

Calf Production, Calf Survival, and Recruitment of Muskoxen on Banks Island during a Period of Changing Population Density from 1986–99

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ABSTRACT. Population estimates for muskoxen (*Ovibos moschatus*) (age > 1 year) on Banks Island increased from 29 168 (SE 2104) in 1985 to a peak of 64 608 (SE 2009) in 1994 and then declined to 45 833 (SE 1938) in 1998. From 1986 to 1999, annual sex and age classification surveys of muskoxen were conducted during summer. We estimated calf production (number of calves per 100 females aged 2 years or more), calf survival, and recruitment (number of yearlings per 100 females aged 2 years or more). Calf production ranged from 31.3 to 56.3 and was similar between periods of increasing and decreasing density (mean = 42.3 vs. 40.8). Calf survival ranged from 23% to 83% and was generally higher while density was increasing than during its decline (mean = 60 vs. 45). Survival at a given density was lower following the 1994 peak in density. Recruitment ranged from 10.0 to 41.7 and was higher ($p = 0.06$) during the period of increasing density than during the decline (mean = 28.0 vs. 17.2). Calf survival and recruitment were lowest following two consecutive severe winters, but animal density explained more of the variation in survival and recruitment than did late-winter snow depth. There was a positive relationship between the proportion of sedge (*Carex* spp., *Eriophorum scheuchzeri*) in the summer diet and calf survival and recruitment. Patterns of calf survival and recruitment plotted against density were consistent with those modelling a density-dependent relationship. Our results suggest that severe weather alone cannot explain the fluctuations in the population dynamics of Banks Island muskoxen and that underlying density-dependent responses acting upon calf survival and recruitment offer an alternative explanation.

Key words: demography, forage, muskoxen, Northwest Territories, *Ovibos moschatus*, population, weather

RÉSUMÉ. Les estimations de population du bœuf musqué (*Ovibos moschatus*) [âge ≥ 1 an] sur l'île Banks ont augmenté de 29 168 (erreur-type 2104) en 1985 à une valeur crête de 64 608 (erreur-type 2009) en 1994 pour ensuite décliner jusqu'à 45 833 (erreur-type 1938) en 1998. De 1986 à 1999, on a procédé en été à des relevés annuels de classification par sexe et par âge des bœufs musqués. On a estimé la production de veaux (nombre de veaux par 100 femelles de 2 ans ou plus), la survie des veaux et le recrutement (nombre de petits d'un an pour 100 femelles de 2 ans ou plus). La production de veaux allait de 31,3 à 56,3 et était semblable durant la période d'augmentation et celle de diminution de densité (moyennes de 42,3 et 40,8 respectivement). La survie des veaux allait de 23 à 83 p. cent et était généralement plus élevée quand la densité augmentait que pendant son déclin (moyennes de 60 et 45 respectivement). La survie pour une densité donnée était plus faible après la crête de densité de 1994. Le recrutement allait de 10,0 à 41,7 et était plus élevé ($p = 0,06$) pendant la période d'augmentation de densité que pendant son déclin (moyennes de 28,0 et 17,2 respectivement). La survie des veaux et le recrutement étaient les plus faibles après deux hivers rigoureux, mais la densité des animaux expliquait mieux la variation dans la survie et le recrutement que l'épaisseur de la neige à la fin de l'hiver. Il y avait une relation positive entre la proportion de carex (*Carex* spp, *Eriophorum scheuchzeri*) dans l'alimentation estivale et la survie des veaux ainsi que le recrutement. Les tendances dans la survie des veaux et le recrutement tracées en fonction de la densité donnaient des courbes en accord avec celles représentant un modèle variant avec la densité. Nos résultats suggèrent que la rigueur du climat ne peut à elle seule expliquer les fluctuations dans la dynamique de la population du bœuf musqué de l'île Banks et que des réactions fondamentales variant avec la densité qui influent sur la survie des veaux et le recrutement offrent une autre explication.

Mots clé: démographie, fourrage, bœufs musqués, Territoires du Nord-Ouest, *Ovibos moschatus*, population, climat

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INTRODUCTION

Historically, muskoxen (*Ovibos moschatus*) on both the mainland and the High Arctic islands of the Northwest Territories experienced drastic fluctuations in numbers

(Barr, 1991). Historical declines have been attributed to overexploitation by humans and severe weather (Barr, 1991; Reynolds, 1998), but the data needed to address these factors critically are lacking. Most population studies of muskoxen have been limited to descriptions of either

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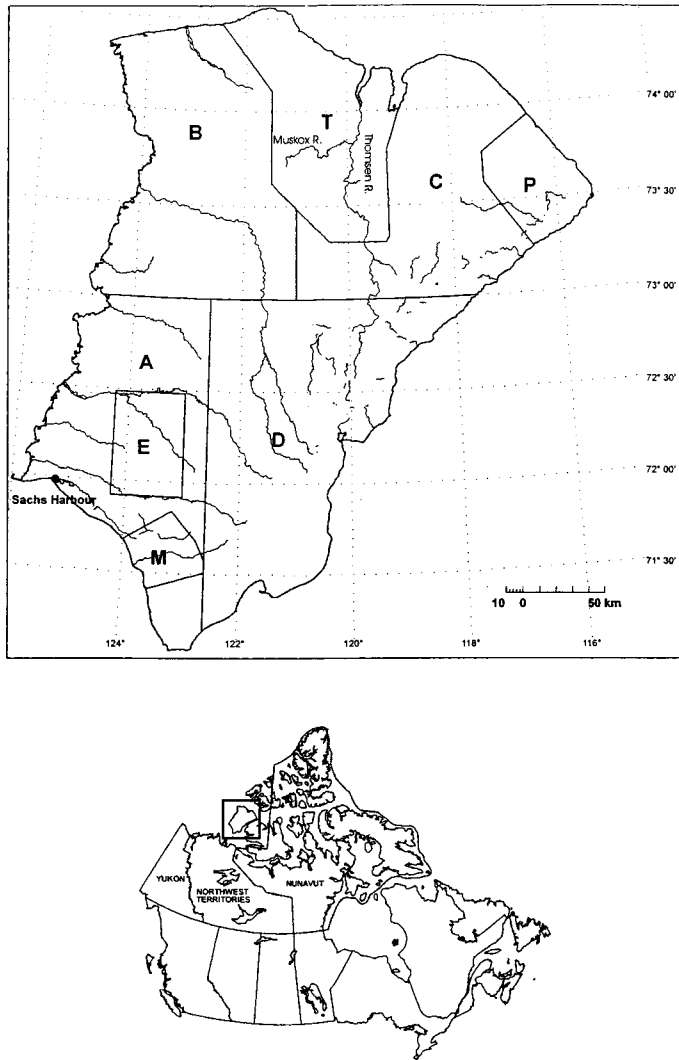


FIG. 1. The study area, Banks Island, showing the eight different strata: A, B, C, D, Egg (E), Masik (M), Parker (P), and Thomsen (T).

current status (Case et al., 1989; Smith, 1989; Yakushkin, 1989; Boertmann et al., 1992; Gunn, 1995) or changes in population numbers, providing little additional demographic data (Le Hénaff and Crête, 1989; Gunn et al., 1991; Olesen, 1993). Extended time series of population data for muskoxen are limited (Reynolds, 1998).

