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The History, Status and Management of Muskoxen on Banks Island

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ABSTRACT. Historical and archaeological records suggest that muskoxen (*Ovibos moschatus*) were once abundant on Banks Island. They declined around the turn of the 20th century and remained at very low population levels until the 1970s. The causes of the scarcity of muskoxen are unknown, but severe freezing rains and subsequent forage unavailability likely played a role. Aerial surveys documented an increase in the estimated population size from 3800 in 1972 to 34 225 in 1989. The rapid increase in muskox numbers has been a source of concern to the local users, who view the muskoxen as detrimental to the caribou (*Rangifer tarandus pearyi*), which have declined in number. Since the mid-1980s, productivity of 3-year-old muskox cows and calf survival have decreased and the prevalence of parasites has increased. Our data do not allow us to distinguish between whether those changes are density-dependent population responses or the effects of the severity of winter weather. Current management focuses on monitoring the trend of population size, the condition and reproduction of the muskoxen.

Key words: muskoxen, *Ovibos moschatus*, Banks Island, numbers, harvest, weather, population regulation

RÉSUMÉ. Des documents historiques et archéologiques suggèrent que les boeufs musqués (*Ovibos moschatus*) se trouvaient jadis en grand nombre sur l'île de Banks. La population a décliné au début du XX^{e} siècle et est demeurée à un très bas niveau jusque dans les années 70. On n'a pas déterminé les causes de la rareté des boeufs musqués, mais on pense que de fortes précipitations de verglas et le manque d'herbage qui s'en est suivi, ont eu un rôle à jouer. Des relevés aériens ont indiqué une augmentation de la taille estimée de la population, de 3 800 individus en 1972 à 34 225 en 1989. L'augmentation rapide du nombre de boeufs musqués est perçue comme un problème par les usagers locaux, qui considèrent le boeuf musqué comme nuisible au caribou (*Rangifer tarandus pearyi*), dont le nombre a décliné. Depuis le milieu des années 80, la productivité des boeufs musqués femelles âgées de 3 ans ainsi que le taux de survie des veaux sont en baisse, et la fréquence des parasites s'est accrue. Nos données ne nous permettent pas de distinguer si ces changements correspondent à une réponse de la population, qui dépendrait de la densité, ou à des répercussions de la rigueur du climat hivernal. La gestion actuelle se concentre sur le contrôle de la tendance démographique, ainsi que sur l'état général et la reproduction du boeuf musqué.

Mots clés: boeuf musqué, *Ovibos moschatus*, île de Banks, nombres, récolte, temps, contrôe de la population

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INTRODUCTION

Since the early 1970s, muskoxen (*Ovibos moschatus*) have been increasing in number on Banks Island, a 70 000 km^2 island in the western Canadian Arctic (Fig. 1). The Banks Island population now constitutes almost a third of the world's muskoxen. High densities and rapid rates of population increase have triggered a variety of concerns among local people and biologists about ecological competition with caribou, range overutilization and catastrophic population decline. As a result, more research attention has been paid to Banks Island muskoxen than other Canadian populations. Much of the information collected has been during routine surveys or part of on-going monitoring programs and, as such, remains in unpublished government reports not readily available to interested persons. Our objective in this paper is to synthesize published and unpublished materials in a review of the history, status and management of muskoxen on Banks Island and to offer some necessarily speculative interpretations of available data.

HISTORY OF MUSKOXEN ON BANKS ISLAND

Archaeological data suggest that Banks Island muskox populations have been at least periodically large enough to support human hunters. Pre-Dorset sites 3400 years old on Banks Island have been found to contain muskox bones (Hahn, 1977). Use of muskoxen also apparently supported Copper Eskimos from Victoria Island when they visited northern Banks Island to salvage iron and wood from the exploration ship *Investigator* abandoned in 1853 (Will, 1984). Bones estimated to represent some 2300 muskoxen have been found at camps seasonally occupied in the late 19th century (Will, 1984), which suggests that muskox populations were substantial during that period. Stefansson (1921) saw no muskoxen during his extensive travels over Banks Island between 1914 and 1916 and believed that few, if any, remained on the island.

In the first half of the 20th century, Banks Island was visited seasonally by fox trappers (Usher, 1966). In 1951, Inuit families settled permanently on the island and were centralized in 1961 at Sachs Harbour (Usher, 1966). Despite extensive travel during fox trapping, locals rarely encountered muskoxen until the 1960s (Urquhart, 1973).

In 1970, fears about possible effects of oil and gas exploration on caribou and foxes prompted the first systematic aerial surveys to describe seasonal distributions of wildlife. Kevan's (1974) survey undertaken in June 1970 was the first to reveal the status of muskoxen, and his estimate of 1567 muskoxen on northern Banks Island in June 1970 was greeted with disbelief that there could be so many (P.G. Kevan, pers. comm. 1986). However, Urquhart's (1973) aerial survey estimating 3800 muskoxen in May 1972 forced the realization that the muskox population had greatly increased from the occasional sightings of the previous decades.

