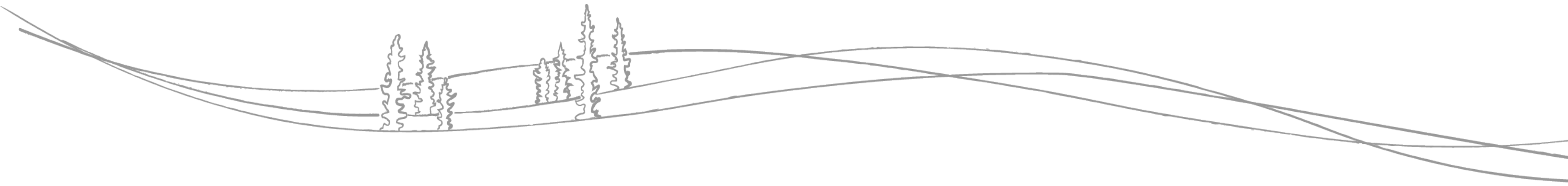

TECHNICAL STATUS REPORT FOR MUSKOXEN (*OVIBOS MOSCHATUS*) IN THE NORTHWEST TERRITORIES

ANNE GUNN [1], BONNIE FOURNIER [2], JUDY WILLIAMS [2] AND JAN ADAMCZEWSKI [2]

[1] SALT SPRING ISLAND, BC

[2] ENVIRONMENT AND CLIMATE CHANGE, GNWT

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ABSTRACT

This report is a technical review of distribution, abundance and ecology of muskoxen in the Northwest Territories (NWT) up to 2019-2020 intended as background for muskox management. The technical information is complementary to Winbourne and Benson's (2021) report based on Traditional Knowledge and Community Knowledge of NWT muskoxen. Muskoxen in the NWT are managed through collaborative management processes in the northern NWT although regional and NWT-wide planning is incomplete.

Mainland and Arctic Island muskoxen differ in genetics, appearance and geographic opportunities for dispersal, and these differences likely justify treating NWT muskoxen as island and mainland ecotypes. However, the 1960 taxonomic assessment based on morphology and more recent genetic studies did not support separation into subspecies. Trends in abundance and distribution for the two ecotypes reflect their different climate and geography.

The overall 2019 estimate was approximately 34,000 adult muskoxen for the NWT, which is a 55% decline from the 86,000 muskoxen estimated in 1998. Just under half the NWT muskoxen were on Banks and northwest Victoria Islands, where numbers declined 82% from their apparent peak in abundance from the late 1990s (91,400) to 2019 (16,300). Estimates for Banks and northwest Victoria are relatively frequent and precise while for the mainland and high Arctic Islands, estimates are infrequent. Since the 1980s, muskoxen on the Arctic Islands have fluctuated in abundance, while longer term trends on the mainland muskox abundance have seen apparent increases; however mainland surveys have varied in area and frequency.

Distribution since 1998 has continued to expand to the northwest toward the Mackenzie River and southeast into the mainland boreal forest, which is similar to the historic distribution before the 1860s. While abundance was increasing along the re-colonizing fronts, the changing survey areas obscured whether abundance was declining behind the dispersing front. Monitoring for pregnancy and survival rates was largely lacking except for productivity (% calves) on aerial surveys.

Evidence on factors limiting abundance is limited for the NWT although research in Nunavut and Alaska suggests wolf and grizzly bear predation may limit muskox abundance, especially when predation interacts with disease and environmental factors. Mortality events driven by pathogens like yersinia and erisypelas have affected several island populations. Muskox pregnancy rates, hence initial productivity of young, can sometimes be low and intervals between calves for breeding females can be 2-3 years or longer. Scarcity of micro-nutrients like copper and selenium can affect health and reproduction. While muskoxen have low genetic variability, the consequences are unclear especially in the face of changes in diseases,

parasites and forage availability as the climate changes. Parasite lifecycles are changing in a hotter climate and together with outbreaks of bacterial diseases may increase muskox vulnerability to environmental stress such as hot summers. Recently, muskox harvest levels have been low in most NWT communities, in part due to negative perceptions of muskoxen and lost hunting traditions.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

Muskoxen (*Ovibos moschatus*) are an adaptable and resilient species persisting through several ice ages (Campos et al. 2010, Raghavan et al. 2014). Muskoxen are a large-bodied social herbivore typical of the tundra. In the last 100 years (1917-2019), muskoxen have recovered from drastic declines that resulted from unregulated commercial harvesting on the Canadian mainland in the late 1800s (Barr 1991, Lent 1999). Numbers on some of the arctic islands (e.g. Banks Island) 100 years ago were also low and have recovered, but then in some cases declined again. Muskoxen have shown the ability to recover after catastrophic ice storms (Munizzi 2017) and severe winters (Miller et al. 1977). For the Northwest Territories (NWT), muskox abundance and distribution were summarized 23 years ago (Fournier and Gunn 1998). That report included muskox populations in what is now Nunavut (NU), which became a separate territory in 1999. Since then, progress has been made in describing muskox nutritional ecology, predator-prey relations, health, abundance and distribution.

Our objective was to compile and update information on NWT muskoxen, especially on abundance and distribution, and describe factors that may limit abundance of muskoxen. This report will serve as background for muskox co-management in the NWT. We relied primarily on technical sources such as government survey reports and research papers. A parallel report on Traditional Knowledge and Community Knowledge of NWT muskoxen was completed in 2021 by Winbourne and Benson (2021). Some sources, such as the community-based research by Tomaselli et al. (2018) and Lent's 1999 book on muskoxen and their hunters, were used in both reports. We summarized the NWT muskox baseline information relative to, where appropriate, the performance of currently used monitoring indicators. We have drawn on recent research findings from across muskox ranges where they likely contribute to understanding mechanisms for the changes in abundance and distribution.

APPROACH AND METHODS

Approach and Information Sources

We summarized common monitoring indicators to provide baseline NWT muskox status and trend information. The report format incorporates components of muskox health (MacBeth and Kutz 2018; Figure 1) into the NWT Species at Risk format for status reports. We grouped the 12 NWT existing aerial survey areas as four regions (Table 1) and relied on unpublished and published government reports to summarize the aerial surveys. For health indicators, we used NWT information and what is known for muskoxen elsewhere.

Table 1. Dates, citations and regions for muskox surveys 1980-2020, NWT. .

Region			**3. Mid-Arctic Islands**			
1. Southeast Mainland				**Northwest Victoria**		**Banks**
Survey Area	**Year**	**Citation**	**Year**	**Citation**	**Year**	**Citation**
Artillery Lake	1989	Graf and Shank 1989	1983	Jingfors 1985	1982	Nagy et al. 2009a (recalculation Latour)
	1998	Bradley et al 2001	1989	Gunn unpublished	1985	Mclean et al 1986
	2010	Cluff Unpublished	1994	Nishi in Fournier and Gunn 1998	1989	McLean and Fraser 1992
	2018	Cluff Unpublished	1998	Nagy et al. 2009d	1991	Fraser et al. 1992a
Alymer Lake	1991	Shank and Graf 1992	2001	Nagy et al. 2009e	1992	Nagy et al. 2009b
	2018	Cluff Unpublished	2005	Nagy et al. 2009f	1994	Nagy et al. 2013a
Thelon Game Sanctuary	1994	Shank in Gunn et al 2009	2010	Davison and Williams 2013a and b	1998	Nagy et al. 2013b
Beaverhill Lake	2000	Gunn et al 2009	2015	Davison and Williams 2019	2001	Nagy et al 2006
Rennie Lake	2011	Adamczewski and Williams unpublished	2019	Davison pers. comm.	2005	Nagy et al. 2009c
2. Northwest mainland				Partial surveys (Minto Inlet)	2010	Davison and Williams 2013c
Paulatuk	1980	Spencer 1980	1992	Heard 1992a	2014	Davison et al 2017
	1983	Case and Poole 1985	1992	Gunn and Nishi In prep.	2019	Davison and Baryluk unpublished
	1987	McLean 1992				
	1997	Larter 1999	1993	Buckland unpublished		
	2002	Nagy et al 2013c	**4. Western Queen Elizabeth Islands**			
	2009	Davison and Branigan 2014	1973	Miller et al 1977		
Great Bear Lake	1997	Veitch 1997	1974	Miller et al 1977		
	2020	Chan Unpublished	1987	Miller, 1987, 1988		
			1997	Gunn and Dragon 2002		
			2012	Davison and Williams 2016		

The Government of the Northwest Territories' (GNWT) Wildlife Management Information System (WMIS) was the source for most aerial survey spatial data, incidental muskox sightings from other species systematic surveys (805 locations 1978-2015) and sightings from pilots, guides and others (1,062 locations 1967-2015).

The GNWT Infobase for species includes muskoxen (www.enr.gov.nt.ca/en/services/muskoxen) and a distribution map which is based on historic and published literature (1877-2013). We also consulted the NWT Cumulative Impact Monitoring Program's Discovery Portal database for NWT environmental monitoring knowledge.

Canada contributes to the Arctic Council's Circumpolar Biodiversity Monitoring Program through support from Environment and Climate Change Canada (ECCC). In 2016, ECCC initiated a terrestrial expert group (Muskox Knowledge Network) to act as a network for sharing information on muskoxen (summarized in Cuyler et al. 2019) and we used the resulting database for survey information. We also used the University of Calgary 2016 muskox health symposium for leads to updates and on-going research (Kutz et al. 2017). We had access to the MERRA spatial climate database updated to 2019 (D. Russell pers. comm., Russell et al. 2013).

METHODS

To describe abundance, we listed the mean estimates for the survey areas. In the original reports, authors varied as to whether they used 95% Confidence Levels or Standard Errors (SE). For the sake of comparability in this report, we converted the SE to 95% Confidence Limits (95% CI = mean ± 1.96*SE). We also calculated the Coefficient of Variation when describing the precision of the surveys CV=μ/σ where: σ=standard deviation and μ=mean. We identified if the estimate was total muskoxen or adult muskoxen (calves not included). Typically, it was the earlier surveys that did not report adult muskoxen (i.e., calves were included in estimates). We estimated the rates of change as an exponential rate (r) (Caughley 1977) using the formula given below:

$$r = \sqrt[t]{\frac{x_t}{x_0}} - 1$$

where x_0 is the population size of the previous time, also known as a reference survey, x_t is the population size of the next or current survey, and t is the number of time-steps between surveys measured in years. The irregular frequency of surveys caused us to apply the exponential rate of change as infilling for the database to be able to sum abundance for 2019 and 1998. We limited the forward projections based on the exponential rate to five years after the most recent estimate.

We estimated the trend in abundance for three generations following the International Union for Conservation of Nature (IUCN) Red List Guidelines. We used IUCN's Excel tool to calculate rate of change (Appendix A). The generation length was seven years (Hansen et al. 2018). In regional accounts, we extended the time period to include earlier surveys to lengthen the time period to detect fluctuations. We followed Clarke (1949) in recognizing a fluctuation as a wave-like variation with a point of reference to distinguish up from down. An 'extreme fluctuation' occurs when population size varies greater than a tenfold increase or decrease (IUCN 2012) and a 'crash' is as at least a 30% decrease in the estimated population size in one year (Gunn et al. 2003).

We mapped WMIS's incidental records of muskox sightings to describe distribution although there were gaps; WMIS does not typically have sightings recorded as part of baseline and monitoring for industrial developments (such as active mine-sites). We grouped the incidental sightings as point observations by decade in ArcMap 10.4 using a generalization cartography tool to aggregate points into polygons for three mainland areas. The same procedure was used for the systematic survey sightings that were 'on transect'. We calculated centroids to measure directional changes in distribution for overall and decadal polygons by using a ‘Calculate Geometry’ function which added centroid points for the mainland regions. Distances between decadal centroids were measured using ArcMap’s ruler. A model was created in ArcMap to calculate the area of overlap between survey blocks, and also between Ecoregions and the Treeline zone with decadal polygons.

TAXONOMY, GENETICS AND POPULATION STRUCTURE

Subspecies and Ecotypes

Muskox taxonomy is based on Tener (1965) who concluded that contemporary *Ovibos* was a monotypic species, largely based on skull measurements. His data set included High Arctic and Greenland muskoxen (359 skulls) compared to barren-ground muskoxen from the Canadian mainland (16 skulls). Taxonomic research emphasis has shifted since the 1960s from morphology to genetics. Genetic variation based on mitochondrial DNA was too low to define subspecies (Groves 1997). Despite the absence of confirmed subspecies, muskoxen are not lacking variation genetically and morphologically (Tener 1965, Groves 1997). Thus, we summarized the evidence for whether that variation is distinctive enough to warrant separate conservation units within the NWT. The ecotype is a population or group of populations adapted to a particular set of environmental conditions (as defined for Canadian eco-types of caribou, COSEWIC 2011).

Evidence for the adaptations to support categorizing island and mainland muskoxen as two ecotypes is morphological, genetic and geographic. Arctic Island muskoxen are relatively distinguishable in appearance from mainland muskoxen in having longer coats of brown guard hairs, paler horns, and whiter saddles, foreheads and stockings. However, metric skull measurements did not differ between the island and mainland muskoxen except for the upper tooth row length (Tener 1965). The presence of lingual styles on the second molar teeth is a non-metric character that differed between the mainland and the islands although with exceptions. Likewise, Henrichsen (1982) reported regional differences in the frequency of dental anomalies for muskoxen in Greenland.

Mitochondrial DNA and micro-satellite nuclear DNA analyses supported clustering of mainland muskoxen separate from Arctic Islands, but with the likelihood of limited gene flow between them (Groves 1997, van Coeverden de Groot 2000, Prewer et al. 2019). Tener (1965) reported based on tooth styles that muskoxen north of Great Bear Lake may interchange with muskoxen from Banks or Victoria Islands. Phylogenetically, mainland muskoxen likely originated from south of the Laurentide ice sheet while Arctic Island muskoxen were isolated in glacial refugia, which would contribute to the genetic differences but does not preclude local adaptations (van Coeverden de Groot 2000, Hansen et al. 2018). Currently, information on life-history and behavior appears similar between mainland and Arctic Island muskoxen. However, geography constrains dispersal behavior as island muskoxen are genetically less variable compared to the mainland despite the presence of sea ice, which would allow muskoxen to move between islands (van Coeverden de Groot 2000).

As well as glacial history and natural dispersal playing a role in muskox genetics, a recent change is the relocation of muskoxen to Alaska from Greenland in the 1930s, including a relocation to the Alaskan North Slope bordering the Yukon (Lent 1999). These Alaskan muskoxen have dispersed through the northern Yukon to reach the NWT in the late 1990s. When and if muskoxen of Greenlandic/Alaskan origin inter-mingle with the NWT muskoxen dispersing from the Great Bear Lake and coastal regions, the effect will include mingling of the putative subspecies and their parasites and pathogens, and possibly an increase in genetic variation. However, the specific baseline genetic variability of dispersing individuals is currently unmeasured (See also Section 7; Diseases).

Genetic Variation

Low genetic variability in muskoxen is a consistent finding among the few genetic analyses carried out to date (summarized in Prewer et al. 2019) and is likely a consequence of bottlenecks during the Pleistocene (Groves 1997). Mitochondrial DNA sequences from Pleistocene compared to early Holocene muskox bones suggest muskox genotypes have changed little since prehistoric times (Groves 1997). However, this current finding of low variability may also reflect the fact that only a fraction of the genome has been sampled, and sampling has mostly focused on neutral variation. We do not know how muskoxen adapted to the extreme Pleistocene climate and landscape changes, even as successive bottlenecks reduced their genetic variability (MacPhee et al. 2005, Hansen et al. 2018). Historic bottlenecks such as the low numbers on Victoria Island in the early 1900s also contributed further to the low variability of those muskoxen (Prewer et al. 2019). However, genetic modeling suggested that even if the current muskox decline reduced the effective population size to about 70 muskoxen, genetic variability would not decline further (Prewer et al. 2019).

Groves' (1997) mitochondrial DNA analysis used samples from the mainland west of Paulatuk and Kugluktuk, as well as from Victoria and Banks Islands. A study conducted a few years later used microsatellite DNA analysis and had extensive Canadian geographic coverage with 169 individuals sampled from 11 locations (van Coeverden de Groot 2000, Van Coeverden de Groot and Boag 2004). Mainland muskoxen clustered as one lineage, whereas Bathurst, Banks and Victoria Islands clustered as a second lineage, and High Arctic Islands clustered as the third lineage. Van Coeverden de Groot (2000) sampled four of the six mainland refugia that had been mapped in the 1930s (Barr 1991). Those isolated refugia are likely why mainland muskoxen have double the average heterozygosity compared to the Arctic Island muskoxen (van Coeverden de Groot 2000).

Prewer et al. (2019) compared microsatellites from muskoxen from Victoria Island and the mainland (Kugluktuk and the Sahtú region) and also reported greater allelic richness and heterozygosity for the mainland than Victoria Island. Hansen et al. (2018) used about 60%

of van Coeverden de Groot's (2000) samples in a finer-scale analysis using single nucleotide polymorphisms (SNPs). However, the statistical power of SNPs compared to microsatellites to determine population structure is untested even though the genome-wide SNP sampling can include potentially adaptive genetic variation.

A concern about low genetic variability is whether it increases susceptibility to disease (Spielman et al. 2004). The major histocompatibility complex (MHC) is the locus which has a key role in the immune system (Mikko et al. 1999, Sommer 2005). Mikko et al. (1999) used polymorphism and DNA sequence analyses for 41 samples from three unspecified Canadian muskox populations and reported almost no variation. However, they also concluded from several other ungulate species that low variability for the MHC locus does not prevent increasing abundance. Subsequently, more recent techniques revealed greater variability in the MHC gene for many species although muskoxen were not sampled (Radwan et al. 2010, Castro-Prieto et al. 2011, Schwensow et al. 2019). Techniques such as whole genome sequencing sample a much larger fraction of the genome and measure rare and low frequency variation, which influences disease susceptibility (Höglund et al. 2019). The introduction of non-invasive sampling (fecal pellets and hair) as already applied for monitoring muskox pathogens and stress (Population Dynamics section) opens up potential for further genetic monitoring (Schwartz et al. 2007) including bar-coding for pathogens (Andersen-Ranberg et al. 2018).

Defining Management Units (Populations)

Muskox management units as populations are currently based on geography (e.g. islands) and aerial survey areas (e.g. mainland). Muskoxen on Banks and northwest Victoria Islands are relatively isolated from the continental mainland (Groves 1997). Movements between islands are rarely observed, and the few observations of muskoxen on the sea ice are likely desperation movements during severe winters and muskoxen in those situations were unlikely to survive (Nagy and Gunn 2009, Miller 1998).

Dispersal on the mainland is apparent as muskox distribution has changed (Distribution section) and the validity of population boundaries is unresolved. Currently, the aerial survey boundaries for the northwest and southeast regions likely reflect two genetic clusters (van Coeverden de Groot 2000) which supports the two regions as populations. However, if distribution changed, then the question of open or closed populations in the management context could become significant and require monitoring including genetic indicators.

DISTRIBUTION

Globally, muskoxen are indigenous only to Canada and northeast Greenland, as the muskoxen in Russia and Alaska are reintroductions. Muskoxen currently in west Greenland, Québec, Norway and Sweden are introductions as those areas do not have earlier historic evidence of muskoxen.

Canadian Distribution

Muskoxen currently occur in Canada's three territories. The muskoxen in the Yukon Territory are recent as they were first sighted in 1985 having dispersed from the Alaskan reintroduction on the North Slope (WMAC 2017, 2019). In 2016, a survey along the Yukon North Slope included portions of the Richardson Mountains (M. Suitor pers. comm.). The Yukon muskoxen have dispersed into the western NWT (Richardson Mountains and west of the Mackenzie River).

The muskoxen in northern Québec (with occasional sightings in Labrador, Chubbs and Brazil 2007) originated from Ellesmere Island in 1967 and were held in a farm until 55 individuals were released between 1973 and 1983 (Le Hénaff and Crête 1989, Chubbs and Brazil 2007). The released muskoxen dispersed and are well established on western and eastern Ungava Peninsula. In 2019, there were an estimated 4,470 muskoxen along the eastern coast of Ungava Peninsula (V. Brodeur pers. comm. 2019).

NWT Distribution

In 2020, muskoxen occurred on 48% (633,294 km^2) of the NWT geographic area, being widely distributed across arctic islands and patchily on the mainland (Figure 2). West of the Mackenzie River, muskoxen are in the Richardson Mountains and occasionally in the Mackenzie Mountains along the Yukon border. East of the Mackenzie River, muskox distribution extends along the coast east into NU, south to Tulita and the Hudson Bay coast. Occasionally, the southern distribution of individual muskoxen can be seen as far as south as the 60th parallel in Saskatchewan (SK) and Alberta (AB). In summer 2019, the Canadian Broadcasting Corporation (CBC 2019) documented a young muskox bull shot near Fort Chipewyan, AB. To our knowledge, this is the southernmost muskox of the current era.

The current mainland distribution is discontinuous with three gaps along the tree-line zone (Figure 1). First, in the northwest NWT, the Mackenzie River and Delta may be a geographic barrier to muskoxen expanding east from the Yukon, and to muskoxen spreading west from the Paulatuk area. Muskoxen have reached the Tuktoyaktuk Peninsula (T. Davison pers. comm. 2020). However, as muskoxen have been recorded near Aklavik and Tsiigehtchic (T. Davison pers. comm. 2020) and the Mackenzie River seasonally freezes, the gap may be closing although it is not certain from which direction the muskoxen have come from. There were four incidental observations of muskoxen (12-40 individuals/group) west of the Mackenzie River recorded between 2004 and 2011.

The apparent gap in distribution east of Great Bear Lake may reflect both muskox scarcity and lack of survey effort. Muskox distribution within the adjacent NU muskox management units is uneven and in 2013, densities were higher toward the coast (LeClerc 2014, MMG 2016). The third gap in distribution along the southeast NWT/NU boundary may also reflect low densities, a lack of surveys and that the area is deeper into the boreal forest (Figures 1 and 2).

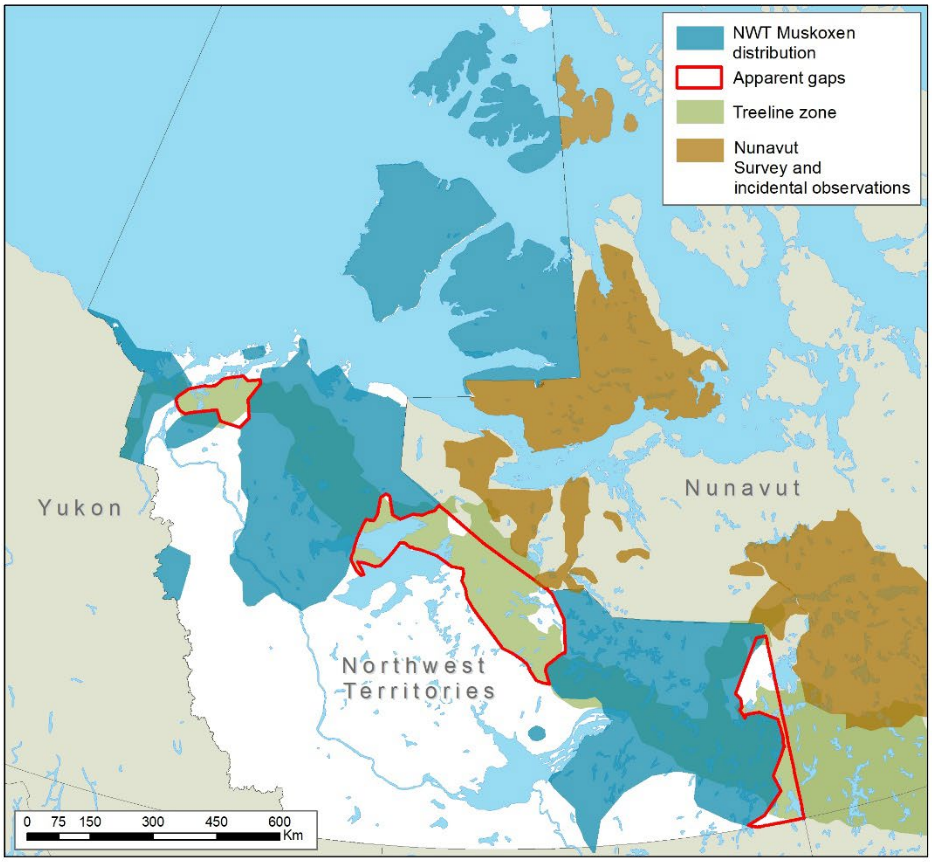

Figure 1. NWT muskox distribution based on aerial surveys and incidental muskox sightings listed in WMIS, 1967-2018. The red outline areas have no recorded incidental sightings. Muskox distribution is based on surveys and incidental sightings adjacent to the NWT and NU boundary.

Search Effort

The aerial survey areas for muskoxen on the NWT mainland cover about 82% of the distribution based on the incidental sightings (Figure 2). The incidental sightings are a mixture of casual observations of unknown effort or observations acquired through systematic sampling but for other species (e.g. caribou surveys). They are likely biased toward the colonization edge of muskox distribution as they are more likely to be recorded when they are 'novel' sightings. For the Arctic Islands, the aerial surveys are island wide except for Victoria Island where the aerial surveys cover the northwest part of the island within NWT. Search effort is more variable on the mainland as standardized aerial surveys are typically a response to where muskox sightings have been reported and people want to hunt muskoxen. Consequently, survey effort progressively shifts to track the expanding edge of distribution, which has meant less effort to measure any changes in abundance and distribution behind the expansion edge.

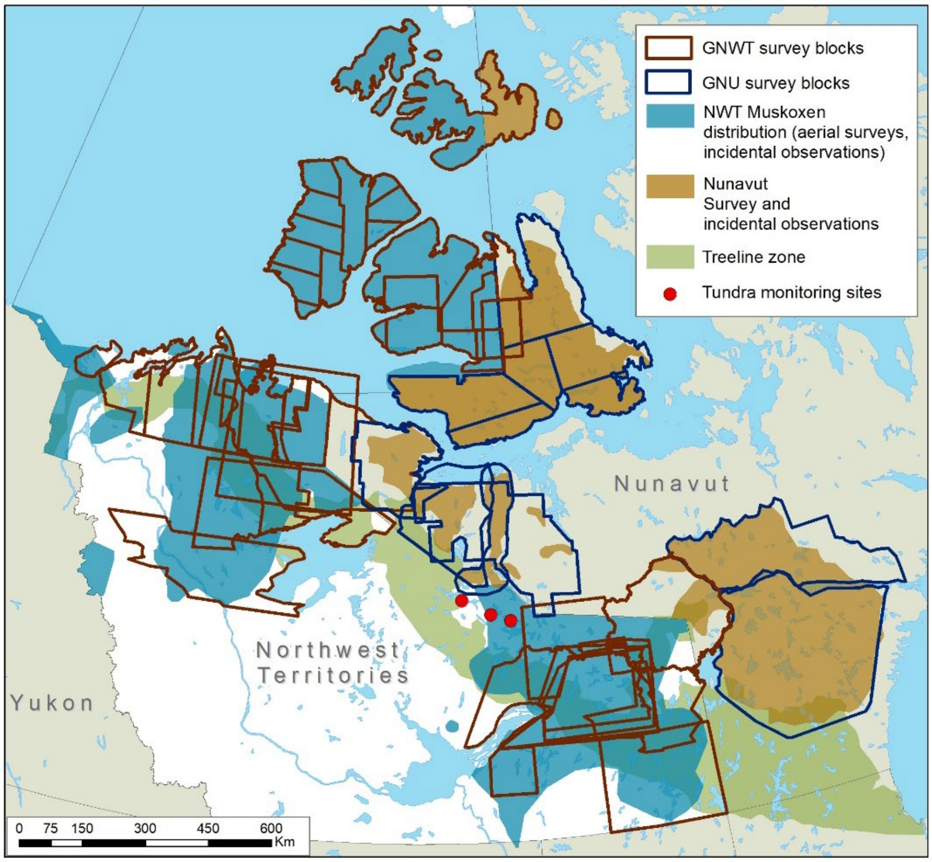

Figure 2. Survey and stratum boundaries relative to muskox distribution based on incidental sightings, NWT and adjacent areas of NU up to 2020. Red dots show three tundra long-term monitoring sites.

