Final Wildlife Research Report, ADF&G/DWC/WRR-2013-1

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Alaska Department of Fish and Game Division of Wildlife Conservation

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Cover Photos: (front) Muskox at Milne Point, April 2008, photo by Stephen M. Arthur;
(back) Muskox near Sagwon Bluff, August 2008, photo by Patricia A. Del Vecchio.

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Summary

From 2007 to 2011 we investigated potential factors that might be limiting growth of the muskox (*Ovibos moschatus*) population in northeast Alaska. Annual counts of muskox abundance ($\bar{x}$ = 191) and estimates of population growth rate ($\bar{x}$ = 0.96) indicated a stable or slowly declining population. Estimates of annual survival ranged from 0.37 to 0.64 ($\bar{x}$ = 0.52) for calves and from 0.74 to 0.91 ($\bar{x}$ = 0.84) for adult cows. Predation by grizzly bears (*Ursus arctos*) was the most important factor limiting population growth, and accounted for 57 and 62% of deaths of calves and adults, respectively, for which a cause could be identified. Other causes of death were much less common, and included disease, accidents (drowning, motor vehicle strikes), starvation, and illegal shooting. Annual birth rates of calves ranged from 0.45 to 0.82 ($\bar{x}$ = 0.66) per adult cow (≥3-year old) and would have been sufficient to allow for population growth if calf and adult survival had been greater. However, reducing rates of predation might not result in a corresponding increase in survival over the long term, as other mortality factors might partially compensate for the change. In particular, dietary limitations related to low availability of trace minerals, such as Cu, and potential interactions between diet and effects of diseases and parasites should be anticipated in this and perhaps other muskox populations. More research is needed to determine when harvests of small, isolated muskox populations should be permitted, and how they should be managed.

Key words: birth rates, mortality, muskox, northeast Alaska, nutrition, population dynamics, predation, recruitment, survival.

Background

Muskoxen (*Ovibos moschatus*) occupy a limited range of habitat types, have a low rate of reproduction compared to many other ungulates, and are vulnerable to excessive mortality due to harvest, predation, or environmental influences. Thus, the species is susceptible to extreme fluctuations in abundance and was once extirpated from much of its range (Klein 2000). Furthermore, muskoxen are the only remaining species of a diverse assortment of large grazing mammals that inhabited arctic regions of North America during glacial and immediate post-glacial periods (Lent 1999). Considerable effort and funds were expended during the 1960s and 1970s to reestablish muskoxen in northeastern Alaska (Lent 1998). This population increased to a peak of approximately 700 muskoxen in 1995, including approximately 100 muskoxen that dispersed eastward into northern Yukon, Canada (Lenart 2011). Limited harvests were established in Unit 26C (Arctic coastal plain between the Canning River and the Canadian border) beginning in 1982 and in Unit 26B (between the Colville and Canning Rivers) in 1990 (Fig. 1). From 1996 to 2006 the total annual harvests from these units ranged from 3 to 20 and consisted predominantly of adult bulls. From 1999 to 2006 the population of muskoxen in northeast Alaska declined to approximately 216 animals. The decline was especially severe in Unit 26C, where muskoxen had virtually disappeared by 2006. In Unit 26B the population declined by 35%, and by 2006 these animals were effectively isolated from muskoxen that had spread eastward into Canada. Harvests were prohibited in Unit 26C from 2003 to 2007, and in Unit 26B beginning in 2006 (Lenart 2011). Predation by grizzly bears (*Ursus arctos*) was documented during periods of both increasing and decreasing muskox abundance (Reynolds et al. 2002), but an apparent increase in predation by bears noted by field personnel and the public during 2000 and 2001 raised concerns among Alaska hunters that predation rates were not sustainable (Valkenburg 2007). However, the importance of predation relative to other potential causes of the decline in the northeastern Alaska population is unknown.

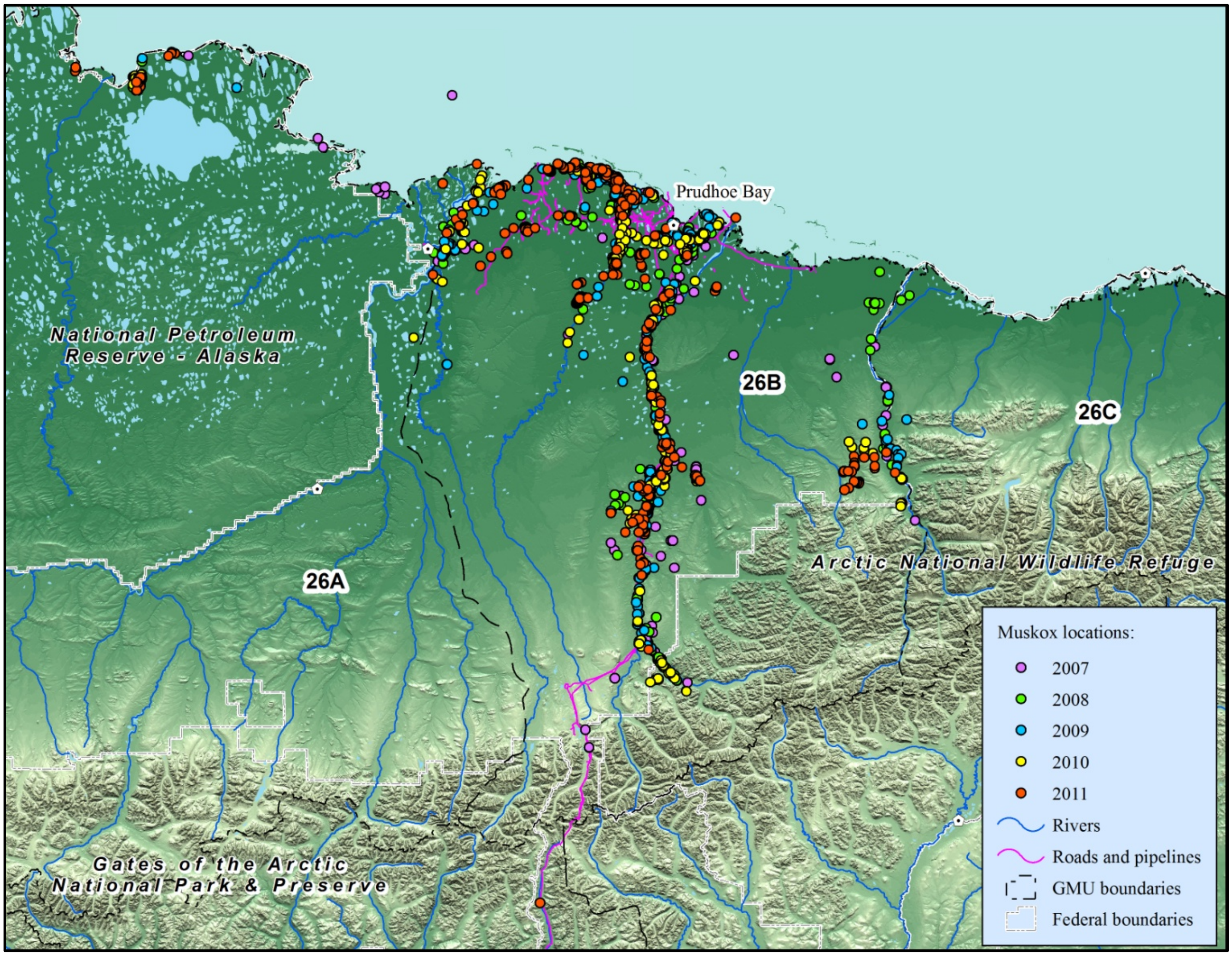

Figure 1. Locations of radiocollared muskoxen in northeastern Alaska, 2007–2011.