Urquhart (1973) estimated that 1000-2000 caribou died of malnutrition after unusually heavy snowfall in mid-October 1970. In fall 1972, hunters reported a decline in numbers and condition of the caribou on southern Banks (Urquhart, 1973), while the frequency of muskox sightings close to Sachs Harbour increased (T.W. Barry, pers. comm. 1987). The hunters attributed the decline to competition between caribou and muskoxen on northern Banks Island during the preceding summer (Boukhout, 1972, cited in Urquhart, 1973). Since that time, local hunters have consistently maintained

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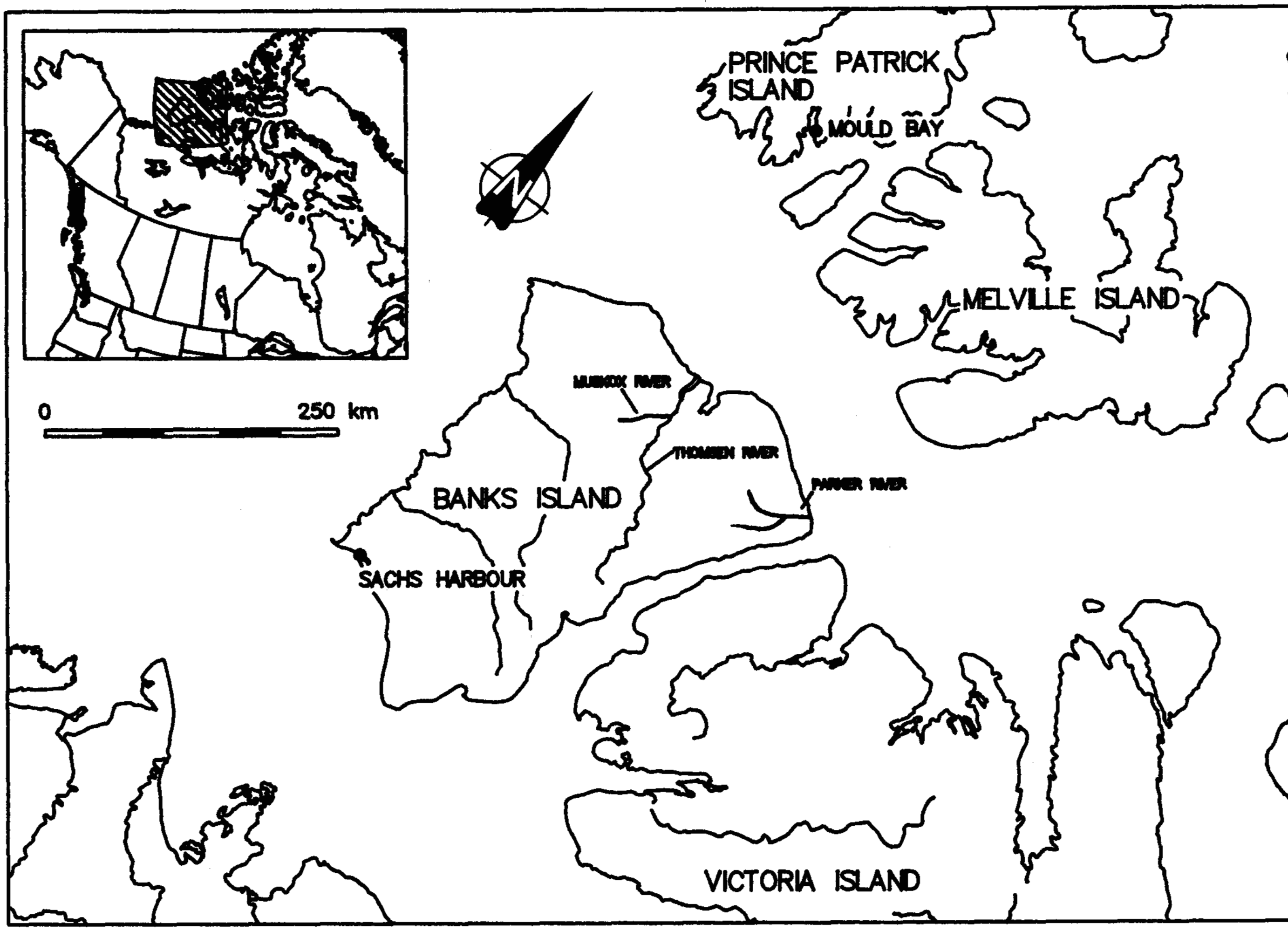

FIG. 1. Map of Banks Island and surrounding area.

their belief in competition as an explanation for the simultaneous increase in muskoxen and decrease in caribou numbers. Wilkinson *et al.* (1976) investigated the feeding habits and range use by the two species in summer 1973 but found no evidence of forage competition.