Three monitoring sites on the NWT tundra (Tundra Ecological Research Station at Daring Lake, Ekati Mine and Point Lake Lodge) have long-term ecological observations, including muskox sightings. These sites are between the northwest and southeast muskox areas (Table 2) and their records suggest muskox occurrence southeast of Great Bear Lake is infrequent. These sightings have not yet been included as incidental sightings in WMIS. The long-term sightings along the major rivers in and south of the Thelon Game Sanctuary are presented in the Biology section.

Table 2. Incidental muskox sightings from three NWT tundra sites with long-term monitoring.

Site & Period	Occupancy & Description	Muskox Observations
Tundra Ecological Research Station at Daring Lake[1]	**Usually occupied mid-May to end of August 1996-2018**	
June 3,2000	30km NE Daring Lake	4 muskoxen seen by heli crew
June 4, 2000	NE of Daring Lake	35 muskoxen seen by heli crew
Ekati Mine[2]	Year-round occupancy since 1995	
1994	Near Lac de Gras	6
1995 June - July	Mine site	4, 4, 9, 28, 1
1996	unknown	13, 15, 25, 2, 20-30, 1, 25
1998 May - June	unknown	Unknown number
1999	Outside the study area	2 and unknown number
2001 May		20-30, 1, 2
2003		1
2010		6
2011 July	Close to mine site	39
2012 August	Close to mine site	50, 3
2017	Within mine site	
Point Lake Lodge[3]	August-September 1986-2018	
2008 August	65° 16 113°N 31’	25 muskoxen including 4 calves

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[1] Karin Clark pers. comm. ENR 2018

[2] Christine Rock pers. comm. 2018; Ekati Diamond Mine’s 2012 Environmental Impact Report, http://reviewboard.ca/upload/project_document/EA1314-01_Ekati_Diamond_Mine_2012_Environmental_Impact_Report.PDF).

[3] Amanda Peterson, Peterson’s Point Lake Naturalist Lodge pers. comm. 2018

Distribution Trends

Overall, current distribution on the mainland has continued the recovery from the 1920s after commercial hunting in the late 1800s left only fragmented distribution in six refugia (Anderson 1930 in Barr 1991). Federal protection from muskox hunting in Canada in 1917 and 1924 contributed to recovery, although it was enacted with no consultation with northern communities (Barr 1991). Expansion of muskoxen from those refugia was initially slow (Barr 1991) but since the late 1990s, the trend for expansion as measured by directional shifts in distribution has continued. The mean number of years between aerial surveys has varied from three to nine years in the NWT (Table 3) but the mainland surveys are relatively infrequent which limits describing distribution trends as well as trends in abundance. Decadal trends in distribution based on the incidental sightings suggest an expansion into areas used historically on the NWT mainland (Figure 3) but the unknown search effort for the incidental sightings limits any occupancy analysis.

Table 3. The interval, period and number of aerial muskox surveys in the NWT for five regions, including mainland and Arctic Islands, up to 2019.

	Southeast mainland (Artillery Lake)	**Northwest mainland (Paulatuk)**	**Northwest Victoria**	**Banks**	**Western Queen Elizabeth Islands**
Surveys	4	6	9	11	5
Period (years)	30	30	33	33	45
Mean frequency of Surveys (years)	9.7	5.8	4.5	3.4	9.8

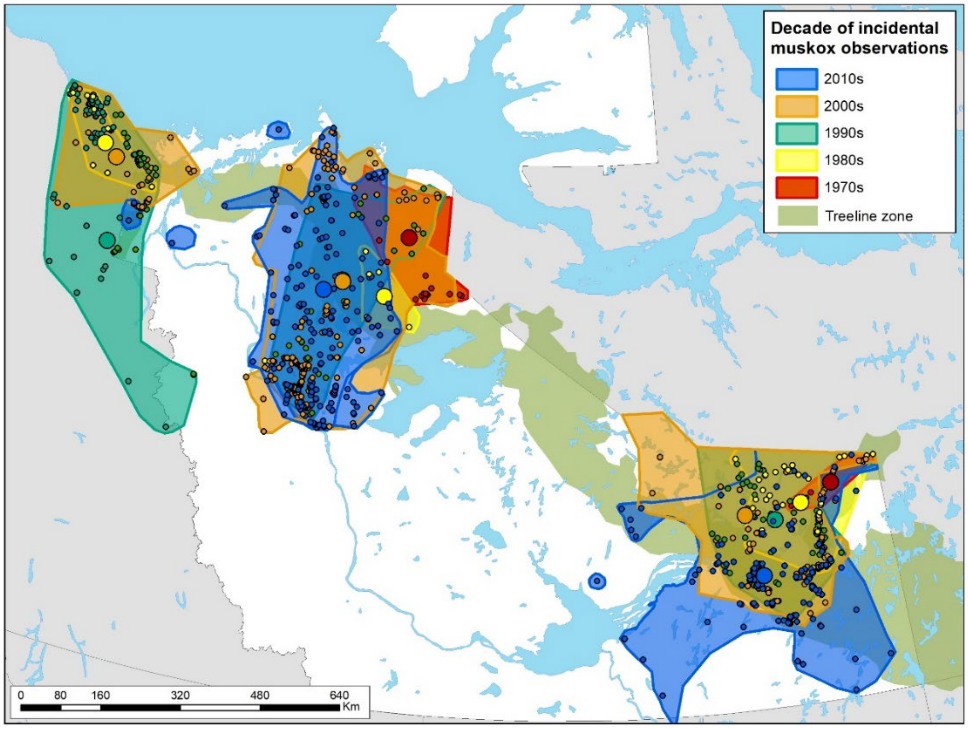


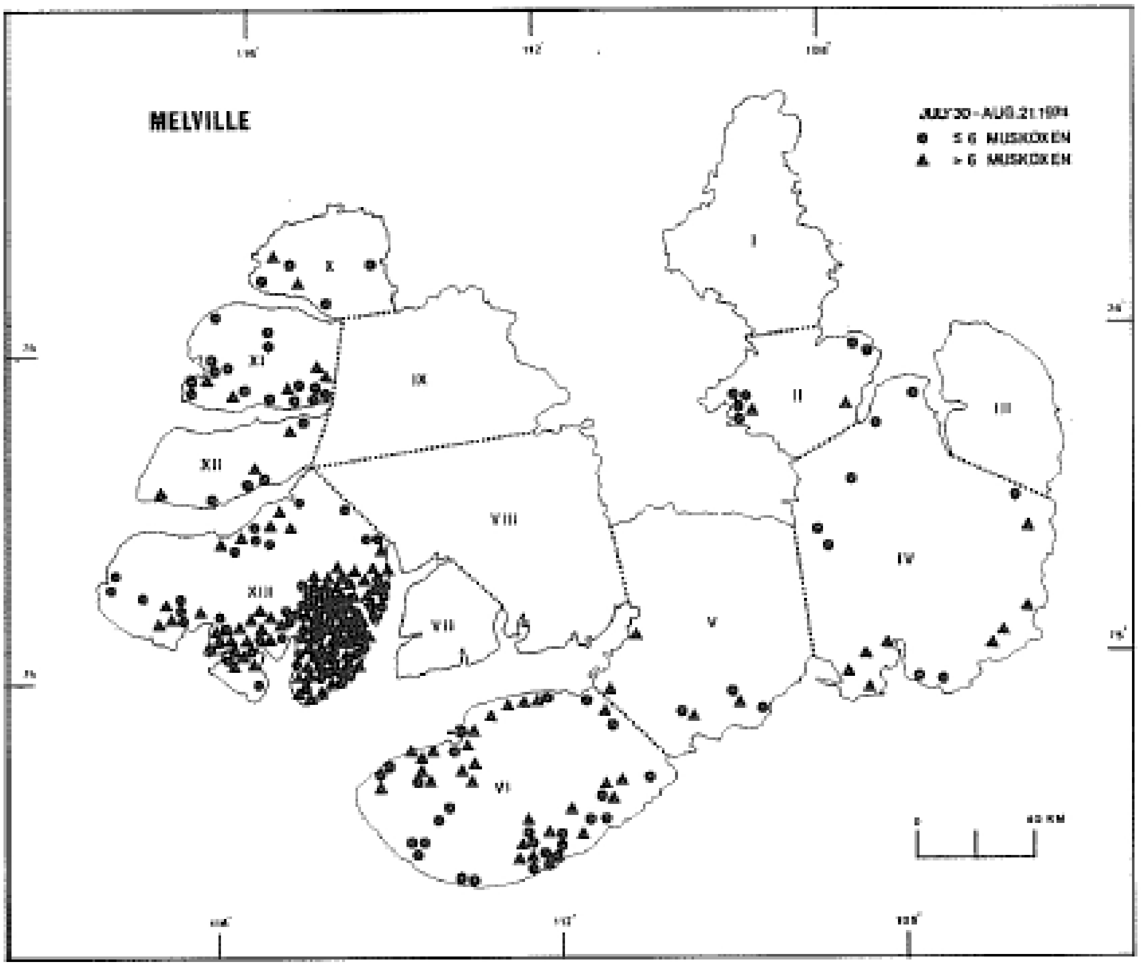
Figure 3. Decadal extent of incidental muskox sightings on the mainland NWT with the decadal centroids, 1970s - 2010s.

Arctic Islands

Western Queen Elizabeth Islands: On Prince Patrick Island, muskoxen were present in the early 1950s, had disappeared by 1961 (Tener 1965) then recolonized between 1961 and 1972 (Miller et al. 1977). The current distribution includes Prince Patrick and Melville Islands but for the smaller western Queen Elizabeth Islands, the presence of muskoxen has varied over time with disappearances after severe winters (Barr 1991, Miller et al. 1977, Gunn and Dragon 2002, Davison and Williams 2016). The role that dispersal over the sea ice between islands contributes to changing abundance is unknown, but it clearly occurs despite the scarcity of muskox observations on sea ice.

Within islands, shifts in distribution occur (Gunn and Dragon 2002, Davison and Williams 2016). In 1997, half the muskoxen (51%) on Melville Island were in the southwest (Dundas Peninsula), which is similar to 1987 when Miller (1988) recorded 31% of the muskoxen on that peninsula, compared to 16% in 1974. The muskoxen likely moved from the high-density strata to the elevated plateau of Dundas Peninsula during or after severe winters (Miller et al. 1977). Most recently in 2012, Davison and Williams (2016) recorded recovery of muskoxen on Melville Island and 19% of the estimated muskoxen were on the Dundas Peninsula.

Other changes in distribution include muskoxen abandoning a former high-density hotspot on Melville Island. The 640 km^2 Bailey Point was formerly a high-density area which was regularly surveyed between 1972 and 1980 (Thomas et al. 1981). Thereafter, regular monitoring ceased. In 1997 and 2004, only one muskox herd was counted on Bailey Point and none in 2012 (Gunn and Dragon 2002, Nagy and Gunn 2009, Davison and Williams 2016). Bailey Point is in Stratum XIII, which in 1974 had 38% of estimated muskoxen, 23% in 1987, 13% in 1997, and 16% in 2012 (Figure 4a&b).



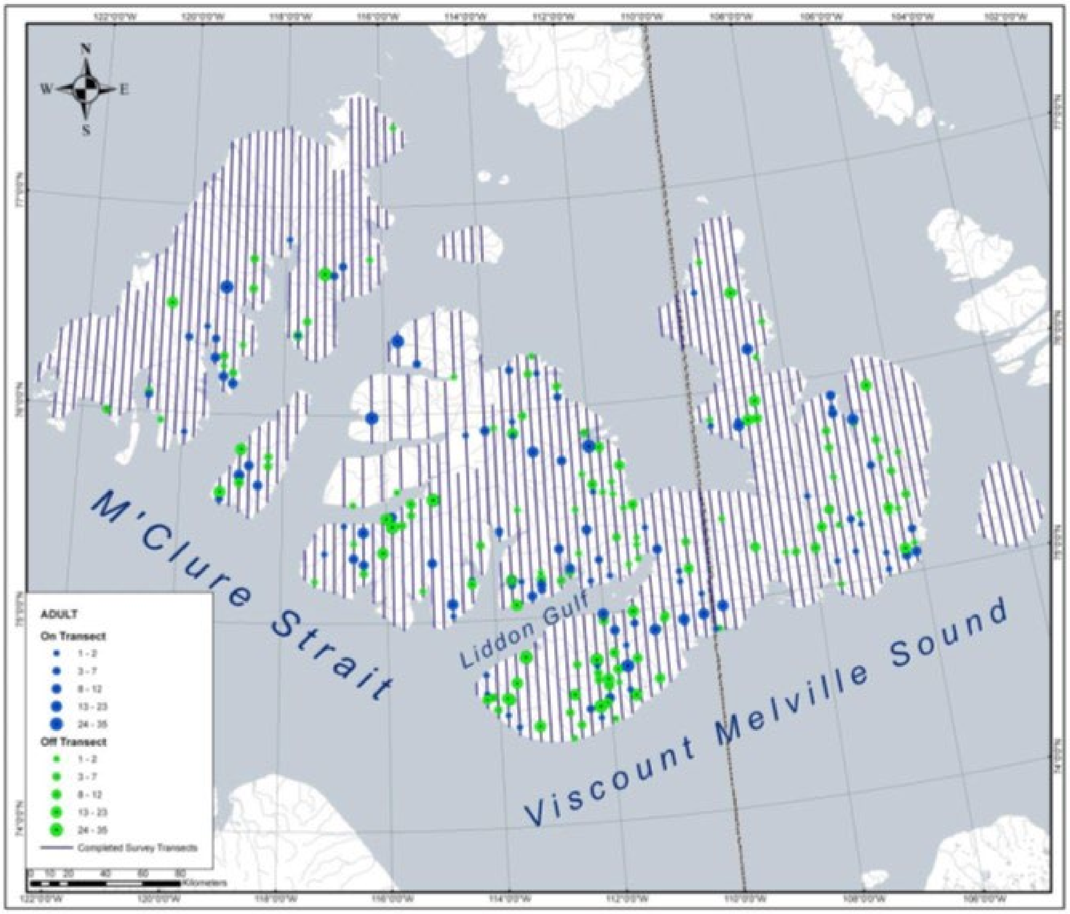


Figure 4a&b. Distribution of muskox groups smaller and larger than average on Melville Island, NWT. August 1974 (top map, 4a) shows high densities on Bailey Point (Figure 5 from Miller et al. 1977) and the bottom map (4b) shows on and off transect muskox observations, August 2012 (from Davison and Williams 2016).

Banks and Victoria Islands

Banks and northwest Victoria Islands have a ≈40-year history of systematic surveys and survey effort, including stratum boundaries, has been relatively consistent. The patterns of distribution during both increases and decreases in abundance have not been analyzed. The aerial survey area does not completely include the entire northwest Victoria Island within the NWT. The survey strata had stayed consistent until 2019 (Davison unpublished), when an additional stratum (head of Prince Albert Sound) was included, possibly as muskoxen had dispersed to that area.

Northwest Mainland

We acknowledge the GNWT completed a mainland muskox survey in March 2021 from the NE corner of the Gwich'in Settlement area East to and including TNNP, however, population estimates were not ready at time of drafting this report.

Richardson Mountains

The original Alaskan North Slope population began with two introductions of 52 and 13 muskoxen in 1969 and 1970 to Alaska's Arctic National Wildlife Refuge (Lent 1999). Some of these muskoxen eventually moved into northern Yukon and the Richardson Mountains. In Yukon and NWT, most animals were seen in the northern half of Vuntut National Park and the Yukon North Slope to the Richardson Mountains. Bulls from this population have been sometimes seen as far south as the Mackenzie Mountains, NWT (Figure 3) and the Tombstone Mountains and Wind River, Yukon (M. Suitor, pers. comm.).

Great Bear Lake

The current muskox distribution into the boreal forest west of Great Bear Lake almost to the Mackenzie River near Norman Wells is recent compared to the early 1900s distribution. At that time, muskox distribution barely reached the Anderson River except for an occasional observation of muskoxen below the treeline (Anderson 1930 in Barr 1991). Case and Poole (1985) summarized how muskoxen spread west and southwest from a refuge northeast of Great Bear Lake to east of Bluenose Lake and to the Rae and Richardson River valleys west of Kugluktuk. West of Bluenose Lake, Tuktut Nogait National Park was systematically surveyed in 2002 and 2009, but the percentage overlap among areas varied (Table 4).

Table 4. Percent overlap of muskox survey areas in the northeastern NWT mainland, 1983-2002. 2009 was similar to 2002 and is not included. GBL = Great Bear Lake; ISR = Inuvialuit Settlement Region.

Northwest Mainland	**GBL 1983**	**North GBL 1987**	**Darnley Bay 1997**	**North GBL 1997**	**ISR 2002**	**West GBL 2020**
Great Bear Lake 1983	100.0	76.6	87.0	29.3	51.8	0.0
North Great Bear Lake 1987	30.3	100.0	73.8	23.4	32.3	0.0
Darnley Bay 1997	11.9	25.6	100.0	0.0	15.6	0.0
Northern Sahtu 1997	17.1	34.4	0.0	100.0	0.0	4.8
ISR 2002	39.6	62.4	87.0	0.0	100.0	0.0
West Great Bear Lake 2020	0	0	0	4.0	0.0	100.0

Coastal Mainland – West of Paulatuk

Since the 1990s, muskoxen have progressively spread west of Tuktut Nogait National Park (Nagy et al. 2013c, Davison and Branigan 2014). During the 1997 survey north of Great Bear Lake, muskox distribution was east of 126°W (Veitch 1997; 128°W in 2004 (D'Hont et al. 2009); and 130°W in 2009 (Davison and Branigan 2014) (Figure 5). The on-transect sightings for 1997, 2002 and 2009 show the westward increase between 2002 and 2009 (Figure 6) as the estimated abundance increased (Davison and Branigan 2014). The area with on-transect muskox sightings decreased in 2002 compared to 1997 (15,740 and 23,040 km^2, respectively) and the area in 2009 was twice that in 2002 (30,440 km^2) and extended the boundary 125 km west.

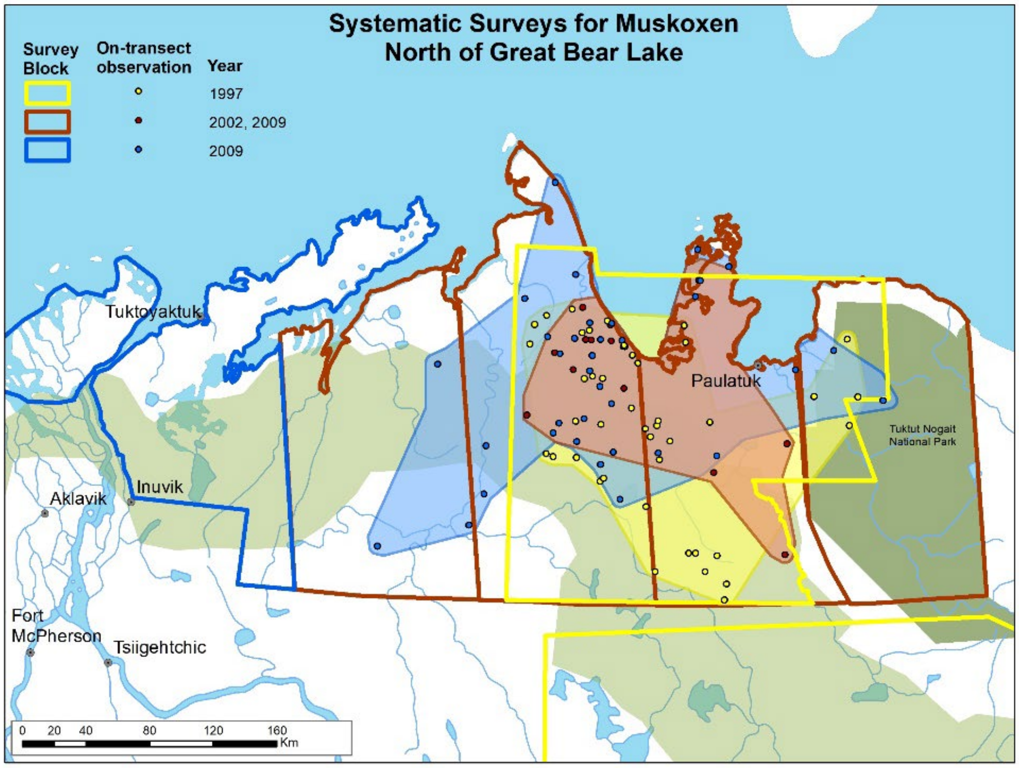


Figure 5. Survey strata and 1997, 2002 and 2009 polygons enclosing on-transect muskox observations (dots), northwest NWT mainland.

More muskoxen were found in 1997 in the Inuvialuit Settlement Region below tree line compared to the 1980s (Larter 1999). In late winter 2004 and 2018, extensive systematic surveys of the western NWT during reconnaissance for barren-ground caribou revealed a low density of muskoxen with further western dispersal (Figure 6a and b) (D'Hont et al. 2009, T. Davison unpublished).

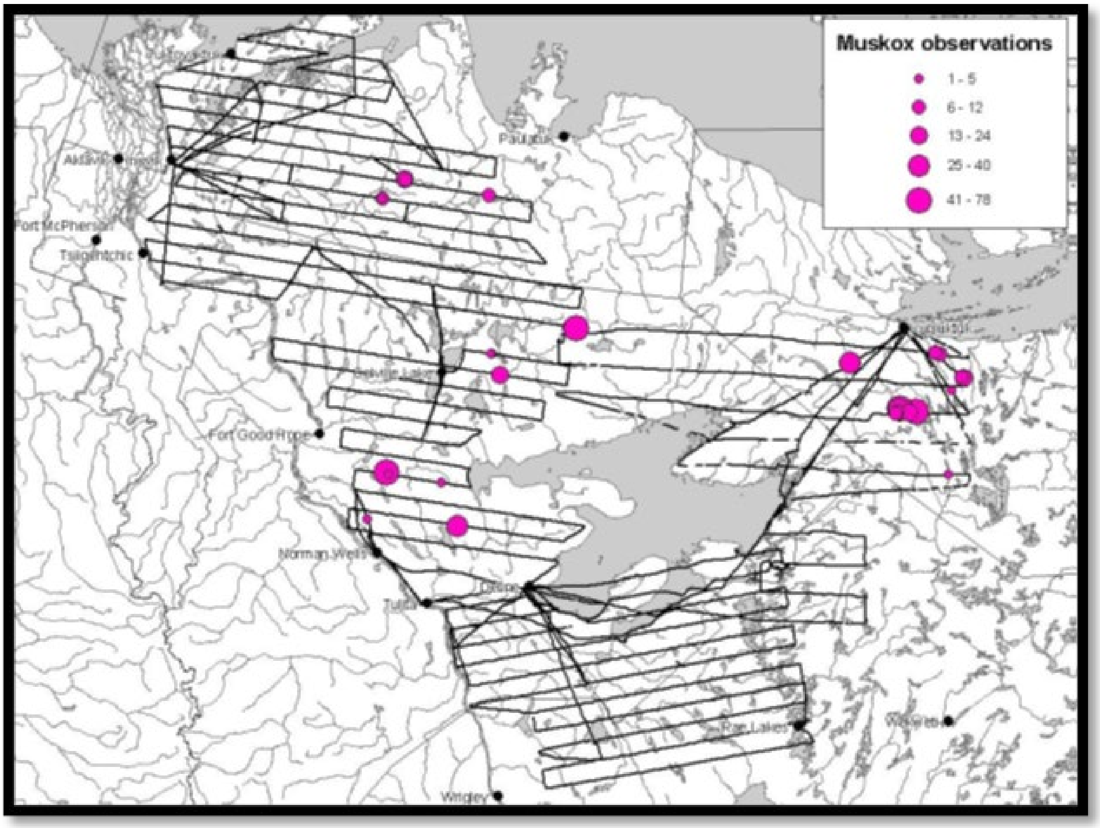


Figure 6a. Muskoxen observed along transects flown February-April, 2004 north and northwest of Great Bear Lake (D'Hont et al. 2009).

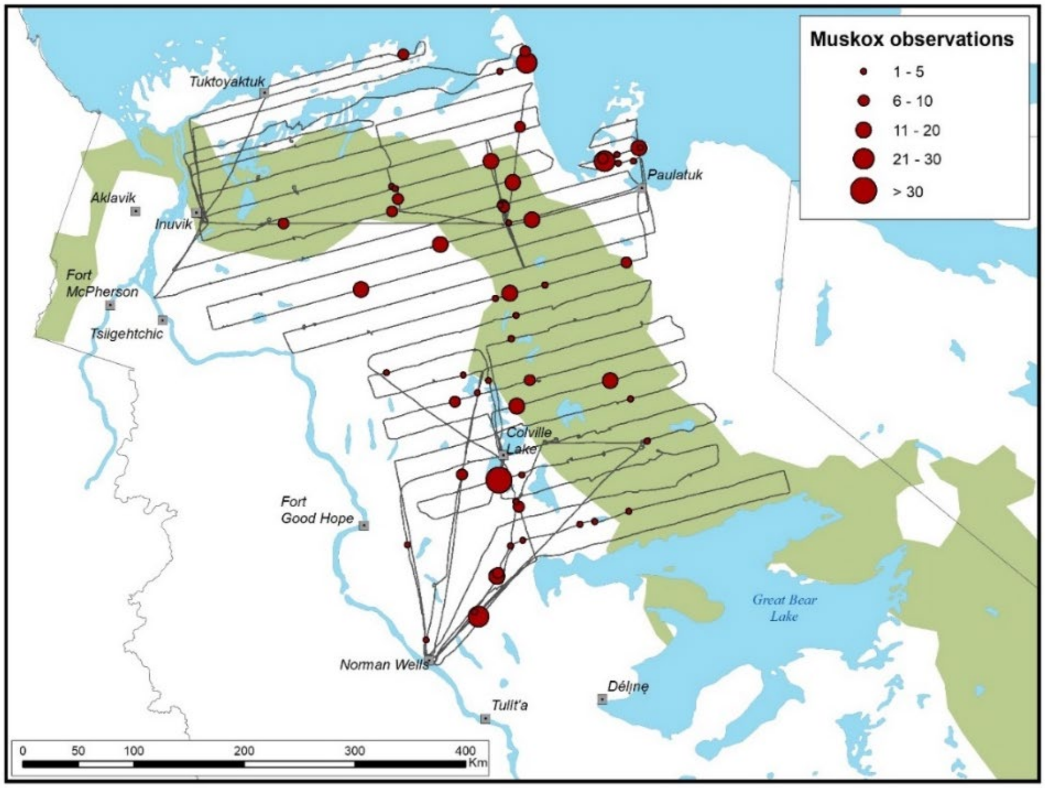


Figure 6b. Muskoxen observed along transects flown during caribou reconnaissance surveys, March 2018 (T. Davison, unpublished).

In 2020, the area west of Great Bear Lake to the eastern edge of the Mackenzie Mountains was surveyed (Rentmeister and Chan 2022) but there was no record muskoxen west of the Mackenzie River[4]. To summarize, muskoxen have recently been expanding westward along the coast from Tuktut Nogait National Park but in the absence of recent surveys or compilation of sightings, trends in distribution in the national park east into NU are uncertain.

Southeast Mainland

Muskoxen had persisted in the Thelon Game Sanctuary through the times of scarcity in the late 1800s and early 1900s and were likely one source of muskoxen expanding their ranges

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[4] Rentmeister and Chan (2022) surveyed an area in the Sahtú region in March 2020 and 2021 north, west and south of Great Bear Lake and estimated a population of 5,793 (95%CI 3,385-9,912) muskoxen with a calf proportion of just 5.6%. that had increased since the more limited regional muskox survey in 1997. This survey and report were completed after the main work of the current technical report.

by the 1980s (Barr 1991). On the southeast NWT mainland, the first aerial survey was in March 1989 when Graf and Shank (1989) found relatively high muskox densities (3.4 muskoxen/100 km^2) northeast of Artillery Lake between the Thelon and Hanbury rivers.