Objectives

This study was designed to document muskoxen population status and distribution, and to determine the relative importance of calf production, age-specific survival rates, specific causes of mortality, nutritional status, and forage quality as potential influences on population trend. Objectives of the study were to:

1. Estimate minimum annual birth rates for muskox cows.
2. Estimate annual recruitment of muskox calves to the yearling age class.
3. Determine relative frequencies of various causes of mortality of muskox calves and adults.
4. Estimate annual survival of adult female muskoxen.
5. Model muskox population growth rate using observed demographic parameters.
6. Assess prevalence of major diseases and parasites in muskoxen in northeastern Alaska.
7. Assess nutritional status of muskoxen in northeastern Alaska.

Methods

Fieldwork for this project occurred between June 2007 and October 2011. We captured and radiocollared adult (≥3-years old) muskox cows during March (n = 10), July (n = 2), and October (n = 10) 2007 and July 2010 (n = 4) in Unit 26B. These captures included 2 muskoxen that had been radiocollared previously by other researchers. Nine other muskox cows that had been radiocollared during previous years were also monitored during this study. We used these radiocollared animals to assist in locating groups of muskoxen during radiotracking flights using single-engine airplanes (Piper Super Cub [Piper Aircraft Corporation, Lock Haven, Pennsylvania] or Cessna 182, 185, or 206 [Cessna Aircraft Company, Wichita, Kansas). Flights were conducted 4–6 times per week (weather permitting) during mid-April through early June and twice-monthly during June–September. Additional tracking flights were conducted during October, February, and March when weather permitted. During each flight, we attempted to locate all known groups of muskoxen, including groups without radiocollared animals. We circled each group and attempted to determine the number calves and older animals present and to locate carcasses of muskoxen that had died. In addition, we observed all known groups of muskox from the ground during April, June, and October 2007–2009 and April 2010 and 2011. During these observations, we approached each group on foot to <100 m, examined each muskox using a 30× spotting scope and counted the numbers of muskoxen in each of the following age categories (assumes a birth date of 1 April):calf (<12 months), 1 year, 2 year, 3 year, and ≥4 year. Muskoxen older than 1 year were also classified by sex. We used our counts of muskoxen observed on these flights as a minimum estimate of population size each year, acknowledging that some small groups or lone animals might not have been observed (see Results). In addition, a systematic survey of muskoxen across the eastern North Slope, including northern Yukon, was accomplished in cooperation with Alaska Department of Fish and Game (ADF&G) management staff and personnel from the U.S. Fish and Wildlife Service (FWS) in April 2011 (Lenart 2011; P. E. Reynolds, FWS/ANWR, 2011 unpublished report).

We estimated minimum numbers of births for each year based on the numbers of newborn calves we observed during our monitoring flights. It is likely that not all births were documented (calves may have died before we observed them); thus, these estimates probably underestimate total numbers of births for the population. However, we were able to document several cases of neonatal mortality and predation (based on sightings of dead calves or blood, hair, and tracks at the scene; see Results), and we monitored with similar intensity during all years, so we believe these counts are a useful index of annual productivity. We estimated numbers of calves alive in October based on counts from our monitoring flights, and numbers of yearlings each April based on both monitoring flights and the ground-based estimates of age/sex composition. We estimated spring-summer survival as the ratio of calves alive in October:minimum number of births; winter survival as the ratio of yearlings in April:calves alive during the previous October; and annual survival of calves as the product of these rates. We estimated annual survival of radiocollared adult cows using standard Kaplan-Meier procedures (Pollock et al. 1989), and birth rates as the ratio of minimum number of births:number of adult (≥3-year-old) cows alive at the start of calving in mid-April (this was the number of cows counted on the April ground survey less any deaths that occurred before start of calving). We used these estimates of productivity and survival to estimate annual growth rate (λ) using a simple population model developed with the PopTools (PopTools version 3.2.5., http://www.poptools.org) add-on for Microsoft Excel® (Microsoft Corporation, Redmond, Washington). For these models, we assumed that birth rates were 0 for cows <3 years old and constant thereafter, sex ratio at birth was equal, and that survival rates for yearling and 2-year-old cows were equal to the rates we estimated for radiocollared cows (≥3-years old).

Whenever possible, we visited locations of dead muskoxen (including both collared and unmarked animals) and attempted to determine the cause of death. We collected tissue samples (heart, lung, liver, kidney, muscle, hair, hoof, and long bones) from dead animals, and blood, serum, and hair from captured muskoxen. These were analyzed to estimate the prevalence of major infectious diseases and parasites. Results of these analyses will be presented in future reports prepared by ADF&G Wildlife Veterinary Services.

We assessed nutritional status of muskoxen using 3 approaches: 1) determining diet composition in late winter; 2) estimating the proportion of metabolized N that was obtained from the winter diet, versus mobilization of N from body tissues; and 3) assessing the availability of trace minerals in soil and forage samples. We collected samples of urine (frozen in snow) and feces from sites where muskoxen were found during April. We initially collected fecal and urine samples from 2 coastal sites and 1 inland site due to the presence of large groups of muskoxen at each site. During 2010 and 2011 we sampled 2 additional inland sites and 1 additional coastal site to increase sample sizes for comparison of diets between sites of differing geography and vegetation composition. Fecal samples were sent to the Washington State University Wildlife Habitat Nutrition Laboratory, Pullman, Washington for microhistological identification of plant fragments. Results from that analysis were corrected for differential digestibility using techniques described by Gustine et al. (2011). Urine and fecal samples were also sent to the University of Alaska Fairbanks for analysis of nitrogen isotopes to indicate sources of metabolized nitrogen (Gustine et al. 2011). Results of the N isotope study will be described in a future report to be prepared in cooperation with D. Gustine, U.S. Geological Survey.

