it is in captivity but that the effects of domestication and husbandry produce an earlier adult weight in captive muskox.
- 3. That late winter weight loss, or lack of weight gain, in the wild muskox begins at the same time as for captive muskox but lasts longer due to prolonged snow cover and lack of supplemental feeding.
- 4. That the weight loss of bulls during the rut in the wild represents the same proportion of body weight as for rutting bulls in captivity and that the effects of rutting are shown in the same cohorts in the wild as in captivity.
- 5. That the effect of gestation and lactation is the same in wild and captive females.

- 6. That in the wild, in any given year, fifty percent of the females produce a calf and that the weight loss during lactation is compensated for by the weight gain in early summer by non-lactating females, thus producing a damped-out summer growth rate for an "average" adult female.
- 7. That the field weight of 177 kilograms and 259 kilograms for wild and captive bulls respectively, thirty-three months old, represents the proportional weight difference between captive and wild muskox between 12 and 60 months of age, for males, and 12 and 36 months for females.
- 8. That adult females are two-thirds the size of adult males (Wilkinson, 1973).
 Tener (1965) reported only one birth weight

of a living calf in the wild. He also gave the weight of a day old calf and one of a week old. I have three weights of dead calves from Devon, one full-term fetus, one still-born, and one dead from unknown causes whose age at death was

unknown. An autopsy showed a completely empty gut and an emaciated carcass. Presumably the calf never nursed and died of starvation. Since there is no significant difference between weights of calves born in the wild and calves born in captivity I think the first assumption is valid.

There are no data to support or reject the second assumption regarding growth rate of calves in their first summer. Wilkinson (1974)after observing muskox on Banks Island during the summer suggested that the calves there were either as large or larger than calves of the same age in captivity. The yearlings collected on Banks Island in March 1973 were lighter than captive animals of the same age. This also holds for a 33 month old bull shot on Devon in February 1973. It is, therefore, safe to assume that muskox in the wild require more time to attain adult weight than do captive muskox.

The assumptions regarding weight losses due to winter and reproduction are speculative and will be discussed more fully later.

Adult sexual dimorphism is well known in muskox (Tener, 1965 ; Wilkinson, 1973), Wilkinson suggested the weight of cows is two-thirds that of - 26

bulls. While this may hold when comparing a cow to a prime breeding bull, I think it is an overestimate of the weight of an "average" bull.

The construction of a reasonably accurate growth curve is important in determining energy requirements for the population and, in turn, the significance of the Truelove Lowland. Accurate adult weights are the most important because the greatest proportion of biomass in the population is that of adult muskox. A reliable growth curve for immature muskox will enable a more refined estimate of energy requirements for the population to be made.

Determining food requirements for muskox

In February and March 1972 I did a series of intake and digestibility studies at the Muskox Farm in College, Alaska. I selected five supposedly pregnant cows, all weighing around 230 kilograms. These cows would have been in the sixth month of an eight month gestation period. I isolated these cows from the rest of the herd and fed them known amounts of alfalfa-brome-timothy hay once daily. When taking daily weights on a platform scale, I also administered

to each animal ten grams chromic oxide (Cr₂0₃), an indigestible indicator, by mixing it with 0.55 kilogram Omolene (Ralston Purina Co., St. Louis), a commercial ration. I followed the above procedure, as outlined by Short (1970) and Theurer (1970) to determine fecal output, for twelve days. Beginning the fourth day, I collected fresh feces from each cow twice daily (10:00 - 11:00 and 16:00 - 17:00). I also retained samples of the hay and Omolene for subsequent chemical and energy content analyses. I repeated this procedure with six growing bulls, each 22 months old.

All forage and fecal samples were stored and transported frozen. Prior to analysis the samples were thawed, dried at 90°C and ground in a Wylie mill. We determined caloric density by bomb calorimetry using a Gallenkamp Bomb Calorimeter. Chemical analyses were kindly done by the staff of Mr. J. McKirdy in the Department of Animal Science, University of Manitoba.

Determining muskox range relationships

Clipping

In July 1970 I selected four locations where exclosures were to be constructed. Two locations were in areas that I knew from observation to be The other both winter and summer grazing sites. two were placed by selecting the site "out of a hat". These locations turned out to be on the edge of favored grazing areas. The four exclosures, 50 m \times 50 m , were constructed by driving six foot steel T-posts into the soil as far as possible (about 30 to 40 cm). We strung three strands of nine gauge galvanized steel wire on the posts, with strands twelve inches apart, the bottom one being about ten inches off the ground. We braced the corner posts so the strain of taut wires would not pull them inwards.

We clipped all the vascular vegetation from 20 randomly selected 100 cm x 20 cm plots; clipping level was just above the moss surface. The clipping was replicated around 20 August 1970. The clip samples were dried, sorted into woody and non-woody vascular vegetation and weighed. These data served as a base line for vascular plant biomass in the vicinity

of each exclosure. All clipping subsequent to that of 1970 was done on plots 50 cm x 20 cm. I reduced the plot size in order to save time in clipping and sorting, recognizing that the accuracy of estimated vascular biomass would suffer. We also sorted all subsequent clippings into the following categories: monocot (live and dead, in July) and dicot to species. In July and August 1971 ten plots were clipped inside and 10 plots were clipped outside each exclosure. On examining the data from sorting I felt this procedure was questionable in determining summer forage removal by muskox. I decided therefore to clip only in July 1972. In addition to the exclosures I began in August 1971 clipping selected areas where I knew muskox had grazed in winter. selected sites and clipped 15 plots spaced two meters apart along a 30 meter transect. The following spring, 1972, I returned to these areas and repeated the procedure. In the spring clipping we recorded the percentage, if any, of the individual plot that had been grazed the previous winter. The spring clipping was sorted into the following categories: Salix, live monocot, dead monocot, and dicot (to species). Live and dead monocot was separated

because the live vegetation would not have been available to muskox the previous winter. This distinction was not made in sorting the August In the fall 1972 I again selected clippings. prospective winter grazing sites and clipped 15 plots at two meter intervals along a thirty meter We did not clip the exclosure meadows. line. In 1973 clipping was restricted to those transects where I had observed muskox grazing the previous Due to lack of time we did not clip winter. around any exclosures. (See Table XIV and Figure 13 for clipping data and locations.)

Grazing Transects

During the winter 1972-73 grazing areas could be identified easily by the disturbed snow cover. All such areas were delineated on a map. In July 1973 I returned to as many winter-grazed meadows as time would permit. In grazed areas I read paired line intercept transects for frequency of grazing. Winter grazing could be identified easily by the reduced amount of standing dead vegetation. The individual lines of a pair were one meter apart. Individual transects were spaced

at twenty meters. (See Table XVI, and Figure 13 for transect data and locations.) In sites that had been grazed I also removed from ten plots, each 20 cm x 50 cm, all remaining monocot litter in order to help estimate muskox grazing efficiency. Muc (pers. comm.) estimated that approximately 25 percent of the litter, including standing dead present in the fall, is removed by subsequent runoff In grazed areas this would be of melt waters. lower than Muc's estimate since winter muskox grazing would remove potential runoff litter. How much of the remaining litter would be lost to runoff is difficult to estimate.