In July 1991, muskoxen were not found west of Aylmer, Clinton-Colden and Artillery lakes but by 1998, a muskox herd was located west of Artillery Lake. By 2010, three herds were seen west of Artillery Lake and by 2018, about 24 muskox herds were observed when an additional stratum to the west of Artillery Lake was added (D. Cluff, pers. comm. 2018). The sightings suggest muskoxen extended their range southeast by about 9 km/year, similar to the rate of muskox spread (about 13 km/year) in the Queen Maud Gulf (Gunn et al. 1984).

The Artillery Lake survey area was surveyed four times and the survey area has doubled in size with an additional stratum to the west (Table 5, Figure 7). Three of the eight southeastern NWT surveys were for areas that had not been previously surveyed and established a baseline for future distribution trends. However, the densities were exceedingly low which reduces the likelihood of measuring trends (Bradley et al. 2001).

Table 5. Overlap between aerial muskox surveys in the southeast mainland NWT 1989-2011**.**

	Artillery Lake 1989	**Aylmer Lake 1991**	**Thelon 1994**	**Artillery Lake 1998**	**Beaverhill Lake 2000**	**Artillery Lake 2010**	**Rennie Lake 2011**
Artillery Lake 1989	100.0	0.0	2.4	70.4	21.4	57.4	0.0
Aylmer Lake 1991	0.0	100.0	0.0	4.7	0.0	11.4	0.0
Thelon 1994	4.0	0.0	100.0	7.0	12.3	2.6	2.6
Artillery Lake 1998	99.6	6.5	6.0	100.0	41.5	79.1	0.0
Beaverhill Lake 2000	26.0	0.0	8.9	35.5	100.0	28.8	7.9
Artillery 2010	97.0	18.8	2.7	94.5	40.2	100.0	0.0
Rennie Lake; Fort Resolution 2011	0.0	0.0	0.0	0.0	14.0	0.0	100.0

Trends in muskox distribution in the Thelon valley and associated rivers can be discerned from annual observations of wilderness tourism operator Alex Hall from the 1980s to 2016. Hall guided canoe trips on these rivers (Figure 7) and recorded how muskox summer distribution expanded about 250 km south of the Thelon Game Sanctuary based on the sightings along the rivers 1986-2006 (Gunn et al. 2009). During that period, small groups and single bulls were seen at increasing distances from the Thelon Game Sanctuary. The upper Thelon River area with muskox sightings was within survey areas flown in 1998-2011 (Figure 7).

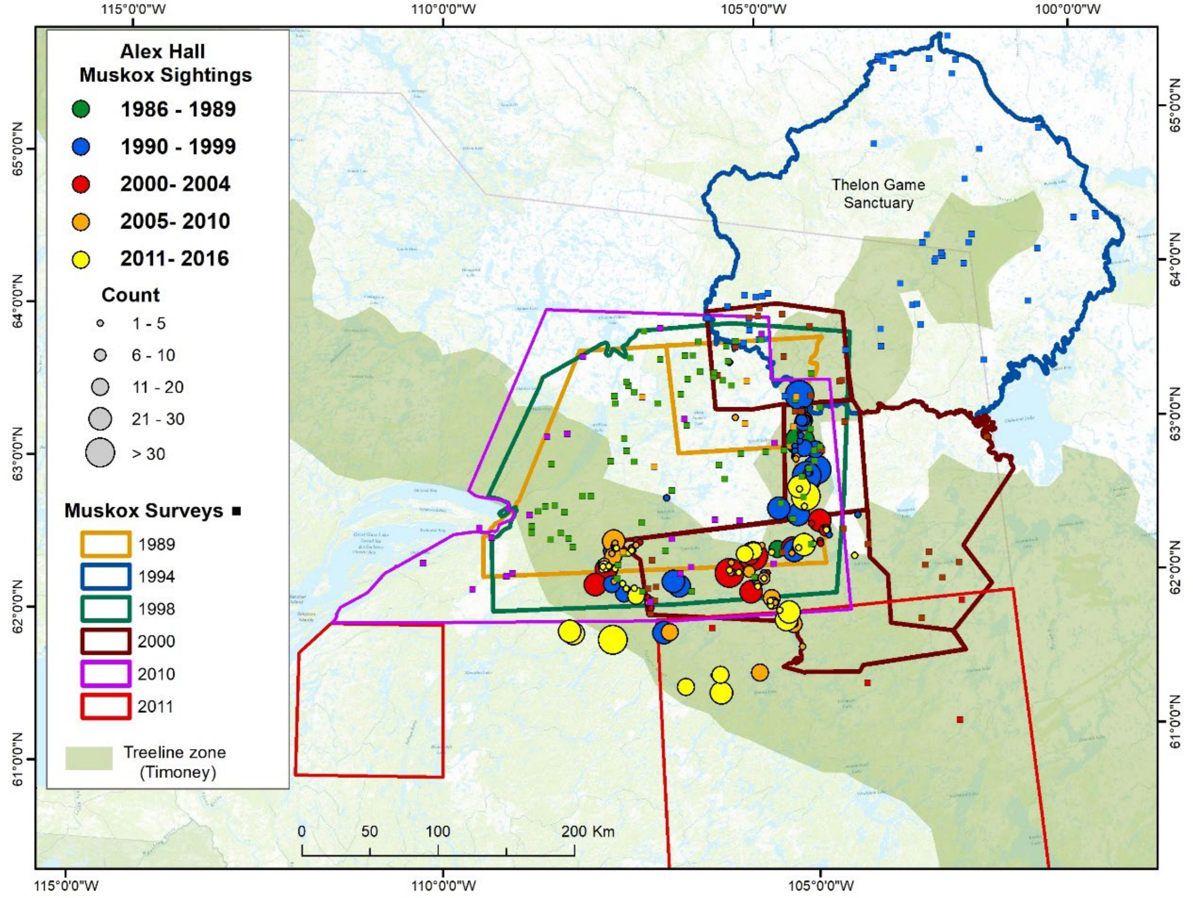

Figure 7. A comparison of decadal changes in muskox sightings on the Thelon River with survey areas and on-transect sightings, 1986-2016, NWT. Observations from Alex Hall made during canoe trips along rivers in and near the Thelon Game Sanctuary between 1971 and 2004 are included with scale to indicate group size.

HABITAT

Habitat Requirements

Muskox habitat requirements are relatively broad as muskoxen occur in eight different ecoregions from 83ºN - 60ºN. Climate is a part of habitat but is included in the Effects of Climate section. While muskoxen are often considered a tundra species, they also occurred historically (Anderson 1930 in Barr 1991) and more recently within the tree-line transition zone and well into the boreal forest (Figure 8).

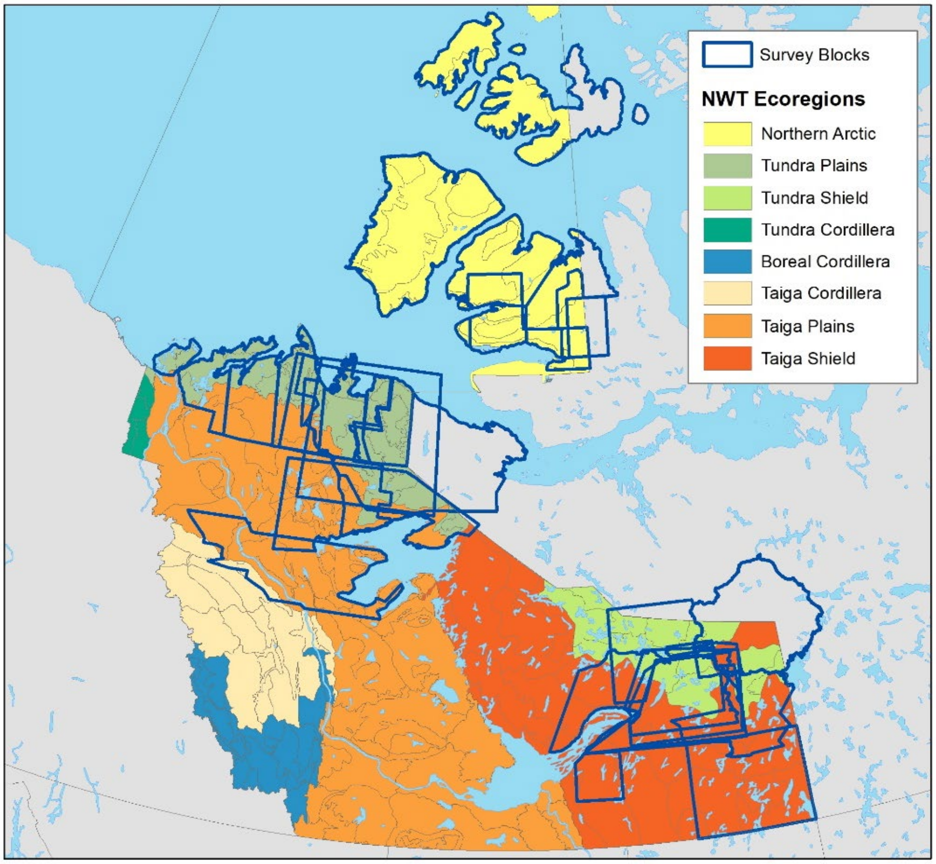

Figure 8. Muskox aerial survey boundaries and NWT ecoregions level II. (www.enr.gov.nt.ca/en/services/ecosystem-classification-program)

The treeline is a forest-tundra transition biome (Timoney et al. 1992) bounded on the north by the southern limit (<0.1% cover) of upland tundra and to the south by the northern limit (<0.1% cover) of trees >3-4 m tall (Figure 9).

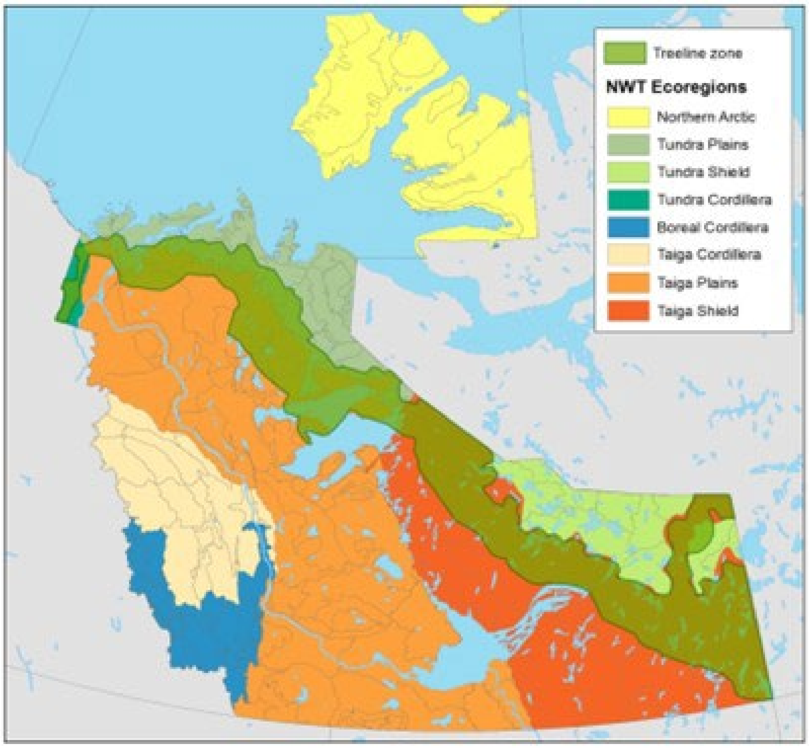

Figure 9. NWT ecoregions and the treeline zone as mapped by Timoney et al. 1992.

The recent expansion of muskox distribution south into the tree line transition zone and beyond into the boreal forest raises questions about if and how the shrub and tree canopies can provide a thermal refuge. Based on the incidental sightings, the trend for muskox use of the tree-line transition zone increased from the 1970s to the 2010s as muskoxen expanded their distribution (Figure 10).

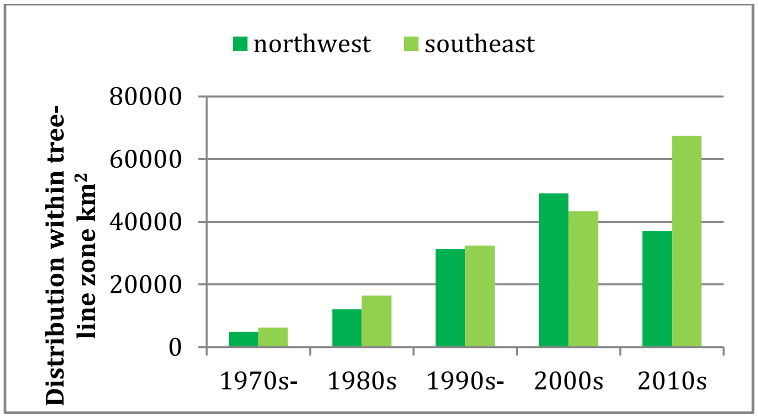

Figure 10. Trend in use of the treeline zone based on incidental muskox sightings in the northwest and southeast mainland NWT over the decades. The area of the treeline zone occupied by incidental sightings was calculated by decade and sampling effort is unknown.

Even within the tundra, environmental and habitat variability can be high. For example, mean July temperatures can vary from <3°C to 9-12°C (Gould et al. 2003). Plant cover varies from <5% to 100% and above ground biomass from <100 g m^{-2} to 4,000 g m^{-2}. Geology is varied from Precambrian Shield to sedimentary rocks which influence availability of minerals for forage plants. For example, levels of soluble phosphorus in soils on muskox winter range in the Thelon Sanctuary were low because the soils are acidic (Tener 1965). Soils and the plant uptake of mineral content are likely significant for muskox physiology as, for example, copper is necessary for immune function (Barboza and Reynolds 2004).

Currently, habitat availability is only partially addressed through vegetation mapping and information on plant biomass and nutritional values is needed to incorporate vegetation mapping for the assessment of habitat availability. This has been partially completed only for southern Banks Island (Larter et al. 2009, 2003a and b).

Information on muskox habitat selection and use on the NWT mainland is fragmentary: in the Thelon Game Sanctuary, muskoxen foraged around rivers, lakes and ponds in the summer, but in the winter, the muskoxen used rolling hills, slopes or plateaus, where the wind kept the snow shallow (Tener 1965). Muskox bedding sites are often on drier, upland sites away from feeding sites, which may reduce their exposure to fecally transmitted parasites as muskox fecal output is highest where they bed and ruminate (Mosbacher et al. 2016). Winter habitat selection is scale dependent from a large regional scale to the fine scale of feeding craters (Schaefer and Messier 1995a, b). Muskoxen adapt to different snow conditions, for example, by using uplands when snow is deeper in lower-lying habitats (Nelleman and Reynolds 1997).

Muskoxen on the NU mainland tundra west of Kugluktuk seasonally migrate from coastal areas to along the Rae River valley among the willow shrubs where the snow is deeper but not as wind packed (Gunn and Fournier 2000). Alternatively, the seasonal migration away from the willow shrubs to the more open tundra in summer may reduce exposure to grizzly bear (*Ursus arctos*) predation (Gunn and Fournier 2000).

Habitat Trends

Muskox habitat is very likely changing based on trends in climate, however the effects of economic development and forest fires are uncertain. Current trends in climate are available through, for example, the MERRA climate database (Russell et al. 2013), although they are incompletely analyzed (Section 9). Trends for industrial development have included pulses of activity as indexed by expenditure in oil and gas development and mining; however, these are for the entire NWT rather than specific to muskox spatial distribution (www.statsnwt.ca/economy). In the 1970s, widespread seismic activity occurred on Banks (Urquhart 1973), Melville and Prince Patrick Islands, but subsequently, oil and gas exploration on the Arctic Islands has been minimal. On the northwestern mainland within the Taiga Plains, seismic and drill camps for oil and gas were active in the 1990s. In the 2000s, three open pit diamond mines were operational on the tundra ranges in the central NWT but muskox exposure to the mines is relatively infrequent. Relating industrial activity to muskox ecology is currently restricted to understanding muskox responses to helicopters and snow machines (Miller and Gunn 1980, McLaren and Green 1982, Reynolds and LaPlant 1985, Miller et al. 1989).

Muskoxen are of interest to tourists although remote access mostly means levels of local tourism are low. For example, tourist visits to Aulavik National Park and Tuktut Nogait National Park averaged <50 individuals per year over the past decade. The number of cruise ships is increasing and landing parties to view wildlife are a potential disturbance (www.enr.gov.nt.ca/en/state-environment/73-trends-shipping-northwest-passage-and-beaufort-sea).

The human population in the NWT has been stable in recent years at about 45,000. The footprint of the communities (Figure 11), if buffered by a 10 km zone of influence, is low at <1% of muskox geographic distribution. Trends in human activities in the vicinity of communities vary; for example, trends in aircraft landings are highly variably over time and among the communities (www.enr.gov.nt.ca/en/state-environment/71-trends-air-traffic). Roads both seasonal (winter) and all-season in the NWT are listed by ecoregion for 2007 as a baseline (www.enr.gov.nt.ca/en/state-environment/81-road-density-and-other-maintained-linear-features). If mines are buffered by 15 km and roads by 5 km, then about 2% of the current muskox geographic distribution is within a zone of influence. These buffers around mines and roads were estimated for barren-ground caribou as areas within which caribou behavior might be influenced (Bathurst Caribou Range Plan 2019).

Figure 11. Communities, operational and planned mines and roads within the NWT muskox range in 2020.

Approximately 12,500 km^2 (about 2%) of the current muskox spatial distribution consists of areas burnt between 2006 and 2016, and the majority of these areas (90%) are located in the southeast (Figure 12). There has been an increase in the total area burned over the last 40 years as a result of increased lightning strikes (Species at Risk Committee 2017). Based on areas burnt and human footprint, by 2018, ~5% of tundra and treeline habitats had been affected by fire and or anthropogenic disturbance. Fires on the tundra are normally rare and small but they do occur in very dry hot summers like 2014.

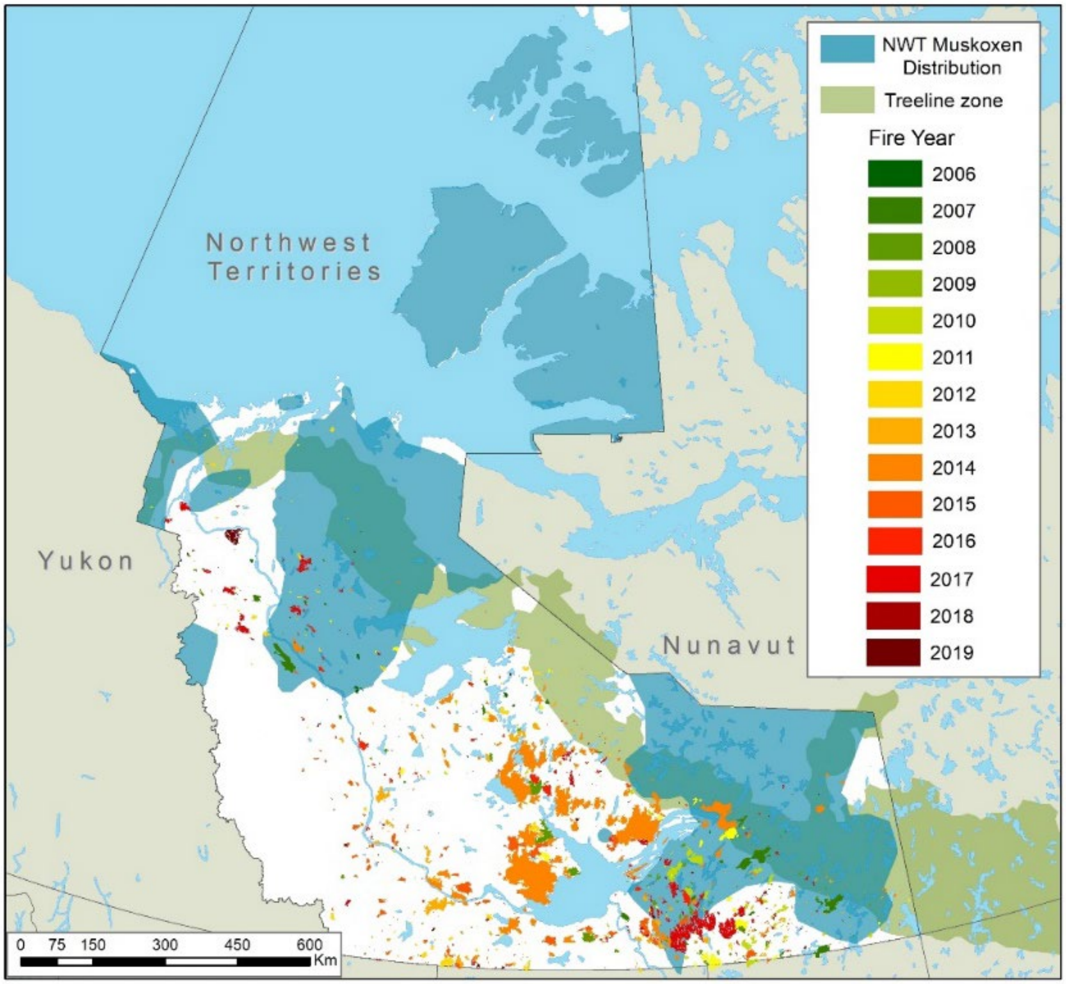

Figure 12. Forest fires in the NWT 2006-2019 (WMIS data), with muskox distribution in 2018 shown.

BIOLOGY

Life Cycle and Reproduction

Muskoxen are capital breeders, i.e. the female's fat reserves provide for fetal growth and early lactation in a highly seasonal and unpredictable environment. Females accumulate large fat reserves during the plant growth season as a buffer during the longer and more variable season of reduced forage availability (Adamczewski et al. 1997). Muskoxen on the NWT Arctic Islands generally breed in August, or in September at lower latitudes (Tedesco 1996). Most conceptions are during the first overt estrous cycle which is about 20 days in length (Rowell and Flood 1988).

Nutrition, especially during August to October, plays a strong role contributing to variation in reproductive rates (White et al. 1989, 1997; Adamczewski et al. 1998). The likelihood of fall pregnancy depends on the cow's condition; cows weighing more than 183 kg in the fall had a 50% probability of pregnancy on Victoria Island in the early 1990s (Adamczewski et al. 1998). Pregnancy rates declined between November and April on Victoria Island (Adamczewski et al. 1997) suggesting that after conception, there may be a second body condition threshold and lactating females in poor condition might be susceptible to pregnancy failure. Most cows will first be bred in their 2nd year and calve for the first time as three-year-olds (Adamczewski et al. 1997). Breeding intervals can be one to three years depending on nutritional condition (Reynolds 1998); cows on Alaska's North Slope had two to three calves per three years between 1982 and 1984, which declined to one calf every three years between 1988 and 1993 as the population began to decline. Cows may calve up to 15-19 years of age (Reynolds 1998). Bulls first breed when they are four to eight years old with most breeding by dominant males; during the breeding season dominant males are intolerant of other breeding-age males.

Calves are born in late winter to spring (mid-April to early June) and weigh about 6-10 kg at birth. Lactation peaks about eight weeks after calving (July) and stays high during August before declining (Adamczewski et al. 1997). Weaning occurs between December and February or even later as some non-pregnant cows continue to lactate for 18 months both in the wild and in captivity (Adamczewski et al. 1997, White et al. 1989).

Nutritional Ecology

Nutrition influences individual and population muskox ecology (Parker et al. 2009) through body condition and growth rates which, in turn, influence the probability of pregnancy, over-winter survival, timing of parturition, and birth mass and calf survival. (Adamczewski 1995, Barboza and Reynolds 2004, Barboza et al. 2006). While Adamczewski (1995) described the plasticity of productivity related to body reserves from muskox carcasses, Barboza and Reynolds (2004) sampled blood sera, hair and feces collected from adult female muskoxen during handling to attach satellite collars. The analyses included isotopic measures of nitrogen and carbon in fecal pellets to reflect diet changes and levels of copper. Expanding the selection of monitoring indicators becomes important now that it is increasingly clear that there are complexities of interactions among weather, forage, micro-nutrients, disease and predation affecting muskox population dynamics (Barboza and Reynolds 2004, Afema et al. 2017, Arthur and Del Vecchio 2017).

Seasonality and Forage Intake Strategies

Seasonality is an over-riding characteristic of Arctic ecology with a short, highly productive plant growth season and a long season of plant senescence when snow cover restricts forage availability. Muskoxen increase their forage intake during the summer into the fall before reducing their intake during winter. The effectiveness of the reduced intake on energy costs is enhanced as muskoxen have a low metabolic rate and eat relatively little for their size (Adamczewski et al. 1994a and b, Barboza et al. 2006). Their alimentary fill is almost a third larger than would be predicted from their body size (Adamczewski et al. 1995) which together with a long retention time and slow metabolism enables them to forage on coarse fibrous forage (Adamczewski et al. 1994a and b, Barboza et al. 2006).

Seasonal changes in the nutritive value of vascular plants and plant parts through the summer growing season are substantial; as the plants grow, their biomass increases but the peak in nutrient quality comes early and declines as the plants senesce (Chapin et al. 1980). Some plants also increase the concentration of secondary compounds (Bryant et al. 1983). Tundra plants trans-locate nutrients underground toward the end of the summer (Chapin et al. 1980, Chapin and Shaver 1989). Changes in forage intake and body reserves reveal how muskoxen adapt to seasonality by increasing forage intake as digestibility declines. However, the time available for foraging, capacity of digestive tract and time for digestion limit the increase in forage intake (Barboza et al. 2006). Forage in the fall may be annually variable in quality due to varying timing of plant senescence. A key variable is the first killing frost, which affects how much of a plant's nutrients are trans-located to the roots (Larter and Nagy 2001a). Adding up to 60% browse such as willow increases intake digestibility and rate of passage (Boyd et al. 1996, Lawler and White 2006).

Forage intake depends on bite size and intake links to reproduction, growth and survival (Parker et al. 2009). Bite size depends on dental morphology and oral anatomy. Muskoxen have been classified as grazing ruminants based on their rumens, omasums and related digestive morphology (Hofmann 1989, 1999; Clauss et al. 2006), but Mathiesen et al. (2000) pointed out that muskox oral anatomy is also consistent with selectivity. Muskoxen select individual flowers and individual plants through the summer (Oakes et al. 1992, Mulder 1999, Mulder and Harmsen 1995). The higher use of willows and forbs was associated with higher muskox productivity on the Alaskan North Slope (Robus 1981).

Forage Selection and Diet in the NWT

Understanding of forage selection and diet contributes to estimating the likelihood of intra- or inter-specific competition with other herbivores and to interpreting trends in productivity. In NWT, the most information is from the 1990s when muskoxen were increasing on Banks Island and from more limited observations from southeast Victoria Island and mainland coastal areas (Table 6).

Table 6. Summary of available information on NWT muskox studies of forage selection and diets based on identification of plant fragments in rumen content samples or fecal pellets.

Study Location	Diet (Years x months)	Selectivity	Forage biomass	Nutrient quality forage measured	Effect on Forage measured	Source
SE Victoria 1989-1995	Diet (3 x 4) Sex and age craters (3 x 2)		(b) Yes Sedges	(b) Yes sedges (d) fecal nitrogen		(a) Gunn and Adamczewski unpublished (b) Pinsonneault 1995 (c) Schaeffer and Messier 1995a,b (d) Schaeffer and Messier 1996
SE Victoria 1997	Plant quadrats		Yes	No	Yes	Griller 2001
SE Victoria 1989-1995	Exclosures		Yes	No	Yes	Hughes 2006
NW Victoria 1992	Functional response curve		Yes Sedges	No	Yes	Gunn unpublished
Queen Maud Gulf 1989-1991	Diet (2 x 1)			No		Gunn and Sutherland 1997
Kugluktuk 1991	Diet (1 x 1)			No		Gunn and Sutherland 1997
Banks 1993-1998	Diet monthly	Yes	Yes	Yes – 5 variables		Larter and Nagy 2004
Banks	behaviour			No		Wilkinson et al. 1976 Shank et al. 1978
Banks	Diet Sex age (1 x 3)	Yes		No		Oakes et al. 1992
Banks	Observation			No	Yes	Mulder and Harmsen 1995
Queen Elizabeth Islands	Diet					Parker 1978

The diets were described (Table 6) from identifying plant fragments in fecal pellets or rumen contents (Larter and Nagy 2004) although fecal plant fragments underestimate highly digestible forbs and lichens. Although lichens were not identified in diet based on fecal pellets from Banks Island muskoxen (Larter and Nagy 2001c), lichens were 21-24% of the above ground standing crop in uplands barrens (Larter and Nagy 1997).