During July 2009 we visited 20 sites that were currently used by muskoxen and 14 sites that had been used by radiocollared muskoxen prior to 2006, but were not occupied during our study. Locations of these sites were determined by examining locations where muskoxen were observed during the current study and by examining data from previous years provided by Patricia Reynolds (FWS, personal communication). At each site, we used a tubular soil sampler (Forestry Suppliers, Jackson, Mississippi) to collect 10 samples of mineral soil from within a 50 m diameter circle, spaced at random distances and bearings from the center. These samples were homogenized by thorough mixing in a stainless steel bowl and approximately 10 cm^3 of the mixture was retained. Homogenized soil samples were placed in paper bags and air dried at 20°C for 2 weeks. At each site we also collected 5 replicate samples of each of 2 species of muskox forage plants (total: 10 samples per site). Vegetation collected at most sites included 1 species of willow (*Salix pulchra* or *S. alaxensis*), and 1 of either sedge (*Eriophorum* spp. or *Carex* spp.) or grass (*Arctagrostis latifolium*). We selected the species to sample based on a subjective identification of the most common species of woody shrub and graminoid or sedge at each site. However, 2 sites were dominated by only shrubs or only graminoids and sedges (1 site each); in those cases we selected 2 species of that plant type. At 6 other sites we collected samples of only a single species due to the sparse vegetation. Vegetation samples were placed in paper bags and oven-dried at 40°C for 48 hours, then ground and passed through a 20 mm screen. Soil and plant samples were sent to the University of Alaska's Palmer Center for Sustainable Living (Matanuska Experiment Farm, Palmer, Alaska), where they were analyzed to determine concentrations of Cu, Fe, Zn, N, S, Mo, and Se, and to determine pH of soil samples. For most minerals, we compared mean concentrations between areas (current or past use), and we performed separate comparisons for each mineral and plant species. However, concentrations of Mo in soil samples were often less than minimum detectable levels (<0.15 ppm), so we compared proportions of sites where Mo was detected in soils. Concentrations of Se were below detectable levels (<0.40 ppm) for all soil samples and 96% of vegetation samples, so no further analysis was possible.

Results

April (precalving) population estimates were 196, 191, 196, 184, and 190 muskoxen during 2007, 2008, 2009, 2010, and 2011 respectively ($\bar{x}$ = 191; Table 1). With the exception of the 2011 estimate, these numbers are minimum counts of muskoxen observed, and are not directly comparable with results of systematic aerial surveys of the entire range of the population that were conducted during 2003 and 2006 (Lenart 2005, 2007). However, a systematic survey conducted during April 2011 found only one group of 7 muskoxen in addition to those located during our intensive monitoring flights, while the monitoring flights located a total of 11 muskoxen that were not observed during the systematic survey (Lenart 2011). Thus, we believe the intensive monitoring flights during 2007–2010 likely accounted for >90% of muskoxen that were present. Data describing age and sex composition of muskox groups were reported by Lenart (2011). Muskox distribution was mainly along the Sagavanirktok, Kuparuk, Colville, and Canning Rivers (Fig. 1). The 2 largest concentrations of muskoxen were found near the Arctic coast south and east of Deadhorse ($\bar{x}$ = 69 muskoxen, 2007–2010) and northwest of Prudhoe Bay in the vicinity of Beechey Point ($\bar{x}$ = 45 muskoxen). A third large group ($\bar{x}$ = 41) ranged from the Ribdon River to Sagwon Bluffs on the Sagavanirktok River. These animals gathered in large groups during winter (October–May) and split into many smaller groups during summer (July–August). Because of the tendency of muskoxen to disperse during summer, we found that herd composition surveys in July were the least reliable, due to the difficulty of locating all of the animals. By October, the groups had reformed sufficiently to enable consistent counts, but weather during this period was unpredictable and often inclement. Thus, the early April period was best suited for estimating herd size and composition.

Table 1. Demographic parameters estimated for muskoxen in northeastern Alaska, 2007–2011.

	Year					
Parameters	2007	2008	2009	2010	2011	$\bar{x}$
April population size	196	191	196	184	190	191
No. 3 yr+ cows in April	77	80	82	88	84	82
Cow deaths before calving	0	2	4	3	2	2
Minimum number of births	35	67	63	52	55	54
Calves alive in October	13	34	45	32	29	31
Yearlings present in April	12	14	32	31	33	24
Births per adult cow (through 31 May)	0.45	0.86	0.81	0.61	0.67	0.68
Annual cow survival[a]	0.74	0.85	0.91	0.76	0.91	0.84
Spring-summer calf survival	0.37	0.51	0.71	0.62	0.53	0.57
Winter calf survival	1.00	0.94	0.69	1.00	0.83	0.89
Annual calf survival	0.37	0.48	0.49	0.62	0.44	0.48

[a] Estimated from radiocollared cows. *N* at risk = 23, 27, 23, 21, 22 for 2007–2011, respectively.

Numbers of neonatal calves observed during spring were lowest in 2007, when only 35 calves were recorded (0.45 births per adult cow). Counts of calves during the other years ranged from 52 to 64 (0.61–0.82 births per adult cow; Table 1). Similarly, spring-summer calf survival during 2007 was only

0.37, and ranged from 0.53 to 0.80 during the following years. Overwinter survival of calves was generally high (0.83–1.0), except for the 2009 cohort. This group had the highest spring-summer survival (0.80), but the lowest winter survival (0.69), so annual survival (0.55) for that year was only slightly above the mean for all years (0.50; Table 1). Annual survival of radiocollared adult cows was also lowest during 2007 (0.74, n = 23). Cow survival was also low during 2010 (0.76; n = 21), but was considerably higher during 2008 (0.85; n = 27), 2009, and 2011 (0.91 during both years; n = 23 and 22, respectively; Table 1). Based on our estimates of birth and survival rates, annual estimates of population growth rate (λ) ranged from 0.80 to 1.05, and averaged 0.96 (Table 2).

Table 2. Demographic parameters and estimated population growth rate (λ) for muskoxen in northeastern Alaska, 2007–2011. Assumes equal survival for all ages ≥1 year, equal sex ratio at birth, equal natality for all adult cows (≥3 years), and that no cows gave birth before age 3.

	Year					
Parameter	2007	2008	2009	2010	2011	$\bar{x}$
Births/female (≥3 yr)	0.45	0.86	0.81	0.61	0.67	0.68
Calf survival	0.37	0.48	0.49	0.62	0.44	0.48
Adult (≥1 yr) survival	0.74	0.85	0.91	0.76	0.91	0.84
λ	0.80	0.99	1.05	0.88	1.01	0.95

The earliest newborn calf we observed in any year was on 14 April 2011. The mean date that calves were first observed was 22 April (Julian date 112). Most (58%) births occurred between 1 May and 15 May, and 83% of documented births occurred by 1 June (Fig. 2). However, we continued to detect neonatal calves occasionally through 10 July, when monitoring flights became less frequent, and we observed a calf that was approximately 1-week old on 1 October 2009 (T. Craig, U.S. Bureau of Land Management, personal communication). Thus, a small number of births evidently occurred throughout the summer. Neither the earliest nor the latest-born calves survived. However, our observations suggested that survival was high for calves born during June and July (see below).