An annual quota for Banks Island of 7 muskoxen was established in 1971 and was subsequently raised to 150 in 1978. Vincent and Gunn (1981) documented the continued increase in muskox numbers to an estimated 19 340 in March 1980, leading to renewed calls for the government to act to slow the increase. In the late 1970s, the Sachs Harbour's Hunters' and Trappers' Association widened its concern from the effect of muskoxen on caribou to expressing fear of a drastic crash by the muskox population. In the hope of slowing down the increase in the muskoxen, the quota was increased to 2000 and the restriction to subsistence use was removed to provide the opportunity for commercial harvests.

METHODS

The trend in size of the muskox population is monitored through systematic aerial transect surveys that began in 1972 (Urquhart, 1973; Vincent and Gunn, 1981) and were improved in 1986 with stratification to allocate survey effort proportional to muskox density (Latour, 1985; McLean *et al.*, 1986; McLean and Fraser, 1989). The natural log of the estimates is plotted against time to measure the rate of increase (Caughley, 1977).

Calf production and early survival are integrated and indexed as the percentage of calves in the total population during summer. Aerial surveys tend to underestimate calf proportions by about 5% because small-bodied calves are inconspicuous as the herd closes together in the muskox defense formation (McLean *et al.*, 1986). We have therefore added 5% to aerial counts to make them comparable with calf proportions estimated from the ground.

In summer 1986 and 1987, the sex-age composition of all herds seen was classified during unsystematic searches by helicopter. The helicopter landed out of sight or distant from the herd. The observers walked to within 200-300 m and used 20× scopes to classify the muskox sex/age classes based on body size, pelage and horn development. The categories were calves, yearlings, male or female 2-year-olds and bulls or cows 3 years and older. In 1986 the sampling was island-wide, but in 1987 sampling was restricted to the Thomsen River area, northern Banks Island.

Data on body condition, pregnancy (presence of a fetus, involuting uterus or lactating) and the incidence of disease or parasitism were collected during commercial harvests from 1981 to 1990 (Tessaro *et al.*, 1984; Rowell, 1989; N.W.T. Department of Renewable Resources, unpubl. data). Condition was indicated by the measured depth of back fat.

Between-year differences were compared using a Kruskal-Wallis One-Way analysis of variance (Lehner, 1979). Incidental data on the condition and health of muskoxen on northern Banks were obtained from necropsies of muskoxen found dead or shot during a study of disease (Blake *et al.*, 1989; B. McLean, unpubl. data).

The incidence of freezing rain and monthly snowfall were obtained from Atmospheric Environment Service, Environment Canada, for Sachs Harbour, which is the only permanent weather station on Banks Island. The records for Sachs Harbour (1956-85) were divided into three 10-year periods. Annual differences in snowfall among the three periods were tested by a Kruskal-Wallis One-Way analysis of variance.

Harvest data are from the Inuvialuit Harvest Study (M. Fabijan, pers. comm. 1990). Data on guided hunts and the commercial harvesting were obtained from the Inuvialuit Development Corporation (T. Beaudoin, pers. comm. 1989).

RESULTS

Population Numbers

Aerial survey data suggest a rapid and continuous increase in population numbers since the first survey in 1972 (Fig. 2). The population estimate in July 1982 of 9400 ± 1050 (S.E.) indicated an apparent decline since the 1979-80 estimate (Latour, 1985), but McLean *et al.* (1986) attributed the reduced estimate to muskoxen missed in the northeast of the island. In July 1985, McLean *et al.* (1986) used two aircraft for extensive reconnaissance and kept the transect lines short to minimize observer fatigue. The survey led to an estimated population size of 25 700 ± 2050 (S.E.) muskoxen (McLean *et al.*, 1986). McLean and Fraser (1989) used a similar approach in June 1989 and estimated that the population had increased significantly to an estimated 34 225 ± 2360 (S.E.); $t_{0.05}$ (2), 53 = 2.006, $0.005 < P(|t| > 2.73) < 0.05$ (Cochran, 1977; Gasaway *et al.*, 1987). The increase in numbers since 1985 has taken place mostly in the southwest of the island. The Thomsen and Parker river areas, both high density areas, declined slightly but not significantly ($t_{0.05}$ [2], 31 = 2.04, $0.05 < P$). The rate of increase (Caughley, 1977) from the four estimates (1972, 1980, 1985 and 1989) is 0.13 (n = 4, r = 0.92).