A recent approach to describing diet is stable isotope analysis (Barboza and Reynolds 2004, Kristensen et al. 2011, Mosbacher et al. 2016, Munizzi 2017). Analyzing isotopes in muskox wool and fecal pellets, Kristensen et al. (2011) concluded that isotope analysis described diet at the level of major plant groupings. By sampling along the length of guard hairs, diet can be described with a resolution of nine-day periods for a 2.5-year sequence (Mosbacher et al. 2016). Diet over a longer timescale (4,000 years) was measured from isotopes sampled from muskox bone collagen and the bones from archaeological sites on Banks Island (Munizzi 2017). The ancient diet had a low contribution of willow compared to sedges (Carex sp.) and limestone sunshine lichen (*Vulpicida tilesii*, syn *Cetraria tilesii*).

Individual variation in diet is high (Oakes et al. 1992, Gunn and Adamczewski unpublished) and forage selection is scale-dependent from bite to patch to region. The scales for forage selection were explicitly addressed for muskoxen wintering on southeast Victoria Island (Schaefer and Messier 1995a, b) and on Banks Island (Larter and Nagy 2001 a and b). Larter and Nagy (2001a, b and c) reported on seasonal diet, summer habitat use and foraging responses to threefold variation in snow conditions on south central Banks Island between 1993 and 1998. Seasonal differences in diet relate to plant growth and timing of plant stages from bud break, flowering and senescence (Robus 1981, Oakes et al. 1992). Weather influences plant growth and diet as for example, forage quality significantly varied on Banks Island from 1993 to 1997, in relation to summer moisture (Larter and Nagy 2001b). During summer, water sedge (*Carex aquatilis*) and legumes had the lowest lignin and fibre content and together with grass, willow leaves had the highest crude protein (CP) content (Larter and Nagy 2001b). In both summer and winter, legumes were highest in digestibility along with grass and willow leaves while energy content in winter was highest in water sedge. Larter and Nagy (2001b) suggested that the higher CP content in water sedge during the winters 1996-1997 and 1997-1998 may have been related to fall precipitation. More frozen green material was seen during winters 1996-1997 and 1997-1998, which increased CP levels of winter forage available for muskoxen. The higher protein caused significantly higher urea nitrogen: creatinine ratios in muskox urine during those winters (Larter and Nagy 2001e).

Shrubs such as willow and legumes have a higher ratio of cell contents to digestible cell wall (more non-structural carbohydrates and protein) than graminoids and are more rapidly digested especially during the fall (Lawler and White 2006). Larter et al. (2002) noted the high fall use of willow on Banks Island and suggested that stems were being used. In June, willow leaves are highly digestible (Larter et al. 2002) and were selected when the muskox rumen mucosa enlarged to increase absorption on Victoria Island (Staaland et al. 1997).

The seasonal changes in forage quality (Larter and Nagy 2001a) and foraging and snow conditions on Banks Island (Larter and Nagy 2001b) were reported at the annual scale (Table 6). Forage distribution among habitat types was pooled (Larter and Nagy 2001c) and for monthly muskox diet, the data were pooled across sex and age classes and years on the assumption that between-year variation was minimal. The sample unit was a composite sample from a muskox group (Larter and Nagy 2004). However, Larter and Nagy (2001a) showed for 1993-1998, high annual variation in the relative proportions of sedge and willow in the summer diet. Larter and Nagy (2001a) attributed an increase in willow use relative to sedge as decreasing the digestibility, as willow is higher in lignin.

Across muskox geographic distribution, the greatest regional variation in diets is from the relative use of shrubs, especially willow. Where willow is less abundant, such as on the Arctic Islands, muskoxen forage more on sedges (reviewed in Robus 1981). As well as regional differences, annual differences are marked. For example, annual differences on southeast Victoria Island in the amount of *Salix* in the diet varied from 56±16.3 mean % relative density of plant wall fragments in November 1991 to 6.7±11.6 % in November 1992 (Gunn and Adamczewski unpublished). On the mainland (Queen Maud Gulf area and Kugluktuk), annual variation was also high (Figure 13).

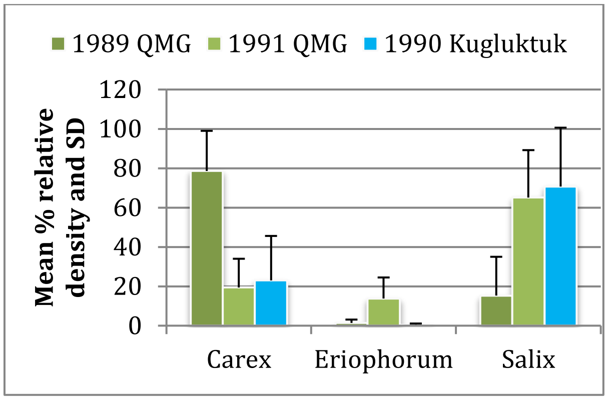

Figure 13. A comparison of the percentage of mean willow and sedge fragments identified in fecal pellets collected in July on the mainland for Queen Maud Gulf lowlands (QMG) and the Kugluktuk area, 1989-1991 (Gunn and Sutherland 1997).

Muskoxen tend to select willow in winter depending on snow conditions. In late winter in Alaska, willows were eaten only when they were in shallow snow (Wilson 1992). On southern Victoria Island, muskoxen selected sedges in winter until May when they shifted to feeding on prostrate willows on the slopes and ridges where snow was shallow (Schaefer and Messier 1996). Grasses and sedges dominated winter diets (Larter and Nagy 1997) on Banks Island and sedges were found to increase from about 50-80% of the diet during the winter (Larter and Nagy 2004).

In summer, muskoxen selectively forage on flowering forbs which are high in protein and digestibility. On Banks Island in July, legumes, including locoweed (*Oxytropis sp.),* were 10-20% of the diet (Oakes et al. 1992; Mulder and Harmsen 1995; Larter et al. 2002) compared to 5% or less on southeast Victoria Island (Gunn and Adamczewski unpublished). In younger muskoxen, nutrient demand and a smaller mouth (incisor arcade) may favour increased diet diversity. On southeast Victoria Island, in April 1989, yearlings, two to three-year-olds, and adults (>3 years) did not differ in their diet dominated by 70% *Carex* (Gunn and Adamczewski unpublished). However, in April 1991, yearlings had the highest percentage of cottongrass (*Eriophorum sp.)* and willows in their diet and the lowest sedges (Gunn and Adamczewski unpublished). In July 1990, August 1989, and November 1990 diet was similar for calves and adults. In September 1990, calves had similar amounts of sedges and willows as subadults and adults, but more legumes (*Astragalus sp.-Oxytropis* sp.) than these other age groups (Gunn and Adamczewski unpublished).

Micro-nutrients

The importance of monitoring micro-nutrients (minerals and vitamins) has only recently been recognized for muskoxen; deficiencies may predispose animals to reductions in health (Barboza and Reynolds 2004, Afema et al. 2017). Micro-nutrients were assessed from muskox liver and serum for southeast Victoria Island in 1989 and 1995, and for Banks Island in 1985 and 1997 (Salisbury et al. 1992; Gamberg and Scheuhammer 1994, Blakley et al. 2000). The sampling was opportunistic, being dependent on the availability of harvested muskoxen on Banks and Victoria Islands, and did not include the individual body condition or diet for the sampled muskoxen.

Based on experience with captive herds, muskoxen are more susceptible to copper deficiency than domestic cattle or sheep (Blakley et al. 1998, White et al. 1998). Copper is essential for the immune system and low copper levels in captive muskoxen, especially calves, can cause illness and deaths and possibly deaths in adults (White et al. 1998, Swor 2002). While dietary protein can increase copper absorption in the intestine, fiber and other minerals can decrease or inhibit absorption (Swor 2002). Copper is stored in the liver and can also be monitored from serum. Serum levels on Banks and Victoria Islands (1985-1997) were low and similar to the threshold for depleted liver levels (Barboza and Reynolds 2004). The tolerance for copper may be narrow as levels of 0.5 μgml^{-1} were associated with pathological changes in a captive muskox cow (Blakley et al. 1998).

Blakley et al. (2000) reported regional, seasonal and annual differences in mean liver copper concentrations during a period when muskox abundance had peaked on Banks and Victoria Islands. The limited sampling frequency prevents any exploration of trends or variation in serum and liver copper levels. Low liver levels affect fetal growth and survival of young muskoxen because the maternal copper accumulates *in utero* and is used through the first 60-100 days from birth to offset low copper levels in milk (Rombach et al. 2002).

Copper is not the only mineral varying regionally and annually. For example, selenium levels in serum were similar between Banks and Victoria islands but liver levels were higher on Banks than Victoria in May 1985 (Blakley et al. 2000). Future monitoring could determine if reduced copper levels are linked to recent declines on Banks and southeast Victoria Islands (Biology section). Archived serum samples could be a useful baseline and contribute to describing levels of individual and yearly variation to determine sample sizes.

Muskox Effects on Their Forage

The effect of foraging on plants is complex and Mulder (1999) identified seven pathways by which herbivores affect forage in the Arctic, while the plants are themselves responding to both grazing and the weather. For example, in the High Arctic, mean summer temperatures annually influenced willow growth more than muskox browsing (Raillard 1992). Willows and graminoids respond to grazing by regrowth (Pinsonneault 1995, Smith 1996, Tolvanen et al. 2002). How forbs responded to selective foraging by muskoxen depended on the timing and extent of the muskox clipping. On northern Banks Island, muskoxen grazed 20% of individual locoweed plants (*Oxytropis borealis* [5] syn *Oxytropis viscida)* and removed the growth tips, which reduced plant growth for the following two years (*Oxytropis viscida* var hudsonica) in Mulder and Harmsen (1995).

Although muskoxen increase their forage intake during summer, they rarely remove much of the green biomass of graminoids and shrubby browse even when local densities are high as in Sverdrup Pass, northern Ellesmere Island (Raillard 1992). The density of muskoxen was relatively low (0.35 muskoxen/km^2), but where they concentrated on the sedge meadows, local density was 6.4 muskoxen/km^2. Even so, they only removed an estimated 4% of available forage (Raillard 1992). In northeast Greenland during 1996-2013, at an average density of 11 muskoxen/km^2 (in a small study area of 47km^2), by fall, muskoxen had removed ~4.6% and 0.19% of available forage in the graminoid-dominated areas and willow snowbeds respectively (Mosbacher et al. 2018).

Muskox Intra-specific Competition

While higher muskox densities likely have stronger effects on forage, empirical evidence that muskox densities have reached a threshold where muskoxen have reduced forage to the detriment of their physical condition or movement to other areas (sometimes termed over-grazing) is conjectural. On Banks Island, increased willow in the muskox winter diet and annual variation in the summer use of sedges in a high muskox density area (ca. 1.6-1.9 muskoxen/km^2) may have been a response to high densities (Larter et al. 2002, Larter and Nagy 2001d). However, the effect of summer moisture on plant quality complicates any relationship and summer moisture varied during the 1993-1997 study on Banks Island. Muskox body size, hence bite size, and nutritional requirements adds complexity to

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[5] http://data.canadensys.net/vascan/taxon/5850

assessing intra-specific forage competition (Forchammer 1995). On Banks Island, young muskoxen and adult females selected herb-dominated habitats within the areas occupied by mixed age-sex herds (Oakes et al. 1992).

Measuring the functional response between forage intake relative to forage abundance is an approach to predicting the effect of muskoxen on their forage (Bayliss and Choquenot 2002). An attempt on northwest Victoria Island in 1992 to measure the functional response had to be supplemented using captive muskoxen (Gunn unpublished). The relationship was linear between forage intake and biomass possibly because muskoxen are efficient foragers and daily intake is relatively low (Adamczewski 1995).

Social Behaviour

Muskoxen are highly social and occur as both mixed sex and age and bachelor groups with only adult bulls typically seen as singles (Gunn 1992a, Lent 1999). Seasonal changes to larger herds in winter are well-documented during aerial surveys and have been used to examine how predation is a likely factor in social behaviour (Heard 1992b).

POPULATION DYNAMICS

Age Structure and Vital Rates

Productivity: Productivity (% calves) is the only vital rate regularly monitored in the NWT. Productivity is the outcome of birth rate and calf survival and is measured as the proportion of calves to total muskox numbers recorded during aerial surveys in summer or winter; population surveys have been carried out in both seasons. During aerial surveys, the percentage of calves is likely under-estimated as calves are not always visible if the muskoxen are grouped, but the information can contribute to interpretation of trends in abundance. Use of photography during muskox surveys can improve accuracy of group counts and % calves.

Average productivity in July-August was similar for the mainland and the Arctic Islands (Table 7). Variability was high for mainland samples (CV=23%) and for Melville and Prince Patrick Islands, the CVs were 30% and 56%, respectively. Banks had the least variable productivity (CV=8%) while northwest Victoria productivity was more variable with CV=17%.

Table7. Summary of mean and SE of the percentage calves to total muskoxen recorded during summer aerial surveys (1982-2012) in the NWT on mainland and islands.

	No. summer surveys	Mean % calves to total muskoxen	SE	Minimum to Maximum
NW mainland	2	13.0	2.95	10-15.9
SE mainland	3	8.4	1.91	5.5-12.0
NW Victoria	9	11.7	2.03	1.4-17.6
Banks	13	12.3	1.04	3.9-18.7
Melville	6	10.6	3.15	0-18.9
Prince Patrick	5	5.2	2.94	0- 16.0

Calf productivity was generally low as measured during aerial surveys for the southeast mainland (Table 7). The low productivity was similar to a 1971-2004 series of observations made during canoe trips along rivers in and south of the Thelon Game Sanctuary (A. Hall, unpublished). Hall consistently recorded low productivity (4.2±0.71 (SE) percent calves to total muskoxen, Appendix J in Gunn et al. 2009). In 1994 and 2000, a comparison was possible with the aerial surveys, and the productivity recorded along the rivers was lower in

1994 (8.3% vs 12% across the entire Sanctuary). In 2000, productivity was similar during the canoe trips (5.3%) as during the aerial survey (5.5%) (Gunn et al. 2009).

However, something changed in the southeast mainland as by 2018, calf productivity and survival of the first three cohorts was exceptional based on a photographic composition survey (Adamczewski et al. 2021). The ten-month calves were 24% of the population which is within the 23-29% (calves/total muskoxen counted) for populations to reach the maximum finite rate of increase. At the same time, regional muskox surveys in the region of the East Arm of Great Slave Lake and Artillery Lake were completed in late winter 2010 and 2018 using distance sampling. The 2010 estimate was 957 muskoxen (95%CI 348-2,631) and the 2018 estimate was 8,098 (95%CI 5,230-12,540) (Cluff et al. unpublished). The 2018 survey area included the 2010 survey area along with an additional area to the west, which however had very few muskoxen. These results suggested an annual rate of increase approaching 30%/year, near the maximum rate of increase. The maximum rate of increase for muskoxen means they could double their numbers every three years under conditions of maximum productivity and survival. The maximum rate was measured during the early stages of reintroductions when the age and sex composition are skewed to younger females (Reynolds 1998). An introduced muskox population in West Greenland (Olesen 1993) had similar demographics during a period of very rapid growth. Latour (1987) cited D. Urquhart, P. Wilkinson and C. Shank (unpublished data) who reported 18-33% calves in the 1970s and 1981 on Banks Island. In the early 1980s on Banks Island the exponential rate of increase was 0.241 which converts to a doubling time of three years. However, by the late 1980s, the rate of increase had slowed to r=0.07.

The high rate of initial increase on Banks Island was in part caused by high pregnancy rates which would have contributed to high productivity (proportion of calves to total muskox numbers). However, regular monitoring of productivity during the aerial surveys (Figure 14) did not begin until 1985 (McLean et al. 1986). Mean % calves was higher during the increasing (1982-1994) than decreasing (2001-2014) abundance (increase 14.1±1.33 SE; decrease 11.4±0.96). Productivity on northwest Victoria Island was similar to but more variable than on Banks Island during the decline (Figure 14).

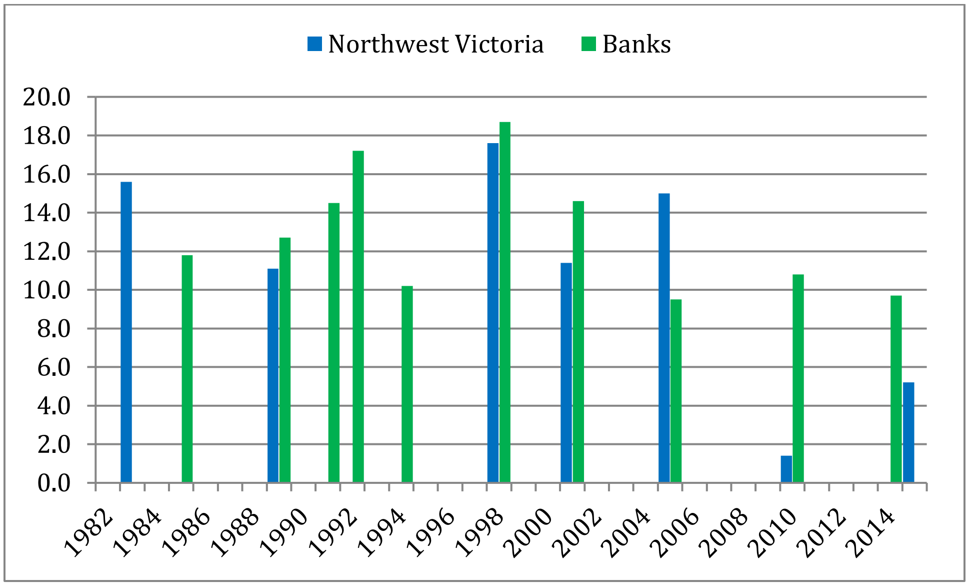

Figure 14. Percentage calves to total muskoxen recorded during aerial surveys on Northwest Victoria and Banks Islands, 1982-2015, NWT.

Additionally, on Banks Island between 1986 and 1998, Larter and Nagy (1999a, 2001d) undertook annual sex and age surveys to classify muskoxen into calves, yearlings and 2+ years, based on their appearance, to calculate productivity and calf survival. These aerial or ground surveys were in June to August and sampled mostly areas of high muskox density. They defined productivity as calves per 2+ year cows as during commercial harvests about 30% of two-year-old females were pregnant (see Nagy et al. 1996). The trends in productivity as a percentage of the population during island-wide aerial surveys or as the ratio to 2+year-old cows were similar during the time when the number of muskoxen on Banks was increasing (Figure 15).

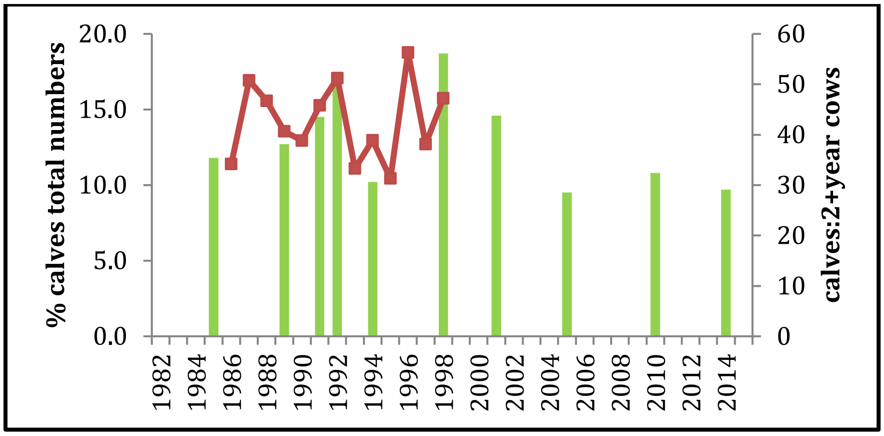

Figure 15. Calves as a percentage of total population from aerial surveys (bars; left axis) and as a ratio to 2+-year-old cows from composition surveys (line; right axis), Banks Island.

Larter and Nagy (1999a, 2001d) defined recruitment as the ratio of yearlings per 100 two-year-old cows and % calf survival as the current recruitment divided by the previous year's recruitment. Recruitment was the ratio of yearlings per 100 2+-year-olds. Between 1986 and 1999, calf survival and recruitment annually varied (range 23-83% and 10.0-41.7 yearlings/100 adult females, respectively) and relationships with snow depth in wet sedge meadows, muskox density and diet were complex (Larter and Nagy 2001d).

Extensive sampling of sex and age composition across Banks Island in summer 1986 found that while the calf:cow ratio for the whole island was 37±1.0 (SE)/100 cows, the ratio varied widely within the island (McLean and Gunn 2005). The calf:cow ratio was higher in low density areas (48±1.95/100 cows) than high density area (32±1.1 /100 cows). The yearling/100 cow ratios was also significantly higher for the low-density areas, 40±1.7 (SE)/100 cows versus 29±1.3/100 cows for the high-density areas, which suggests that areas of low and high density have to be sampled to estimate a representative value, as generally occurs during aerial surveys.

Pregnancy rates: Data on muskox pregnancy rates are only available during commercial or scientific harvesting or when serum is collected during live captures. Pregnancy rates on Banks Island were initially as high as 95% in November 1983 (Latour 1987) for three-year and older cows. The rate for two and three-year cows decreased from 8% to 0% and 88% to 43%, respectively, during 1982-1985 and 1986-1991 (Fraser et al. 1992b). The pregnancy rates of 4+-year cows changed from 95 to 83% for the same two periods. Subsequently, during the 1990s, adult pregnancy rates declined to between 35% and 68% although 30% of the two-year-old females were pregnant (Larter and Nagy 2001a). Pregnancy rates for cows >3 years of age on southern Victoria Island averaged 64% in November 1989-1992 and 58% in April (Adamczewski 1995). There have been scattered observations of live-born twins but they are very much the exception (Tener 1965).

Adult sex ratio: Adult sex ratios are relatively easy to determine as the sexes are distinctive in body size and horn shape. However, sampling the sex ratio does require sampling a cross section of group sizes and types as the males can occur as solitary individuals or in bull-only groups. The adult sex ratio was 78±3yrs males/100≥3 years females overall, including all observations, but only 52±1.6 (SE) males/100 cows in mixed groups (McLean and Gunn 2005). Relatively little information is available to determine if there are trends in the adult sex ratio over time as sex and age composition surveys are infrequent. Environmental conditions such as severe winters or disease can skew adult sex ratios as bulls are more vulnerable to diseases such as yersinia (Blake et al. 1991, McLean et al. 1993). For example, between 1988 and 1991, adult male mortality on northern Banks Island was significantly higher than expected among carcasses examined, but the overall adult sex ratio for live muskoxen classified was 76.6±4.75 SE bulls:100 cows (McLean unpublished). Bulls lose body weight during the rut (Thing et al. 1987) and are likely more vulnerable to malnutrition during severe winters. In August 1983, during the rut on Bailey Point, Melville Island, after two severe winters, the adult sex ratio was only 31 bulls/100 cows (>3 years old), the percentage of single bulls was low and bull only groups were not seen, which suggested disproportionate mortality for adult males (Gunn et al. 1989).

Age structure: Information on age structure is mostly lacking again because sex and age composition surveys are infrequent, despite the importance of these variables in understanding changes in population size (Caughley 1977, Coulson et al. 2004). Muskoxen through their body size, horn development and eruption pattern of the lower dentition are readily classified into the first four- or five-year classes (e.g. Henrichsen and Grue 1980, Gray 1987, Olesen et al. 1994)[6]. The timing of sex and age composition surveys requires a standardized approach to defining the age classes (Gorn and Dunker 2015). Latour (1987) reported that examining annuli in the tooth cementum was inconsistent in separating year classes but using tooth eruption and horn growth enabled classification of the first four-year classes from 228 muskoxen killed during a commercial harvest in April 1981.

Adult mortality: Adult mortality is difficult to measure unless a large sample of individuals are marked, and their fate determined. Another approach to estimating mortality is population modeling using productivity, harvest levels and population trends. Neither approach has yet been attempted for muskoxen in the NWT. In large-bodied mammals, although recruitment rates are more sensitive to environmental conditions than adult survival rates, population rate of change is most sensitive to changes in adult survival rates. Searching for carcasses and determining the cause of deaths provides information on the

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[6] A photographic approach to sex and age classification (1, 2, 3 and 4+ year old males and females) was used in the East Arm area in March 2018 (Adamczewski et al. 2021) and these surveys were repeated in 2020, 2022 and 2024 (Adamczewski unpublished).

relative proportion of causes, although not the rate. McLean et al. (1993) examined carcasses on northern Banks Island and found high annual variation over a four-year period in the relative number of deaths from Yersinia, winter malnutrition and wolf (*Canis lupus*) predation (Figure 16).

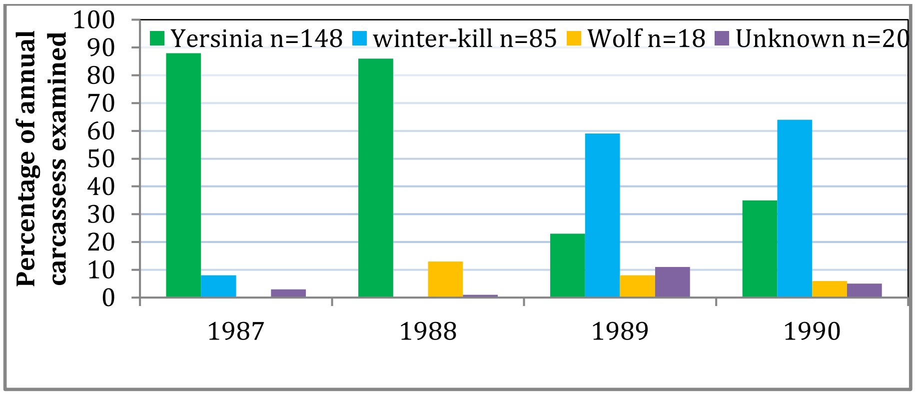

Figure 16. Causes of death 1987-1990 for muskox carcasses found during aerial and ground searches on northern Banks Island (McLean et al. 1993).

Movements, Migration and Dispersal

Information on seasonal muskox movements in the NWT is limited and largely unmeasured. The exception occurred when ten adult cows were tracked with satellite collars in the Sahtú region near Norman Wells between 2007 and 2009 (WMIS, B. Tracz, unpublished). The cows maintained small annual ranges with overlapping seasonal ranges (Table 8, Figure 17)[7]. Seasonal ranges were measured by creating minimum convex polygons around collar locations grouped by season.

Table 8. Mean seasonal home range areas (km^2) for adult muskox cows in the Sahtú region, 2007-2009, NWT.

Season	Sample size	Mean range size (km^2)	SE
Winter	11	112.8	35.33
Spring	8	184.4	40.94
Summer	7	566.4	234.86
Fall	11	257.7	83.48

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[7] In 2024, this collared muskox data set was the subject of a detailed analysis of range use by postdoctoral associate N. Luymes at Laurier University, working with Dr. F. Stewart.