Determination of daily fecal output by individual muskox

If digestibility can be accurately estimated, then daily intake can be determined based on daily fecal output. Digestibility will be defined and discussed later. By observing single adult males during periods of snow cover, and by noting their position, it is possible to follow their trails in the snow and collect 24 hour fecal samples. This method works if it does not snow, if the feces are not obliterated by windblown snow, if the animal

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does not fall onto another animal's trail, or if the beast does not double back on itself. All are very From numerous attempts I was probable events. able to collect two 24 hour samples, one from May In summer we 1971 and another from October 1971. had to locate a single animal and observe his every move in such a way so as not to disrupt his activity cycle or alarm him. Out of six such attempts we collected one 12 hour sample. Too many factors mitigated against predictable success of this exercise for us to continue it. All samples collected were dried at 90°C and analysed for energy and chemical content. Caloric determinations were made as described above. In addition to the above samples, fecal samples were collected monthly for chemical and energy analyses. Forage samples were collected during the growing season, after freeze-up, and in April 1973 for the same analyses.

RESULTS AND DISCUSSION

Population size and distribution

On the basis of aerial surveys flown in May 1972 and May 1973 I estimate the population using the five lowlands to be between 250 and 275 animals. Survey results for 1970 and 1971 (Table III) are incomplete. Lack of experience, unfamiliarity with the range and incomplete coverage are responsible The results of the August 1973 for this deficiency. survey are questionable due to incomplete coverage, poor visibility and incompetence of the pilot. Freeman (1971) reported the population of the same area to be 230 to 300 animals for 1966-67. His range extended west along the entire shore of Bear Bay, while the range I studied extends along Bear Bay as far west as Sverdrup Inlet. Kiliaan (pers. comm.) reported small isolated herds of muskox near Sverdrup Inlet and Thomas Lee Inlet.

Harington (1964) suggested that the average density of muskox for northeastern Devon was 0.279 per square kilometer for the fifty years prior to 1960. The maximum density he reported was 0.528 per square kilometer. If the present population stands at

TABLE III

Muskox observed on population surveys

Date		Area*						Total	
		l	2	3	4	5	6		
197	70								
22	May	14	21	13	32			70	
10	June		2		52			54	
18	June		14	8	33			55	
19	June		14	4	36	8		62	
15	July	23	17	10	17	65		132	3 M
10	August		21	10	37	27	•*	95	н. 1
19	August	11	10	2	40	48		111	
197	71								
27	May	7	28	17	42	62		156	
12	June		11		9	101		121	
2	July	10	22	13	21	50		116	
197	72								
8	Мау	29	70	1	99	50	2	251	
197	73								
22	March	16	114	5	49	53	0	237	
25	April		61	11	41	50		163	
11	May	25	89	15	53	73	13	268	
16	August	57	27	9	167	18	9	287	

1. Newman Smith Lowland

2. Truelove Lowland and Valley

- 3. Skogn Lowland
- 4. Sparbo-Hardy Lowland

5. Sverdrup Lowland

6. East of Sverdrup Glacier to Eastern Glacier

TABLE IV

Densities of muskox observed on surveys

Date						
		l	2	3	4	5
<u>197</u>	0					
22	Мау	.100 ¹	.347	.255	.330	
10	June		.033		.780	
18	June		.231	.526	.495	
19	June		.231	.263	.540	.354
15	July	.165	.281	.658	.255	2.876
10	August		.347	.658	.555	1.195
19	August	.079	.165	.132	.560	2.124
197	71					
27	May	.050	.462	1.118	.630	2.743
12	June		.182		.135	4.469
2	July	.072	.363	.855	.315	2.212
19	72					
8	Мау	.208	1.155	.066	1.484	2.212
<u>19</u>	73					
22	March	.115	1.881	.329	.735	2.345
25	April		1.007	.724	.615	2.212
11	May	.179	1.469	.987	.795	3.230
16	August	.409	.446	.592	2.504	.796

* Areas defined in Table III.

1. Muskox per square kilometer

260 muskox, the density is 0.867 per square kilometer, a 65 percent increase. Density cannot be calculated from Freeman's 1966-67 observations due to his imprecise definition of the range (Freeman, 1971). His densities however would agree very nearly with mine if I ignore his Bear Bay muskox. This would put the population during 1966-67 at 230 for the area east of Truelove Inlet, a density of 1.434 per square kilometer. Using the results of the May 1973 survey for the same area the density was 1.515 muskox per square kilometer.

The number of muskox occupying the Truelove Lowland varied widely from season to season and even from week to week (Figure 3). In May and June of every year there was a general decrease in muskox on Just prior to, or during, snow melt and the lowland. runoff (approximately a five day period), muskox were Muskox would leave the lowland via the absent. Truelove Valley, across the frozen Truelove Inlet and along the northeast coast onto Skogn Lowland. During June and July of 1970 and 1971 (see Table IV) Ι observed high densities on Sverdrup Lowland. Presumably muskox, including those from Truelove Lowland, moved to Sverdrup Lowland due to an earlier snowmelt there. Muskox returning to the lowland after the melt entered

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via the northeast coast and usually either moved along the base of the escarpment south toward the Truelove Valley or west into the outcrops along the north coast. Fluctuations during the snow free period are due mainly to animals moving into and out of the Truelove Valley This activity ceased following the from the lowland. first snow fall. I never observed muskox in the Truelove Valley between the end of August and February Fluctuations during the study (see Figures 4 to 7). observed in September and October of 1971 are due to movements between Skogn and Truelove Lowlands. The stability observed during this period in 1972 was due to the presence of only one herd and two or three single bulls. The bulls left in late October following polar bear activity in the meadow they had occupied for seven days. In early November the herd moved into this same meadow and left the lowland following more polar bear activity there. Although there is no direct evidence from the Canadian Arctic of polar bear preying on muskox, Chr. Vibe and Thor Larsen (pers. comm.) have made observations of this activity on East Greenland.

Figure 3 illustrates the rapid buildup of muskox on the Truelove Lowland in December and January. The fluctuations observed in February, March and April 1973 are due to movement between the lowland and Truelove Valley.

Figure 3. Fluctuations in muskox numbers occupying the Truelove Lowland during the period spent in the field. Points on the curve show the total number of muskox present on the 10, 20, and last day of each month of the field study.



Figure 4.

Distribution of muskox during May and June. (See Figure 2 for physiographic features of the Truelove Lowland.)

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Figure 5. Distribution of muskox during July and August.



Figure 6. Distribution of muskox during September and

October.



Figure 7. Distribution of muskox between 1 November 1972 and 30 April 1973.



Figures 4 to 7 show the monthly distribution of observed muskox on Truelove Lowland and in Truelove Valley for the duration of the study.