Recently, populations of muskoxen worldwide have increased dramatically (Smith, 1989). Re-established and introduced populations have increased in Quebec (Le Hénaff and Crête, 1989), Alaska (Reynolds, 1998), West Greenland (Olesen, 1993), and Russia (Yakushkin, 1989). Indigenous populations in Greenland (Boertmann et al., 1992) and in the Northwest Territories have also increased (Barr, 1991; Nagy et al., 1996). The population of muskoxen on Banks Island, Northwest Territories, which represents a substantial proportion of worldwide muskoxen numbers, has undergone a spectacular increase. From an estimated 3800 animals (age >1 year) in 1972 (Urquhart, 1973), the population increased exponentially at ca. $r = 0.12$ until 1994, when numbers peaked at 64 608 (SE 2009) (Larter

and Nagy, 1997). Since 1994, numbers have declined: the 1998 estimate was 45 833 (SE 1938) (J. Nagy and M. Branigan, unpubl. data).

Reynolds (1998) described the population dynamics and range expansion of a re-established population of muskoxen in northeastern Alaska from 1977 to 1995. The population increased and declined, but never exceeded 1000 animals. Calf production declined over time, and both calf production and calf and yearling survival were negatively correlated with snow depth in late spring. Sex- and age-classification surveys of muskoxen have been conducted annually on Banks Island since 1986 (Larter and Nagy, 1999). More recent studies have documented such factors as seasonal diet (Larter and Nagy, 1997), overwinter changes in health and condition of muskoxen (Larter and Nagy, 2001a), and winter foraging behaviour (Larter and Nagy, 2001b). These data provide the opportunity to describe the demography of the world's largest indigenous population of muskoxen over a 14-year period in which animal densities increased, peaked, and declined. Whether or not the population has exhibited some stages of the classic ungulate eruption described by Riney (1964) and Caughley (1970) is open to debate. However, the interactive model of population growth that these studies described predicts that calf production and overwinter survival will be high when population is increasing and lower when it is stabilizing or declining. Since less forage is available per capita during periods of high density, the result is lower recruitment following peak population density.

We hypothesized that there would be an underlying, density-dependent response by the muskox population that would be expressed in reduced calf production, calf survival, and/or recruitment after peak density. Alternatively, with no underlying density-dependent response, calf production, calf survival, and recruitment would be more related to winter weather conditions than to population density. Here we examine the relationships between population density and calf production, calf survival, and recruitment. We discuss these relationships in the context of winter weather conditions and summer diet.

STUDY AREA

Banks Island, the westernmost island in the Canadian Arctic Archipelago, covers approximately 70 000 km² (Fig. 1). The climate is Arctic Maritime along coastal areas, where weather stations are located, tending toward Arctic Desert inland (Zoltai et al., 1980). Winters are long and cold: mean monthly temperatures are below 0°C from September through May, and mean minimum daily temperatures range from -30° to -40°C from December to March. Summers are short and cool, with mean maximum daily temperatures ranging from 5° to 10°C from June through August. There is little precipitation, an annual mean of 9 cm (Zoltai et al., 1980). Sachs Harbour (population 125) is the only permanent settlement on the island.

Habitat descriptions were adapted from Kevan (1974), Wilkinson et al. (1976), and Ferguson (1991). There are four major terrestrial habitats: wet sedge meadow (WSM), upland barren (UB), hummock tundra (HT), and stony barren (SB). WSM is generally level hydric and hygric lowland characterized by *Carex aquatilis*, *Eriophorum scheuchzeri*, and *Dupontia fisheri*. UB is well drained and found on the upper and middle parts of slopes; its vegetation is dominated by *Dryas integrifolia* and *Salix arctica*. HT is found on moderately steep slopes and is characterized by individual hummocks, which are vegetated primarily by dwarf shrubs (*D. integrifolia*, *S. arctica*, and *Cassiope tetragona*). SB has a coarse, gravelly substrate and sparse vegetation. This habitat is found on windblown areas, ridges, and gravel and sand bars. A more detailed description of the flora of Banks Island can be found in Wilkinson et al. (1976), Porsild and Cody (1980), and Zoltai et al. (1980).

Muskoxen and Peary caribou (*Rangifer tarandus pearyi*) are the dominant resident herbivores. During summer, there is a substantial population of nesting snow geese (*Chen caerulescens*). The major resident predators are arctic wolves (*Canis lupus arctos*), polar bears (*Ursus maritimus*), and arctic foxes (*Alopex lagopus*). Muskoxen are harvested both commercially and for subsistence. Since 1988, the annual subsistence harvest has been fewer than 300 animals. Large-scale commercial harvests of muskoxen were conducted in 1991 (2031 animals), 1992 (1798), 1993 (738), and 1997 (1300). The harvests were conducted in both the Egg and the Masik strata, on the southern part of the island (Fig. 1), with approximately half of the animals coming from each area.

METHODS

Sex and Age Classification Surveys

Muskoxen on Banks Island generally calve during April and early May, and most calves are born by mid-May (Latour, 1987). Body size, pelage, and horn development are sufficiently different between the sexes to identify the sex and age of the four most recent cohorts of muskoxen in the field (Tener, 1965; Henrichsen and Grue, 1980; Olesen and Thing, 1989). Classification surveys identified calves, yearlings, 2-year-old females and males, and females and males aged 3 years or more. Surveys were conducted annually from 1986 to 1999. Eight of the 14 surveys were conducted in June, and all took place between 13 June and 12 August. We acknowledge that calf mortality occurs during this period and may bias the results; however, we deemed classification surveys conducted during this 2-month period as suitably comparable. All classification surveys (except in 1990) were conducted by helicopter to maximize coverage. After groups of muskoxen were located from the air, the survey crew was positioned by helicopter out of the animals' line of sight and subse-

quently viewed the animals with a spotting scope. The 1990 classification survey, part of a larger field operation, was ground-based. Groups of muskoxen were classified with spotting scopes or binoculars whenever encountered. A more detailed accounting of each classification survey can be found in Larter and Nagy (1999). Classification surveys were conducted mostly in areas of high muskox density. From 1986 to 1990, they were conducted primarily in the Thomsen stratum in the north, and from 1991 to 1998, primarily in the Egg and Masik strata in the south (Fig. 1). In 1999, all three high-density areas were surveyed.