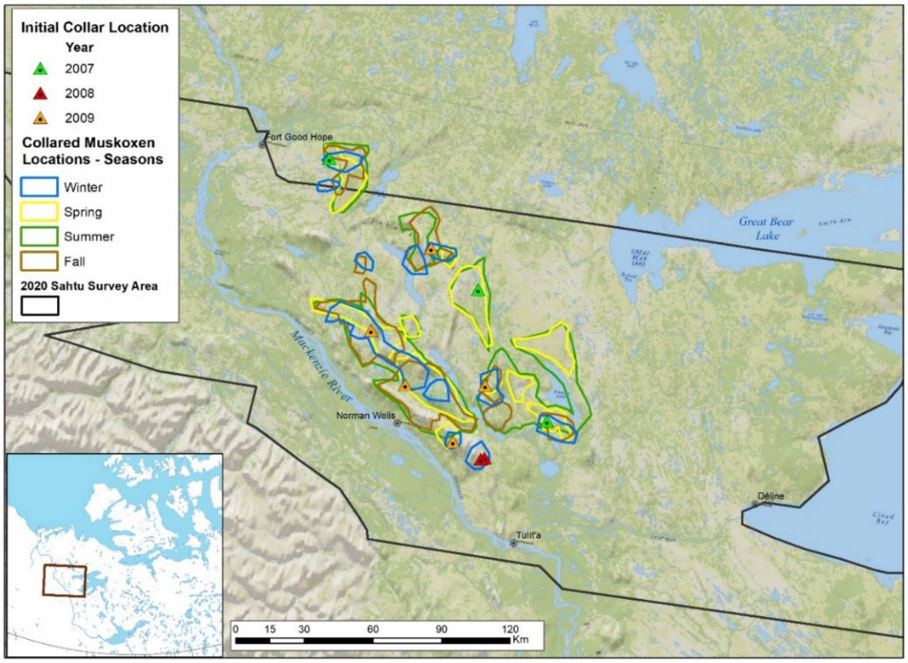

Figure 17. Seasonal ranges for ten satellite collared muskox cows and capture sites, 2007-2009, in the Sahtú region in the NWT.

This limited information on movements is similar to findings elsewhere across muskox ranges based on the few studies using satellite collared muskoxen. On the North Slope Alaskan tundra, satellite collared adult cows used smaller home ranges (about 16-35 km^2) in winter than summer (Reynolds et al. 2002a). Mean daily movements in summer (2.6 km/day) were greater, especially in July, than in other seasons (1.1-1.4 km/day). However, adult cows also moved long distances (>160 km), but then returned after two years (Gorn and Dunker 2015). At a finer timescale, using GPS collars in northeast Greenland, individual movements were variable (Schmidt et al. 2016).

Seasonal migrations have been infrequently documented in muskoxen. In northwest mainland NU, muskox cows fitted with VHF radio collars tracked from April to November seasonally moved on average 85 km from valleys to coastal uplands, probably in response to snow conditions and foraging (Gunn and Fournier 2000). Larter (1999) reported muskoxen wintering below the treeline and moving to summer on the tundra. Historical reports also record that muskoxen moved 65-80 km south of the treeline in winter between the Anderson River and western Great Bear Lake, (in 1864: Clarke 1940 cited in Barr 1991).

Dispersal is usually classified as innate or environmentally forced directional movement (Caughley 1977). Environmentally forced dispersal is infrequent. NWT hunters report environmentally forced dispersal during winters with ground-fast icing; muskoxen were seen out on the sea ice west of Banks Island in the fall of 2001 after rain followed by freezing temperatures and snowfall (Nagy and Gunn 2009).

The dispersal of bulls is likely innate behaviour as they mature and search for breeding opportunities. Dominant bulls are intolerant of other bulls in the breeding season, although multiple bulls may be found together in other seasons. Single bulls are often the first muskoxen seen in new or re-colonized ranges. The bulls then may lead mixed sex and age groups to expand the ranges, which would be similar to behaviours in wood bison *Bison bison athabascae* behaviour (Gates and Larter 1990). On the southeast NWT mainland, bull muskoxen disperse into unoccupied areas preceding the occurrence of mixed sex and age groups (Gunn et al. 2009). The gap in information on the relationship between the density of muskoxen and the mechanism(s) for emigration to unoccupied ranges is a concern for management. Currently the directional shifts in distribution in the NWT support the role of emigration/immigration as a factor in changing abundance. However, whether the dispersal is innate or density-dependent is a key monitoring gap.

Abundance

Measuring Abundance

The aerial surveys used to estimate abundance are standardized, which improves detecting trends: an overall review such as Boulanger et al.'s (2017) review for bison, another social ungulate, could increase standardization. The standard survey design is strip transects except in 2010 and 2018 for Artillery Lake (D. Cluff unpublished) and in 2020 and 2021 north and west of Great Bear Lake (Rentmeister and Chan 2022) which were line transect designs (distance sampling). The line transect design is efficient in low density areas, as observations that otherwise would be off-transect in a strip survey are used toward estimating abundance. Distance sampling has recently evolved to allowing inclusion of habitat variables to increase the efficiency of the sampling (Boulanger et al. 2017).

Accuracy of survey estimates includes the probability of detecting muskoxen, which depends on aircraft altitude, type and strip width (Tables 9-14). Survey altitude varies and because the aerial surveys are often for caribou as well as muskoxen, aircraft altitude is usually about 150 m above ground level. Counting errors are possible especially if muskoxen group together tightly in response to the survey aircraft, and are less likely during summer surveys when groups are smaller. Most recent muskox surveys in the NWT include photos of larger groups, which allows for more accurate counts.

Precision is the consistency of the survey estimates and is typically increased through increased coverage and stratifying survey effort using either reconnaissance surveys or prior knowledge, especially for the Arctic Islands. Graf and Case (1989) recommended that precision, as measured by the coefficient of variation (CV), for NWT muskox surveys should be 0.15 or lower. On Banks and Victoria islands, the mean CV has been 6-8% since 1982, obtained through a combination of stratification and increased coverage (Table 11). On the mainland the CVs averaged 28-35%, which is not unexpected as the survey areas were large, some groups were large and densities were often low. CVs exceeding 30% usually resulted from surveys with coverage lower than 15% (Fournier and Gunn 1998). Although some of the earlier surveys used low coverage (e.g. 4-6%), surveys now tend to use a standard 20% coverage (5 km spacing on transects, 1 km strip width) which increases statistical power to detect trends in abundance.

NWT and Global Muskox Populations

In 2020, the NWT had approximately 34,000 adult muskoxen (rounded to the nearest 1,000) based on the most recent aerial surveys (Appendix A). The estimate is uncertain as only five of 12 survey areas had estimates within the last five years. The NWT shares mainland, Melville and Victoria Island muskoxen with NU. Together with NU and the Yukon Territory, the total in 2020 was about 80,000 adult endemic muskoxen. The NWT had 46% of Canada's total endemic muskoxen, which is 68% of the global muskox population (Figure 18).

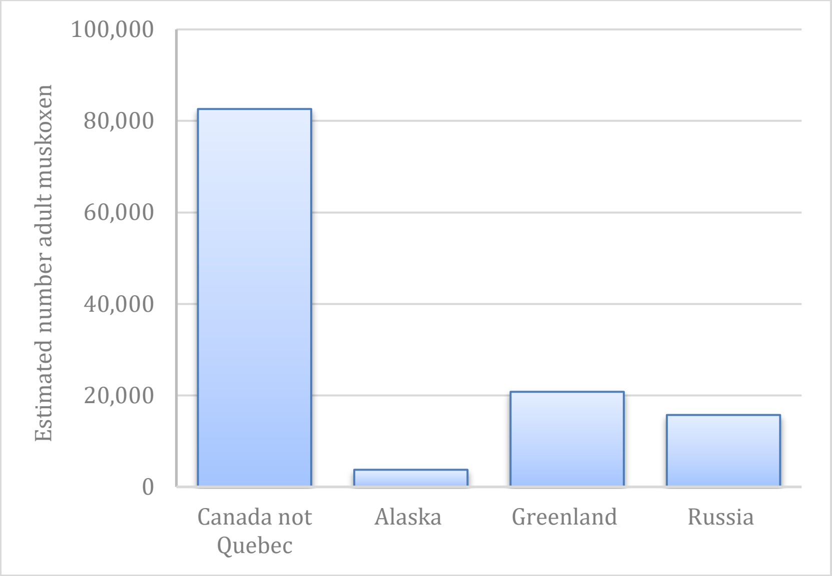

Figure 18. Estimated numbers of endemic muskoxen by country in 2020. The Québec muskoxen are introduced from release of captive muskoxen and so are not included for the global comparison.

Fluctuations and Trends

Overall Trends

The 2020 estimate for the NWT of 34,000 adult muskoxen is a 55% decline from the 97,080 muskoxen estimated in 1998 (three generations, Appendix A), assuming a constant exponential rate of change based on two available survey results from 1991-2019 for ten management areas (Western Queen Elizabeth Islands, Banks Island, northwestern Victoria Island, Paulatuk area, North and West Great Bear Lake area, Artillery Lake area, Aylmer Lake area, Thelon, and Richardson Mountains). The overall trends are weighted by the steep declines (-80%: from surveys in 1994-2019) on Banks Island and northwest Victoria (-76%: from surveys in 1998-2019), of previously large populations. These declines were not offset by increases on the western Queen Elizabeth Islands and the mainland.

Trends were not estimated for the three mainland survey areas without at least two estimates covering three generations (Appendix A). Earlier trends included slow recovery between the 1940s and the 1980s (Barr 1991) and then increasing trends, accelerated especially on Banks and northwest Victoria Islands, where numbers peaked in the 1990s. Trends on the mainland are harder to summarize as survey areas have changed (Fournier and Gunn 1998).

Regional Trends

Western Queen Elizabeth Islands (Prince Patrick, Eglinton, Melville and Byam Martin)

The most recent estimate for the western Queen Elizabeth Islands is 3,716 ± 2,367 CI in 2012 (Davison and Williams 2016) (Table 10). The overall trend over the past three generations calculated using the survey results from 1997 and 2012 is an 85% increase in abundance, but CVs were high (Table 9, Figure 19).

For Melville Island, the 39 year period of surveys includes a 32% decline between 1973 and 1974 on Melville Island, based on extrapolated numbers as western Melville was not surveyed in summer 1974 (Miller et al. 1977), an increase to 1986 (Miller 1988,) a decline to 1997 and an increase to 2012 (Gunn and Dragon 2002, Davison and Williams 2016). For the two western islands, the fluctuations were more marked than on the large island of Melville. The trend for Prince Patrick Island was low numbers in 1986 and 1997, followed by an almost five-fold increase between 1997 and 2012. Muskox numbers on Eglinton Island were low in the early 1970s and 1997 and similarly experienced an almost six-fold increase between 1997 and 2012 (Miller 1987). Muskox occurrence on Byam Martin Island has been sporadic (Table 9).

Table 9. Estimated numbers of adult muskoxen (and 95% Confidence Limits) for Melville, Prince Patrick, Eglinton and Byam Martin islands, 1973-2012 (included calves in 1973 and 1974).

	Melville		**Prince Patrick**		**Eglinton**		**Byam Martin**		**Source**
	mean	**95%CI**	**mean**	**95%CI**	**mean**	**95%CI**	**mean**	**95%CI**	
1973	3,991	1,807	168	331	26	35	125	128	Miller et al. 1977
1974	1,997	1,152	232	270	28	49	0		Miller et al. 1977
1986/1987	4,761	731	62	0	101	0	96	60	Miller 1987, 1988
1997	2,258	525	96	82	37	41	0		Gunn and Dragon 2002
2012	2,998	770	504	319	214	198	0		Davison and Williams 2016

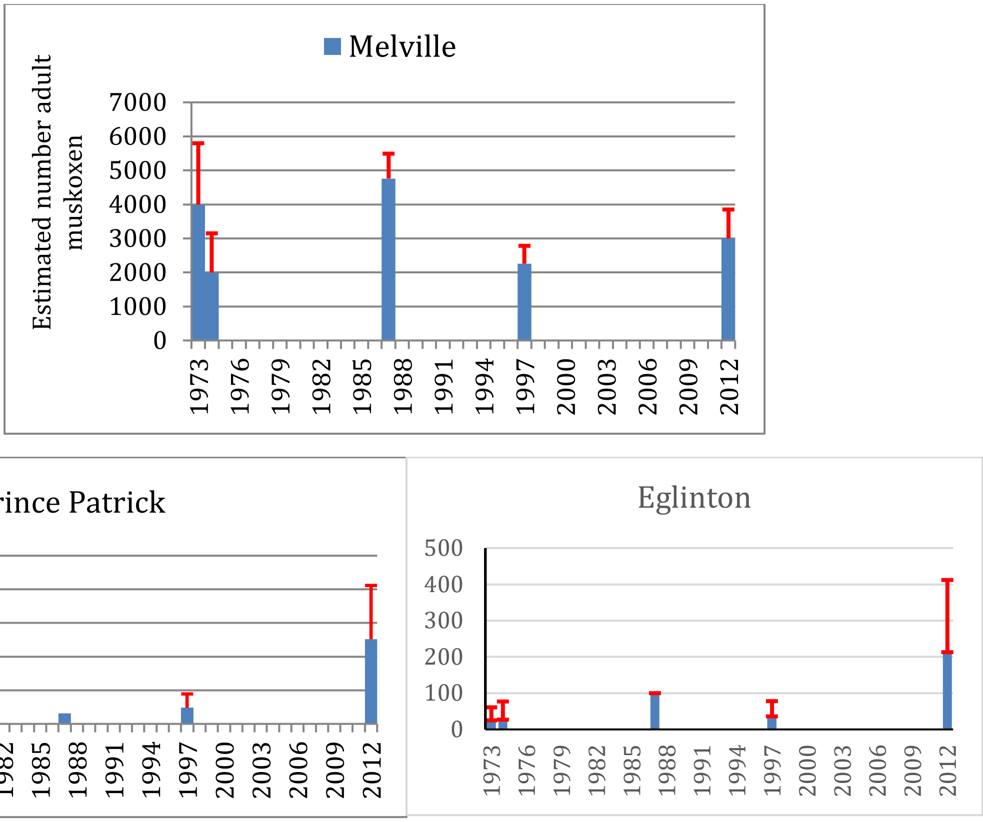

Figure 19. Trends in muskox estimated abundance (with 95% Confidence Intervals) on Melville, Prince Patrick and Eglinton Islands, 1973-2012.

Survey design was fixed-wing strip transects except for a helicopter and line transect design in 1986-1987 (Table 10). The islands were flown in a single year except in 1986 and 1987 when Melville and Byam Martin Islands were flown in 1986 with Prince Patrick and Eglinton Islands flown in 1987. In 1974, the western half of Melville Island was not surveyed (Miller et al. 1977).

Table 10. Survey attributes, western Queen Elizabeth Islands, July-August, 1973-2012.

Year	Coefficient of Variation			Aircraft type	Altitude (m)	Each Strip width (m)	Coverage (%)
	Melville	**Prince Patrick**	**Eglinton**				
1973	0.23	1.01	0.69	Helio-Courier	150	400	12.5-25
1974	0.29	0.59	0.89	Helio-Courier	150	400	12.5-25
1986		--		Helicopter	90	ca. 857	27
1987	0.08		0.57	Helicopter	90	ca. 857	27-54
1997	0.12	0.44		Helio-Courier	100	500	12-18
2012	0.28	0.63	0.93	Helio-Courier	120	500	14-19

Banks Island

The most recent estimate of muskoxen on Banks Island is 10,979±1148 (95% CI) in 2019 (Davison and Baryluk 2021). The trend for the past three generations, calculated using survey results from 1994 and 2019 is a 28% decline (Table 11, Figure 20). The rate of decline accelerated between 2010 and 2014 when the halving rate reached 2.8 years, based on an exponential rate of -0.245.

Between 1982 and 1994, muskox numbers on Banks Island increased although the rate of increase has not been constant, being punctuated by years with low productivity (Figure 14). From 1985 to 1994, the rate was a doubling time of three to nine years. Between 1994 and 1998, muskoxen apparently declined, although this may have reflected survey issues, and then recovered by 2001 to a similar level as 1994 (Nagy et al. 2006, 2013a and b).

Banks Island has had a high survey frequency (Table 11) with relatively standardized methods since 1982 (Table 11). The surveys prior to 1982 were either not island-wide or had different methods (McLean et al. 1986, McLean and Fraser 1992, Nagy et al. 1996). The 1982 survey was the first survey to stratify the island but an area on the north was not covered (McLean et al. 1986) although Nagy et al. (2009a) recalculated the estimate.

Table 11. Estimated numbers of adult muskoxen (and 95% Confidence Limits) and survey attributes, Banks Island, 1982-2019.

Year	Dates	Estimate	95%CI	CV	Altitude	Each Strip width (m)	Reconnaissance + no. strata	Coverage	Citation
1982		12,481	3,047	0.12	120		rec+3		Nagy et al. 2009a
1985	6-14 Jul	25,700	4,018	0.08	180	1,000	rec+4	10, 25,42	Mclean et al 1986
1989	22-28 Jun	34,270	4,625	0.07	120	600	rec+4	10, 25,42	McLean and Fraser 1992
1991	27 Jun - 3 Jul	47,670	7,783		150	500	4	10	Fraser et al. 1992a
1992	21-30 Aug	53,526	4,032	0.04	100	500	8	20, 40	Nagy et al. 2009b
1994	early Jul	66,297	5,106	0.04	100	500	8	20, 40	Nagy et al. 2013a
1998	early Jul	45,922	4,097	0.04	100	500	8	20, 40	Nagy et al. 2013b
2001	7-15 Jul	68,585	6,972	0.05	100	500	8	20, 40	Nagy et al 2006
2005	24 Jul -1 Aug	47,209	3,997	0.04	100	500	11	20, 40	Nagy et al. 2009c
2010	17-26 Jul	36,676	4,031	0.06	100	500	11	20, 40	Davison et al. 2013c
2014	8-18 Jul	13,767	1,948	0.07	100	500	11	20, 40	Davison et al 2017
2019	24 Jul -20 Aug	10,979	1,148	0.07	120	500	11	12-20, ave. 17.1	Davison and Baryluk 2021

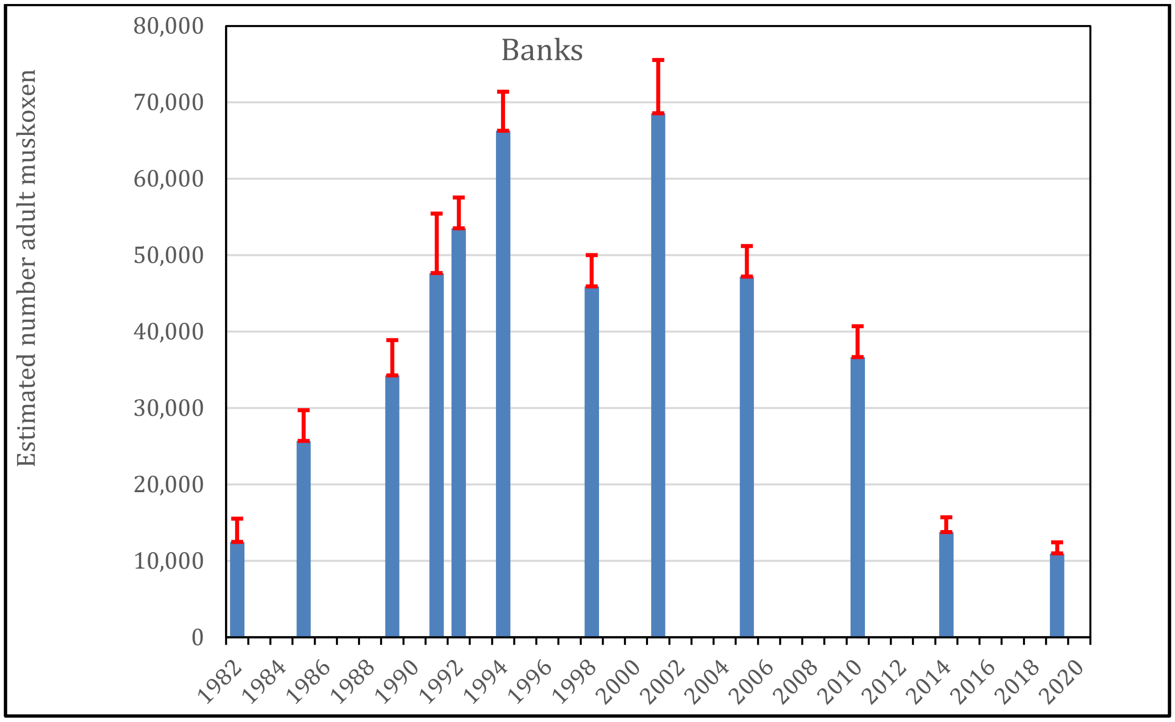

Figure 20. Estimated muskox numbers (and 95% Confidence Limits), Banks Island, 1982-2019, NWT (data sources Table 11).

Northwest Victoria Island

The most recent estimate of muskoxen on northwest Victoria Island (Table 12) is 5,550 ± 1,672 (95% CI) in 2019 (Davison and Williams 2022). The three-generation trend calculated using surveys 1998 and 2019 is a 76% decline (Table 12, Figures 21 and 22, Appendix A).

Table 12. Estimated numbers of adult muskoxen (and 95% Confidence Limits) and survey attributes, northwest Victoria Island, 1983-2019 (included calves in 1983, 1989 and 1994).

Year	Month	Estimate	95 % CI	CV	Altitude (m)	Each Strip width (m)	Strata	Coverage %	
1983	8-17 August	6,430	976	0.08	300	1,000	4	11.3	Jingfors 1985
1989	19-31 August	12,847	2,470	0.09	300	1,000	5	10, 20, 30	Gunn Unpublished
1994	July	19,989	7,421		120	500	3	10.2	Nishi in Fournier and Gunn1998
1998	early July	22,829	1,676	0.07	100	500	4	20	Nagy et al. 2009d
2001	16-21 July	21,756	3,221	0.82	100	500	3	20	Nagy et al. 2009e
2005	6-8 July	14,170	2,156	0.85	100	500	3	15.6	Nagy et al. 2009f
2010	August	11,602	1,637		120	500	3	19.9	Davison and Williams 2013 a and b
2015	14 April-6 May	11,708	1,867			500	4	19.8	Davison and Williams 2019
2019	8-24 May	5,550	1,672		120	500	4	16.5	Davison and Williams 2022
Minto Inlet survey area									
1992	24-26 March	8,900	820	0.09	183	1,000	2		Heard 1992a
1992	August	7,214	176	0.024	183	1,000	2	40	Gunn and Nishi Unpublished
1993	July	6,921	486	0.07	183	1,000	2		Gunn and Nishi Unpublished

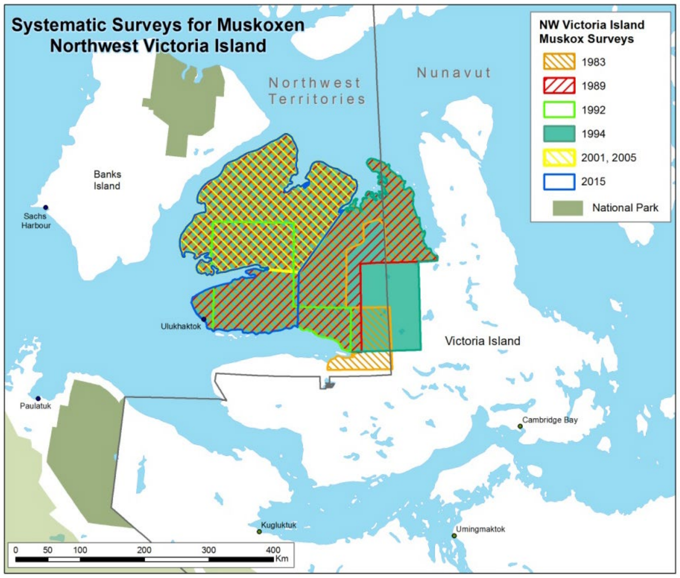

Figure 21. Survey areas flown on northwest Victoria Island 1983-2015, NWT.

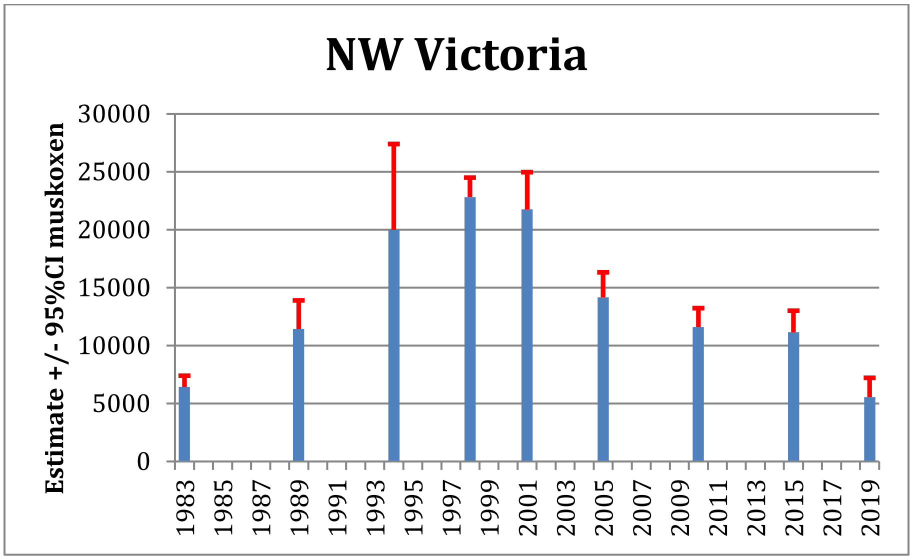

Figure 22. Estimated adult muskox abundance (with 95% Confidence Intervals) on northwest Victoria Island, 1983-2019.

An apparent increase between 2010 and 2015 is the result of an additional stratum flown in 2015 (Davison and Williams 2019; Figure 21); without the additional stratum, the trend was stable between 2010 and 2015. Muskox abundance peaked 1998-2001 (Nagy et al. 2009 d and e) followed by a low rate of decline (r=-0.039) for 2001-2015.

The aerial surveys in 1983 and 1989 were similar but had larger survey areas (76,000 km^2) and extended further east than the 1998-2015 surveys (36,000 km^2). For estimating the trend in this report, we used Stratum 1 for 1989 as it was similar to the 1998 survey area. The 1994 survey was designed to look for calving caribou on western Victoria Island and the muskox counts were incidental (Nishi and Buckland 2000). Between 1998 and 2015, the survey area was standardized, and the strata changed in 2001, then subsequently remained the same (Nagy et al. 2009 d and e).

Estimating trends of muskoxen on northwest Victoria Island is also complicated by uncertainty from the lack of geographical boundaries for the eastern extent of survey areas. Jingfors (1985), for example, suggested that the lower estimate in 1983 compared to 1980 (Jakimchuk and Carruthers 1980 in Jingfors 1985) might have been muskoxen moving from Prince Albert Sound east into the area surveyed as southeast Victoria Island in March 1983. The southern boundary of the survey area changed in 2015 as an additional stratum was added south of Minto Inlet (Davison and Williams 2019) but is not included in estimated trend (Figure 22).

The rate of decline on northwest Victoria Island was lower than on Banks Island. Possibly, muskox movements elsewhere on northwest Victoria Island are a factor in the lower rate of change.

An aerial survey in March 1992 was to determine if a muskox removal (commercial harvesting experiment; Table 12) would increase caribou densities (Heard 1992a). July/August surveys in 1992 and 1993 followed up with a similar area to March 1992, but as the Minto Inlet surveys were a different survey area, they are not included as part of the trend analysis for northwest Victoria Island (Gunn and Nishi unpublished).

Northwest Mainland

Richardson Mountains

West of the Mackenzie River, muskoxen are few as in April 2016, only 98 of the 287 total muskox count on the Yukon North Slope and the Richardson Mountains were within the NWT (M. Suitor, pers. comm. 2016). The trend is unknown.

Paulatuk and Great Bear Lake Areas

The most recent estimate of abundance along the coastal area mainland near Paulatuk is 2855 ± 2,677 (95%CI) in 2009 (Davison and Branigan 2014). The trend is possibly stable but uncertain because of changes in distribution and survey areas (Appendix A). The estimates increased between 2002 and 2009 (r=0.114) and comparing 2009 to 1997, the trend is about a 20% increase (Appendix A) or recovery from the lower estimate in 2002 (Table 13, Figure 23). The muskox survey areas varied between 1980, 1983, 1987 and 1997 but then the amount of overlap between consecutive surveys increased for 2002 and 2009 although the 2009 survey was extended west (Figure 24).