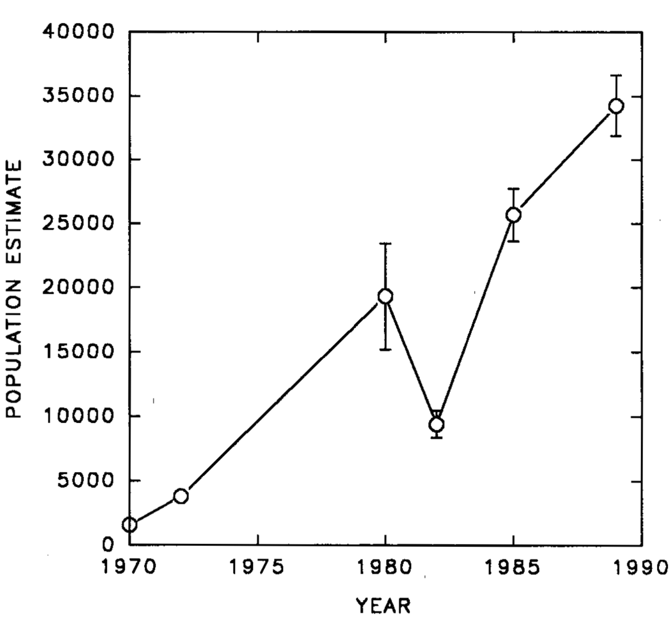

FIG. 2. Population estimates (± 1 standard deviation) for muskoxen on Banks Island, N.W.T., 1969-89 (data from Urquhart, 1973; Latour, 1985; Vincent and Gunn, 1981; McLean *et al.*, 1986; McLean and Fraser, 1989).

Reproduction

Pregnancy rates are high (Table 1), suggesting that most cows calve every year. Calving by 2-year-olds occurred in 1982 and 1983 but sample sizes were small and may not be representative (Rowell, 1989). The pregnancy rate of 3-year-old cows in 1986 statistically decreased significantly from that of the adult cows (Rowell, 1989) and the decline continued in 1987 and 1990 (Table 1).

The only measure of productivity in the 1970s comparable to the data collected in the 1980s is the proportion of calves to total population (Table 2). The trend in calf percentages is difficult to determine because of the small sample sizes used in the early estimates, but the 23-25% seen in 1970 and 1971 were not equalled in the past decade (Table 2), indicating a recent decline in calf production. The three estimates of yearling production since 1979 show a decline (Table 2).

Condition

Fat deposits were measured regularly in commercial harvests between 1985 and 1990 (Table 3). In earlier commercial harvests the muskoxen had abundant subcutaneous and internal fat deposits but measurements were not collected (Latour, 1987; J.Rowell, unpubl. data). The Kruskal-Wallis analysis suggests there were significant differences in back fat between years (P = 0.0001) in adult cows (Table 3). Back fat was significantly thicker in 1985 than in 1986 (P = 0.05, multiple comparisons; Gibbons, 1985).

There are few reports of muskoxen found dead from natural causes prior to 1986. Information gathered after 1986 is restricted to the confluence of the Muskox and Thomsen rivers. Blake *et al.* (1989) examined a large sample in July 1986 and found that 2 of 31 carcasses and 7 of 21 skeletons showed evidence of reduced fat reserves. In 1988 only 2 of 47 dead muskoxen were considered to have died from malnutrition, but in June 1989, 67 of 69 carcasses had died from malnutrition.

Parasites and Disease

Initially, the muskoxen examined during the commercial harvests were largely free of disease and parasites (Tessaro *et al.*, 1984). The proportion of muskoxen infected with the

TABLE 1. Pregnancy rates of 2-, 3-, and 4+ year-old cow muskoxen, Banks Island, N.W.T. (from Rowell, 1989, and B. McLean and J. Nagy, unpubl.)

	% pregnant or lactating (sample size)		
Year	2-year	3-year	4+year
1990	0.0 (9)	15.4 (13)	54.6 (22)
1987	0.0 (9)	20.0 (5)	100.0 (26)
1986	0.0 (10)	67.1 (12)	96.7 (71)
1985	0.0 (8)	75.0 (4)	92.0 (13)
1983	33.3 (6)	100.0 (9)	94.3 (34)
1982	8.3 (12)	84.6 (13)	100.0 (19)

TABLE 2. Calf and yearling percentages of muskoxen, Banks Island (5% has been added to aerial surveys as a correction — see text)

Month/year	Type of survey[1]	Total number classified	% of total animals	Source
		Calves		
July 1989	A	6632	17.7	McLean and Fraser, 1989
July 1987	H	1112	17.0	McLean, unpubl. data
July 1986	H	3894	13.7	McLean, unpubl. data
July 1985	A	5975	16.8	McLean *et al.*, 1986
July 1979	G	1482	14.2	Zoltai *et al.*, 1980
June 1972	A	—	23.1	Urquhart, 1973
June 1971	A	416	25.4	Urquhart, unpubl. data
		Yearlings		
July 1987	H	1112	8.0	McLean, unpubl. data
July 1986	H	3894	12.0	McLean, unpubl. data
March 1979	A	1243	18.2	Vincent, unpubl. data south of 73°N
March 1971	A	565	9.7	Urquhart, unpubl. data

[1]Surveys classified as follows: A = aerial (fixed-wing); H = helicopter-supported ground; G = ground.