Reproduction

Tener (1965) reviewed the literature dealing with reproduction and productivity of muskox. My findings agree with his. Breeding in muskox begins in late July and may last into early October. Wilkinson (pers. comm.) suggested that females are seasonally polyestrus having a 25 to 30 day cycle. This may account for the October rutting of bulls observed on Devon in 1971. The gestation period т is eight months (240-250 days). On Devon, calving Tener (1965) occurred from late April to late May. reported a calving season from mid-April to early Judging by the surveys of May 1972 and 1973 June. the peak in calving is probably the first week of Twinning occurs, but rarely (Tener, 1965; May. Wilkinson, 1971). Although direct evidence is lacking, under normal conditions in the wild cows of breeding age bear a calf in alternate years. Cows in captivity at Fairbanks bear a calf annually. In the captive herd the calves are weaned prior to

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the cow's next breeding season whereas on Devon I observed 13 and 15 month old calves nursing. Nursing may prevent the cow from coming into estrus by increasing her energy requirements for maintenance (Pedersen, 1958). Also, prolactin stimulates progesterone production by the corpus leuteum (Turner and Bagnara, 1971) and thus may prevent a female muskox from coming into estrus while lactating.

In cows the age of sexual maturity is probably dependent on nutrition. Tener (1965) reviewed reports from captive animals in Vermont, U.S.A. and Edmonton, At the Alberta Game Farm near Edmonton a Canada. She was bred by a yearling two year old gave birth. On Devon in June 1971 I saw a three year old bull. cow nursing a calf of the year; she would have conceived Tener's (1965) discussion of this as a two year old. subject suggests that cows in the wild normally give birth to their first calf at four years. On the basis of my limited observations I would agree, adding that under favourable nutrient conditions calving may occur at a younger age.

The bulls, I believe, are sexually mature long before they are permitted to breed. Most breeding is done by bulls older than six years (judging by pelage and horn development). On 5 October 1971 I noticed

a two year old bull mounting an adult cow. No adult bull was present in this herd for a period of eight days. I do not_know_if_any of the three cows in this herd conceived during this time.

Population composition and productivity

When flying a survey in a helicopter we always attempted to classify all animals for sex and age. The same was done on ground surveys. Table V shows the results of these surveys.

It is interesting that on all surveys except that of 10 August 1970 more cows than bulls were seen. This may be due to inaccurate classification. It is easily possible that some three and four year old bulls It is also possible that an were classified as cows. unequal sex ratio is the normal situation. Gray (1973) reported a near-equal adult sex ratio for Bathurst Island during his four year study. Tener (1965) listed sex ratios for Bathurst Island, 1961, Lake Hazen, 1948, Fosheim Peninsula, 1951 and 1960, and the Thelon Game Sanctuary, 1952 and 1956 and reported sex ratios in favor of cows in all cases except for Lake Hazen where the ratio was 103.3 bulls to 100 cows. Spencer and Lensink (1970) observed adult males outnumbering adult

TABLE	v
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Sex and age composition observed on surveys*

Date	Adult <u>Males</u>	Adult Females	Calves	Yearlings	<u>2 yr.</u>	3 yr. <u>Males</u>	4 yr. <u>Males</u>
1970					•		
10 August	36	33	15	5	6	0.	0
1971							
27 May	62	52	27	5	10	0	0
12 June	25	37	21	6	(21)
2 July	39	47	20	5	5	0	0
1972							
8 May	75	93	48	21	11	3	0
1973							
25 April	40	53	01	32	26	4	8
ll May	54	84	50	36	34	2	8
16 August	65	95	57	32	28	. 7	3

* See Table II for survey transportation.

1. Survey done prior to calving.

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females on Nunivak Island (209 males:150 females). Reports on sex ratios in calves are conflicting. Wilkinson (1971) reported that out of 79 calves born at the Muskox Farm, 45 were females. Spencer and Lensink (1970) reported that of 59 calves captured on Nunivak in 1964 only 14 were females. For the moment, I think it best to assume that an equal sex ratio exists at birth.

Looking at the three surveys done by helicopter in May of 1971, 1972 and 1973 (Table VI) we see an increase in the proportion of immature animals in the population and a decrease in the adults. Calf crops are higher than what Leslie (Appendix 2 in Tener, 1965) would predict. Leslie assumed an equal sex ratio, that cows begin breeding at three years, that cows breed in alternate years and that one half of the calves die prior to one year of age. Under these conditions the population should have eight to fifteen percent calves. According to Leslie (ibid.), with less than 50 percent calf mortality the calves would make up 15 to 23 percent of the population. A calf crop of greater than 23 percent would indicate that cows were breeding at a younger age of that some cows are beeeding annually, or both. Spencer and Lensink (1970) suggested the latter conditions for Nunivak

My data for Devon from 1971 to 1973 show Island. that most calves survived (Table VI), and that occasionally a two year old cow did conceive. This situation however has not always existed. In August 1970 we observed 15 calves (15.8 percent), (Table V). The following May however we saw only five yearlings This low yearling count reflects (3.2 percent). considerable winter mortality. It is also possible that the incomplete August 1970 census resulted in an apparently inflated-calf crop. I think both conditions are possible. Hussel (1970) reported frequent sightings of calves in 1966. In 1967 calves were seen rarely. Hussel reported that in 1967 12 fresh carcasses were found, including possibly two of calves. No live calves were reported for 1968. Living calves were again reported in 1969. From Hussel's reports it seems clear that severe mortality occurred during the winter of This probably affected 1967 calf crops and 1966-67. possibly 1967 breeding. Such reductions in cohort production and/or survival account for the lack of sub-adults seen in 1970-71.

We observed only seven cases of mortality between 1970 and 1973. Three (one adult male and

TABLE VI

Date	% Adults	<u>% Calves</u>	% Yearlings	% Sub-adults
27 May 1	971 73.1	17.3	3.2	6.4
* 8 May 19	972 68.1	19.1	8.4	4.3
*11 May 19	973 51.5	18.7	13.4	12.7

Age composition of population

* Calving season not yet complete.

two adult females) in May 1971 were accidental at a time of thick snow cover. All three carcasses were in an emaciated condition, as were the animals we immobilized that same year. This thick snow cover apparently did not seriously affect 1971 calf survival (Table VI). We found the fresh (recent) carcass of an adult male after the melt in 1971. The cause of death could not be determined but the carcass was emaciated. Two dead calves (both males) were found in May 1973. An autopsy on these carcasses showed that one was probably stillborn. The emaciated condition of the other pointed toward starvation as the probable cause of death. An adult bull was found dead in the Truelove River in August 1973. It probably drowned in attempting to cross the river during a particularly heavy discharge following a rain.

From the results shown in Table VI, I conclude that the population on northeastern Devon is in a period of increase, and will probably continue to increase until abiotic density-independent factors result in mortality and/or reduced or total lack of breeding success occurs, similar to that observed by Gray (1973).

Although the sex ratios for Devon muskox do not agree with Nunivak the age composition appears similar. In April 1968 the Nunivak age composition was: adults, 53.5 percent; sub-adults, 31 percent; yearlings, 16.2 percent; calves, 20.2 percent. Since 1947 the average calf crop on Nunivak has been 19 percent. Spencer and Lensink (1970) assumed a seven percent annual loss due to mortality which is not sex and age specific. Under these growth conditions the Nunivak population doubled every four and a half years. For Devon it seems that under favourable conditions the population growth would equal that of Nunivak for one or two years but that environmentally-induced mortality can be expected to stop population growth and/or produce a loss. Such conditions occur at irregular intervals but could possibly average once every five years. Vibe (1967) described periodic muskox population declines produced by severe winter conditions in East Greenland.