Table 13. Estimated numbers of adult muskoxen (and 95% Confidence Limits) and survey attributes, northwest mainland, 1980-2009 (includes calves in 1980 and 1983)[8].

Year	Month	Adult	95% CI	CV	Altitude (m)	Each strip width (m)	Reconnaissance +no. strata	Coverage (%)	
Paulatuk region									
1980		3,290	1674					11.9	Spencer 1980
1983	8-21 March	3,315	1262	0.201	300, 150	1,500, 750	Reconn+4	10, 25	Case and Poole 1985
1987	23 August – 3 September	3,040	2540	0.42	200	750	1	10	McLean 1992
1997	10-19 March	2,567	1419	0.29	200	750	1	10	Larter 1999
2002	27-29 March, 5-13 May	1,215	256	0.30	110-132	500	4	10	Nagy et al 2013c
2009	9-23 March	2,855	1356		110	500	6	10	Davison and Branigan 2014
North Great Bear Lake									
1997	11-21 March	1,460	920	0.31	200	500	Reconn+2	10, 25	Veitch 1997
North, South and West Great Bear Lake									
2020 &2021	March	5,793	4,121	0.279	100-200		Distance sampling, 10km spacing	Ca. 10	Rentmeister and Chan 2022

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[8] Estimate for the Sahtu region in 2020-2021 is added for comparison with the 1997 survey as these were the only regional muskox surveys over this period.

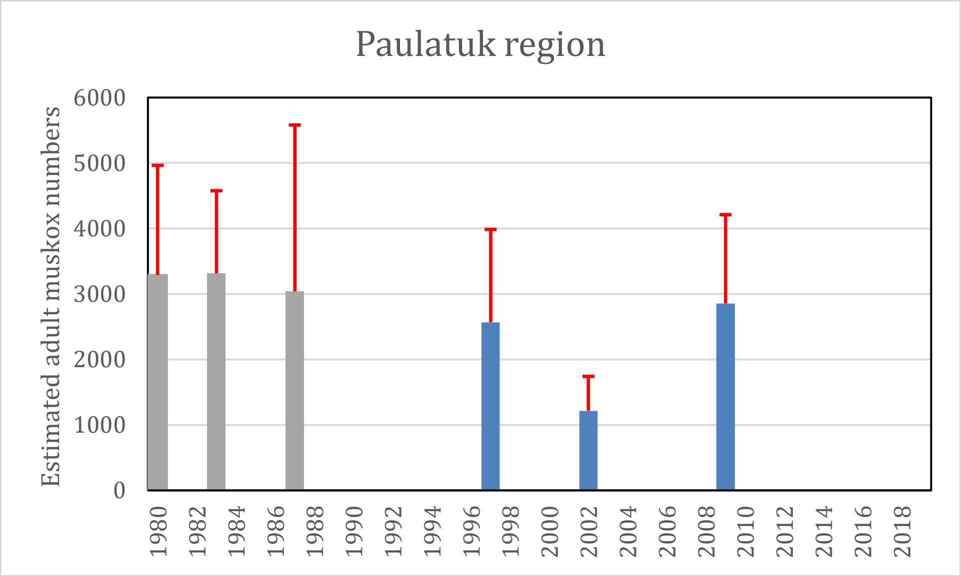

Figure 23. Trends in mean numbers of muskoxen (with 95% Confidence Intervals) estimated in the northwest NWT mainland, 1980-2009. Grey bars are different survey areas than blue bars.

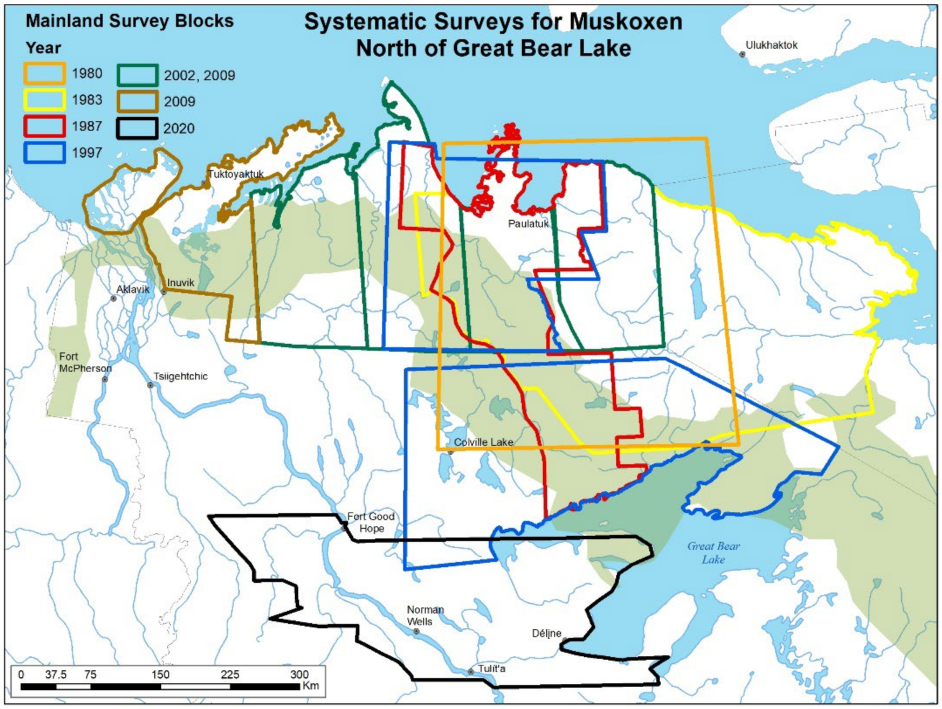

Figure 24. Survey areas flown on northwest NWT mainland 1980-2020. Areas of ocean within survey blocks were not flown.

The previous 1997 muskox survey in the northern Sahtú Settlement Area (Veitch 1997) estimated 1,460 ± 920 (95% CI) non-calf muskoxen in the survey area and a corresponding density of 2.6 muskoxen per 100 km^2. In 2020 and 2021, an aerial survey covered 98,625 km^2 in the Sahtú region north, south and west of Great Bear Lake, including an area west of the Mackenzie River (Rentmeister and Chan 2022). Muskox abundance was estimated at 5,793 non-calf muskoxen, ranging from 3,385 to 9,912 (95% CI). Re-analysis of 1997 survey results and comparable 2020/2021 survey area results suggested 1,278 muskoxen in 1997 compared to 1,654 muskoxen in 2020-2021 in the same area. The time interval since 1997 and differences in surveyed areas and methods prevent a determination of population trend.

Adjacent to the NWT/NU boundary, by the 1980s, muskoxen had also spread east of Bluenose Lake to Nunavut's's Rae and Richardson River Valleys, where their numbers sharply declined between 1987 and 1994, then stabilized between 1994 and 2017 (Dumond 2007, LeClerc 2018). It is unknown how the abundance east of Bluenose Lake relates to trends west of Bluenose Lake.

Southeast Mainland

Artillery Lake Area

The most recent estimate for the Artillery Lake survey area is 8,116 ± 4,526 (95%CI) in 2018 (Table 15). The 2018 estimate was for a larger survey area than the 2010 Artillery Lake area as it included an area to the west of the 2010 survey, however that western portion in 2018 had very few muskoxen (Figure 25). The trend for three generations (using surveys 1998-2018) for the Artillery Lake area (Figure 26) shows a large increase of 237%, based on high productivity and survival (Adamczewski et al. 2021). Muskox numbers doubled between 1989 and 1998 in the Artillery Lake survey area (Bradley et al. 2001) and then declined to 2010, but the decline was not statistically significant (Table 14). Subsequently, the exponential rate of increase between 2010 and 2018 was 0.210, a doubling rate of 3.3 years. The trends are based on three late winter and one summer survey with similar methods until 2018, when the design switched from strip to linear transect (distance sampling).

The first systematic muskox survey in 1989 established a survey area between the East Arm of Great Slave Lake and the western boundary of the Thelon Game Sanctuary and this area centered on Artillery Lake was then covered in 1998, 2010 and 2018 (Figure 26). The area north centered on Clinton-Colden Lake and west of Artillery Lake was flown in 1991 but only had a few muskoxen concentrated northeast of Clinton-Colden Lake (Shank and Graf 1992).

Table 14. Estimated numbers of adult muskoxen (and 95% Confidence Limits) and survey attributes, southeast NWT 1989-2018. Calves were included in 1989 and 1991.

Year	Dates	Estimate	95% CI	CV	Altitude (m)	Each strip (m)	Coverage (%)	Survey area km^2	
Artillery Lake									
1989	20-31 March	563	302	0.27	185	1000	16, 50	34,407	Graf and Shank 1989
1998	16-28 July	1,606	545	0.17	185	1000	29	46,864	Bradley et al 2001
2010	15-20 March	957	508	0.53			.	59,200	Cluff pers. comm.
2018	28 February – 2 March	8,098	4,442					79,740	Cluff pers. comm.
Alymer									
1991	24-27 July	359	506	0.72	185	1000		33,825	Shank and Graf 1992
2018	28 February – 2 March	3,064	551						Cluff pers. Comm.
Thelon									
1994	20 July – 7 August	1,095	359	0.26	185	1000	13.3	58,615	Shank in Gunn et al 2009
South Thelon									
2000	August	1,320	302		185	1000	19.8	41,326	Gunn et al 2009
2011	20-26 April	too few			185	500			Adamczewski and Williams unpub.

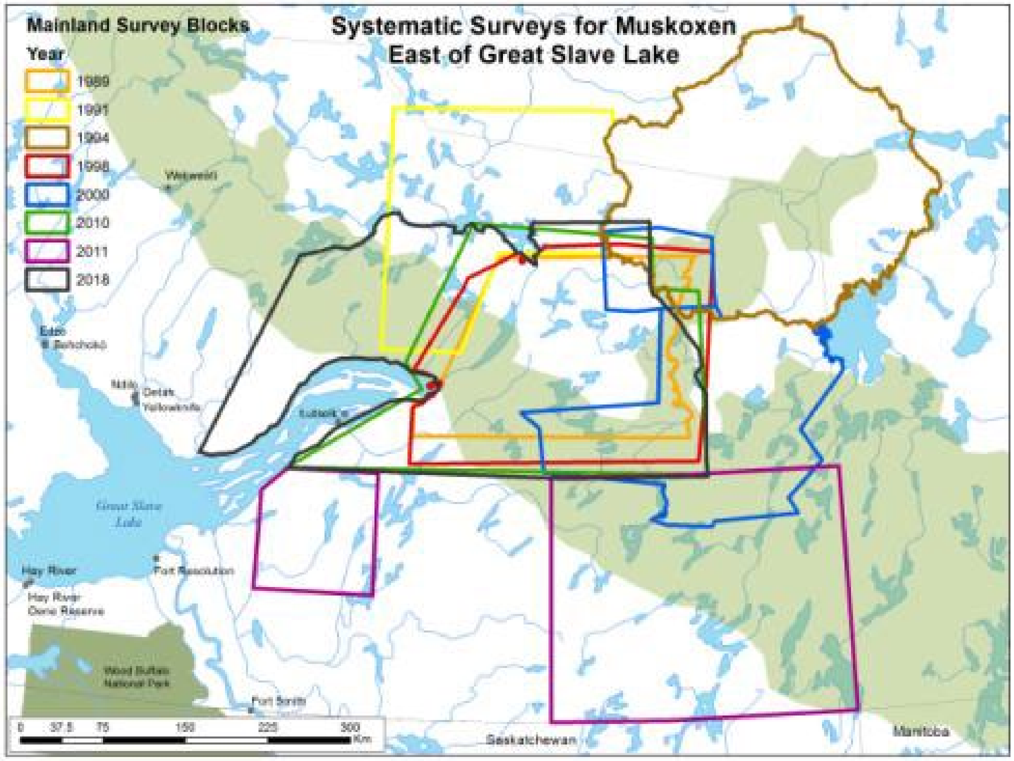

Figure 25. Muskox survey area boundaries 1989-2018, southeast NWT.

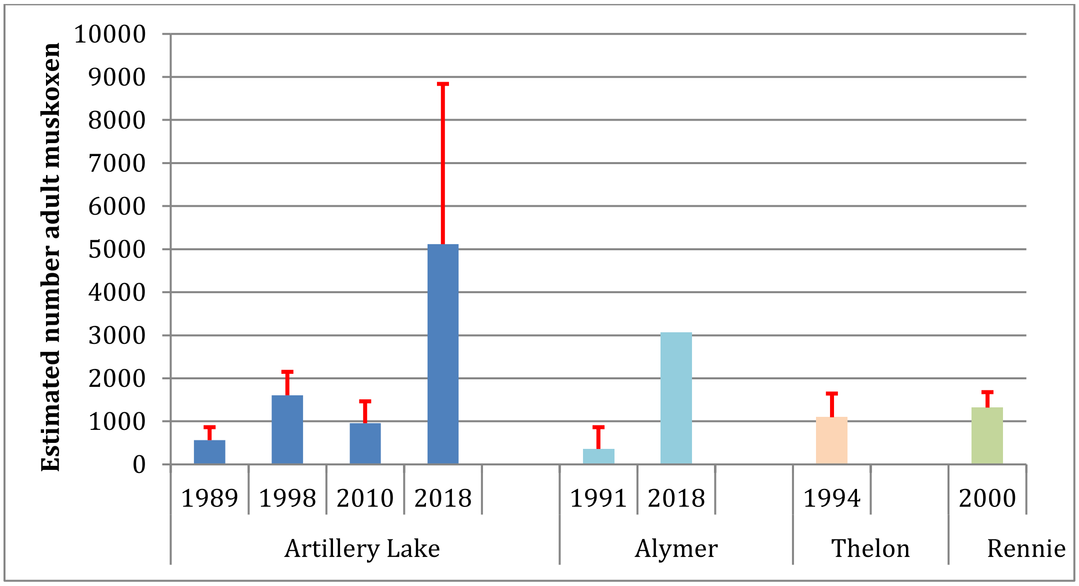

Figure 26. Estimated abundance of muskoxen 1989-2018 (with 95% Confidence Intervals) for the southeast NWT.

The western boundaries of the 2018 survey area were extended west about 120 km along the north shore of Great Slave Lake compared to 2010, which indicated muskoxen dispersing west since 2010. At the same time as abundance increased in the Artillery Lake survey area, abundance decreased in the Thelon Wildlife Sanctuary and east of Artillery Lake. The evidence is conjectural as the strata vary among surveys, which prevents a direct comparison of estimated abundance by strata. From 1998-2018, the number of muskox sightings declined in the eastern part of the survey areas. The 1989 and 1998 muskox locations have not been digitized which limits comparison, but from the survey maps, the number of groups in the 1989 high density area increased in 1998 then sharply declined from 21 to two groups in 2018.

The South Thelon survey areas (Beaverhill Lake in 2000 and Rennie Lake in 2011) south of the Thelon Game Sanctuary and Great Slave Lake, respectively were the first time those areas had been systematically surveyed for muskoxen (Table 14 and Figures 25-26). The Rennie Lake survey in 2011 was challenged by low coverage and particularly by the presence and sign of many thousands of Qamanirjuaq caribou in much of the survey area; these factors limited detection of muskoxen in the area (Williams and Adamczewski unpublished).

An index that suggests that muskox abundance has changed since the 1990s in the Thelon Game Sanctuary and south of the Sanctuary is from annual sightings along the major rivers during guided canoe trips (A. Hall, pers. comm.). The sighting rate of muskoxen/day along the Thelon, Hanbury, Baillie and Clarke rivers was entered into WMIS and reveals muskox dispersion south of the Sanctuary from 1984-2004 (Gunn et al. 2009). The rate of sightings within the Thelon Game Sanctuary (A. Hall pers. comm.) suggests an increase and then a decline in muskoxen along the major rivers (Figures 27, 28). The only systematic aerial survey of the Sanctuary was in 1994 (Shank in Gunn et al. 2009), which was about when the daily muskox sightings peaked. Rivers are often paralleled by dense willow thickets which are favored by bull muskoxen (Tener 1965) Ih might be why 61% of the 454 groups were bulls, including 142 singles from 1971-2015.

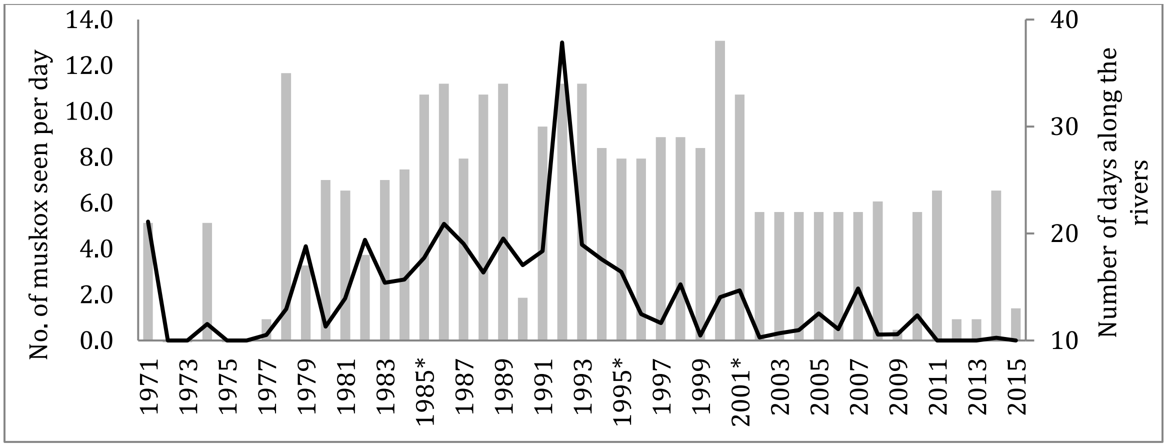

Figure 27. Sighting rate of muskoxen/day (black line) and number of days each year 1971-2015 in the Thelon Game Sanctuary (grey bars). *Includes sightings along the Bailey and Back rivers. (A. Hall, pers. comm).

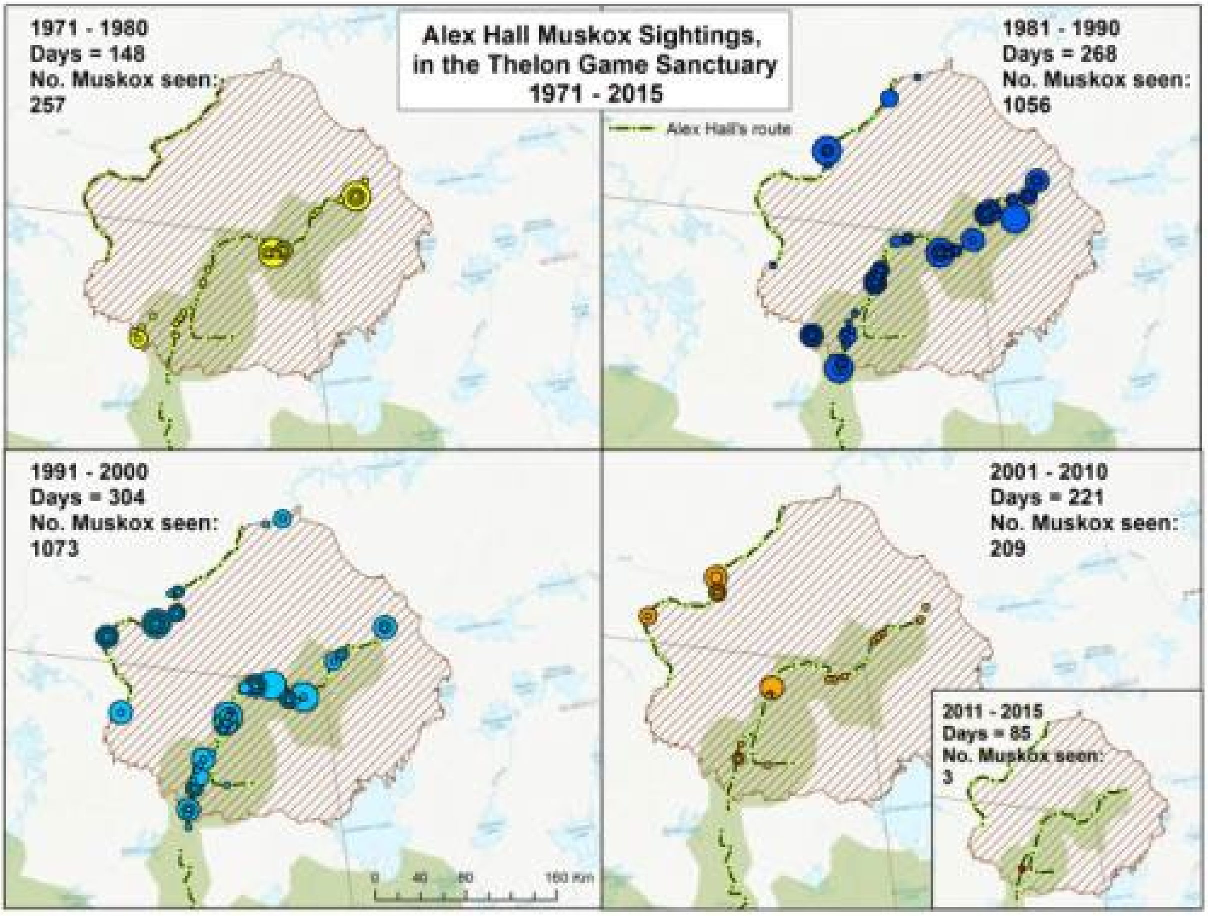

Figure 28. Alex ’all's sightings (days spent and number of muskoxen seen) along the Thelon River and Back River within the Thelon Game Sanctuary, 1971-2015. (A. Hall, pers. comm).

The mean number of days in the Sanctuary 1971-2015 was 24.6±1.11 SE (range 11-38 days) (Figure 29). The daily rate of muskox sightings was relatively low (mean 2.2±0.37 SE; range 0-13) and after 2010, no muskoxen were seen except for a group of three in 2014 (Figure 29) (A. Hall pers. comm.).

Fluctuations

On Banks Island, variations in the isotope composition of muskox bone collagen from archaeological sites revealed fluctuations over the last 4,000 years but not their periodicity or amplitude (Munizzi 2017). Inuit knowledge of muskox abundance over historic times speaks to marked historic changes in abundance on Banks and Victoria islands (Gunn 1990).

Estimates of abundance based on aerial surveys extend back to the early 1980s for the Arctic Islands (Figure 29). The timing of the peaks for Banks and NW Victoria Islands was similar (late 1990s) but amplitudes differed. This may reflect that northwest Victoria is almost half the size of Banks Island and muskoxen can disperse to and from the remainder of Victoria

Island. The timing of the peaks for the High Arctic Islands (Melville, Prince Patrick and Eglinton) differed. We identified one crash (30% reduction in a year) for 1973/1974 on Melville Island while the 62% decline on Banks was over a four-year period (2010-2014).

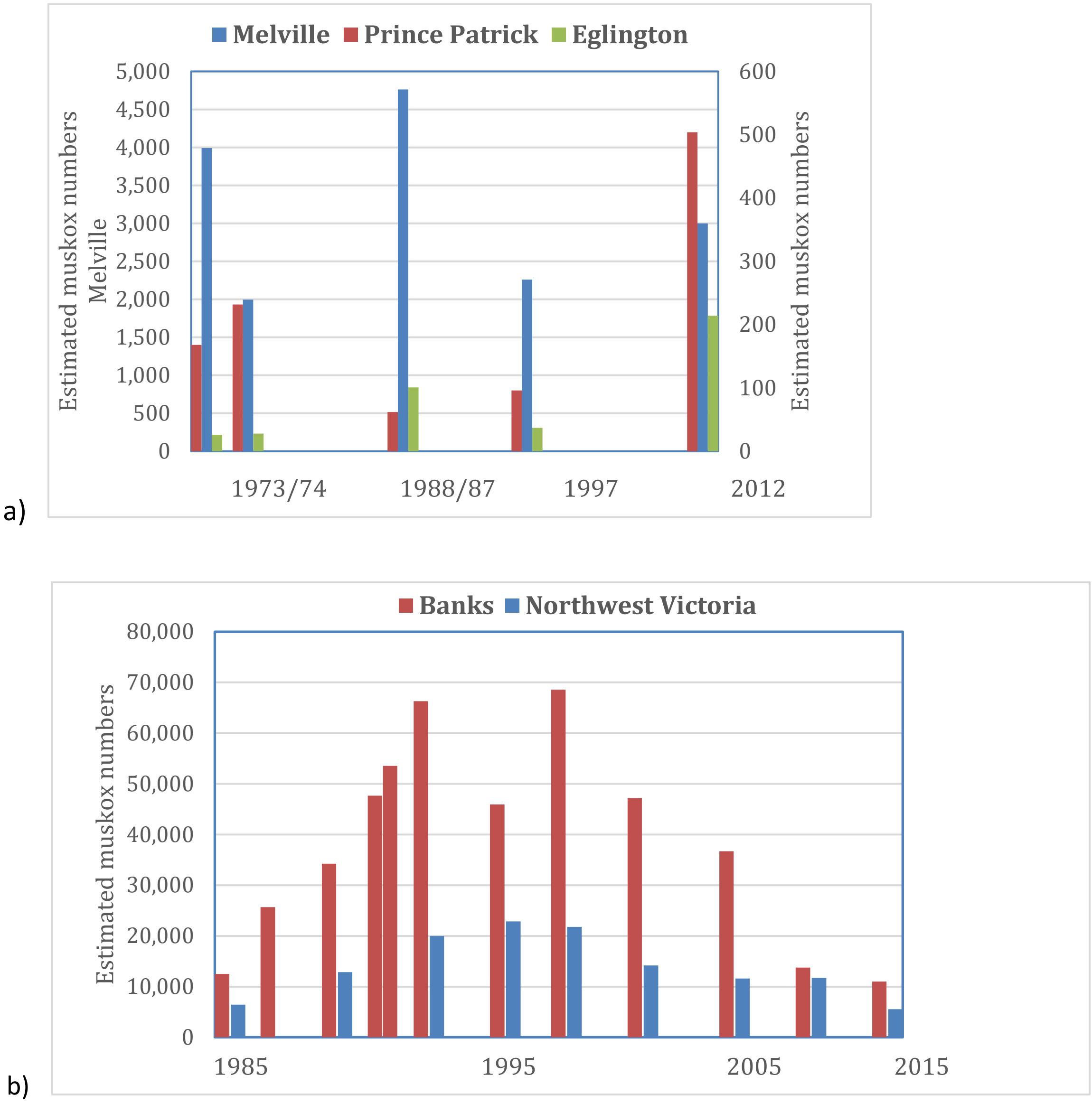

Figure 29. Fluctuations in abundance for (a) Melville, Eglinton and Prince Patrick Islands and (b) Banks and northwest Victoria Islands, NWT.

For the mainland, the five survey areas had three or fewer estimates, which restricts inferences about trends. Since historic times, trends on the mainland were collapses coincident with unregulated hunting in the late 1800s and the subsequent recovery over about 100 years (Barr 1991, this report). In the context of muskox management, the recoveries may be an irruptive oscillation after an 'introduction' or 're-introduction' of a herbivore to new or long-unused range and reveal regional differences in the timing and extent of the recoveries with consequent uncertainties about their underlying mechanisms. When muskoxen were re-introduced into Alaska and Russia, rapid increases have followed, which may be the initial stages of eruptive oscillations typical of introduced herbivores with a single eruptive peak, decline and then oscillations at a lower abundance (Caughley 1970).