TABLE 3. Mean depth and standard deviation of back fat (sample size) measured (cm) from muskox cows taken during commercial harvests on Banks Island, N.W.T., 1985-90

Year/ month	Age of cows (years) 2.0	3.0	4+	Source
90/05	0.7±0.3 (15)	1.0±0.4 (13)	1.0±4.2 (22)	J. Nagy, unpubl. data
87/05	0.0 (4)	0.0 (1)	0.9 (1)	B.McLean, unpubl. data
86/05	0.0 (2)	0.6±0.4 (4)	0.7±0.4 (17)	B.McLean, unpubl. data
85/05	0.5±0.2 (10)	1.4±0.4 (4)	1.6±0.6 (13)	K. Jingfors, unpubl. data

nematode *Ostertagia* spp. increased from 16% in 1983, to 68% in 1985, to 90% in 1986 (Rowell, 1989) and to 84% in 1987 (B. McLean, unpubl. data). Likewise, the proportion of animals with lungworm (*Dictycaulis* spp.) increased in animals taken in the 1986 commercial harvest. The prevalence of lungworm was <5% in the commercial harvests of 1982, 1983 and 1985 but increased to 81% in 1986 and 33% in 1987 (J. Rowell and B. McLean, unpubl. data). Yearling muskoxen seem to be particularly susceptible to lungworm infection. In June 1987, heavy lungworm burdens were carried by 10 yearlings found dead and 5 emaciated yearlings that were shot.

Yersiniosis is a bacterial disease caused by *Yersinia pseudotuberculosis*. The acute and fatal form of the disease in muskoxen appears to be restricted to the muskox high density area of the Thomsen-Muskox river area, where it was first diagnosed in 1986 (Blake *et al.*, 1989), and has been the focus of subsequent studies (B. McLean, unpubl. data).

Weather

May and October snowfalls (Table 4) were significantly different among the three periods, 1956-65, 1966-75 and 1976-85 ($P > 0.05$). The number of years with above average snowfall was highest in 1976-85 and least in 1956-65. There were no years with incidence of freezing rain in October exceeding 3.0 mm from 1956 to 1965, 1 year from 1966 to 1975 and 4 years from 1976 to 1985.

Harvest

The current quota of 2000 muskoxen is assigned to the whole island. The Sachs Harbour Hunters' and Trappers' Committee (HTC) distributes the tags. Hunters from Sachs Harbour took 271 muskoxen in 1989-90 (Inuvialuit Harvest Study, M. Fabijan, pers. comm. 1990). The estimated replacement cost is about $250 000/year, based on an average carcass weight of 90 kg and a beef replacement value of $10/kg.

Table 4. Comparison of May and October snowfall for three 10-year periods, Sachs Harbour, Banks Island, N.W.T.[1]

	May snowfall (mm)			October snowfall (mm)		
	1956-65	1966-75	1976-85	1956-65	1966-75	1976-85
Mean	41.4	106.4	108.1	125.0	199.2	260.2
S.E.	14.0	30.1	47.9	14.4	45.9	51.2
Minimum	8.0	0.0	7.0	76.0	48.0	90.0
Maximum	160.0	295.0	460.0	193.0	442.0	531.0

[1]Data from Atmospheric Environment Service, Environment Canada, Downsview, Ontario.

Sport hunting began in 1980. Non-resident hunters must organize their hunts through an outfitter and must be accompanied by a local guide. In 1989-90, 19 muskoxen were killed on guided hunts. These hunts bring about $3000 into the community for every muskox killed.

In 1981, the Inuvialuit Development Corporation and the Sachs Harbour HTC started commercial harvesting of muskoxen for meat sales in the N.W.T.'s "country food" outlets. Subsequent harvests were conducted to meet Agriculture Canada's inspection requirements for exporting meat across territorial and provincial boundaries. The economic value to the Sachs Harbour HTC of the 470 muskoxen commercially harvested between 1985 and 1987 was $117 600 (T. Beaudoin, pers. comm. 1989).