Assuming no mortality and 18 percent annual natality, the population of 230 muskox reported by Freeman for 1967 (Freeman, 1971) should have increased to 739 by June 1973. The observed population was 236 on 11 May 1973 and 287 on 16 August 1973,

about 65 percent lower than the predicted. Assuming from Hussel's reports (1970) that there was ten percent mortality in April and May 1967 following Freeman's census; that there was no mortality in 1967 and 1968 and an eight percent natality in 1969 and 1970 (according to our observations of calves and yearlings in 1970 and yearlings and sub-adults in 1971) the 1973 population should have been 380 muskox. The observed population is now about 30 percent below the predicted. Therefore assuming no consistent rate of mortality, one winter of severe conditions in seven held the population's annual increment to only 9.3 percent. Including a five percent winter mortality independent of sex or age the 1973 population would be 287 or an annual increment of 3.5 percent for seven years. Under favourable conditions the increment (assuming the censuses are correct) between May 1972 and May 1973 was 6.7 percent. The above history of occasional increased mortality combined with fluctuating natality suggests "boom" or "bust" rates of population change. Vibe (1967) reported that between 1938 and 1960 there were six winters during which muskox populations suffered considerable losses on northeastern Greenland. He described the winters of 1938-39 and 1953-54 as "catastrophic". In both cases during the following summer no calves and very few yearlings were observed among the animals surviving the winter.

Growth and change in body weight of muskox

Birth weights of male muskox born dead in captivity were 11 kilograms (n=9) and females were 12 kilograms (n=12) (Wilkinson, 1973). Figure 8 shows the growth of captive muskox to 36 months. This curve is based on Wilkinson (1973) and unpublished data of the Muskox Farm at College, Alaska. Weights of one to six cohorts were averaged to produce the curve.

Sexual dimorphism is observed very early The dimorphism in immature muskox is due in life. to differential growth rates, the rate of males slightly exceeding that of females. The dimorphism in adults is, I feel, due more to a prolonged growth In captivity, muskox in males than in females. females approach adult body weight in their fourth summer whereas bulls reach adult weights in their Allen (1913) and Wilkinson fifth or six summer. (1973) said that adult wild muskox females are two-thirds the size of adult males. In the wild I think females reach adult body weight in their fifth or sixth summer while males probably approach adult weights in their sixth or seventh summer or perhaps later.
Using Wilkinson's data (1973, and unpublished) for captive muskox and data on wild muskox from available sources (Table VII) I have constructed a growth curve for wild muskox (Figure 9).

Seasonal fluctuations in body weight are a combined function of nutrition, environmental stress, and reproductive condition. Figure 10 shows effects of reproductive condition on captive adult muskox (Wilkinson, 1973 and unpublished). Five lactating cows lost an average of 29 kilograms each in three weeks following parturition (Wilkinson, unpublished). During the same period four non-pregnant, non-lactating cows lost an average of 6.2 kilograms. The reason given by Wilkinson for this latter loss is the transition from dry hay to fresh pasture.

An intriguing feature of the seasonal fluctuations in body weight of captive muskox is the weight loss during late winter and spring for non-pregnant as well as pregnant females. Figure 8 shows a weight loss for adult males during the same period. This loss occurs despite the <u>ad libitum</u> availability of good quality (10 percent protein) feed. White (in press) reported a similar phenomenon for caribou. Segal (1962) suggested that the rate of metabolism in Russian reindeer is 30 percent lower in

Figure 8.

Growth curve of domestic muskox to 36 months

of age.



winter than in summer. White (*ibid*.) also reported that weaned reindeer fawns tend to regulate at a constant dry matter intake regardless of protein content and that this may regulate winter growth. If these shifts hold for muskox, they may be responsible for the weight loss in late winter. Reducing metabolic rate at a time of low energy and nutrient availability would reduce weight loss. The survival advantage of such a mechanism to a boreal ruminant may be very significant.

The effects of rutting and breeding on body weight of individual adult muskox is shown in Figure 10. It is clear that there is a greater weight loss associated with rutting than with breeding proper, both before and after the breeding period. Wilkinson (1973) reported that immature bulls as young as 28 months showed weight loss during the rut. This may be due to intra-specific aggression by older bulls in the paddock rather than active rutting on the part of the young bulls. Wilkinson (1973) stated that the weight loss following breeding resulted from aggression in establishing the dominance hierarchy after the breeding bulls were reintroduced to the paddock.

Figure 11 illustrates the estimated body weight and fluctuations in body weight of adult wild muskox. Due to the lack of age:weight data all males greater than four years and all females greater than three years are considered adult. For females the estimated weights of pregnant or lactating females and non-reproductive females are averaged producing a "normal" female.

If the estimated seasonal weights of adult wild muskox are accurate, seasonal energy balance can be determined. Energy balance will be negative during periods of weight loss and positive during periods of weight gain. It appears that bulls are in a positive energy balance only two months of the year, are neutral four months, and negative six months. Cows are positive for five months and negative seven months Superficially it would appear that the result (Figure 11). is a net annual deficit in energy balance for both adult males and adult females suggesting that prolonged survival of adults is difficult if not impossible. However calculating the monthly percent change in estimated body weight (Figure 12) shows that annually the net change is +0.5 percent for bulls and +0.4 percent for cows. To me this suggests that mechanisms regulating body weight changes in muskox respond more directly to conditions of positive energy balance than they do to conditions of negative energy balance.

TABLE VII

Field Weights for Wild Muskox

Sex	Age	Weight (kg)	Season	Location	Source
	Ad.	325	August	Melville Is. NWT	Fischer, 1821 in Wilkinson, 1973
?	?	163		18	n
?	?	167	81	11	II .
F	3 yr.	177	Spring	Nunivak Is.	Lensink in Wilkinson, 1973
F	3 yr.	168	. 0	Alaska	11
М	11 mo.	78 (n=30)	53	n	- Ir
F	11 mo.	75 (n=33)	17	n	11
м	23 mo.	119 (n=6)	••	n	
F	23 mo.	109 (n=11)	11	11	11
F	35 mo.	127 (n=3)	11	tt.	II
м	38 mo.	182	July	Thelon Game Sanc.	Tener, 1965
м	Ad.	325	July	Lake Hazen	Tener, 1965
м	Ad.	373	August	Melville Is. NWT	Parry, 1820 in Tener, 1965
м	Ad.	263	August	Thelon Game Sanc.	Hanbury, 1899 in Tener, 1965
F	l day	12	April	Thelon Game Sanc.	Tener, 1965
F	l week	17	May	Fosheim Pen.	Tener, 1965
F	?	18	Spring	Fort Conger	Tener, 1965
м	11 mo.	89 -	March	Banks Is. NWT	NWT Government
м	11 mo.	84	tr	11	н
M	· 11 mo.	95	11 .	H	и .
м	ll mo.	92	. #	H	U

Table	VII cont'd	· · ·	1			
М	11 mo.	106	March	Banks Is NWT	NWT Government	
F	ll mo.	95	. "	tt	11	
F	ll mo.	77	11	11	II.	
F	11 mo.	97	11	U	11	
?	?	144	. U	H	u	
М	Ad.	259	July	Melville Is. NWT	Miller, unpublished	
М	Ad.	191	July	N	n	
М	Ad.	234	May	Devon Is.	This study	
M	Ad.	309	f1		TI .	
М	Ad.	302	(I	11		
М	Ad.	264	. 11	tt .	11	
М	Ad.	223		If		÷
М	Ad.	291	February	11	TT CONTRACTOR OF	
M	Ad.	286	88	11	tt.	
М	34 mo.	177	1. 18	· • •	· #	

Figure 9. Growth curve of wild muskox to 48 months of age.