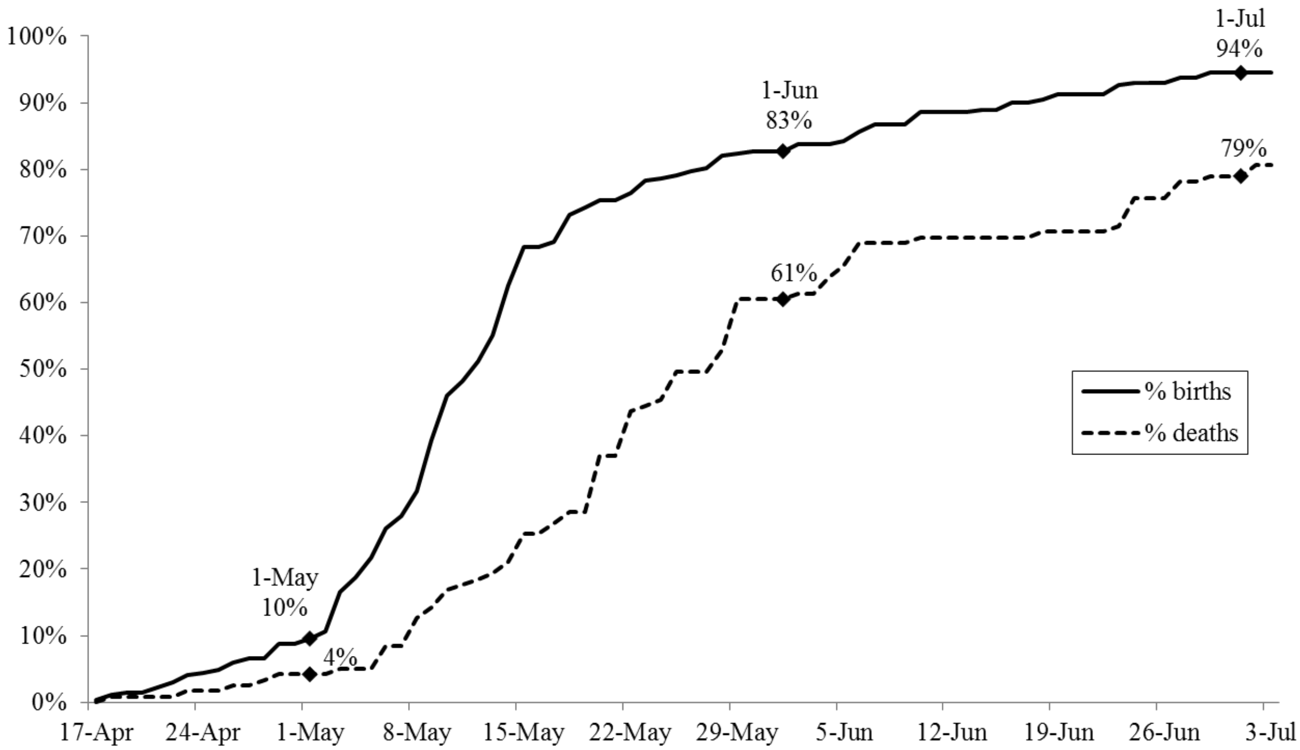

Figure 2. Cumulative percentages of births and deaths of muskox calves from northeastern Alaska during spring and early summer, 2007–2011.

Predation by grizzly bears was the most common cause of death of calves, and accounted for 25 (57%) of the 44 deaths for which there was sufficient evidence to assign a cause (Table 3). In addition, 74 calves disappeared and were presumed to have died (63% of the 118 calves observed). It is likely that bears, wolves (*Canis lupus*) or wolverines (*Gulo gulo*) consumed these calves, preventing us from finding the remains. However, we cannot assume that predators killed all of these, as some may have been scavenged following death from some other cause. Other causes of death that were observed included abandonment (11%; usually due to a bear attack causing the muskox group to flee); disease (7%); starvation, goring by another muskox, and vehicle collision (2% each); and unknown perinatal (18%; defined as deaths within the first week of life for which predators were not involved but a specific cause was not identified). The 3 calves that died of diseases that could be identified included cases of pneumonia, peritonitis ("navel ill"), and chlamydophila.

Table 3. Causes of death of muskoxen in northeastern Alaska, 2007–2011.

	Year							
Age/Cause of death	2007	2008	2009	2010	2011	$\bar{x}$	Totals	%
Calves								
Predation	10	2	1	4	8	5	25	57
Disease	1	2	0	0	0	1	3	7
Starvation	0	0	1	0	0	0	1	2
Perinatal, nonpredation[a]	1	4	0	0	3	2	8	18
Abandoned	0	2	0	1	2	1	5	11
Gored by adult	0	0	1	0	0	0	1	2

Age/Cause of death	Year 2007	2008	2009	2010	2011	$\bar{x}$	Totals	%
Vehicle	0	0	1	0	0	0	1	2
Total known cause	12	10	4	5	13	9	44	100
Missing, fate unknown	10	24	16	13	11	15	74	
Cows (≥1 yr old)								
Predation	2	8	3	12	5	6	30	67
Vehicle/shot	0	0	3	0	3	1	6	13
Drowning[b]	3	0	1	0	0	1	4	9
Other nonpredation[a]	1	1	0	0	1	1	3	7
Unknown[c]	2	0	0	0	0	0	2	4
Total	8	9	7	12	9	9	45	100
Bulls (≥1 yr old)								
Predation	1	0	0	3	5	2	9	56
Vehicle/shot	0	0	0	0	2	0	2	13
Disease	1	1	0	0	0	0	2	13
Other nonpredation[a]	1	1	0	0	1	1	3	19
Unknown	0	0	0	0	0	0	0	0
Total	3	2	0	3	8	3	16	100
All Adults and Yearlings								
Predation[d]	5	8	4	18	10	9	45	62
Vehicle/shot	0	0	3	0	5	2	8	11
Disease	1	1	0	0	0	0	2	3
Drowning	3	0	1	0	0	1	4	5
Other nonpredation	2	2	0	0	2	1	6	8
Unknown[e]	8	0	0	0	0	2	8	11
Total	19	11	8	18	17	15	73	100

[a] Includes starvation and unconfirmed disease or injury with no evidence of predation.
[b] Includes 2 deaths possibly influenced by capture effects (2007).
[c] Includes 1 animal that died and 1 collared animal that disappeared, presumed dead.
[d] Includes 6 for which sex was not determined.
[e] Includes 6 that disappeared while on sea ice (2007), presumed drowned or killed by predator.

Predation by grizzly bears was also the most common cause of death for adults and yearlings, and was responsible for 45 (62%) of 73 deaths that were assigned to a specific cause (Table 3). Other mortality causes for adults and yearlings included human actions (11%; includes vehicle collisions and illegal shooting); drowning due to falling through thin ice (5%); disease (3%; consisted of 1 case each of pericarditis and pneumonia); and unknown nonpredation (8%; no evidence of predation but cause was not definitively determined). Of the 4 cases of drowning, 2 may have been influenced by stress of capture prior to the drowning event and 1 case occurred during a bear attack on the muskox group (this adult female muskox was also suffering from an advanced case of pneumonia). An additional 8 (11%) adults or yearlings disappeared and likely died of unknown causes. One of the deaths assigned to predation was an adult cow that died of stress myopathy following an incident in which a bear attacked and killed 2 other adult cows from the same group. Although the bear did not directly injure this cow, the stress of running from the predator caused the animal to die within 2 days of the attack.

Bear predation of both calves and older muskoxen began soon after bears emerged from their winter dens and continued through the period when bears were active (March–October). However, predation was most prevalent during spring: 61% of predation on calves and 87% of predation on older muskoxen occurred before 1 June (Figs. 2 and 3). An additional 18% of calf predation and 11% of predation on older muskoxen occurred during the month of June. Some additional mortality may have occurred during summer, when our monitoring flights were less frequent and muskoxen were more widely dispersed. However, total counts of muskoxen seen on tracking flights were similar between late June and October, suggesting that mortality during that period was much less than during spring.