Population Estimates

Island-wide censuses were conducted on Banks Island during the summers of 1985, 1989, 1991, 1992, 1994, and 1998 to estimate muskox and Peary caribou population sizes. Censuses were conducted using fixed-wing aircraft and strip-transect techniques with a stratified design; the transect was the sampling unit (Norton-Griffiths, 1978). Beginning in 1992, the island was stratified into eight strata on the basis of muskox density (determined from previous surveys) and geographic area (see Fig. 1). Percent coverage was 20% for all strata except the Egg and the Masik, where coverage was 40%. Prior to 1992, the number and locations of strata varied, and percent coverage varied from 5% to 20% (Nagy et al., 1996). For all population surveys, transect lines were flown at fixed altitudes, and animals were counted within fixed strips on either side of the aircraft. Markers were placed on the aircraft wing struts to bound the strips (following Norton-Griffiths, 1978). Altitude and strip width varied between population surveys (120–180 m above ground level; 0.5–0.6 km wide) but did not vary within a survey. All raw data from population surveys prior to 1992 were reanalyzed using the eight strata (Nagy et al., 1996). Population estimates for all years were derived by the Jolly (1969) method for unequal-sized sampling units.

We calculated the instantaneous rate of population growth (r) for whole-island and strata populations between population surveys following Caughley (1977). We used r to interpolate whole-island and stratum population size for those years between population surveys, which provided whole-island and stratum population estimates for 1985–99. This calculation assumed a constant r between censuses. Animal density for 1985–99 was derived from these data; it was calculated for the entire island and for each stratum by dividing the estimated population size by the total area of the island or the stratum (Table 1).

Estimating Calf Production, Calf Survival, and Recruitment

Information collected during commercial harvests of muskoxen in the early 1990s indicated ca. 30% pregnancy in 2-year-old females (J. Nagy, unpubl. data). Therefore, we defined adult females as females aged 2 years or more.

TABLE 1. Population estimates (N) of animals (age ≥ 1 year), density (animals/km²), calf production (calves per 100 adult females, age ≥ 2 years), calf survival (%), and recruitment (yearlings per 100 adult females, age ≥ 2 years) for all Banks Island and for the three high-density strata, Thomsen, Egg, and Masik. Calf survival is reported in the year winter started.

	Banks Island					Thomsen					Egg					Masik				
	N	Dens.	Prod.	Surv.	Recr.	N	Dens.	Prod.	Surv.	Recr.	N	Dens.	Prod.	Surv.	Recr.	N	Dens.	Prod.	Surv.	Recr.
1985 ¹	29 168	0.42				12 883	1.51				1342	0.50				933	0.68			
1986	31 014	0.44	34.2	70	29.4	12 449	1.46	28.8	85	21.3	1539	0.58				1165	0.85			
1987	32 834	0.47	50.8	77	23.9	12 029	1.41	55.0	71	24.5	1764	0.66				1455	1.06			
1988	34 761	0.49	46.7	23	39.3	11 624	1.37	46.7	23	39.3	2022	0.76				1817	1.32			
1989 ¹	37 046	0.53	40.7	48	10.7	11 257	1.32	40.7	48	10.7	2411	0.91				2524	1.84			
1990	41 603	0.59	38.8	80	19.7	12 080	1.42	38.8		19.7	3057	1.15				3081	2.25			
1991 ¹	48 704	0.67	45.8	83	30.8	13 030	1.53				4120	1.55	44.7	54	31.9	3923	2.86	51.2	93	31.0
1992 ¹	52 959	0.75	51.2	81	38.0	15 737	1.85				4354	1.64	48.5	86	24.2	2684	1.96	52.5		47.5
1993	58 223	0.83	33.3	55	41.7	18 607	2.19				4701	1.77	33.3	73	41.7	3217	2.34			
1994 ¹	64 608	0.92	38.9	35	18.1	22 665	2.66				5105	1.92	45.2	21	24.2	3994	2.91	33.3	32	13.5
1995	59 065	0.84	31.3	40	10.0	18 930	2.22				4617	1.73	29.3	35	9.4	3507	2.56	32.4	48	10.6
1996	53 997	0.77	56.3	33	12.7	15 810	1.86				4177	1.57	54.9	41	10.5	3079	2.24	57.9	25	15.5
1997	49 364	0.70	38.1	57	18.7	13 205	1.55				3778	1.42	43.2	47	22.7	2703	1.97	33.3	71	14.6
1998 ¹	45 833	0.65	47.2	49	21.8	11 726	1.37				3438	1.30	45.9	72	20.3	2452	1.73	48.5	92	23.4
1999	41 901	0.60	31.3		23.0	9794	1.15	36.2		26.1	3110	1.17	29.7		21.2	2153	1.57	21.7		20.0

¹ Indicates years when population surveys were conducted. N was estimated for other years by determining r and assuming constant annual growth between survey years.

We determined the total number of calves observed per 100 adult females from each classification survey. We realize that these data do not address neonatal mortality, but we believe this measure provides conservative estimates of calf production that are comparable over the 14-year period. We estimated calf survival by dividing the number of yearlings per 100 adult females by the number of calves per 100 adult females from the previous year. This estimate assumed that female recruitment matched adult female losses. We used the number of yearlings per 100 adult females to estimate recruitment.

We derived estimates of calf production, calf survival, and recruitment on an island-wide basis so that we could assess the relationship with density expressed over the 14-year period during which the Banks Island population increased, peaked, and declined. These estimates were determined from classification surveys conducted in areas of known high density because it was assumed that any effects of density would occur in those areas. We also calculated the same demographic data and assessed their relationships with density for each stratum surveyed: Thomsen, Egg, and Masik.

We compared estimates of calf production, calf survival, and recruitment during periods of increasing density (1986–94) and decreasing density (1995–99), using a one-way ANOVA. (Calf survival estimates for 1994–95 are included within the period of increasing density.) We used correlation analysis to explore the relationships between density and calf production, calf survival, and recruitment.

Winter Snow Measures

We defined severe winter as freezing rains in early winter that caused die-offs of caribou. Accounts of severe

winter weather events prior to winter 1992–93 have been documented previously (Nagy et al., 1996). We documented severe winter weather events from 1993 to 1999.

Reynolds (1998) found calf and yearling survival were negatively correlated to late-winter snow depth. Since muskoxen on Banks Island typically feed in wet sedge meadows (WSM) during winter (Larter and Nagy, 2001b), we used mean snow depth in WSM during late winter as an index of relative winter severity. From 1994 to 1998, we measured snow depth in WSM annually between 20 April and 4 May. Ten stations were located along fixed transects. At each station, we took seven measurements of snow depth, two with a snow tube and five with a Rammsonde penetrometer. In 1993, we were limited to five measurements with a snow tube, taken at two stations in WSM on 21 March.