Figure 10. Effects of reproduction on body weight of adult muskox in captivity.



Figure 11. Seasonal fluctuations in the body weight of adult wild muskox in relation to reproductive and environmental conditions.



Figure 12.

Percent change in body weight of adult wild muskox. Calculation of percent change was determined as follows:

$$\left(\begin{array}{c} \frac{bw}{x} \\ \frac{bw}{bw} \\ \frac{bw}{x+1} \end{array} \times 100 \right) - 100$$

where bw_x is the body weight of the individual adult muskox in month x.



Forage digestibility and energy intake of captive muskox

Digestibility is an expression for the feed:feces ratio or, the efficiency of digestion. It is also a good measurement of forage quality (Short, 1970). I have used three independent techniques in calculating forage digestibility for the experiments conducted at the Muskox Farm at College, Alaska.

> 1. Chromic Oxide. Chromic oxide $(Cr_2 0_3)$ is indigestible and therefore a good indicator when added in known quantities to the feed of experimental animals. Fecal output can be determined by the following calculation (Theurer, 1970):

Fecal dry matter = gm. indicator administered output (gms.) gm. indicator/gm. fecal dry matter

Since I fed a known amount of hay and grain I could determine the feed:feces ratio. From chemical analyses the percent ash was determined for feed and feces in order to calculate organic matter digestibility. Organic rather than dry matter digestibility was preferred because of a high ash content in the forage due to air-borne dust.

2. Nitrogen Fecal Index. Lancaster (1954) found the following regression reliable for calculating the feed:feces ratio. Y = X + 0.9 where X is the percent nitrogen in the fecal organic matter and Y is the feed:feces ratio. Percent digestibility is calculated by the formula:

% digestibility = $\frac{Y - 1}{Y}$ (100)

where Y again is the feed:feces ratio.

3. Lignin Ratio. Lignin is used as a naturally occurring indicator since it occurs both in the forage and in the feces. Digestibility is calculated as follows:

% digestibility = 100 - 100
$$\begin{pmatrix} \% \text{ lignin in forage} \\ \hline \% \text{ lignin in feces} \end{pmatrix} \begin{pmatrix} \% \text{ organic matter} \\ \hline \% \text{ organic matter} \\ \hline \% \text{ organic matter} \\ \hline \% \text{ in feces} \end{pmatrix}$$

Using this calculation lignin need not be indigestible (Theurer, 1970). I assume the chemical analyses of forage and feces exposes the same lignin.

The results of these experiments are summarized by Tables VIII and IX. Statistical anslysis of variance at 0.95 showed no significant difference between the digestibility of the pregnant cows and that of 22 month old bulls.

About 64 percent of the organic matter was removed from the feed, whereas 66 percent of the energy in calories was removed. The coefficient for metabolizable energy is 0.82 (Blaxter, 1967). Therefore 54 percent of the energy was metabolized. Metabolizable energy intake (M.E.I.) for the cows was 128.7 C/kg^{•75}/day, and for the bulls 146 C/kg^{•75}/day (1C = 1,000 calories). For non-lactating female caribou in summer White et al. (1974) reported an M.E.I. of 196 C/kg^{.75}/day; well above my values for Also, as suggested earlier the heat muskox. production in winter is possibly much lower for caribou making a detailed comparison of the above data impossible.

The average weight of the cows used for the experiment was 235 kilograms (range 224 - 247); the bulls weighed 193 kilograms (range 182 - 200). The cows gained an average of 0.14 kilograms per day while the bulls gained 0.15 kilograms per day.

Energy requirements of wild muskox

Using the lignin ratio and the nitrogen fecal index I have calculated the digestibility of monocot forage from Devon Island (Table X). Daily fecal output

TABLE VIII

Percent organic matter digestibility* observed in feeding trials

	Chromic Oxide	<u>Lignin Ratio</u>	Nitrogen Fecal Index
Cows	64.7 ± 5.2	64.4 ± 1.4	63.2 ± 1.3
Bulls	64.7 ± 1.5	64.1 ± 0.9	62.2 ± 1.1

 Measurements of apparent digestibility are usually overestimates (Short, 1970).

TABLE IX

Energy intake for muskox during feeding trials

	O.M.I. ¹ (g/kg/day)	G.E.I. ² (C/kg/day)	D.E.I. ³ (C/kg/day)
Cows	13.1	62.1	40.1
Bulls	15.4	73.0	46.7

1. organic matter intake

2. gross energy intake

3. digestible energy intake

is known from collecting feces produced during a known time interval (Table XI). As muskox probably select fresh forage when it is available, a digestibility of 75 percent for the snow-free period is probably an underestimate. As the digestibility and fecal output is known, daily dry matter intake can be estimated (Table XII). Caloric density of organic matter in the forage is 4.78 C/g. (Calculated from Muc, 1972) and does not show significant seasonal changes (Muc, 1974). Table XIII gives the estimated daily energy intake of muskox on Devon Island. The summer values are based on the June and July data above. The winter values are based on the October data above and the experimental work from Alaska using captive muskox.

The February D.E.I. value estimated for free ranging muskox is 52.8 C/kg/day, whereas the same value for pregnant muskox cows in captivity is 40.1 C/kg/day. I do not find it unreasonable to see a 30 percent greater energy requirement for free-living muskox versus non-active captive muskox. Sheep at pasture expend 21 percent more energy than do their penned counterparts (Blaxter, 1967). The D.E.I. for the 22 month old bulls in captivity was 46.7 C/kg/day. According to this the above value for wild muskox is probably an underestimate, especially when applied to all age groups.

Having estimated the food requirements, the growth and the body weight (Figure 9) of muskox and knowing the number of muskox occupying the Truelove Lowland (Table XIV) we can now estimate the amount of forage harvested by muskox for the year ending 30 April 1973.

Table XV shows the results from converting "muskox days" (Table XIV) to kilograms per day. This value is multiplied by the daily forage requirement for the particular month (Table XV) which in turn is multiplied by the days per month to ascertain the total amount harvested during the month.