DISCUSSION

Population Dynamics

The rate of increase of the muskox population on Banks Island between 1972 and 1989 was 0.13 ($r = 0.92$), which is comparable to population growth rates recorded elsewhere. Muskoxen introduced to Nunivak Island, Alaska, increased at an annual rate of 0.14 ($r = 0.99$) between 1949 and 1966 (Spencer and Lensink, 1970). Muskoxen transplanted to Alaska's North Slope between 1969 and 1970 increased at a rate of 0.19 ($r = 0.98$) between 1978 and 1986 (Reynolds, 1986). In west Greenland, a population introduced in 1965 grew at a rate of 0.17 (r = 0.98) between 1965 and 1982 (Thing *et al.*, 1984).

Calving by 3- and 2-year-olds on Banks Island (Rowell, 1989) is indicative of high levels of nutrition and is typical of rapidly increasing populations elsewhere (Jingfors and Klein, 1982; Thing *et al.*, 1987). The breeding interval is usually 1 year in rapidly increasing populations (Reynolds, 1986), although if nutritional status is poor, cows may calve in alternate years or even less frequently (Thing *et al.*, 1987; Gray, 1987). The high pregnancy rates on Banks Island indicate that most cows are calving every year.

Twinning is a rare phenomenon in muskoxen. Dinneford and Anderson (1984) found 4 of 102 pregnant cows to be carrying twins in the rapidly increasing populations of Nunivak and Nelson islands, Alaska. On Banks Island, only 1 of 23 cows examined during the commercial harvest in 1989 was carrying twin fetuses (P. Fraser, pers. comm. 1990). The occurrence of twin fetuses at a rate of less than 1% of the pregnant cows suggests that twinning is not a significant factor in the population dynamics on Banks Island.

Mortality is the least quantified aspect of the population dynamics and is probably as low as 5-7%, based on the observed rate of population increase. Wolves (*Canis lupus arctos*) are rare on Banks Island (Urquhart, 1973; Kevan, 1974; Latour, 1985; McLean *et al.*, 1986; McLean and Fraser, 1989). We suggest that the rarity of wolves may be related to the periodic high numbers of arctic foxes (*Alopex lagopus*) triggering epidemics of rabies and canine distemper, which spread to the wolves. Fox numbers are particularly high on Banks Island even during the low phases of the population cycles (Hiruki and Stirling, 1989). The scarcity of wolves suggests that at current muskox densities, wolves are not a significant cause of mortality and predation is currently unimportant in regulating the muskox numbers.

The harvest is currently less than 2% of the estimated population size and, therefore, not a significant limiting factor. Expansion of the commercial harvests to reduce the size of the population has been promoted as a management tool (Gunn *et al.*, 1989a). A fully developed commercial harvest will require establishment of markets, large investments in capital equipment and greater efficiency in procurement, processing and transportation. Investment is risky because of the uncertainty about the stability of population numbers and runs the additional risk of creating a momentum for harvesting even if a population decline becomes apparent.

Our understanding of the role of diseases and parasites in the population dynamics of muskoxen is rudimentary and possibly underestimates their significance. Muskoxen occur at high densities, graze intensively, taking in large volumes of forage, and show marked fidelity to seasonal ranges. Those attributes favour the transmission of diseases or parasites such as yersiniosis or lungworm, with infective stages dependent on being ingested with forage.

Weather

We suspect that the most significant long-term factor in muskox ecology on Banks Island may be weather. In Greenland and on the High Arctic islands, winter thaws, icing conditions and deep snow reduce forage availability, causing malnutrition and leading to low productivity and high mortality (Vibe, 1967; Parker *et al.*, 1975; Miller *et al.*, 1977; Gray, 1987). Relatively minor and short-lived weather events can potentially have prolonged and cascading population effects. For example, Albon *et al.* (1987) showed for red deer (*Cervus elaphus*) that temperature during the last two months of gestation affects the entire cohort's birth weight, age at first reproduction, survivorship during adulthood, as well as the birth weights of the next generation. The result was a fivefold difference in the number of surviving young produced by cohorts born after differing temperature regimes.

The effects of weather on the population dynamics of Banks Island muskoxen are difficult to determine. First, the significant factors may be subtle and transitory. Second, weather records are few. Sachs Harbour is the only weather station on Banks Island and weather records only start in 1954. And last, the sensitivity of muskoxen to various weather conditions is poorly understood (Gunn *et al.*, 1989b). We chose May and October snowfalls as snowfall peaks in those two months (Maxwell, 1980), but relating standard meteorological measurements to muskox ecology is problematic in the absence of detailed studies. The climate may be changing on Banks Island. Since the early 1960s, spring snow disappearance has been occurring earlier in the western Arctic (Foster, 1989) and warmer winters tend to be snowier (Barry, 1982). Total snowfall for Sachs Harbour during the months of October and May (Table 4) and the incidence of freezing rain have increased in the 1970s and 1980s compared to the 1960s.