We used multiple regression analysis (Neter and Wasserman, 1974) to determine whether the independent variables (snow depth in late winter and density) explained significant variation in dependent variables (calf production, calf survival, or recruitment) from 1992–93 to 1997–98.

Diet Composition

Composite samples of fresh (< 4 h old) faeces from three to five individual pellet groups were collected from groups of muskoxen during June, July, and August from 1993 to 1996. Larter and Nagy (1997) found more variation in diet composition between groups than within any group and deemed that sampling groups would give a better measure of the diet over a larger portion of the population. As part of a separate study, samples were collected from groups of muskoxen residing in areas where density was high (ca. 1.6–1.9/km²) and low (ca. 0.3–0.4/km²), but for the purposes of this study we present only

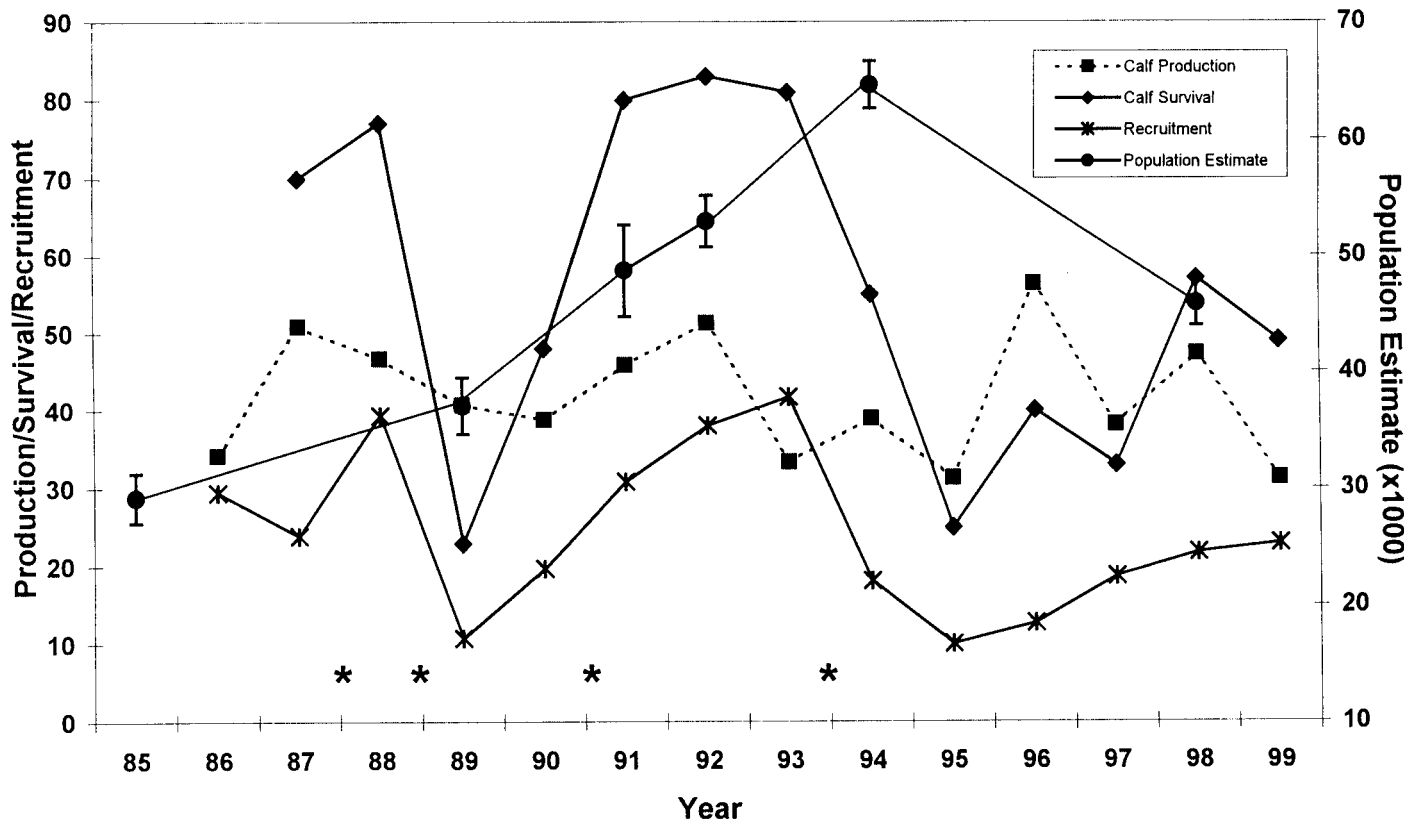


FIG. 2. Annual muskox calf production (number of calves per 100 adult females, age ≥ 2 years), calf survival (%), recruitment (number of yearlings per 100 adult females, age ≥ 2 years), and estimated (\pm SE) muskox population (age ≥ 1 year) for Banks Island from 1985–99. An asterisk (*) indicates a severe winter.

data from the high-density area. Four to ten groups, representing between 73 and 165 individuals, were sampled each month.

Faecal samples were thawed, air-dried for 24 hours, oven-dried at 60°C for 48 hours, and ground through a 1 mm screen with a centrifugal mill. Subsamples (1 g) were forwarded for analysis to the Composition Analysis Laboratory, Ft. Collins, Colorado. Diet composition was determined by analyzing plant fragments (Sparkes and Malechek, 1968) according to Hansen et al. (1976). The microhistological technique has inherent limits, such as an inability to separate some species and a limited percent of identifiable fragments in the slides (Johnson et al., 1983; Barker, 1986). We deemed this method suitable because (1) differing proportions of forage classes, not changes in individual species composition, were of importance; (2) this method had been used previously with muskoxen from Banks Island; and (3) previous work had shown negligible amounts of unidentifiable fragments (Larter and Nagy, 1997). Diet was separated into the following forage classes: sedge (*Cyperaceae*), willow (*Salix arctica*), grass (*Gramineae*), rose/saxifrage (*Rosaceae* and *Saxifragaceae*), legume (*Leguminosae*), lichen (*Cetraria* spp., *Cladonia* spp., *Cladina* spp., *Peltigera* spp., and *Thamnolia subuliformis*), and other (other forbs, moss, and *Equisetum* spp.). For this study, we present data for sedges and willows separately but lump the remaining classes into a third category called “other.”

Summer diet composition was determined by pooling the monthly dietary components of each group, weighted by the number of individuals per group. Because of the lack of independence between forage-class proportions, we conducted parametric tests only on the sedge component, which was deemed to be the most important forage for muskoxen (Larter and Nagy, 1997). We used a one-way ANOVA to test for interannual differences in the sedge component of the diet and the Tukey test to identify these differences ($\alpha = 0.05$). We used correlation analysis to test for any relationships between summer sedge and calf production, calf survival, and recruitment.