Currently, we cannot distinguish whether muskox abundance regularly fluctuates or is more strongly influenced by stochastic events (e.g. non-equilibrium grazing system) and how this may differ between the Arctic Islands and the continental mainland. Given a relationship between metabolic rate, longevity and the duration of cycles in Arctic herbivores (Gunn 2003) regular fluctuations are likely. However, at higher latitudes, climate variability has an increasingly unpredictable effect on the relative length of the annual plant growth season, which may increase the likelihood of a non-equilibrium grazing system (Gunn 1992b). The recent fluctuations in muskox numbers on the High Arctic Islands have been declines coincident with extremes in weather and island scale differences which may reflect regional weather variations and dispersal. On Banks and northwest Victoria Islands, mechanisms for the declines are unclear despite intensive studies on Banks for diet, forage quality and quantity during the phase of increase. A role for predation is possible while effects of disease outbreaks are uncertain (Section 7). The studies and monitoring have not yet contributed to an underlying model essential for effective management (Bayliss and Choquenot 2002).

INTERSPECIFIC RELATIONSHIPS

Interspecific relationships of muskoxen include parasites and pathogens, as well as key predators wolves and bears. Other interspecific relationships exist because muskoxen share their ranges with small and medium-sized herbivores, of which some migrate and others are winter residents. The periodic influx of migrant herbivores (geese, caribou, ptarmigan) introduces complexity in describing their relationships with resident herbivores and with shared predators. Concerns over competition between muskoxen and caribou and potential negative effects of muskoxen on caribou have been raised in several communities in the NWT, particularly where caribou have declined and muskoxen have increased (Winbourne and Benson 2021).

Parasites and Disease

Information on muskox pathogens and parasites has recently increased, but absence of systematic surveillance hinders distinguishing between trends in disease prevalence and intensity or increasing information. Information about parasites and diseases often depends on when hunters see sick or dead muskoxen. On Victoria Island and the nearby coastal mainland (Gunn et al. 1991b), hunters' observations led to follow-up studies notably on the lungworm *Umingmakstrongylus pallikuukensis* (Kutz et al. 2001). The studies instigated a Muskox Health Research Program (University of Calgary's Faculty of Veterinary Medicine). The program is collaborative with communities and includes an innovative interview technique for hunters to document prevalence of diseased muskoxen as abundance declined (Tomaselli et al. 2018, Peacock et al. 2020). The advantage of the research program is that follow-up to hunter's reports can be prompt and detailed. Tomaselli et al. (2016) described how on southeast Victoria Island, a hunter had killed an adult bull in late August 2014 and reported lesions on its muzzle. Subsequently, a necropsy found contagious ecthyma, brucellosis and two species of nematode lung worms (*Umingmakstrongylus pallikuukensis* and *Varestrongylus eleguneniensis*). The lungworm burden was severe as the 212 nodules (0.5–5 cm in diameter) comprised 26% of the total lung weight. Yet despite the parasites and diseases, the bull had 2 cm of back-fat.

Brucellosis is infrequent in muskoxen but may be under-reported as abscesses within a bone are not found without bone sectioning (Tomaselli et al. 2016). The contagious ecthema diagnosis was also unexpected as it had not been previously confirmed in Canadian muskoxen although it was suspected in a muskox on Banks Island in the 1990s (N. Larter pers. comm.).

The finding of multiple health conditions also occurred in cases where muskox declines led to research to determine the under-lying causes. In eastern Alaska, carcass examination and serum testing from live-captured adult females in a declining muskox population identified viral and bacterial diseases and nematode parasites (Afema et al. 2017). The blood cell counts indicated a general immune response to infections and high parasite loads. Clinical signs included hoof lesions which likely increased muskox susceptibility to predation and in turn, the hoof lesions may have been related to low copper levels in the forage (Afema et al. 2017). An additional complication was that some diseases suspected of being newly introduced to North Slope muskoxen included bovine viral diarrhea, respiratory syncytial virus, *Chlamydophila* spp., *Brucella* spp., *Coxiella burnetii*, and *Leptospira* spp.

In western NU, research suggested an interaction between predation with disease and parasitism was causing declining muskox abundance. Muskox calf and adult survival was low 1989-1991 and grizzly bear predation was suspected as five of eight radio collared cows were killed by grizzly bears (Gunn and Fournier 2000). The lungworm *U. pallikuukensis* was common and likely reduced lung capacity, and probably increased muskox vulnerability to grizzly bears. Additionally, in March 1991, pregnancy rates were low (36%) as measured in 36 cows which were ear-tagged during a pilot treatment of lungworm (Gunn and Fournier 2000). Four of the ten treated cows in fall 1991 were serum positive for toxoplasmosis which was high prevalence (though based on a limited sample) compared to 6.4% prevalence across Victoria Island (Kutz et al. 2000); toxoplasmosis can reduce pregnancy rates (Kutz et al. 2000).

Hunters' reports and observations during aerial surveys have also identified disease outbreaks. Disease outbreaks were likely to be detected on Banks Island because muskoxen were commercially harvested between1987-2007. These harvests provided an opportunity to examine many carcasses. In addition the local community (Sachs Harbor) harvested for personal consumption, and aerial surveys were flown every three to five years, all of which contributed to monitoring. Five outbreaks (>50 carcasses) were detected (Table 15), although follow-up observations were limited (Mavrot et al. 2020). Extrapolating the outbreak counts to the population is difficult in the absence of any follow-up sampling, which hampers estimating a role of the outbreaks in population dynamics on Banks Island.

Table 15. Observations and sampling for muskox disease on Banks Island, 1986-2013.

Dates	Initial observation	Sampling/diagnosis	Citation
July 1986	67 fresh carcasses	20/29 sampled positive for *Yersinia*	Blake et al. al 1991
1987-9090	localized search; 72, 56, 109, 34 carcasses	88 and 86% *Yersinia* in 1987 and 1988; 23 and 35% in 1989 and 1990	McLean et al. 1993
July-Aug 1996	66-86 carcasses	12 carcasses with signs consistent with *Yersinia*; *Yersinia* not found on testing	Larter and Nagy 1999b
1997	commercial harvest	20% liver lesions consistent with *Yersinia*	Larter and Nagy 1999b
July 2004	Unsystematic aerial survey: 471 carcasses	No sampling; fall 2003 severe icing; carcasses emaciated	Nagy and Gunn 2009
July-Aug 2012	Aerial survey: 150 carcasses	7/7 sampled positive for *Erysipelothrix*	Kutz et al. al 2015
Jun-July2013	Several carcasses	2/6 sampled positive for *Erysipelothrix*	Kutz et al. al 2015

The outbreaks on Banks Island were from two bacterial diseases, yersiniosis and erysipelas. Yersiniosis was diagnosed especially during hot summers (Blake et al. 1991, McLean et al. 1993, Larter and Nagy 1999b). *Yersinia pseudotuberculosis* was first diagnosed in 1986 (Blake et al. 1991). Rates of yersiniosis varied between 1987 and 1990 when 84% of 184 carcasses were adult bulls (McLean et al. 1993). Larter and Nagy (1999b) reported an outbreak in August 1996 with 66-86 carcasses and the 12 individuals (five adult bulls) examined had signs consistent with *Yersinia,* but it was not found on testing (Table 15).

Erysipelothrix rhusiopathiae (erysipelas) was unexpected when first diagnosed on Banks (Table 12) in 2012 (Kutz et al. 2015, Mavrot et al. 2020). Subsequently, erysipelas was found in archived samples from 28 muskoxen found dead on Banks and Victoria Islands from 2009 to 2013 (Kutz et al. 2015), which triggered a retro-active testing of over 600 archived muskox serum samples (1976-2015) from across Canada and Alaska. The testing found that the disease had been present and widespread since the 1980s (Mavrot et al. 2020), which raises the possibility that it contributed to mortality events prior to 2012. Determining factors influencing when disease becomes fatal is complex; for example, erysipelas is suspected to interact with environmental variables including unusually hot summers (Kutz et al. 2015).

Warmer summers may increase stress on muskoxen and stress plays a role in the immune system, which is also affected by forage intake and forage quality such as low copper levels (Afema et al. 2017). The role of micronutrients such as copper is also summarized in Section 5 (Biology). Stress can be monitored with glucocorticosteroids levels over the immediate (Lund 1992, Harms et al. 2012) or longer-term timescales (Di Francesco et al. 2017). Qiviut cortisol levels accumulate in the hair from April to November and the qiviut is shed a year later in May-July. Cortisol levels in hunter-killed muskoxen revealed high individual and annual variability, and lower levels in summer and in females. Cortisol levels were higher for the declining muskoxen on Banks and Victoria islands than on the mainland (Di Franceso et al. 2017). Cortisol levels over a shorter timescale were measured in snow urine of muskoxen relative to changes in forage availability; increased cortisol levels were associated with reduced nutrition (Larter and Nagy 2001e).

A warmer climate is changing parasite diversity (Davidson *et al.* 2011) in the north as well as leading to changes in life-history and spread. The lungworm *U. pallikuukensis* has shifted from a two-year life cycle to a one-year cycle (Kutz et al. 2001, 2005) which likely facilitated spread of the lungworm from the Kugluktuk area of the mainland to Victoria Island (Kutz et al. 2013). While recorded for northwest Victoria Island, the lungworm has not yet been recorded for Banks Island and is absent in some portions of the NWT mainland (S. Kutz. pers. comm. 2017). *Varestrongylus eleguneniensis* is another lungworm that has recently been recognized as infecting muskoxen, and has now been found on Victoria Island, possibly introduced from the mainland by seasonal migrations of the Dolphin and Union caribou (Kutz et al. 2013). Unlike for caribou, a warmer climate will not likely increase any threat of insect harassment for muskoxen. Arthropod parasites are almost unknown for muskoxen as the muskox's thick pelage seemingly protects them from mosquitoes (Culicidae) and blackflies (Simulididae), with the exception of the eyes and nose. On Victoria Island, only three of 90 muskoxen collected in late winter had a few warble larvae (*Hypoderma tarandi*) which were undeveloped (Gunn et al. 1991b). Behavioural responses of muskoxen to biting flies in summer are highly limited compared to those of barren-ground caribou.

As well as a warmer climate affecting the parasites and disease vectors, a warmer climate has implications for heat stress and forage intake which, in turn, will modify how parasites and diseases reduce individual host fitness. Host fitness depends on the immune system, especially how the individual host either tolerates or is resistant to parasites and disease organisms. Tolerance, for example, to parasitic nematodes is an evolutionary strategy to reduce costs of immune system maintenance. Gaps remain, however, in linking a warmer climate, body condition, immune functioning and the vulnerability to diseases and parasites.

Gaps in our understanding of population responses to diseases and parasites and how the responses could change with a warmer climate can be met by changes in monitoring. This could include working more closely with hunters, especially on the mainland both where muskoxen are increasing and expanding their distribution as well as where abundance is declining. Additionally, non-invasive disease monitoring will become more important such as metabarcoding RNA in fecal samples, which for example identified gut bacteria including the genera *Erysipelothrix* and *Yersinia* in Greenland and Norway (Andersen-Ranberg et al. 2018).

Interspecific Forage Competition

Concerns about whether muskoxen compete with or displace caribou are long-standing especially in areas where muskox are returning to former range and where people have had less experience with them. People in several communities in the NWT have stated that muskoxen negatively affect caribou, although views are diverse about this relationship (Winbourne and Benson 2021). The concerns have led to scientific research in northern Canada and Alaska on whether muskoxen negatively affect caribou (or reindeer) through overlap in diet, foraging behavior and habitat selection (Parker 1978, Shank et al. 1978, Larter and Nagy 1997, Ihl and Klein 2001).

In the 1990s on Banks Island, when muskoxen were approaching peak abundance, Larter and Nagy (1997, 2001b) found that caribou and muskox diets overlapped, especially for willow (*Salix arctica*) in June, and suggested that summer availability of willow may be potentially reduced following winters when high numbers of muskoxen and arctic hares (*Lepus arcticus*) fed on willow (Larter 1999). During winters with deeper snow and density, muskoxen foraged more in upland than in low lying sedge meadows and ate more willow (Larter and Nagy 1997, 2001a). In 1993, warm temperatures and freezing rain in September led to ice layers in the snow, but muskoxen did not select areas of shallower snow because they were able to dig through snow and ice that was six times harder than where caribou cratered (Larter and Nagy 2001a). These 1990s studies on Banks Island were a baseline for annual and seasonal variability in forage availability, quality and diet during the increase and peak of muskox abundance, but they were inconclusive about competition other than the potential existed.

On the Alaskan Seward Peninsula, Ihl and Klein (2001) found that “although muskoxen and reindeer overlap in their use of feeding areas, they select forage plants differently from each other.” Recently, using a novel approach of measuring isotope signatures in bones from archaeological sites over the last 4,000 years, Munizzi (2017:310) wrote that muskoxen and caribou “have persisted on Banks Island at different times and under variable ecological conditions by capitalizing on their relative dietary flexibility to avoid forage competition”.

Predation

Initially, information on muskox predation was mostly through opportunistic field investigations rather than estimates of kill or predation rates (Tener 1965, Lent 1999). Observations from the Arctic Islands described variability of muskoxen in wolf diet; for example, 97.5% of 98 wolf scats had muskox hair at two wolf dens on northern Ellesmere (B. Troke *in* Marquard-Petersen 1998). In contrast, in the early 1950s, 16.7% of 85 wolf scats had muskox remains compared to 83.3% with Arctic hare remains on western Ellesmere Island (Tener 1952). However, Tener (1954) also commented that wolf kills were ‘many’ of the 28 muskox carcasses opportunistically examined, and Freeman (1971) recorded that half of 16 non-calf carcasses on Devon Island were likely wolf kills. On the mainland (Thelon Game Sanctuary), Kuyt (1972) commented that muskoxen were infrequently identified in wolf scats (19 of 595 scats collected 1960-1965).

More recently, GPS collars on wolves were used to estimate kill and predation rates. Anderson et al. (2019) estimated that wolves annually killed 6.5-13.3% of muskoxen on central Ellesmere Island and eastern Axel Heiberg Island in Nunavut. The predation rate was estimated from a wolf kill rate based on clustered locations of GPS collared wolves, wolf density (seven adult wolves/1,000 km^2) and muskox density (30-61.4 muskoxen/1000 km^2). Anderson et al. (2019) examined carcasses at the cluster locations and found 14 muskox calves among the 39 muskox kills in 2017/2018. The kill rate was about one adult muskox killed/eight days for a pack of four wolves. Anderson et al. (2019) indicated that wolves also rely on other prey in this area, most likely arctic hares.

Anderson et al.’s (2019) estimated wolf predation rate for Ellesmere Island may be applicable elsewhere, especially on Banks Island. In 2005, the densities of wolves and muskoxen in the Thompson valley were similar to those recorded on western Ellesmere where Anderson et al. (2019) estimated an annual predation rate of 6-13% of the muskoxen. Supporting evidence on Banks Island about the importance of wolf predation is that muskox remains were found in 90% of 115 wolf stomachs from hunter-killed wolves and 87% of 38 opportunistically collected wolf scats from 1992-2001 (Larter 2013) on Banks Island, while on northwest Victoria Island, muskox remains were in 88% of 27 stomachs (1998-2001). On northern Banks, only 10% of 187 carcasses examined were wolf kills during 1987-1990 (McLean et al. (1993). However, the numbers of wolves and sighting rates were low in the late 1980s and increased during the 1990s (Table 16). Wolf harvests were <10 wolves annually from 1988-1989 to 1991-1992, but 50 wolves were harvested in winter 1992-93 (Larter and Clarkson, 1994 cited in Nagy et al. 1996).

Table 16. Numbers of wolves seen and sighting rates during aerial surveys on Banks and northwest Victoria islands, 1985-2014.

Year	Banks Island				Northwest Victoria Island		
	Total hours[1]	Adult wolves	Pups	Sighting rates/100h	Total hours[1]	Wolves	Sighting rates/100h
1985		13					
1987		0					
1989		8	5				
1992		2		1.5			
1994		23		17.7			
1998		26		20.0		5	6.4
2001		40		30.8		11	11.0
2005		28		21.5	78	12	15.4
2010	127	28	6	22.0	100	18	23.1
2014/2015	130	15		11.5	100	16	16.0

[1] Survey hours were not reported except in 2010 and 2014 and because island coverage is similar, those average hours were used to estimate sighting rates.

Comparing the trend in muskox abundance to wolf sightings on Banks Island suggests wolf numbers increased after the peak in muskox abundance (Figure 30a) although we acknowledge uncertainties in the wolf sightings as to the consistency of sampling effort. The exponential rate of change (%) is negatively related to wolf sightings and exponential trend in the muskox population (Figure 30b). The wolf sighting rate vs exponential rate of change for both Banks and Victoria Islands is for one survey lag for the rate of change and sample size is a limitation (K. Chan pers. comm. 2020). Calf productivity was positively but weakly related to population trend (r^2= 0.24, p=0.50) and the relationship between calf productivity and wolf sightings was weak (r^2= 0.16, p=0.60).

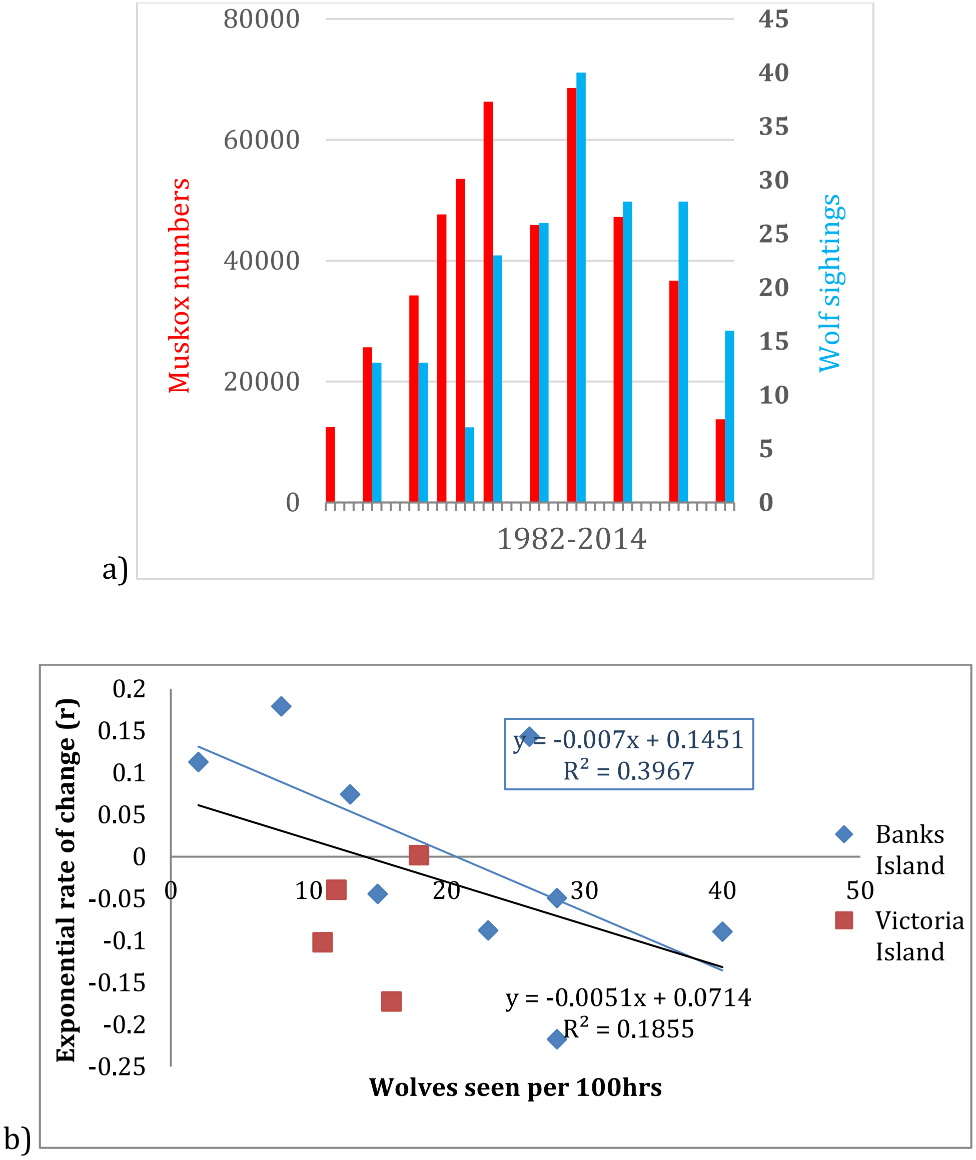

Figure 30. (a) Wolf sighting rates versus muskox abundance and (b) muskox exponential rate of change regressed against wolf sighting rate (lagged one year) for Banks and northwest Victoria Islands: blue line is Banks and black line is both Banks and Victoria Islands.

In the NWT, observations of grizzly bear predation on muskoxen suggested the potential for bear predation to be a factor (Gunn and Miller 1982, Case and Stevenson 1991, Clarkson and Liepins 1993, Gunn and Fournier 2000, Dumond 2006). Grizzly bear predation on muskoxen may increase on islands such as Banks and Victoria as bear sightings there are increasing (Tomaselli et al. 2018, Species at Risk Committee 2017). On the mainland, bear sighting rates within muskox distribution are few as only five of 16 aerial surveys were summer surveys when grizzly bears are active. Sightings on the mainland's northwest region were annually variable (Table 17) and the bears were relatively numerous as they have access to caribou calving and summer-fall ranges and possibly beached whales (Species at Risk Committee 2017). Grizzly bear sightings were higher than wolf sightings on the western caribou calving grounds, at least in 2007 and 2008 when systematic surveys were conducted across eight calving grounds in NWT and NU (Poole et al 2014) and muskox distribution overlaps the caribou calving grounds.

Table 17. Sighting rates of grizzly bears during aerial surveys, mainland NWT.

		bears/100 hours	
1994 July	Thelon Game Sanctuary	3	Gunn et al. 2009
2000 July	Beaverhill Lake	9	
2002 May	Tuktut Nogait National Park area	30	Nagy et al. 2013c
2002, 2003, 2004 June	Tuktut Nogait National Park area	11, 18, 26	Nagy and Johnson 2007
2007 May	Tuktut Nogait National Park area	33	Dumond 2007

Grizzly bear densities on NWT muskox ranges are variable and appear to be higher in the west toward the Mackenzie River. Boulanger and Branigan (2017) estimated 9.7 bears/1,000 km^2 (CI=6.7-18.4) in 2013 and 2014 for the area surrounding the Inuvik to Tuktoyaktuk Highway. In 2008-2009, Dumond et al. (2015) used DNA mark-recapture to estimate about six bears/1,000 km^2 for the northwest coastal area including Kugluktuk.

Estimates of grizzly bear kill and predation rates are currently limited to radio collared muskoxen on the Alaska North Slope, which revealed a high rate of grizzly bear predation and suggested that some individual bears specialized in muskox predation (Arthur and Del Vecchio 2017, Reynolds et al. 2002a). The muskoxen had been introduced to the area in the 1970s, abundance initially increased and by 1982, grizzly bear predation was observed (Reynolds et al. 2002b). Between 1982 and 2001, the number of grizzly bear-killed muskoxen increased mostly due to multiple kills (Reynolds et al. 2002a). Muskox abundance declined after 1999 which triggered studies into the cause of the decline. Between 2007 and 2011, grizzly bears were the proximate cause of death for 62% of adult cows and 58% of muskox calves in cases where cause of death could be assigned. A further 11% of calf mortality was abandonment, possibly when a bear attack scattered the muskox herd (Arthur and Del Vecchio 2017). In a separate study (Afema et al. 2017), six of ten grizzly-bear killed muskoxen also had underlying health problems such as hoof lesions, suggesting compensatory predation. On the northwest mainland adjacent to the NT/NU boundary and Kugluktuk, grizzly bear predation was a likely factor in declining muskox abundance between 1987-2007 (Gunn and Fournier 2000, Dumond 2007), kill and predation rates were not estimated.

While the northeast Alaskan example suggests that as muskoxen colonize NWT mainland grizzly predation could increase, there are uncertainties. The presence of alternate prey such as caribou and moose will affect kill and predation rates of muskoxen. Potentially, muskoxen may subsidize predation rates on caribou (i.e., muskoxen as an alternate prey may support more wolves in a two-prey system) but the effect will depend on the relative densities of the prey species. Alternatively, a decline in caribou, if it led to a decline in wolf abundance as happened on the Bathurst herd's summer range (Klaczek 2015), may reduce predation on muskoxen. The high productivity and high survival of calves and adults in muskoxen on the southeast mainland (Adamczewski et al. 2021) is coincident with declines in the Beverly herd (Adamczewski et al. 2015). Additionally, the Bathurst herd has not wintered in the vicinity of eastern Great Slave Lake since 2006 (Adamczewski et al. 2015, Virgl et al. 2017). Wolf and grizzly bear sightings declined in and south of the Thelon Game Sanctuary (A. Hall pers. comm.) and the change in the Bathurst herd may have limited any winter incursion of wolves to the eastern Great Slave Lake area and reduced predation on muskoxen. In recent years (2016-2020), based on satellite collared caribou, the only barren-ground caribou herd wintering east and south of Great Slave Lake has been a portion of the Qamanirjuaq herd south and east of Artillery Lake (M. Campbell, Government of NU, pers. comm. 2021). The herd's winter distribution includes northern Manitoba, southeastern NU and into the southeastern NWT.

ACCIDENTS AND TRAUMA

Recorded accidents causing mortality in muskoxen include muskoxen becoming marooned on islands in lakes (Griller 2001, Cluff et al. 2009) or breaking through thin lake ice and drowning (Lenart 2015). Freezing rain, leading to reduced forage availability in early winter 2003, resulted in muskoxen moving onto the sea ice off Banks Island and presumably dying (Nagy and Gunn 2009). On Nunivak Island in Alaska muskoxen occasionally leave and become stranded on drifting sea-ice (Patten 1997). Other accidents including freezing rain binding muskoxen to the ground (Vibe 1967, P. Groves pers. comm.) and injuries during the rut (Wilkinson and Shank 1976) are known to occur, but typically accidents involve individuals and do not have population-scale effects.

Tooth breakage

Tooth breakage and jaw pathology (Henrichsen and Dieterich 1984) are potential indicators of poor muskox health, although the current baseline information is restricted to Victoria Island and the neighboring mainland. Forage intake and rumination depend on bite size and healthy teeth, which can affect reproduction, growth and survival (Parker et al. 2009). Bite size is dependent on dental morphology and oral anatomy. Many muskoxen monitored 1989-1991 and 2015-2016 had broken or cracked incisors (F. Mavrot, in prep., Gunn and Lee in prep.). While the implications and causes of the tooth damage are uncertain, low micro-nutrient levels, especially copper, and changing mechanical forces from browsing on larger diameter twigs are possible causes (Clough et al. 2010). The larger twigs may be a response to the warming climate (Forbes et al. 2010). The frequency of incisor damage is likely an indicator for potential changes in forage intake.

Contaminants

Currently, there are gaps in assessing contaminants in muskoxen; an example was from southern Victoria Island in the early 1990s (Salisbury et al. 1992). Migratory tundra caribou herds share the mainland ranges of muskoxen but the exposure of muskoxen to aerial contaminants may be lower than for caribou as caribou diet frequently includes lichens and mushrooms, which are known for their propensity to take up contaminants. Mushrooms are not mentioned in accounts of muskox diets and the role of lichens is ambiguous (Section 5 Biology).

CLIMATE AND CLIMATE CHANGE

Effects of Climate

Climate is a driving influence in muskox ecology through interactions with plant growth and availability and exposure to parasites and predators. Muskoxen, through their nutritional ecology, are resilient to annual variation in forage availability (Schaefer and Messier 1995a, Larter and Nagy 2001b), however, analyses of muskoxen and climate are largely lacking.

Banks Island on the eastern edge of the Beaufort Sea is subject to fall incursions of warm, moist Pacific air masses periodically causing rain freezing as ice within or on snow-covered ground (Rennert et al. 2009). The resulting extremes in ground fast icing and deep snow restrict access to forage. Between 1986 and 1999, calf survival and recruitment were low following two consecutive severe winters (defined as having freezing rains in early winter sufficient to cause die-offs of caribou, Larter and Nagy 1994, 2001c). During increasing and peak abundance phases on Banks Island (1993-1998), muskox density explained more variation in survival and recruitment than late-winter snow depth measured in wet sedge meadows (Larter and Nagy 2001c).