Some mortality of muskoxen on Banks Island can be related anecdotally to particular weather events. For example, the low percentage of yearlings seen in March 1971 (Table 2) coincided with above average snowfalls both in winter 1970 and in the previous spring, when these calves were born (AES data). The proportion of muskox calves was low in July 1986 and animals in the May 1986 harvest were thin (Tables 2 and 3). Snowfall recorded at Sachs Harbour was above average in May 1986 and the melt was unusually late. At Mould Bay, Prince Patrick Island (the nearest weather station to northern Banks Island), however, the October 1985 snowfall was the record amount (38.6 cm) for the recorded period (1948-89), which may indicate that snowfall was also heavy on northern Banks.

During the aerial survey of June 1989, 120 dead muskoxen were counted (McLean and Fraser, 1989) on northern Banks Island. Those deaths may have been caused by malnutrition from forage unavailability. Heavier snowfall than usual on northern Banks Island is suggested by above average snowfall in October 1988 and May 1989 for Mould Bay.

Considerably more work needs to be done to determine long-term trends in weather patterns and in relating weather conditions to patterns in mortality and reproduction. We suggest that the severity of winter snow conditions may dominate annual mortality but plant phenology and duration of the plant growing season may dominate reproductive rates (assuming a tight relationship between physical condition and reproduction, such as Thomas [1982] recorded for caribou). In some years, the effects of winter weather on physical condition could conceivably override the effects of plant phenology and growing season.

Interspecific Interactions

Most Sachs Harbour hunters believe that increasing muskox numbers have caused the decline in Banks Island caribou from 11 000 in 1972 (Urquhart, 1973) to 2700 ± 340(S.E.) in 1989 (McLean and Fraser, 1989). Some possible mechanisms are competition for food resources and the behavioural displacement of caribou from favoured feeding areas.

Differences in dentition, digestive anatomy and body size predict that the two species have different feeding habits. Muskoxen are better adapted to utilizing large volumes of relatively coarse material, which they digest very efficiently (R.G. White, pers. comm. 1989), compared to caribou, which tend to be "concentrate selectors" (Hofmann, 1989). The two species do not usually use the same habitats or have the same food habits (Wilkinson *et al.*, 1976; Parker and Ross, 1976; Parker, 1978; Thomas and Edmonds, 1984). Winters with deep, hard and prolonged snow or ice cover will, however, force muskoxen to forage on exposed slopes and ridges where caribou usually feed (Parker, 1978; Thomas and Edmonds, 1984). Overlap in diet does not necessarily confirm the existence of ecological competition since the resource used by one species must be limiting to the other for competition to occur. There is no evidence of competition between muskoxen and caribou, but a practical method for establishing its non-occurrence has not been devised.

The feeding behaviour of caribou might give the impression that muskoxen are physically displacing caribou. Caribou feed on the move, briefly pausing to take a bite before moving on. Muskoxen are sedentary and feed intensively in one location. When seen together, caribou are more likely to be seen to move away by virtue of their feeding behaviour, giving the impression that they are being displaced.

Range Condition

Little is known about responses of arctic vegetation to grazing and browsing. Low densities of muskoxen increased the productivity of grazed sedge meadows on Ellesmere Island (Henry and Svoboda, 1989). Sedges and grasses have a large proportion of their biomass below ground, as do some willows (Chapin *et al.*, 1980), which increases their resilience to grazing and browsing. However, questions remain, such as the responses of forbs and willows to grazing and browsing and the effect of weather on their resilience to grazing and on their nutritional quality.

Population Limitation

Population ecologists conceptually differentiate among limiting factors whose effects are or are not influenced by population density. The theoretical significance of this differentiation is critical since the relative importance of density-dependence and independence determines whether the population will fluctuate randomly or in some predictable manner. In practice, it is difficult to determine whether a particular factor acts density-independently or -dependently (Begon and Mortimer, 1981) and whether the population is actually being limited in a density-dependent manner (e.g., Solow and Steele, 1990). Some speculative conclusions can nevertheless be derived.

Forage is the ultimate density-dependent factor in the population dynamics of herbivores. Caughley (1970) described four sequential stages in an entirely density-dependent relationship between plants and plant-eaters: 1) initial rapid increase in animal numbers, 2) decline in plant biomass and temporary stabilization in animal numbers, 3) rapid decline in animal numbers, and 4) a series of smaller fluctuations in plant biomass and animal numbers. This generalized pattern may apply to the muskox population on Banks Island. Population growth has been rapid since about 1970, corresponding to Caughley's rapid increase phase. Since the mid-1980s, productivity has declined, mortality of calves and yearlings has increased, and parasitism has become more prevalent. The validity of each of these conclusions might be questioned individually but in concert they indicate that the population is now entering Caughley's initial stabilization phase. The prediction from Caughley's model is that the population will next move to the rapid decline phase. The transition from undergrazed to overgrazed vegetation can be rapid and can be triggered by poor weather (Noy-Meir, 1981). Sudden vegetation responses could drive a relatively slow, density-dependent decline of a herbivore into an abrupt and unpredictable decline.