RESULTS

Population Estimates

Island-wide and individual-stratum population and density estimates from all censuses from 1985 to 1998 are presented in Table 1. We defined the period of increasing density as 1986–94 and the period of decreasing density as 1995–99 (Fig. 2). In the Thomsen stratum, animal density was relatively stable from 1986 to 1990 (1.32–1.46/km²; Table 1) and then showed the same pattern of increase to 1994 and subsequent decline as did island-wide estimates. In the Egg stratum, animal density mirrored island-wide estimates from 1986 to 1999, increasing, peaking, and

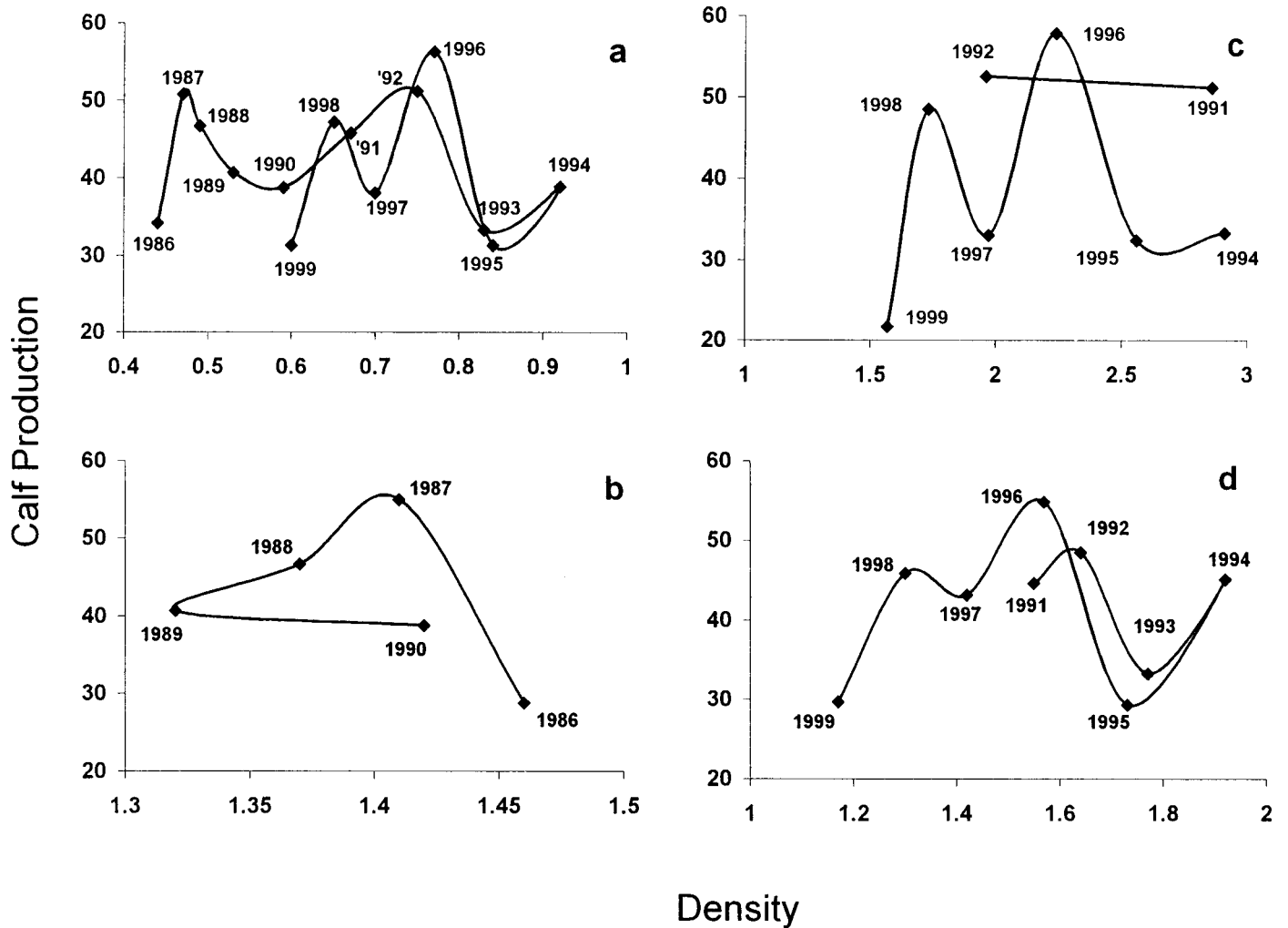


FIG. 3. Relationships between calf production (number of calves per 100 adult females, age ≥ 2 years) and animal density (muskoxen per km^2): a) island-wide, 1986–99; b) Thomsen area, 1986–90; c) Masik area, 1991–99 (note no data for 1993); and d) Egg area, 1991–99.

declining. In the Masik stratum, density increased from 1986 to 1991 and decreased from 1994 to 1999, showing variability between 1991 and 1994 (Table 1).

Calf Production and Calf Survival

Calf production showed considerable interannual variability with no relationship with density over the 14 years (range: 31.3–56.3 calves per 100 adult females; $r = -0.11$, $p = 0.71$) (Figs. 2 and 3a; Table 1). Substantial variability and a lack of relationship occurred during periods of increasing density ($r = -0.19$, $p = 0.63$) and decreasing density ($r = 0.09$, $p = 0.88$). Calf production island-wide was similar ($p = 0.76$, $F_{(1,12)} = 0.1$) in periods of increasing and decreasing density (mean = 42.3 versus 40.8 calves per 100 adult females). We found a similar lack of relationship between density and calf production in the three individual strata (Fig. 3b–d).

Calf survival showed considerable interannual variability (range 23–83%) (Figs. 2 and 4a; Table 1). Although survival was not significantly different between periods of increasing

and decreasing density (mean = 60 vs. 45%, respectively; $p = 0.25$, $F_{(1,11)} = 1.5$), survival was higher at similar density during the increasing phase than during the decline. Survival showed a decreasing trend prior to peak density (Fig. 4a). If data collected prior to 1990–91 (largely associated with the severe winters) are excluded, there is a significant negative relationship between calf survival and density ($r = -0.88$, $p < 0.05$), and calf survival is higher ($p < 0.01$, $F_{(1,8)} = 19.5$) before peak density than afterwards. Survival has shown moderate increases since the 1994 density peak, but it has remained below the levels reached at comparable densities while the population was increasing (Fig. 4a).

Calf survival and density were negatively related over a wide range of density in the Egg ($r = -0.40$, $p = 0.32$) and Masik ($r = -0.30$, $p = 0.56$) strata, but they were positively related over a limited range of density in the Thomsen stratum ($r = 0.73$, $p = 0.27$; Figs. 4b–d). Calf survival showed increases in both the Masik and Egg strata subsequent to peak density. The pattern of density versus calf survival for the Egg stratum is consistent with that of a density-dependent relationship (Fig. 4d).