On the western Queen Elizabeth Islands, Octobers with deeper than normal snowfall and freezing rain correlated with reduced productivity and adult deaths in muskoxen in 1973-1974, 1985-1986 and 1996-1997 (Miller et al. 1977, Miller 1987, Gunn and Dragon 2002). Winter 1985-1986 had exceptional snowfall and multiple days with freezing rain in early winter; this may have caused muskoxen to move from Prince Patrick Island to Eglinton Island where their calves survived, although at a low rate, while muskoxen remaining on Prince Patrick had no calves (Miller 1987). On Prince Patrick Island, snowfall in September 1996 totaled 46.6 cm (1950-1989 mean is 14.9±10.3 [SD]) and only two calves were seen in summer 1997 on Melville Island and none on Prince Patrick Island (Gunn and Dragon 2002).

The frequency of extreme weather events for muskoxen and defining an extreme relative to muskox ecology are currently not well described. An additional limitation is detecting trends when annual variability in weather is high. For example, based on the MERRA climate database extends from 1980 to 2018, trends in October snow depth on Banks Island were not detectable as annual variability (CV) was high and increased from 20% to 60%. Extreme years with deep early snow were 1993, 2003 and 2008.

Although emphasis has been on how winter conditions affect the relative availability of forage, timing of snow melt and the onset of plant growth are also factors affecting muskox condition. From the MERRA baseline climate data (Russell et al. 2013), the onset and end of the plant growth season is annually variable as indexed by plant growing degree days (GDD, cumulative days) on Banks Island (Table 18). The beginning of the season (the date when

GDD10 was reached) and the end of the season (GDD 10-20 August) had high variation while the earlier plant growth started, the higher the maximum for the year.

Table 18. Mean and variability in the growing season as indexed by GDD for Banks Island (MERRA data 1980-2018). GDD10, GDD100, and GDD250 are days after May 29 when the number of growing degree days exceeded 10, 100, and 250 respectively[1]. GDDMax represents the maximum number of growing degree days measured between 1980-2018. GDD 10-20 August represents the end of the growing season.

	GDD10[9]	GDD100	GDD250	GDDMax	GDD 10-20 August
Mean	14.23	31.13	76.95	472.72	39
Standard Deviation	6.16	5.55	9.69	104.84	18.9
Coefficient of Variation	43.27	17.83	12.60	22.18	49

[1] Growing degrees (GDs) is a cumulative term as the number of temperature degrees above a certain threshold base temperature (0^0c) and is calculated as GDD = (T_{max}+T_{min}/2)-T_{base}.

High summer temperatures can stress muskoxen, especially in the absence of shade on the tundra. Muskox behavioural responses to heat stress are unknown except in captivity where muskoxen sought water pools (P. Flood unpubl.). The thermo-neutral range has not been measured for adult muskoxen (Munn and Barboza 2008), but higher temperatures (>20°C) reduce appetite and food absorption associated with shutdown of rumen bacteria (R. G. White, pers. comm. 2016). Panting is a cooling mechanism but increases water intake. Increased respiration rate and volume may increase exposure to pathogens, which would be accentuated by heat-stress, thus reducing immune function (Reinhold and Elmer 2002 cited in Ytrehus et al. 2015).

Another sign of increasingly warmer summers on Banks Island is that the years with the highest number of June and August days >20°C were in 2007, 2011, and 2013 (Figure 31), although the likely stress associated with outbreaks of diseases on Banks Island was recorded in 1986, 1996 and 2012. Warmer temperatures contribute to higher evapotranspiration which can limit plant growth for the upland plant communities which muskoxen may use in winter. On Banks Island, Larter and Nagy (2001b) reported that crude protein levels in sedges varied between wet and dry years.

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[9] We determined the dates (days after May 29) when the GDD first exceed 10 and 100.

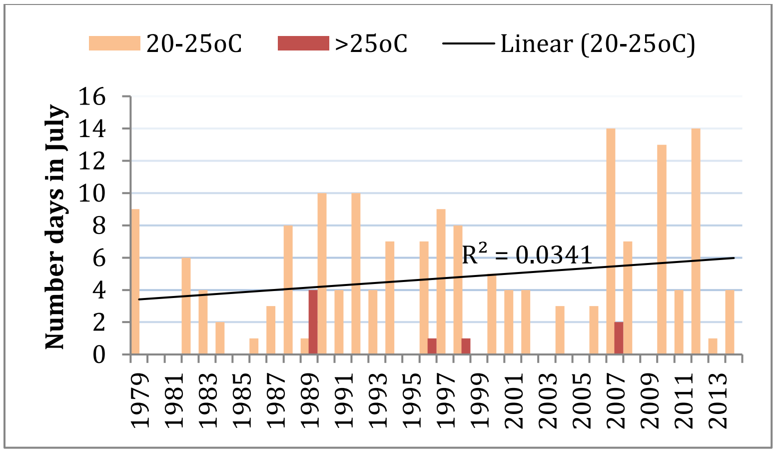

Figure 31. Number of days in July with daily maximum temperatures of more than 20°C and 25°C, Banks Island, 1979-2014 (MERRA data from CARMA).

Climate Change

While global signals for a warmer Arctic climate are strong, they vary regionally (Bhatt et al. 2017). Global warming is so far reaching that it will change muskox habitat, demography and distribution but relatively little has been reported to explore muskox vulnerability to the likely changes. An exception is concerns for disease as a trend toward warmer summers will modify conditions for parasites and diseases with complex and cascading effects (Kutz et al. 2009, Davidson et al. 2011, Ytrehus et al. 2015). In particular, the complex disease syndrome related to stress includes warmer summers during declines in Alaska and NT/NU (Mavrot et al. 2020). Changes in forage quality as well as quantity are almost a certainty. For example, experimental warming increased phenolic content of the tussock cotton-grass *Eriophorum vaginatum* by 38%, reducing forage quality on tundra in central NWT (Zamin et al. 2017). However, what is less certain is how, and to what extent, muskoxen can adapt to changes among the different forage species and can compensate by changes in diet selection.

The muskox's large body mass and dark pelage increase the likelihood of thermal stress especially during summer or exertion. The extent of behavioural plasticity such as reduced activity (movement and foraging) or seeking thermal cover (water and/or shade) to help muskoxen cope with rising temperatures is uncertain especially relative to habitat selection at different scales. Muskoxen found south of treeline in the boreal forest may be affected differently from those on the tundra.

MANAGEMENT AND HARVESTING

Co-management

Within the NWT, muskox spatial distribution encompasses four settled land claim settlement areas, territorial boundaries, and large areas in the southern NWT with unresolved land claims. The Inuvialuit Settlement Region is home to the first co-management authority in the NWT in 1984 and an analysis of Inuvialuit management for caribou and beluga revealed successful governance of large-scale common-pool resources (Tyson 2017). The Inuvialuit Settlement Region includes muskoxen on the western Arctic Islands and the northwest mainland and has developed management plans (Nagy et al. 1998). The muskoxen shared with the Yukon are included in the Wildlife Management Advisory Council (North Slope) 2017 management framework and 2019 research plans. Muskoxen north of Great Bear Lake also are within the jurisdiction of the Gwich'in and Sahtú land claim settlement areas and associated co-management boards. Muskoxen in the central and southeastern NWT are within the boundaries of the Wek'èezhìı Renewable Resource Board (Tłįchǫ land claim), and within asserted territories and areas of unsettled claims of the Akaitcho Government, the North Slave Métis Alliance, the NWT Métis Nation and the Athabasca Denesuline. Co-management of muskoxen may become a priority for each of these areas and Indigenous governments and Indigenous organizations. The Advisory Committee for Cooperation on Wildlife Management is a group made up of the chairs of a number of co-management boards in the NWT and NU; this group has been concerned with declines in three barren-ground caribou herds and may, in future, focus on muskoxen.

Harvesting

Hunting muskoxen has been part of Indigenous cultures in northern Canada and Alaska for thousands of years (Lent 1999) and on Banks Island, for example, muskox hunting dates back to the pre-Dorset period 4,000 years ago. The archaeological record suggests three to five records of heavy muskox utilization on Banks Island in the pre-Dorset period (Hahn 1977 cited in Lent 1999) and then during the 17th-19th century Inuinnait occupation (Hodgetts 2013, Munizzi 2017).

By the mid-20th century, recovery in muskox abundance in the NWT (then still including NU) led to recognition that the suspension of harvesting should be lifted (Lent 1999). The government's objectives for setting harvest levels were initially conservative and were based on community quotas. However, increasing muskox numbers on Banks and Victoria Islands in the early 1980s led to increased quotas for meat, hide and qiviut sales partly to forestall a predicted crash (Gunn et al. 1991a, Nagy 2004). On Banks Island, the average commercial harvest was 124 muskoxen/year (range 0-260) for 1980-1990. In 1991, the quota increased to 5,000 and large-scale harvesting started with 2,525 muskoxen harvested on southwest Banks (Nagy et al. 1996). However, this level of harvest was rarely achieved and in more recent years, the scarcity of muskoxen on southern Banks Island, near the only community of Sachs Harbour, has meant that no commercial harvests have taken place.

In 2021, for most of the NWT, Aboriginal harvest of muskoxen is not limited but harvest levels are generally low due to negative perceptions of muskoxen and in some areas, lost traditions of hunting muskoxen from a long period when muskoxen were scarce and hunting was prohibited (Winbourne and Benson 2021).

Current NWT regulations list seasons for resident and non-resident hunters with quotas on Melville Island, Banks Island, northwest Victoria Island, and four areas on the mainland (Table 19, Figure 32). The regulations list seasons which generally are closed during calving (except year-round I/MX/05, northwest mainland) and other restrictions include that a hunter must not knowingly approach by vehicle (including a snowmobile or all-terrain vehicle) any closer than 1.5 km to the muskoxen.

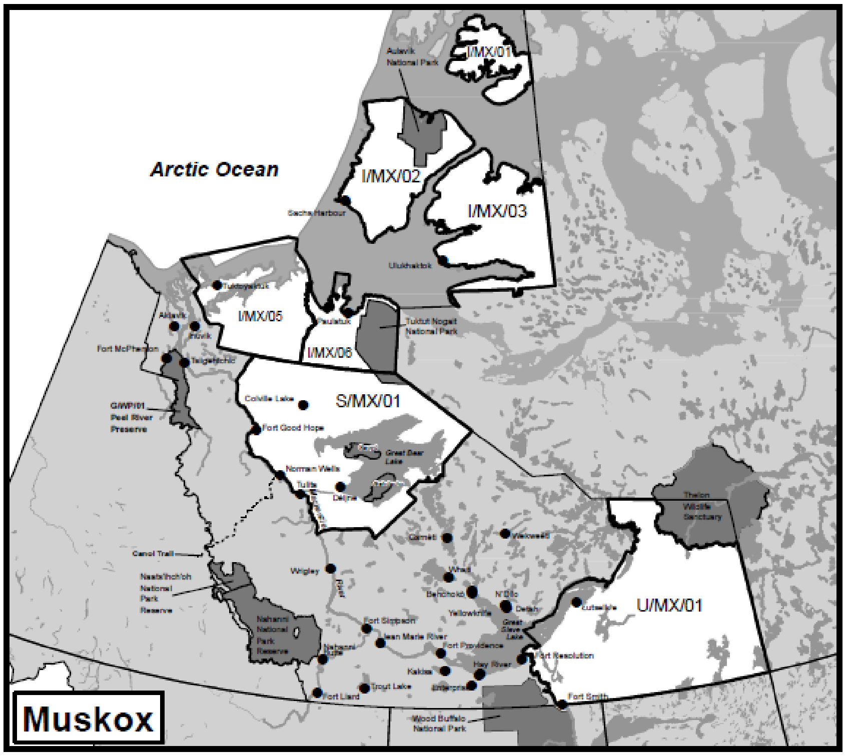

Figure 32. GNWT-ECC hunting zones for muskoxen, 2019. www.enr.gov.nt.ca/sites/enr/files/resources/3512-gnwt-enr-hunting_reg_2019_en-web.pdf

Table 19. Inuvialuit muskox harvests, 2000-2011 (GNWT unpubl. data). Quotas are in parentheses.

Community and quota	2000-2001	2001-2002	2002-2003	2003-2004	2004-2005	2006-2007	2007-2008	2008-2009	2009-2010	2010-2011
Melville (12)	0									
Banks (10,000)	192	887	228	122	131	116	419	395	60	90
NW Victoria (1,000)	346	420	384	479	240	244	208	270	211	217
Paulatuk (50)	52	32	34	22	23	27	14	32	20	10
Tuktoyaktuk (25)						27	14	32	20	10

The Inuvialuit Settlement Region has Community Conservation Plans which guide land use planning and identify important habitats and an approach for the use of those habitats. In addition, muskox ranges are within Aulavik National Park (Parks Canada. 2010), Tuktut Nogait National Park and Thaidene Nëné National Park Reserve.

CONCLUSIONS

The overall 2019 estimate of muskoxen in the NWT was approximately 34,000 adult muskoxen, which is a 55% decline from the 86,000 muskoxen estimated in 1998. The overall declining trend for muskoxen in the NWT is weighted by the steep decline of key populations on the southern Arctic Islands of Banks and northwestern Victoria. The aerial survey frequency and coverage to estimate muskox abundance is sufficient to measure the trend for those two island populations. The northwestern High Arctic islands have a low survey frequency but results suggest an overall recovery from earlier crashes in the 1990s.

Surveys on the mainland NWT reveal muskoxen returning to historic distribution patterns observed prior to the unregulated commercial overharvesting in the late 1800s that reduced muskoxen to scattered refugia in the early 1900s. Muskoxen have re-established historic ranges in the boreal forest and are known at least as far south as the AB and SK borders. Describing recent trends in muskox abundance on the mainland is hampered by low survey frequency, low coverage and changing survey areas. Regionally, survey areas have progressively tracked the colonizing edge rather than areas previously surveyed.

Limited investigations and infrequent monitoring to estimate demographic mechanisms (adult and calf survival, fecundity and dispersal) are insufficient to fully understand factors driving either increasing or declining abundance in the NWT. The increasing trends on the mainland and recolonization are usually initially characterized by high productivity and survival rates. However, recolonization has in some areas been slow and regionally uneven and the causes are uncertain.

Among the factors driving declines are likely predation together with disease outbreaks and environmental stress (such as hot summers) based on evidence from Alaska, NWT and NU. Low calf percentages observed on multiple aerial surveys may reflect a combination of low pregnancy rates and high calf vulnerability to predators. Scarcity of micro-nutrients like selenium and copper can affect health and productivity. Harvest rates of muskoxen across the NWT have generally been low, in part due to negative perceptions of muskoxen and in some regions due to lost hunting traditions.

The question of whether caribou (or reindeer) and muskoxen compete has consistently driven research across the Yukon, NWT, NU and northern Québec wherever a recolonizing muskox distribution or increasing muskox abundance brings them onto caribou ranges, particularly where caribou numbers have declined. An intensive study on Banks Island in the 1990s occurred when muskox numbers were peaking but caribou had been in a long-term decline and suggested limited seasonal overlap in diets and range use. Other scientific evidence has generally also suggested limited overlap in range use of muskoxen and caribou, and they have co-existed for thousands of years through multiple ice ages. There are strong perceptions of muskoxen having a negative effect on caribou in some communities in central and southern NWT communities, though less so in the northern NWT.

The long-term picture of muskoxen has been that they are resilient and adaptable and have survived the abrupt switches during inter-glacial and glacial periods. However, as the current climate heats up, diseases and habitat changes may increase muskox vulnerability to poor health and declines, and potentially to predation. Our review finds that technical information as a basis for management planning is uneven across the NWT regions and over the previous 20-30 years.

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[10] In 2023 the GNWT Department Environment and Natural Resources (ENR) was re-named Environment and Climate Change.

PERSONAL COMMUNICATIONS

Vincent Brodeur, Wildlife Division, Government of Quebec.

Mitch Campbell, Department of Environment, Government of Nunavut

Kevin Chan, Environment and Climate Change, Government of Northwest Territories.

Karin Clark, Environment and Climate Change, Government of Northwest Territories.

Dean Cluff, Environment and Climate Change, Government of Northwest Territories.

Tracy Davison, Environment and Climate Change, Government of Northwest Territories.

Pam Groves, University of Alaska, Fairbanks, Alaska

Late Alex Hall, Fort Smith.

Nic Larter, Environment and Climate Change, Government of Northwest Territories.

Susan Kutz, University of Calgary.

Cristine Rock, Dominion Diamond, Ekati Mine.

Don Russell, Whitehorse.

Mike Suitor, Department of Environment, Government of Yukon.

Robert G. White, University of Alaska, Fairbanks.

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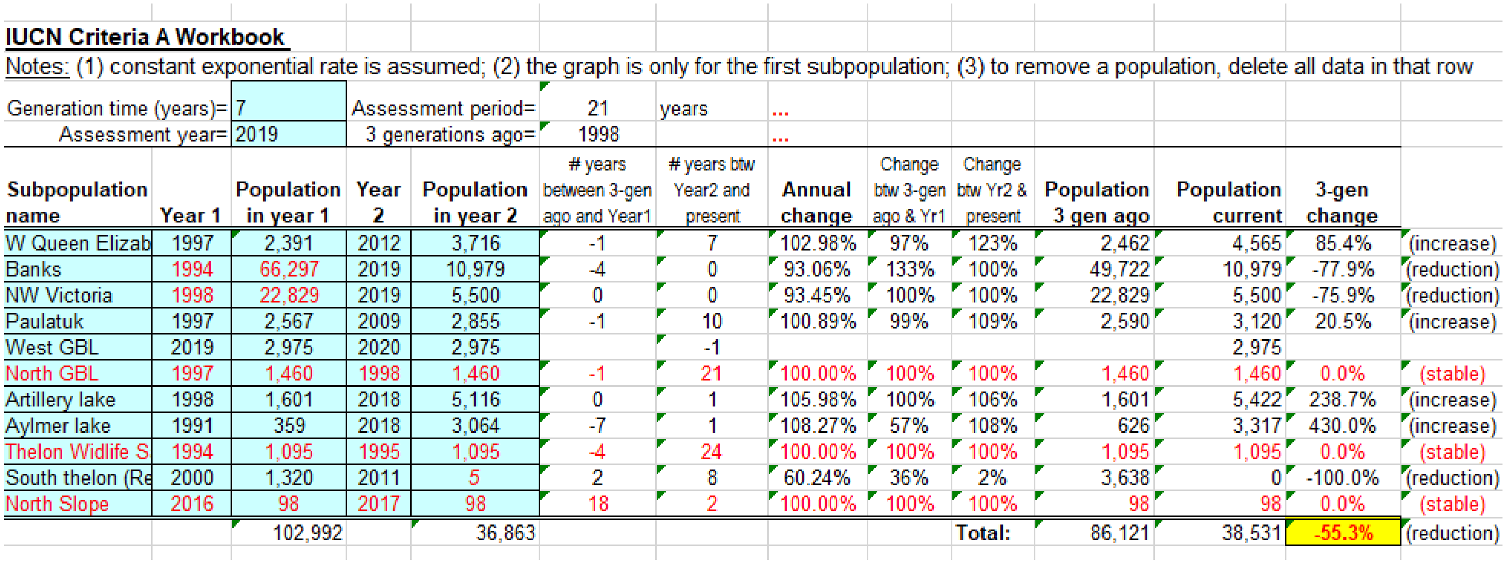
APPENDIX A. TRENDS IN REGIONAL ABUNDANCE FOR THREE GENERATIONS FOLLOWING INTERNATIONAL UNION FOR CONSERVATION OF NATURE RED LIST GUIDELINES

https://nc.iucnredlist.org/redlist/content/attachment_files/CriterionA_Workbook_13112018.xls



IUCN Criteria A Workbook

Notes: (1) constant exponential rate is assumed; (2) the graph is only for the first subpopulation; (3) to remove a population, delete all data in that row

Generation time (years)= 7 Assessment period= 21 years ...

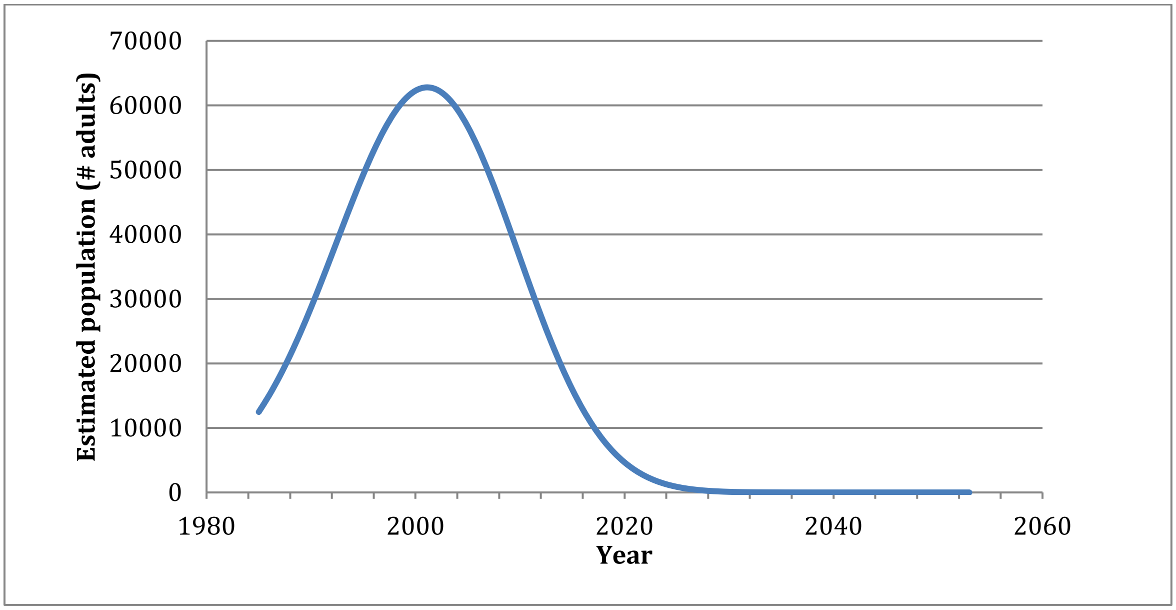
Assessment year= 2019 3 generations ago= 1998 ...

Subpopulation name	Year 1	Population in year 1	Year 2	Population in year 2	# years between 3-gen ago and Year1	# years btw Year2 and present	Annual change	Change btw 3-gen ago & Yr1	Change btw Yr2 & present	Population 3 gen ago	Population current	3-gen change	
W Queen Elizab	1997	2,391	2012	3,716	-1	7	102.98%	97%	123%	2,462	4,565	85.4%	(increase)
Banks	1994	66,297	2019	10,979	-4	0	93.06%	133%	100%	49,722	10,979	-77.9%	(reduction)
NW Victoria	1998	22,829	2019	5,500	0	0	93.45%	100%	100%	22,829	5,500	-75.9%	(reduction)
Paulatuk	1997	2,567	2009	2,855	-1	10	100.89%	99%	109%	2,590	3,120	20.5%	(increase)
West GBL	2019	2,975	2020	2,975		-1					2,975		
North GBL	1997	1,460	1998	1,460	-1	21	100.00%	100%	100%	1,460	1,460	0.0%	(stable)
Artillery lake	1998	1,601	2018	5,116	0	1	105.98%	100%	106%	1,601	5,422	238.7%	(increase)
Aylmer lake	1991	359	2018	3,064	-7	1	108.27%	57%	108%	626	3,317	430.0%	(increase)
Thelon Widlife S	1994	1,095	1995	1,095	-4	24	100.00%	100%	100%	1,095	1,095	0.0%	(stable)
South thelon (Re	2000	1,320	2011	5	2	8	60.24%	36%	2%	3,638	0	-100.0%	(reduction)
North Slope	2016	98	2017	98	18	2	100.00%	100%	100%	98	98	0.0%	(stable)
		102,992		36,863					**Total:**	86,121	38,531	-55.3%	(reduction)

APPENDIX B. EXPONENTIAL RATE OF INCREASE FOR BANKS AND NORTHWEST VICTORIA ISLANDS RELATIVE TO WOLF SIGHTINGS DURING AERIAL SURVEYS

(K. Chan pers. comm. 2020).

Estimated population of adults on Banks Island based on the trendline analysis in Figure 23.

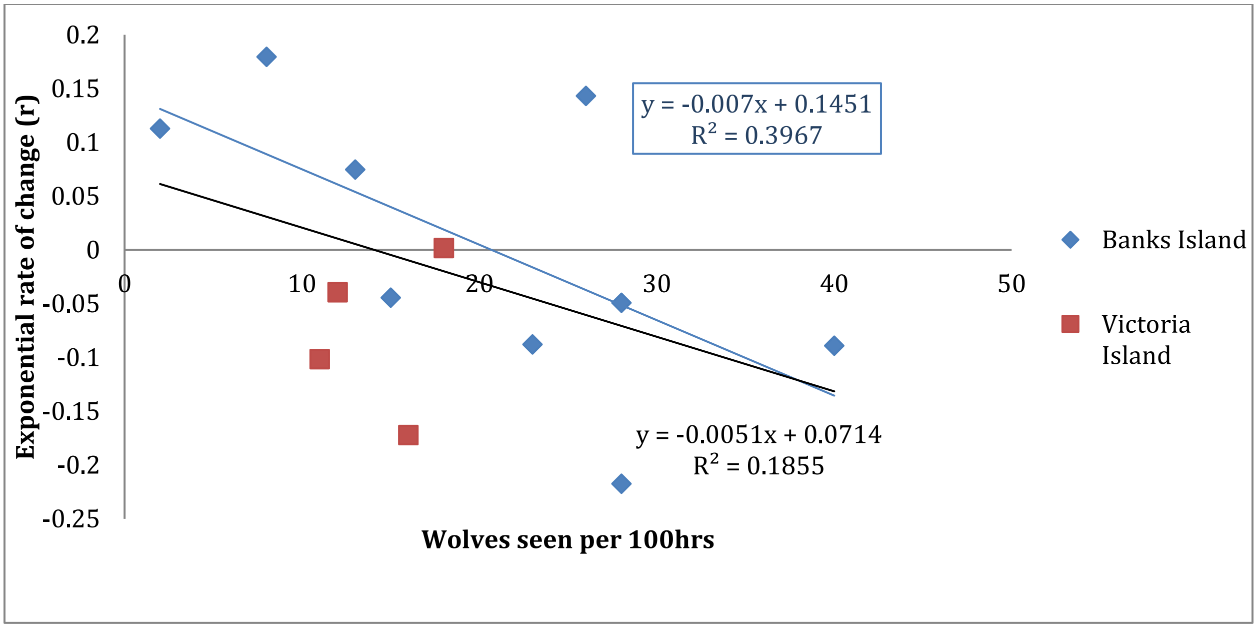


These are the r values calculated for Banks Island using the equation presented in the methods.

Year	**Muskox**	**t**	**r**	**Wolves**
1982	12,481			
1985	25,700	3	0.272217	13
1989	34,270	4	0.074596	8
1991	47,670	2	0.179412	
1992	53,526	1	0.122845	2
1994	66,297	2	0.112922	23
1998	45,922	4	-0.08771	26
2001	68,585	3	0.143061	40
2005	47,209	4	-0.08915	28
2010	36,676	5	-0.04924	28
2014	13,767	4	-0.21727	15
2019	10,979	5	-0.04425	

These are for Victoria Island (adjusted as wolf sightings for Victoria Island are 2014 rather than 2015).

Year	**Muskox**	**t**	**r**	**Wolves**
1998	22,829			5
2001	21,756	3	-0.01592	11
2005	14,170	4	-0.10165	12
2010	11,602	5	-0.0392	18
2015	11,708	5	0.001821	16
2019	5,500	4	-0.17212	



Exponential rate r vs. wolf sighting rate for both Banks and Victoria Island with a one survey lag for the rate of change. In other words, the wolf densities from the previous survey are matched with the rate of change from the subsequent survey. The blue trendline is for the Banks Island data while the black trendline is for data from both Banks and Victoria Islands.