Figures 4 to 7 show the approximate distribution of muskox observed during the field study. The problems imposed by the scale of the map prevent a more precise distribution map. By transposing the data from the daily maps prepared in the field to a large photo mosaic of the lowland I have calculated the area utilized by muskox during the period of snow cover in the year ending 30 April 1973. The areas utilized are predominantly meadows of the hummocky sedge type (Muc, 1974). The total area utilized was 327 hectares. The standing

TABLE X

Percent organic matter digestibility

of monocots from Devon Island

	Ligni		
Month	Live	Dead	Nitrogen Fecal Index
Мау		72.7	68.4
June	83.8	69.7	66.8
July	84.4	63.1	73.8
August	83.4	73.8	75.3
September		72.6	70.0
October			65.8
January			67.8
March			66.2
April		74.6	

TABLE XI

Daily fecal output of adult bull muskox

Date	Estimated weight (kg)	Daily fecal output		
		<u>Total (g)</u>	<u>(g/kg)</u>	
14 June 1971	227*	990	4.4	
31 July 1971	281*	1542	5.5	
22 October 1971	268	1606	6.0	

* On 9 May 1972 this bull weighed 264 kg.

TABLE XII

Estimated daily forage intake by adult bull muskox

Date	Digestibility (%)*	Fecal output (g)	Intak	<u>e</u>
	. •		<u>Total (g)</u>	<u>(g/kg)</u>
14 June 1971	75	990	3960	17.4
31 July 1971	75	1542	6170	22.0
22 October 1971	65	1606	4590	17.1

* probably an underestimate

TABLE XIII

Estimated daily energy intake for muskox on Devon Island

May17.081.352.8June17.583.762.7July22.0105.278.9August22.0105.278.9September20.095.662.1October20.095.662.1December20.086.055.9January18.086.055.9February17.081.352.8March16.076.549.7	Month	0.M.I. (g/kg)	G.E.I. (C/kg)	D.E.I. (C/kg)
June17.583.762.7July22.0105.278.9August22.0105.278.9September20.095.662.1October20.095.662.1November20.095.662.1December20.086.055.9January18.086.055.9February17.081.352.8March16.076.549.7	May	17.0	81.3	52.8
July22.0105.278.9August22.0105.278.9September20.095.662.1October20.095.662.1November20.095.662.1December20.086.055.9January18.086.055.9February17.081.352.8March16.076.549.7	June	17.5	83.7	62.7
August22.0105.278.9September20.095.662.1October20.095.662.1November20.086.055.9January18.086.055.9February17.081.352.8March16.076.549.7	July	22.0	105.2	78.9
September20.095.662.1October20.095.662.1November20.095.662.1December20.086.055.9January18.086.055.9February17.081.352.8March16.076.549.7April16.076.549.7	August	22.0	105.2	78.9
October20.095.662.1November20.095.662.1December20.086.055.9January18.086.055.9February17.081.352.8March16.076.549.7April16.076.549.7	September	20.0	95.6	62.1
November20.095.662.1December20.086.055.9January18.086.055.9February17.081.352.8March16.076.549.7April16.076.549.7	October	20.0	95.6	62.1
December20.086.055.9January18.086.055.9February17.081.352.8March16.076.549.7April16.076.549.7	November	20.0	95.6	62.1
January18.086.055.9February17.081.352.8March16.076.549.7April16.076.549.7	December	20.0	86.0	55.9
February17.081.352.8March16.076.549.7April16.076.549.7	January	18.0	86.0	55.9
March16.076.549.7April16.076.549.7	February	17.0	81.3	52.8
April 16.0 76.5 49.7	March	16.0	76.5	49.7
	April	16.0	76.5	49.7

TABLE XIV

Muskox Days for Truelove Lowland:

May 1972 - April 1973

Month	Bulls	Cows	Calves	Yrlngs.	2 yrs.	3 yrs.
May	165	587	303	224	66	60
June	62	192	101	64	17	20
July	97	125	101	28	34	15
August	104	238	130	89	42	17
September	90	268	150	114	28	0
October	78	261	146	112	25	0
November	13	117	65	52	13	0
December	197	323	96	58	26	26
January	446	1084	440	234	29	132
February	483	1101	478	246	105	103
March	571	1208	685	363	153	146
April	300	805	500	225	8	64

crop in this meadow type, averaged over three seasons, is 77.8 g/m^2 . (Muc, 1974 and pers. comm.). The other meadow type utilized by muskox is of the "frost boil sedge" type with a standing crop, averaged over two years, of 60.8 g/m^2 . (*ibid*). Of these amounts approximately 10 percent is forb and shrub material (Muc, 1972) that would not be available to muskox subsequent to die back and breakage at freeze-up. Therefore I will assume that about 65 g/m^2 . are available to muskox during the period of snow cover. On this basis the muskox would remove 135.1 kg/hectare or 13.5 g/m^2 ; about 20.8 percent of what is available to muskox in those areas where they grazed during the period of snow cover. Is this in agreement with what we find when estimating forage removed from winter grazed areas?

Removal of vegetation by grazing and abiotic factors

The only other terrestrial vertebrate herbivores present in the study area were: the greater snow goose (*Chen caerulescens atlantica* Kennard), the arctic hare, and the collared lemming. Geese, being migratory, are present from early June to early September (but in low

TABLE XV

Forage removed from the Truelove Lowland

by muskox grazing

Month	Total muskox (kg/day)	Food requirement (g/kg/day)	Monthly harvest (kg)
Мау	6,756.6	17.0	3,560
June	2,333.5	17.5	1,230
July	2,201.8	22.0	1,500
August	3,369.1	22.0	2,300
September	3,557.2	20.0	2,130
October	3,337.7	20.0	2,070
November	1,376.2	20.0	830
December	4,842.4	20.0	3,000
January	14,934.8	18.0	8,340
February	17,343.2	17.0	8,260
March	18,763.5	16.0	9,310
April	11,387.5	16.0	5,470

Total annual predicted harvest

48,000

densities.) Arctic hare are present but were rarely observed. Lemming densities are very low (Speller, 1972). Muskox therefore, are the only vertebrate agent whose grazing effect may be measured on a meaningful scale.

Vegetation is also removed by abiotic agents such as wind and flowing water. The amount removed by wind is unknown. Muc (1974, and pers. comm.) estimated that 25 percent of the fall standing crop is removed by spring runoff. His estimates are based on examination of areas that were not intensively grazed by muskox the preceding winter. Undoubtedly the amount removed by runoff from an intensively winter grazed meadow would be less than that from an ungrazed meadow.

The methods used in determining forage removal by muskox were not sensitive enough to determine the effect of summer grazing. This is due to the rapid plant growth in a short growing season and very low densities on the Truelove Lowland during the snow free period (Figure 3).

The diet of muskox is predominantly monocot vegetation. In an examination of fecal fragments from Devon Island muskox, Rackette (1974, unpublished) found

monocots making up 97.7 percent of the identifiable fecal material in August 1972. Comparing percent monocot in feces to percent monocot in rumen contents of three bulls collected from Cape Newman Smith by Inuit hunters in February Rackette found 83.8 percent and 87.7 percent monocots respectively. The non-monocot material in the feces as well as the rumen contents was Salix arctica is found in almost exclusively Salix. association with the monocots making up the meadow flora of the study area. Tener (1965) found Salix to be a dominant portion of muskox diet on the Fosheim Peninsula as well as in the Thelon Game Sanctuary. Salix hummock is a common habitat type While on the Fosheim on the Fosheim Peninsula. Peninsula in July 1972 I found Salix arctica made up 32 percent of the cover when the total cover in this habitat type was 36 percent, (unpublished data). Live Salix tissue made up 31 percent, dead Salix 66 percent and monocot less than four percent of the total above ground plant biomass. The study area on Devon Island has no such habitat type. Our observations of muskox grazing activities also show almost exclusive grazing of meadows. For these reasons the discussion of the effects of forage removal by muskox grazing is restricted to meadows alone (Figure 13).