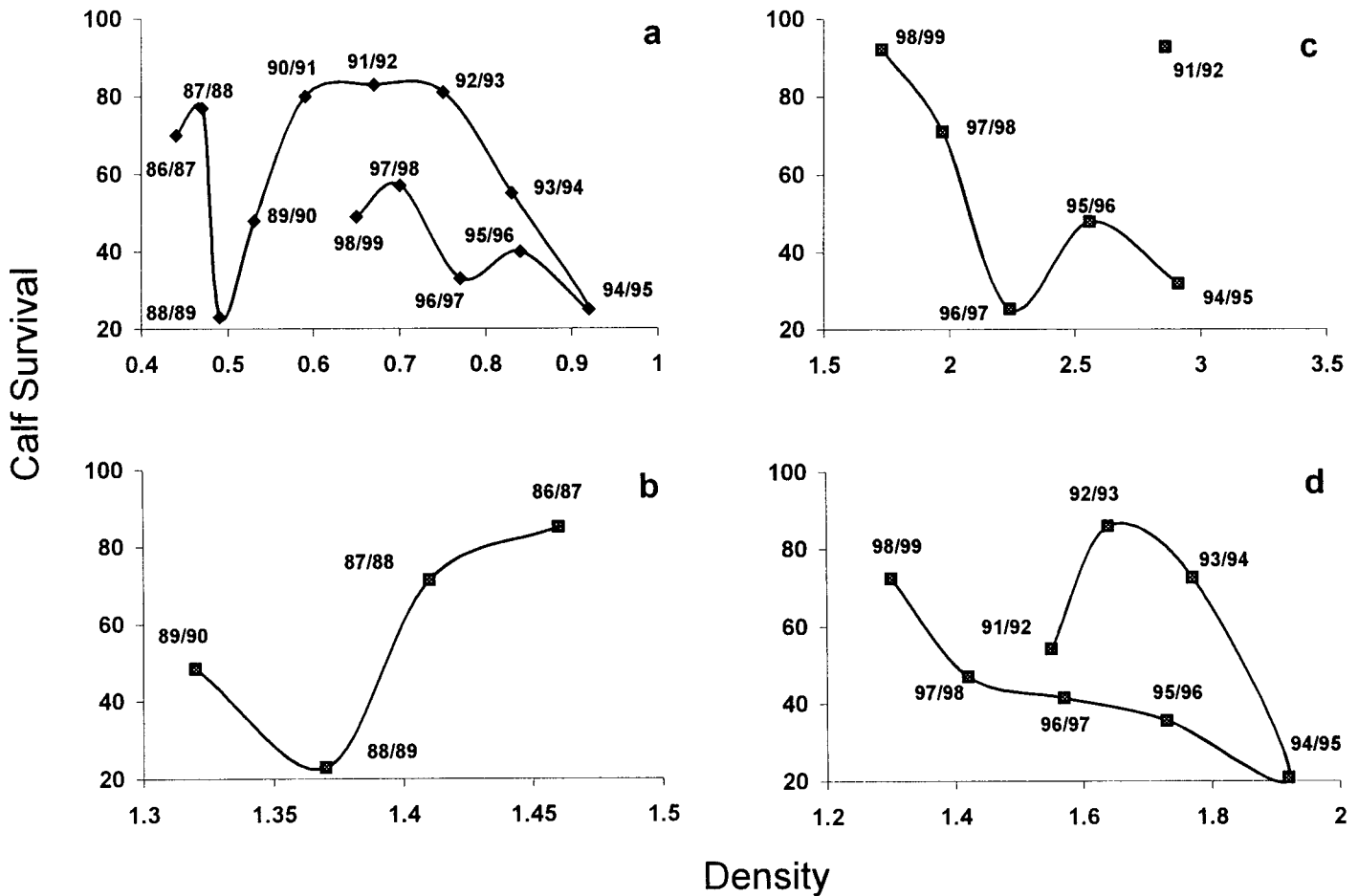


FIG. 4. Relationships between calf survival and animal density (muskoen per km²): a) island-wide, 1986–87 to 1998–89; b) Thomsen area, 1986–87 to 1989–90; c) Masik area, 1991–92 and 1994–95 to 1998–99; and d) Egg area, 1991–92 to 1998–99.

Recruitment showed considerable interannual variability (range: 10.0–41.7 yearlings per 100 adult females) (Fig. 5a; Table 1). Recruitment tended to be higher during the period of increasing density than during the decline (mean = 28.0 vs. 17.2 yearlings per 100 adult females, respectively; $p = 0.06$, $F_{(1,12)} = 4.3$). If data collected prior to 1991 (largely associated with the severe winters) are excluded, recruitment was higher ($p < 0.02$, $F_{(1,9)} = 12.1$) during the period of increasing density. After the 1994 peak, recruitment showed a negative relationship with density ($r = -0.99$, $p < 0.05$; Fig 5) and was generally lower than at similar densities before the peak.

Winter Snow Measures

Severe winter weather events occurred during the winters of 1987–88, 1988–89, and 1990–91. Freezing rains also occurred in early winter 1993–94, but this event was not accompanied by a die-off of caribou. Calf production following these winters was similar to that of other years (Figs. 2 and 3a). Calf survival was lowest and recruitment was also low following the second of the two consecutive severe winters (1988–89). Calf survival and recruitment levels during other severe winters were similar to those of other years (Figs. 2, 4a, 5a).

Late-winter snow depth in WSM showed substantial interannual variation from 1993 to 1998 (range: 48.2 ± 5.3 to 15.3 ± 0.7 cm, mean \pm SE). Neither density nor late-winter snow depth explained the variation in calf production ($R^2 = 0.35$, $p = 0.53$, $F_{(2,3)} = 0.8$) during this time period. In contrast, both factors explained significant variation in recruitment during these six years ($R^2 = 0.97$, $p < 0.01$, $F_{(2,3)} = 49.6$), but density had a negative effect, whereas late-winter snow depth had a positive effect. Although neither factor explained significant variation in calf survival ($R^2 = 0.80$, $p = 0.09$, $F_{(2,3)} = 4.5$) during these winters, density had a negative effect of borderline significance ($p = 0.07$).