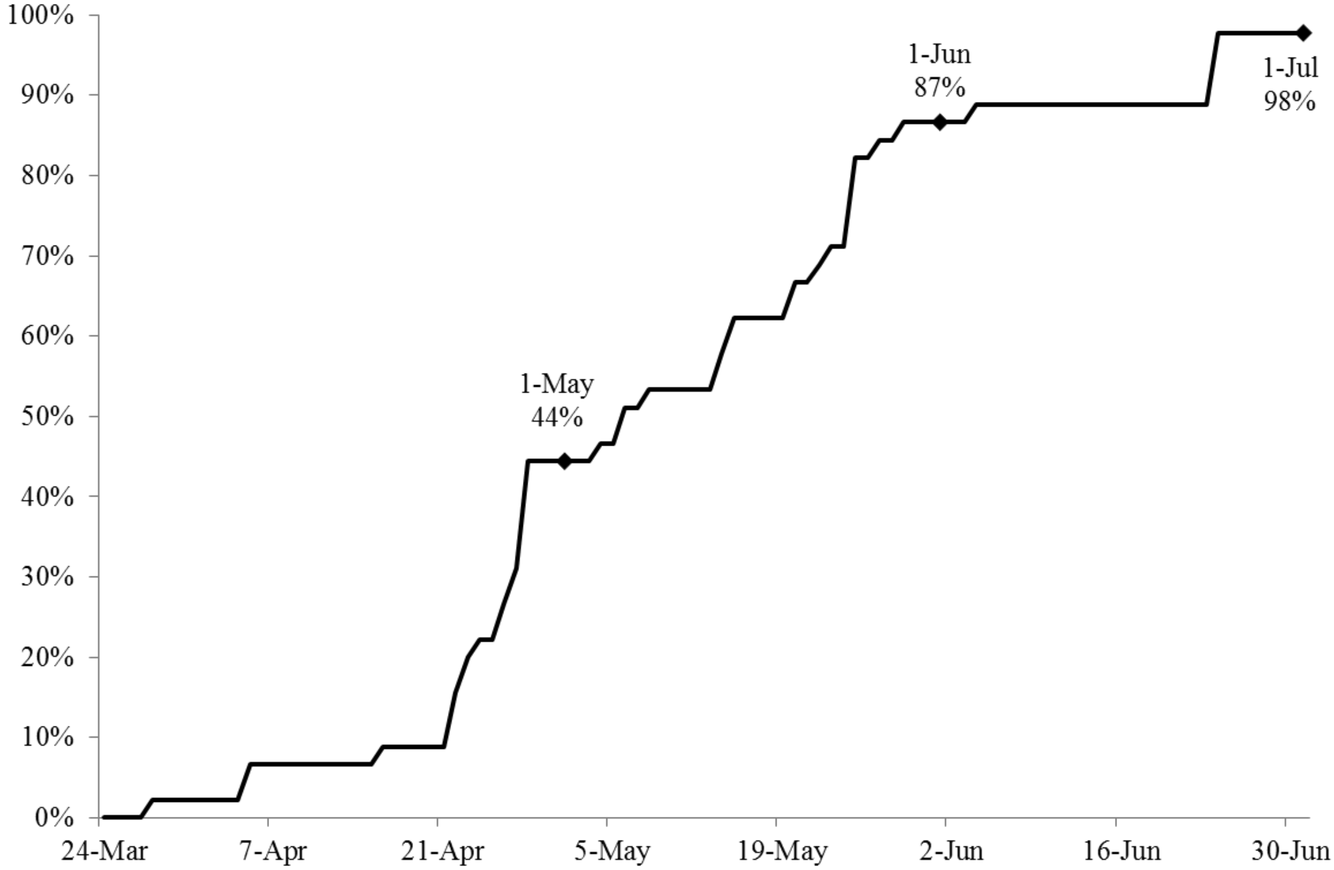

Figure 3. Cumulative percent of deaths of muskoxen older than calves in northeastern Alaska, 2007–2011.

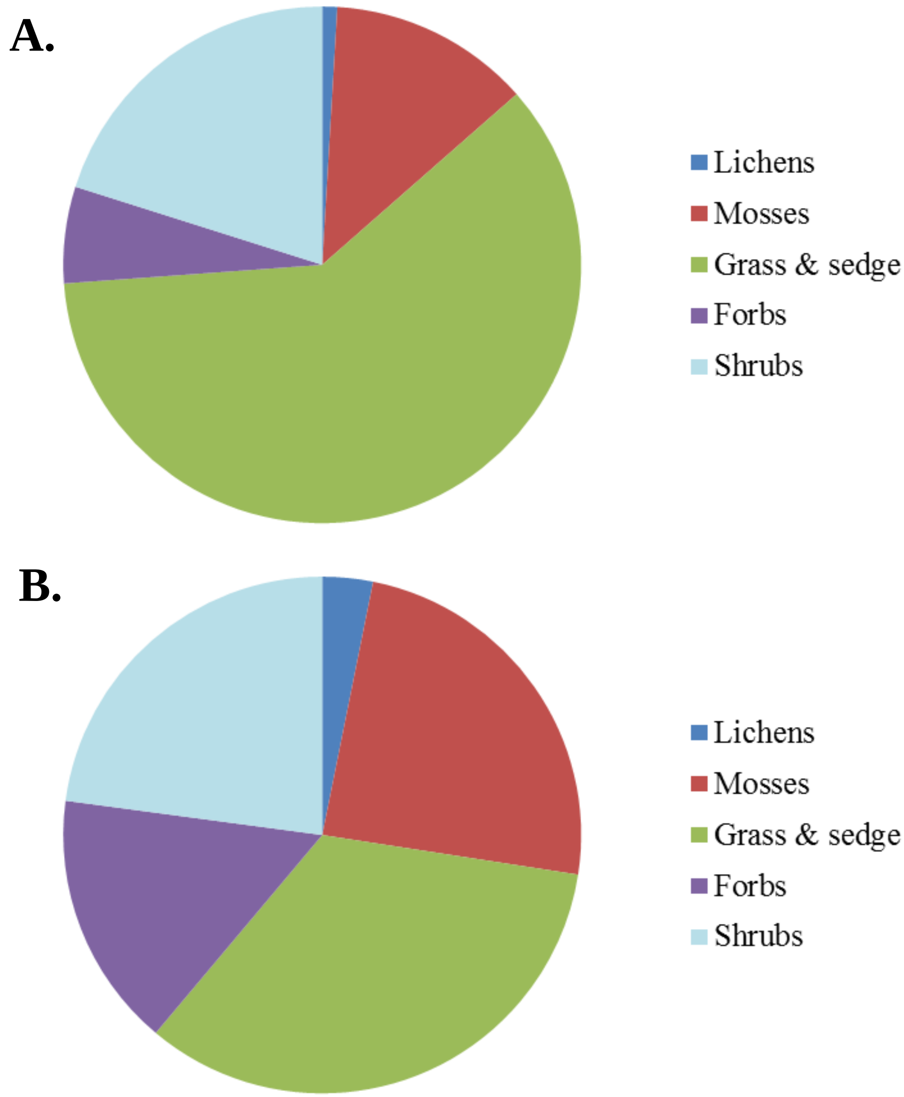

Figure 4. Proportions of vegetation types in diets of muskoxen from northeastern Alaska, assessed by microhistological examination of fecal samples, corrected for differential digestibility. A: coastal sites; B: inland sites.