Tables XVI and XVII give the results of clipping inside and outside the exclosures as well as the clipping transects in meadows without exclosures. The biomass of *Salix* (Table XVI) is extremely variable and could not be treated statistically to be meaningful. Any differences observed are due more to the variable distribution of *Salix* than to its removal by grazing. For this reason *Salix* is not included in Table XVII.

Table XVII is a summary of Table XVI. Loss due to runoff only (from inside the exclosures) ranged from 11 to 62 percent. Loss due to runoff and grazing ranged from 16 to 78 percent. Since we did not collect any samples after winter grazing ceased but before runoff began, it is impossible to separate the grazing loss from the runoff loss. For this reason I am unable to determine the amount removed by grazing alone.

In the clipping experiments we restricted our sampling to small areas and in the case of the clipping transects, to areas of maximum removal by muskox grazing. The grazing transects sampled large areas where we were sure winter grazing had occurred. Table XVIII gives the results of these grazing transects. The area grazed ranged from 23 to 40 percent of the total area sampled. The amount of litter

Figure 13.

Locations of grazing investigations on the Truelove Lowland. (See Figure 2 for physiographic features of the Truelove Lowland.)



TABLE XVI

Clipping Results from Exclosures and Winter Grazed Meadows

	Exclosures	Monocot	(g/m ²)	Sali	<u>x</u> (g/m ²)
Date	Location	Inside	Outside	Inside	Outside
August 1970	l	(58.3 ± 3	.4)	(10.5	± 2.4)
	2	(63.1 ± 3	.6)	(6.9	± 1.6)
	3	(56.1 ± 8	.1)	(7.3	± 1.7)
	4	(54.8 ± 3	.5)	(1.8	± 0.7)
July 1971	1	21.9 ± 4.8*	22.2 ± 3.0*	5.3	5.6
	2	52.6 ± 8.7*	47.7 ± 15.7	8.1	1.3
	3	25.7 ± 4.6*	31.8 ± 8.8*	8.8	7.4
	4	44.6 ± 4.9*	23.3 ± 3.7*+	26.2	6.1
September 1971	1	36.7 ± 3.2	40.4 ± 2.8	5.8	4.9
	2	55.1 ± 5.1	62.9 ± 4.1	3.0	5.3
•	3	55.8 ± 6.0	64.8 ± 1.6	20.6	11.8
_	4	83.3 ± 10.5	50.9 ± 3.7*	11.5	15.1
July 1972	1	32.6 ± 6.4	15.2 ± 3.7*+	8.6	2.4
,	2	49.2 ± 3.1*	22.6 ± 4.1*+	6.9	5.2
	3	46.5 ± 6.2*	29.6 ± 6.4*+	4.2	3.0
	4	55.6 ± 4.5*	42.8 ± 2.6*+	3.8	8.7

Table XVI cont'd.

	Winter Grazed Meadows				
	Location	Monocot	Salix		
September 1971	5	67.2 ± 9.2	trace		
· · · ·	6	65.9 ± 8.1	1.3		
	7	90.9 ± 9.0	2.1		
	8	76.8 ± 9.7	3.1		
	10				
July 1972	5	15.6 ± 1.3*	10.3		
	6	16.9 ± 3.3*	1.5		
	7	21.4 ± 3.4*	2.3		
	8	22.0 ± 4.0	4.5		
	10				
September 1972	5	65.1 ± 7.3	8.8		
	6				
	7	72.4 ± 15.6	1.8		
	8	76.0 ± 11.8	2.3		
	10	48.2 ± 6.7	18.9		
July 1973	5	35.4 ± 9.9*	8.7		
	6				
	7	28.7 ± 7.2*	1.5		
	8	29.7 ± 9.7*	1.9		
	10	36.4 ± 10.9	3.0		

1 mean and standard error.

* significantly different from previous sampling at 95% using standard t-test
+ significantly different from control area at 95% using standard t-test
TABLE XVII

Date	Location	Runoff only*		<u>Grazing</u> an	d Runoff**
		_g/m ²	%	g/m^2	%
1970-71	1	36.4	62	36.1	62
	2	10.5	17	15.4	24
	3	30.4	54	24.3	43
	4	10.2	19	31.5	59
1971-72	1	4.1	11	25.2	63
	2	5.9	11	40.3	64
	3	9.3	17	35.2	54
	4	27.7	33	8.1	16
	5			51.6	78
	6			49:0	74
	7			69.6	77
	8			54.8	71
1972-73	5			29.7	46
	Ŧ			43.7	61
	8			46.3	60

Forage loss estimated by clipping

* fall - spring inside

** fall - spring outside

TABLE XVIII

	Forage Available*	Litter Remaining+	Area	Forage	Transect
Location	<u>(g/m²)</u>	<u>(g/m²)</u>	grazed (%)	$\frac{\text{removed}++}{(\%)}$	length (m)
4 + 8	76.0 ± 11.8	11.3 ± 2.0	40 ± 6	30	2400
9	63.6 ± 2.4	12.7 ± 3.2	26 ± 2	23	3600
10	48.2 ± 6.7	5.6 ± 1.4	23 ± 2	20	3900
11 .	63.9 **	10.9 ± 1.8	20 ± 2	17	5620
12	67.3 ± 3.6	6.l ± 1.0	31 ± 3	28	1380
	$\bar{x} = 63.8$			$\bar{x} = 23.6$	

Forage removed from meadows grazed in the winter of 1972-73

* Monocot biomass present September 1972.

** Data from Muc (1974)

- + Litter remaining following grazing and runoff in plot where 100% of area had been grazed prior to runoff.
- ++ Percent forage removed from entire meadow.

remaining in plots that were totally grazed ranged from 9.1 to 20.2 percent of that which was present the previous fall. The amount of vegetation that was removed from the meadow by all agents ranged from 17 to 30 percent.

By sampling litter in areas of total grazing we minimized if not eliminated the effects of runoff. Litter remaining in areas of total grazing was either deposited by runoff water or remained as litter following grazing. Probably both agents are responsible with the latter playing a greater role.

The close agreement between the observed 23.6 percent forage removed in those meadows sampled and the predicted 20.8 percent based on the predicted energy required and area intensively utilized indicates that I have come close to approximating reality. If this is so, it would appear that muskox harvest only a small portion of the total standing crop on the Truelove Therefore, the natural factors regulating Lowland. population size will probably always keep a wild muskox population from harvesting more than the sustained yield of its food supply. Accordingly only density independent agents could produce starvation with possible subsequent die-off in a natural muskox population in its native range.