Diet Composition

Two forage types, sedge (*Carex* spp. and *Eriophorum scheuchzeri*) and arctic willow (*Salix arctica*), comprised a majority of the muskoen's summer diet, but their proportions varied from year to year. From 1993 to 1995, the proportion of summer dietary sedge decreased, rebounding somewhat in summer 1996 (Fig. 6). There were significant differences ($p = 0.005$) in dietary sedge component from 1993 to 1996; the sedge component was significantly ($p < 0.05$) smaller in 1995 than in 1993. Both

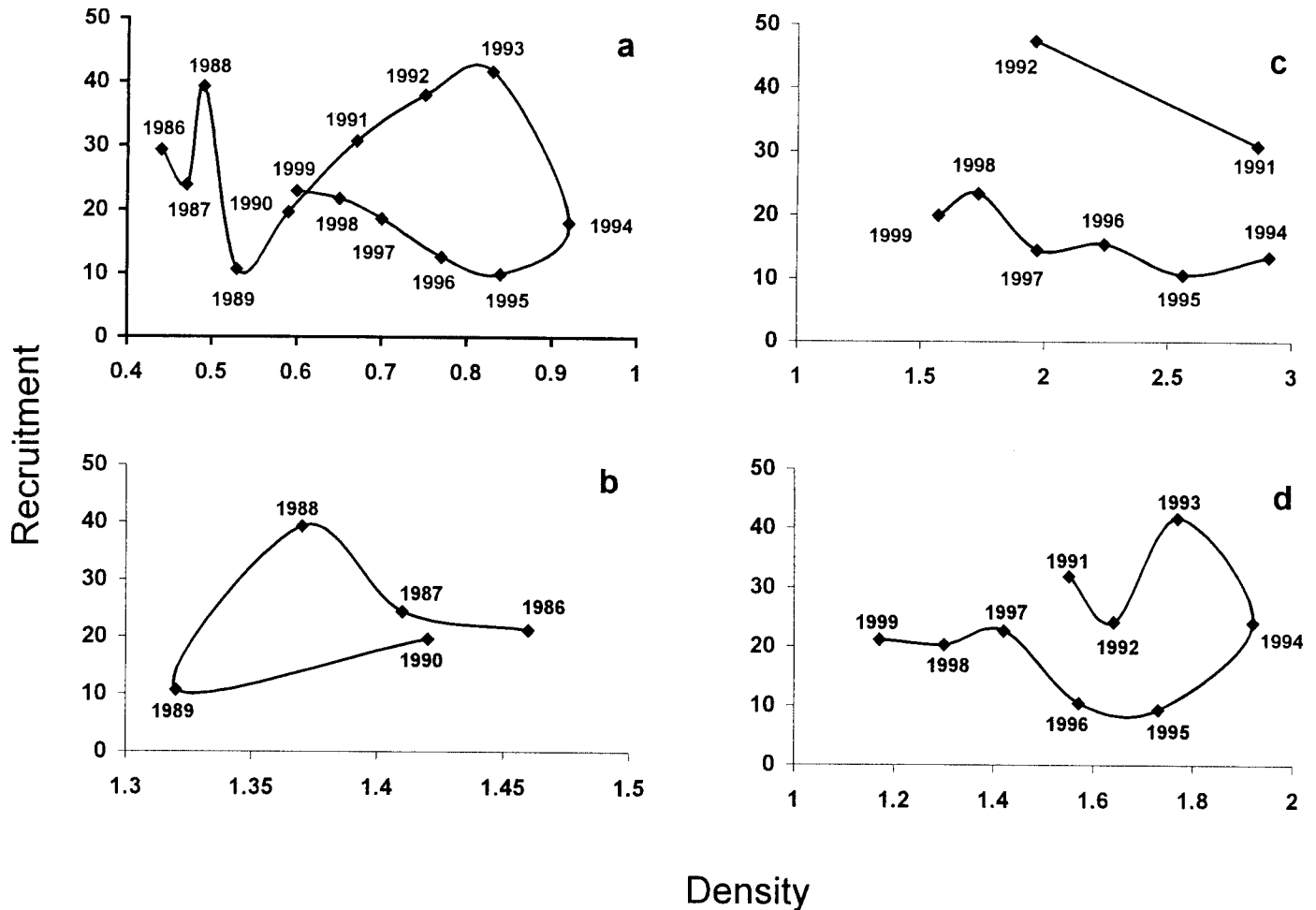


FIG. 5. Relationships between recruitment and animal density (muskoxyen per km²): a) island-wide, 1986–99; b) Thomsen area, 1986–90; c) Masik area, 1991–99 (note no data for 1993); and d) Egg area, 1991–99.

recruitment and calf survival were positively related to the summer dietary sedge component ($r = 0.74$, $p = 0.26$ and $r = 0.57$, $p = 0.43$, respectively). In contrast, calf production and the dietary sedge component of the previous summer had a negative relationship ($r = -0.38$, $p = 0.62$). None of these relationships were particularly strong (Fig. 7).

DISCUSSION

Caughley (1970) and Riney (1964) described an interactive model of population growth for herbivores that included four stages: 1) initial population growth, 2) stabilization in numbers, 3) decline in numbers, and 4) a stable oscillation of population size around less-than-peak numbers. During initial population growth, calf production, survival, and recruitment are high. During stabilization and population decline, calf production, survival, and recruitment are reduced, and the age of first reproduction may increase. These demographic changes result from decreasing available forage per capita. Our findings are generally consistent with this hypothesis.

Calf survival and recruitment of muskoxyen on Banks Island were higher during the period of population increase

than during peak population and initial decline, and both showed a pronounced decline as the population peaked. Higher survival and recruitment during the period of population increase occurred even in the face of three severe winters, when freezing rains resulted in annual die-offs totalling 460 Peary caribou (Nagy et al., 1996). Survival and recruitment showed a decreasing trend as the amount of sedge in the summer diet decreased. Although calf production showed no indication of a general trend over the study period, the number of 1-year-old females that were pregnant during commercial muskox harvests dropped to zero between 1993 and 1997 (J. Nagy and M. Branigan, unpubl. data). Messier et al. (1988) found a similar density-dependent response in the pregnancy rates of caribou from the George River herd as population size peaked.

Findings from the only other long-term study on muskoxyen (Arctic National Wildlife Refuge, Alaska) also support the Riney (1964) and Caughley (1970) model. Calf production was greatest (87 calves per 100 females aged 3 years or more) when the population was increasing ($r = 0.24$) between 1977 and 1980. Calf production subsequently declined as the rate of population increase slowed (61 per 100 in 1983–86), decreased (49 per 100 in

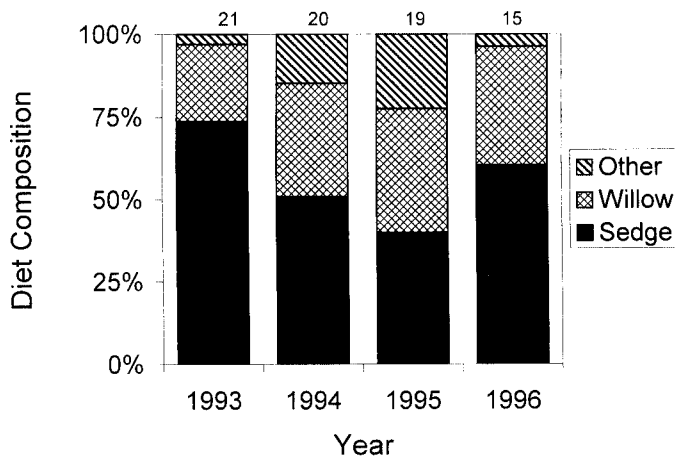


FIG. 6. Annual changes in summer diet composition of Banks Island muskoxen from areas of high muskox density (1.6–1.9 animals per km²). Values above the histograms are the number of muskox groups sampled.