Microhistological analysis of fecal samples indicated that grasses and sedges were the most common plant type in diets of both coastal and inland muskoxen groups, followed by shrubs and mosses (Table 4). Our sample sizes were insufficient to allow meaningful statistical comparisons, especially considering the need to control experiment-wise error rates over multiple comparisons. However, there was some evidence that inland groups consumed higher proportions of lichens, forbs, and mosses and smaller proportions of grass and sedge, compared to coastal groups (Table 4, Fig. 4). These differences parallel differences in vegetation composition of the areas inhabited by these groups (Walker et al. 2005).

Table 4. Proportional occurrence of vegetation types in fecal samples of muskoxen from northeastern Alaska, 2007–2011, corrected for differential digestibility.

			Vegetation types						
Year	Group	Location	Lichens	Forbs	Mosses	Grass and sedge	All shrubs	Evergreen shrubs	Deciduous shrubs
2007	Beechey	Coastal	0.027	0.002	0.139	0.730	0.102	0.014	0.088
2008	Beechey	Coastal	0.017	0.245	0.169	0.254	0.315	0.077	0.237
2010	Beechey	Coastal	0.018	0.002	0.107	0.770	0.103	0.009	0.094
2011	Beechey	Coastal	0.003	0.021	0.048	0.628	0.300	0.016	0.284
2007	Deadhorse	Coastal	0.001	0.169	0.213	0.570	0.047	0.015	0.033
2008	Deadhorse	Coastal	0.004	0.063	0.034	0.360	0.540	0.064	0.475
2010	Deadhorse	Coastal	0.008	0.028	0.096	0.817	0.051	0.019	0.032
2011	Deadhorse	Coastal	0.002	0.005	0.106	0.652	0.236	0.033	0.203
2011	Kuparuk	Coastal	0.004	0.009	0.221	0.649	0.116	0.018	0.098
	$\bar{x}$	Coastal	0.009	0.060	0.126	0.603	0.201	0.029	0.172
2007	Ribdon	Inland	0.054	0.062	0.366	0.403	0.115	0.033	0.082
2008	Ribdon	Inland	0.081	0.016	0.137	0.678	0.088	0.032	0.056
2010	Ribdon	Inland	0.018	0.037	0.498	0.112	0.335	0.139	0.196
2011	Ribdon	Inland	0.007	0.022	0.107	0.252	0.612	0.032	0.581
2010	Canning	Inland	0.000	0.745	0.072	0.107	0.077	0.000	0.077
2010	Ivashak	Inland	0.044	0.003	0.347	0.474	0.131	0.028	0.104
2011	Ivashak	Inland	0.017	0.236	0.174	0.331	0.243	0.037	0.205
	$\bar{x}$	Inland	0.032	0.160	0.243	0.337	0.229	0.043	0.186
	t[a]		2.168	1.048	1.996	2.727	0.312	0.790	0.172
	P[a]		0.048	0.312	0.066	0.016	0.760	0.443	0.866

[a] *t*-test comparing mean proportions between coastal and inland sites.

We found no differences in mean concentration of Cu, Fe, Zn, N, or S, or in pH of soil samples from areas used either currently or in past years (Table 5). However, the proportions of sites where Mo was detected was greater for sites used in the past (71%) compared to sites used currently (30%; $\chi^2 = 5.67$; $P = 0.02$). Similarly, concentrations of most minerals did not differ between areas for most forage plants. The only exceptions were for Cu in *Arctagrostis latifolium* (past > current; $t = 2.4$, $P = 0.04$); Fe in *Eriophorum vaginatum* (current > past; $t = 2.90$, $P = 0.03$); and S in *A. latifolium* (past > current, $t = 2.58$, $P = 0.03$; Table 6).

Table 5. Concentrations (ppm or %) of mineral nutrients and pH of soil samples from sites used either currently or in past years by muskoxen in northeastern Alaska, 2009.

	Current use		Past use			
Mineral	$\bar{x}$	SD	$\bar{x}$	SD	t[a]	P[a]
Cu (ppm)	2.99	2.28	4.20	2.49	−1.45	0.16
Zn (ppm)	7.34	5.39	7.00	4.88	0.19	0.85
Fe (ppm)	291.75	251.49	350.00	183.93	−0.78	0.44
N (ppm)	0.34	0.26	0.46	0.33	−1.13	0.27
S (%)	0.55	0.35	0.51	0.31	0.36	0.72
pH	6.58	0.74	6.39	1.00	0.62	0.54

[a] *t*-test comparing mineral concentrations or pH between sites.

Table 6. Concentrations (ppm or %) of mineral nutrients in vegetation samples from sites used currently or in past years by muskoxen in northeastern Alaska, 2009.

	Plant	Current use			Past use				
Mineral	species[a]	$\bar{x}$	SD	n	$\bar{x}$	SD	n	t[b]	P[b]
Cu (ppm)	Alat	3.23	0.85	10	4.48	0.42	3	2.40	**0.04**
	Cspp	3.30	0.47	4	3.49	0.57	5	0.53	0.61
	Evag	3.73	1.02	6	3.29	0.39	4	0.82	0.43
	Sala	4.40	1.01	10	3.78	1.07	7	1.22	0.24
	Spul	3.79	0.48	7	3.53	0.63	6	0.83	0.43
Zn (ppm)	Alat	28.32	18.08	10	20.33	6.77	3	0.73	0.48
	Cspp	39.85	14.94	4	38.80	22.81	5	0.08	0.94
	Evag	60.21	17.04	6	55.10	14.44	4	0.49	0.64
	Sala	225.38	50.59	10	184.89	70.79	7	1.38	0.19
	Spul	297.29	63.76	7	261.47	86.38	6	0.86	0.41
Fe (ppm)	Alat	177.73	165.54	10	181.27	69.38	3	0.04	0.97
	Cspp	62.70	28.06	4	126.80	82.30	5	1.47	0.18
	Evag	90.50	28.53	6	55.95	4.91	4	2.90	**0.03**
	Sala	337.86	614.39	10	203.00	199.20	7	0.65	0.53
	Spul	71.23	35.51	7	51.77	8.98	6	1.40	0.21
N (ppm)	Alat	1.46	0.45	10	1.33	0.09	3	0.50	0.08
	Cspp	1.69	0.19	4	1.46	0.40	5	1.04	0.34
	Evag	1.81	0.32	6	1.55	0.29	4	1.29	0.23
	Sala	1.99	0.25	10	2.00	0.19	7	0.09	0.93
	Spul	2.04	0.26	7	1.87	0.16	6	1.37	0.20

Mineral	Plant species[a]	Current use			Past use			t^b	P^b
		$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*		
S (%)	Alat	0.22	0.24	10	0.74	0.50	3	2.58	**0.03**
	Cspp	0.72	0.41	4	0.25	0.30	5	2.04	0.08
	Evag	0.40	0.45	6	0.09	0.00	4	1.69	0.15
	Sala	0.67	0.81	10	0.39	0.17	7	1.04	0.32
	Spul	0.25	0.14	7	0.27	0.30	6	0.21	0.84
Mo (ppm)	Alat	0.93	1.24	10	0.67	0.61	3	0.34	0.74
	Cspp	1.06	1.32	4	2.04	1.70	5	0.94	0.38
	Evag	0.58	0.19	6	1.89	2.24	4	1.16	0.33
	Sala	0.21	0.22	10	0.30	0.22	7	0.83	0.42
	Spul	0.16	0.11	7	1.38	1.49	6	2.00	0.10

[a] Plant species: Alat = *Arctagrostis latifolia*; Cspp = *Carex* spp.; Evag = *Eriophorum vaginatum*; Sala = *Salix alexensis*; Spul = *Salix pulchra*.
[b] *t*-test comparing concentrations for each species between sites. Significant differences indicated in bold type (P <0.05).