Weather is the archetypal density-independent population-limiting factor, but it can also subtly influence and interact with other density-dependent factors. The increasing frequency of freezing rain events and increasing snowfall could reduce forage availability, which would account for the decline in productivity of 3-year-old cows and decreased survival of calves and yearlings. Decreased forage availability and consequent poor condition probably would increase susceptibility to parasitism.

Our appreciation of the relative significance of density-dependent and -independent population factors would be aided by a better understanding of the size of Banks Island muskox populations in the latter half of the 19th century, the causes for the decline in Banks Island muskoxen around the turn of the century, and why it took Banks Island muskoxen more than half a century to recover.

The large bone assemblages at the late-19th-century archaeological sites suggest that muskox populations were substantial at that time. Will (1984) suggests that the population might have been as large as contemporary estimates. However, examination of journals from members of the *Investigator*'s crew suggests that muskoxen were uncommon on the north end of the island (Barr, 1989). Stefansson (1921) attributed the disappearance of Banks Island muskoxen to overhunting by the Copper Inuit. However, it seems unlikely that muskoxen could have been exterminated over the entire 70 000 km^2 of the island. The simultaneous decline of muskoxen on Victoria Island (Gunn, 1990) argues for a more widespread cause, such as weather. In 1939, Billy Banksland, who had guided Stefansson, remarked: "All the muskoxen are gone. They died out long ago when the rains came and froze on the land, covering the grass with a mantle of ice leaving nothing for them to eat" (de Coccola and King, 1986:334).

Muskoxen are capable of doubling their populations every 5 years, yet they remained rare on Banks Island for nearly 60 years. One possibility is that muskoxen became extinct on Banks Island around the turn of the century and population recovery awaited a fortuitous colonization event, perhaps from Victoria Island. Another possibility is that wolves kept muskox numbers from increasing. If wolf numbers were maintained by a healthy caribou population, even the occasional instance of a wolf killing a muskox could have kept muskoxen rare or slowed their recovery. A third possibility is that high muskox populations in the last century might have degraded the vegetation to such a degree that recovery required decades. Caughley *et al.* (1987), in their study of the dynamics of kangaroos and vegetation, described the difference in the scales of time for the plants compared to the herbivores. This difference would likely be even more pronounced in the Arctic, where the vegetation is dominated by perennials.

Are There Too Many Muskoxen on Banks Island?

Whether Banks Island is overpopulated with muskoxen is largely a judgement that will vary with value systems. Local people at Sachs Harbour believe that the large muskox population is causing a decline in caribou, which are valued more than muskoxen. Some people have stated that there are too many muskoxen "for their own good" and that individual muskoxen will suffer increasingly from disease, parasitism and starvation. This concept implies responsibility for "quality of life" for wild animals in relation to our anthropocentric standards of acceptability. Others believe that the large numbers of muskoxen indicate that the system is out of ecological equilibrium, which will result in catastrophic and irreversible consequences, such as extinction and range destruction. The problem may be our perception of equilibrium and the short acquaintance with the system rather than the dynamics of the weather-muskox-vegetation system.

Management

Local residents have long been in favour of a management reduction in the muskox population to reduce competition with caribou. The Government of the Northwest Territories has chosen not to intervene in this manner because of the enormous costs and logistical problems (Shank, 1990), the uncertainty about future muskox population trends and hesitation to accept the competition hypothesis. A workshop was held during the Second International Muskox Symposium to address desirability of intervention. The participants agreed on the inadvisability of population reduction measures (Gunn *et al.*, 1989b) but did suggest that steps could be taken to encourage increased harvesting and monitoring of the muskoxen.

The quota was raised to 5000 in 1990 and the Inuvialuit Development Corporation is working to establish markets for an increase in commercial harvesting. Current management continues to depend on monitoring the trend of population size and survival of the first three cohorts using standardized systematic aerial and sex-age composition surveys respectively. Further data on productivity, condition and prevalence of parasites and disease will be acquired through monitoring of commercial harvests.

Caughley *et al.* (1987) introduced the term "centripetality" instead of "stability" to emphasize that the factors displacing the system may be sufficiently multidirectional and forceful to prevent the reaching of equilibrium. Caughley *et al.* (1987) described a kangaroo-plant system with rainfall as the driving force, which has parallels with the role of weather in arctic ecosystems. The parallel suggests that arctic ecosystems are unlikely to be stable and that long-term fluctuations in their mammal populations are inevitable. The challenge will be to adapt our management, including harvest strategies, to these long-term fluctuations.

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