Significance of the Truelove Lowland to the productivity of muskox on northeastern Devon Island

99

The total area below 200 meters between Sverdrup Inlet and Sverdrup Glacier on northeastern Devon Island is 301.4 square kilometers. Of this area approximately 51 square kilometers (18.8%) are meadow habitat. The Truelove Lowland represents 14.7 percent of the land surface of the range but the Truelove Lowland meadows represent 34.6 percent of the meadow habitat available to the muskox in this area.

To determine the significance of the Truelove Lowland to the muskox population occupying northeastern Devon Island I will fix the population at 243 animals; based on May 1972 and May 1973 censes. That means that 243 animals were in the population from 1 May 1972 to 30 April 1973. The composition of this constructed population is: 73 adult males, 86 adult females, 36 calves, 34 yearlings, 6 two-year-olds, and 8 three-year-old males. The reason for setting the number of calves at 36 rather than the total number observed in May 1973 is that we know that at least 36 calves were in the population for the year. The same reasoning holds for the other cohorts in the population.

Figure 14 illustrates the percentage of the individuals in the population utilizing the lowland while Figure 15 shows the percentage of the biomass of the population occupying the lowland. If muskox were distributed randomly over the land surface of their range one would expect 14.7 percent occupying On an annual basis 17.0 percent of the the lowland. muskox days of the population were spent on the lowland. If muskox were distributed at random over the meadow area in their range 34.6 percent of the population should utilize the lowland. In fact, from Figure 19 neither condition appears to hold. Table XVII shows what percentage of each cohort occupies Truelove Lowland monthly. The lowland was under-occupied in relation to the rest of the range as a whole during the entire period of "total day" plus the early portion of the period of snow cover. It was over-occupied most the period of "total night", maximum snow cover, and coldest ambient temperature. It is interesting that the greatest rate of increase in muskox numbers and biomass on the lowland coincides with the period when the population approaches and enters a period of The lowland is zero or negative biomass change. most important for cows, calves and yearlings during

Figure 14. Percentage of individuals in the population on Truelove Lowland for the year ending 30 April 1973.



Figure 15.

Percentage of the total population biomass utilizing the Truelove Lowland for the year ending 30 April 1974.



TABLE XIX

Percent of cohort in population utilizing Truelove Lowland in the year ending 30 April 1973

	Adult	Adult			<u>2 year</u>	<u>3 year</u>
Month	males	females	Calves	Yearlings	_olds_	olds
Мау	7.3	22.0*	27.2*	21.3*	35.5*	24.2*
June	2.8	7.4	9.4	6.3	9.4	8.3
July	4.3	4.7	9.1	2.7	18.3*	6.1
August	4.6	8.9	11.7	8.4	22.6*	6.8
September	4.1	10.4	13.9	11.2	15.6*	0
October	3.5	9.8	13.1	10.6	13.4	0
November	.6	4.5	6.0	5.1	7.2	0
December	8.7	12.1	8.6	5.5	14.0	10.9
January	19.7*	40.7**	39.4**	22.2*	15.6*	53.2**
February	23.6*	45.7**	47.4**	25.8*	62.5**	48.5**
March	25.2*	45.3**	61.4**	34.4*	82.3**	58.9**
April	13.7	31.2*	46.3**	22.1*	4.4	26.7*
x	10.7	20.2*	24.5*	14.6	25.1*	20.3*

* Utilization greater than 14.7%

** Utilization greater than 34.6%

this period which probably means cows with calves and yearlings. Since the observed number of two-year-olds and three-year-old males is so low in the "constructed" population" it is difficult to judge the importance of the lowland to these cohorts. The lowland is also important for calving cows in May. Summing up then, the Truelove Lowland provides ample amounts of forage in a small area during the season when forage is most difficult to obtain.

Productivity of muskox on northeastern Devon Island

Based on the proposed growth and weights of wild muskox (Figure 9) the constructed population weighed 43,429 kilograms on 1 May 1972 (Figure 15). The population reached its maximum weight of 50,000 kilograms in January 1973. Over the year ending 30 April 1973 the constructed population increased 5198 kilograms or 12.0 percent. I will attempt to show how much biomass each cohort in the population contributed to this increase relative to the standing crop of primary producers in the natural system.

In this exercise I will deal only with net annual production, that is, the weight gain in kilograms of the cohort as a whole from 1 May 1972 to 30 April 1973.

TABLE XX

Contribution of individual cohorts to the biomass increment of the Devon Island muskox population

	% of population	<u>% of net</u>	% of forage	<u>Ratio*</u>
		production	harvested	
Adult bulls	30.0	0	42.0	
Adult cows	35.4	13.2	39.3	3.0:1
Calves	14.8	53.0	5.1	10.4:1
Yearlings	14.0	22.9	8.1	2.8:1
2 Year-olds	2.5	4.7	1.9	2.5:1
3 Year-old bulls	3.3	6.2	3.7	1.7:1

* Percent of net production/percent of forage harvested

In the case of adult males the net annual production is zero due to seasonal fluctuations in body weight. Their gross annual production however would be 1971 kg ; equal to 38% of the net annual production for the entire population.

To determine the forage required by each cohort on an annual basis I will use values presented in Table XIII, and multiply them by the weight of the cohort for each month, adding them to produce annual values to calculate how much forage each cohort requires annually. From Table XX the expected pattern emerges in that the youngest cohort in the population is the greatest contributor to its biomass increment. Also, this segment of the population, that contributes the most biomass to the net annual production in the population, is also the cohort which has the bwest relative forage requirement. Such are the inequities of the System.

SUMMARY

The object of this study was to determine the productivity of muskox on northeastern Devon Island, Productivity of an animal population may be N.W.T. considered in two ways. One is the growth and regulation of numbers of individuals in the population, Another approach is measuring or population dynamics. the biomass increment or change resulting from fluctuations in population size and growth of individuals of the A major component of the latter approach population. is the cost of production; in this case forage requirements The major points emerging from this of the population. study are briefly outlined below:

- The muskox population on northeastern Devon Island was in a period of increase and stood at approximately 275 at the close of the field study. Population size is probably regulated by abiotic density independent agents.
- 2. Female muskox may produce their first calf in their third year but probably most are at least four years old. Calves in the wild are not necessarily weaned before 12 months.

- 3. Female muskox probably approach adult body weight in their fifth summer while males may grow until their sixth or seventh summer.
- 4. Cultured hay used in feeding trials with domestic muskox had a digestibility of 64 percent while native sedges had a minimum digestibility of 66 percent in winter and 84 percent in summer.
- 5. Forage requirements for maintenance of domestic muskox were 13.1 - 15.4 grams organic matter per kilogram body weight per day in February 1972. For wild muskox the estimated organic matter intake ranged from 16 g/kg/day in March and April to 22 g/kg/day in July and August.
- 6. On the basis of body weight and forage requirements of muskox a predicted 20.8 percent of the forage was removed from winter grazed meadows on the Truelove Lowland for the year ending 30 April 1973. Examination of these meadows in August 1973 showed that an average 23.6 percent of the standing crop had been removed.

7. The numbers of muskox utilizing the Truelove Lowland ranged from zero during the period of spring melt and runoff to 114 in March 1974. It was most heavily utilized in the season when forage is the most difficult to secure.

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APPENDIX I

Word Model Predicting Forage Requirements Of Muskox On The Truelove Lowland