Discussion

This study was intended to be a broad-based investigation into potential factors that might influence the status of the muskox population in northeastern Alaska. Thus, these results are best viewed as a guide for future, more definitive studies focused on specific hypotheses. With that caveat in mind, it seems clear that predation by grizzly bears was the single most influential force acting to limit muskox population growth during this study. Although the results of our survey of diseases and parasites are not complete, we found no indication that any particular pathogen was widespread or especially virulent in the population (ADF&G, unpublished data, Fairbanks). Our minimum counts of population size and our estimates of population growth rate were in good agreement, and both indicated a stable or slowly declining population. We found no other significant sources of mortality, and our estimates of calf production would be sufficient to allow for population growth if calf and adult survival were to increase. However, simply reducing the number of deaths due to predation might not result in an overall increase in survival, if this is accompanied by an increase in mortality from some other cause (e.g., disease or poor nutrition). In particular, there is some evidence to suggest that nutritional deficiencies might become important if losses to predation were reduced. For example, concentrations of Cu in muskox forage plants were well below minimum levels recommended for domestic ruminants (>5 ppm; National Research Council 2007). Conversely, concentrations of Zn in willow species commonly consumed by muskoxen greatly exceeded the maximum concentrations recommended for livestock. Concentrations of Zn in excess of 100 ppm can reduce the ability of ruminants to absorb Cu (National Research Council 2007), and might exacerbate deficiencies caused by the already-low levels of Cu found in the plants we studied. Thus, muskox groups whose diets contain large amounts of willows may face dietary challenges resulting from insufficient availability of Cu. Low levels of Cu have been reported elsewhere in tissues of wild muskoxen (Barboza et al. 2003) and were implicated in deaths of muskoxen in captivity (Blakley et al. 1998).

Another potential dietary issue is suggested by the prevalence of mosses in the diet of the inland muskox groups we studied. Ihl and Barboza (2007) suggested that consumption of mosses by muskoxen results in a net cost of dietary protein because during digestion mosses retain most of the protein they contain and adsorb particles of other forage plants, reducing availability of nitrogen from those foods. We noted that captured muskoxen from the inland groups were notably fatter than those from coastal areas, as were carcasses of muskoxen that we necropsied (this study, unpublished data). Thus, we believe that diets of the inland groups provided muskoxen with sufficient amounts of energy, but may have been deficient in nitrogen and perhaps Cu and Se.

The precipitous decline in muskox abundance in Unit 26C (Arctic National Wildlife Refuge) between 1998 and 2006 was a primary stimulus for this study. However, because the decline occurred before the study began, our data provide some clues but no definitive indication of possible causes. The change from a period of significant growth to a rapid decline suggests a major change in predator behavior or abundance, increased incidence of disease, reduced quality or abundance of food, or a change in some other limiting factor. Harvest of muskoxen in this area was thought to be well below the level that might influence the population, although the effects of selective removal of mature bulls might be more important than is currently supposed (Schmidt and Gorn 2013). There is no evidence that abundance of grizzly bears increased substantially during that period, and predation of muskoxen by bears was recorded throughout the period when the muskox population increased (Reynolds et al. 2002). However, most bear predation that we observed occurred during spring. The only other ungulate prey available to bears in northeastern Alaska at that time were moose (*Alces alces*) and caribou (*Rangifer tarandus*). The moose population throughout the area declined significantly beginning in 1988, and remained low through the early 2000s (Lenart 2010). Similarly, during the spring calving season the large Porcupine caribou herd migrated into the area occupied by muskoxen in northern Unit 26C for most of the 1980s and 1990s (Griffith et al. 2002), but the herd shifted its calving distribution eastward into northern Canada beginning in 2000 (ADF&G, unpublished data, Fairbanks). Thus, availability of moose and caribou calves as prey for bears during spring was greatly reduced during the period when the muskox population declined (Fig. 5), which may have caused some bears to increase predation on muskoxen.

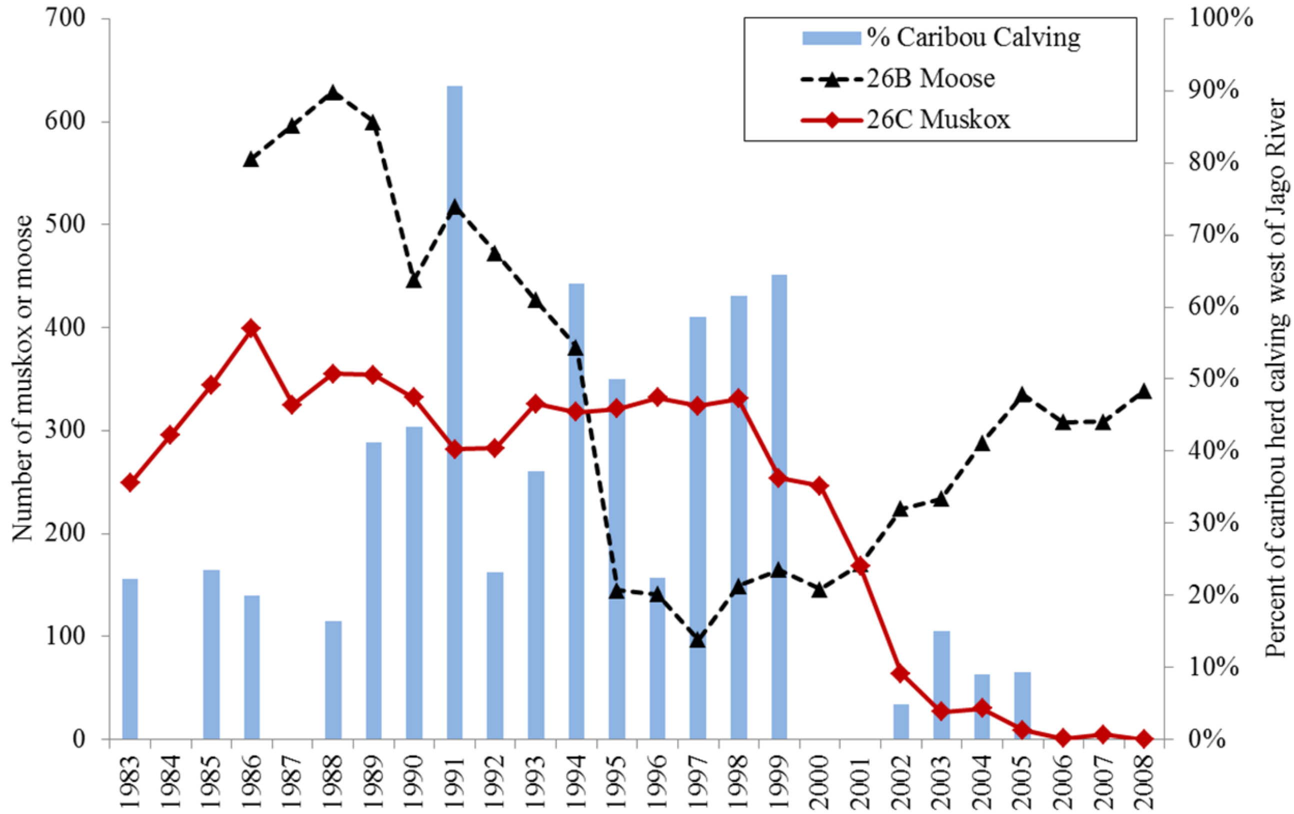

Figure 5. Abundance of muskoxen (solid line) in Unit 26C, abundance of moose in Unit 26B (dashed line), and proportion of the Porcupine caribou herd calving west of the Jago River (bars) in northeastern Alaska, 1983–2008. Populations of moose within Unit 26C were low throughout the period, except in areas bordering Unit 26B.

Changes in climatic conditions may also have played a role in the muskox decline. Mean winter temperatures in northeastern Alaska reportedly increased by >2°C from 1980 to 2000 (Johannessen et al. 2004). However, since 2000, this warming trend has been accompanied by a reduction in number of growing degree days during summer, as reported by the U.S. National Weather Service station at Deadhorse airport, on the Arctic coast of northeastern Alaska (Fig. 6). A possible explanation for this is an apparent increase in cloud cover and fog that we observed along the coast during our spring fieldwork. Other recent changes that are consistent with predicted effects of a warming climate include increased winter precipitation, more frequent occurrence of icing events, thawing of permafrost, increasing depth of the active layer of soil, and drying of the soil due to increased drainage during winter (Hinzman et al. 2005). Effects of these changes on the quality and quantity of forage available to muskoxen are unknown and difficult to predict, but will likely be significant in the future.

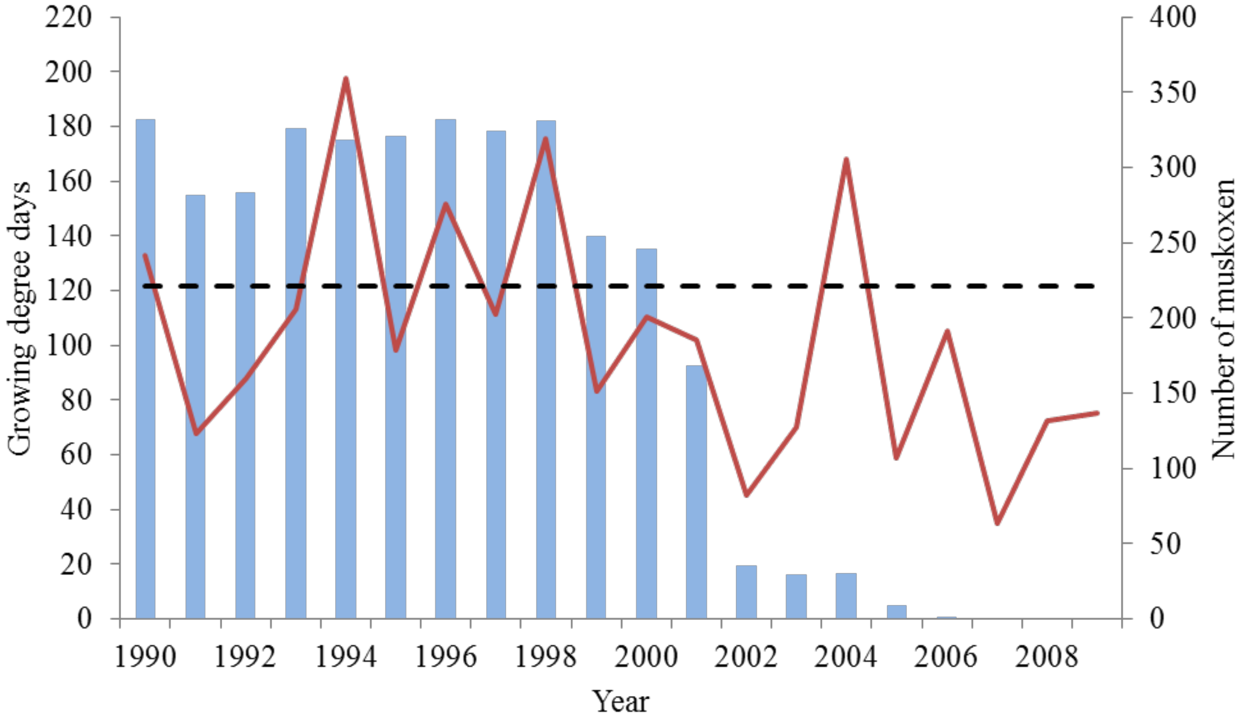

Figure 6. Growing degree days measured at Deadhorse airport (solid line), and abundance of muskoxen (bars) in Unit 26C, northeast Alaska, 1990–2009. Dashed line is the mean number of growing degree days from 1990 to 1999.

An additional effect that should be considered is the potential for interactions among forage quality and the incidence of diseases and parasites. Dietary concentrations of trace minerals, particularly Cu, are important factors affecting the ability of animals to resist disease and parasite infestation (Underwood 1977, National Research Council 2007). At the same time, an overabundance of intestinal parasites may reduce the ability of an animal to absorb nutrients from the diet, creating a feedback mechanism. For example: low dietary Cu may lead to an increased parasite load, which further reduces availability of Cu (Adogwa et al. 2005). Thus, muskoxen inhabiting an area where the concentration of Cu in forage plants is below optimum levels may gradually build up parasite populations, which might eventually reach levels sufficient to inhibit absorption of what little Cu is available in the forage. In this case, an area that initially appears capable of supporting muskoxen might prove unable to maintain a population over the long term. It is impossible to determine retrospectively if such a process played a role in the decline of muskoxen in Unit 26C, but this could be investigated in other areas currently showing signs of a population decline (e.g., the Seward Peninsula of western Alaska).

It should also be noted that the potential negative effects discussed above are neither a comprehensive list nor are they mutually exclusive; any or all of these could have contributed in some way to the muskox decline (i.e., the cause may have been “death by a thousand cuts” rather than a single negative influence). Considering the harsh environment occupied by muskoxen, their low reproductive potential, and the general tendency of arctic species to fluctuate in abundance over time, periodic declines and even local extinctions may be an inherent characteristic of muskoxen. Long-term survival may thus depend on the ability of local populations to recover from steep declines, or to be reestablished by animals dispersing from other areas. This suggests that significant management efforts, such as predator management, range improvement, or augmenting populations through translocations of additional muskoxen may be required to maintain small, isolated muskox populations. The diversity of threats faced by muskoxen and the history of localized extinctions in Alaska suggest that hunting of muskoxen should be managed conservatively. Additional research is needed to determine how best to manage harvest programs, and under what conditions harvesting from small populations should be permitted.

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