1987–90), and possibly stabilized (38 per 100 in 1991–95) (Reynolds, 1998). Overwinter survival of calves did not decline over the period of population decline and possible stabilization in the Alaskan study.

Limited demographic data from rapidly increasing populations of muskoxen also support the model. Jingfors and Klein (1982) documented 100% overwinter survival of calves for an increasing population in Alaska. Le Hénaff and Crête (1989) reported high calf production during a 3-year period when an introduced population of muskoxen in Quebec showed a rapid increase in population. Olesen (1993) estimated that half of the 2-year-old females reproduced in a rapidly increasing population of muskoxen in West Greenland.

Access to high-quality summer forage can influence both production, through fecundity, and overwinter survival of calves. If access is restricted, females may be unable to gain enough body mass to come into estrus (White et al., 1997) and calves may not gain adequate body reserves for winter. Between 1993 and 1995, there was a significant decrease in the sedge component of the summer diet of muskoxen, while the willow component generally increased (Fig. 6). This change in summer diet was measured in areas of high (1.6–1.9 muskox/km²) and low (0.3–0.4 muskox/km²) density, during peak population density. Although studies of muskox diet have shown muskoxen to be quite capable of utilizing willow during summer (Wilkinson et al., 1976; Thing et al., 1987; Larter and Nagy, 1997), a diet high in willow browse may not be advantageous. Muskoxen represent the classic grazer (Hofmann, 1989, 2000): they have a large gut capable of processing large amounts of low-quality forage and a very slow rumen turnover rate (Adamczewski et al., 1994). Willow leaves and newly growing stems show a consistent increase in lignin content, which reaches 10–25% by mid-August, whereas lignin content in sedge (*Carex* spp.) is 3% or less throughout the summer (Larter and Nagy, 2001c). Lignin is not only virtually indigestible, but it interferes

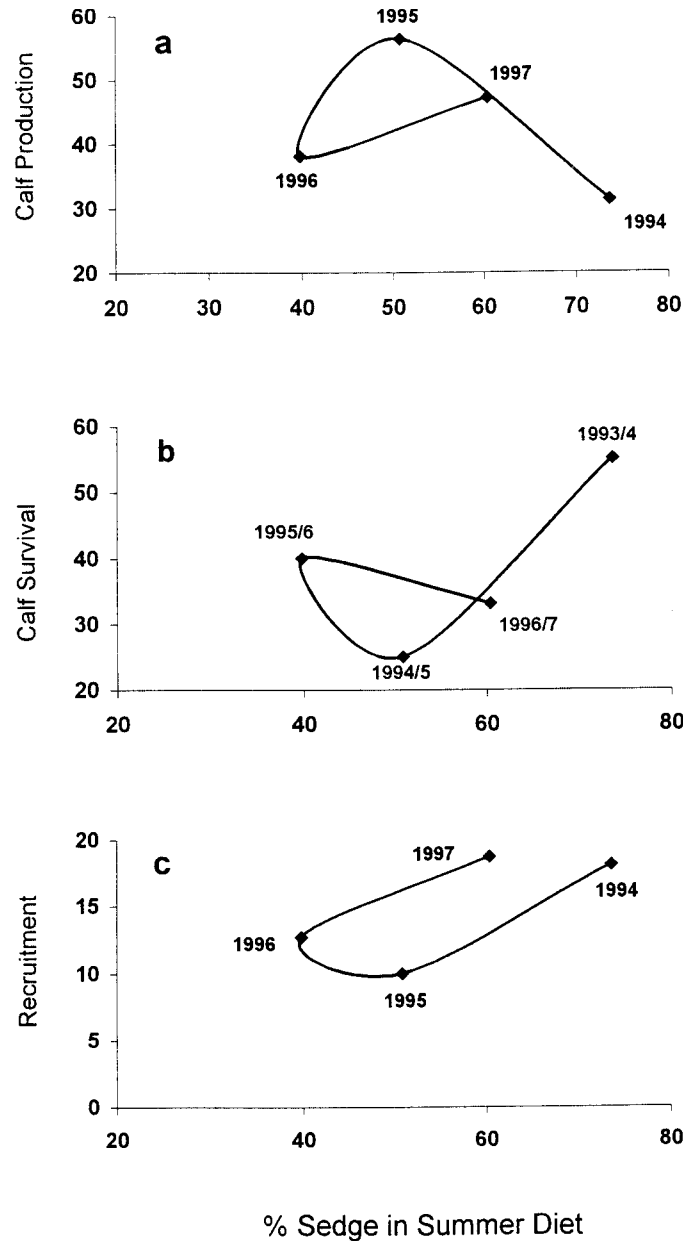


FIG. 7. Relationships between the proportion of sedge in the summer diet (1993–96) and a) calf production the following year (1994–97); b) calf survival (1993–94 to 1996–97); and c) recruitment the following year (1994–97).

with cellulose digestion (Van Soest, 1963), consequently lowering the rate of protein assimilation (Bell, 1971). Increasing proportions of willow, a potentially inferior summer forage, may represent a delayed density-dependent response by muskoxen to changes in per capita availability of forage, and of sedge in particular.

Severe winter weather is believed to cause fluctuations in muskox population dynamics (Parker et al., 1975; Miller et al., 1977; Gray, 1987; Gunn, 1990) and has been considered the most significant long-term factor in the ecology of muskoxen (Gunn et al., 1991). Since severe winter weather events can affect entire cohorts, they could have potentially prolonged population effects (Albon et

TABLE 2. Ratios of calves and yearlings per 100 adult females (age ≥ 2 years) from various muskox populations.

Population/Location	Date(s)	Ca:100 Fem	Yr:100 Fem	Reference
Banks Island, NWT	1985–99	31.3–56.3	10.0–39.3	This study, island-wide
Victoria Island, NWT	1986	50.8–61.4	26.1–43.0	B. McLean, unpubl. data
Rae-Richardson, NWT	1987	22.8	20.2	Gunn, 1995
ANWR, Alaska ^{1,2}	1983–95	30–76	36.5	Reynolds, 1998; personal communication
Seward Peninsula, Alaska	1992	59.6	24.3	S. Machida, unpubl. data
Jameson Land, Greenland ²	1982–90	28–67	7–45	Pedersen and Aastrup, 2000
Nunivak Island, Alaska ²	1937–48	0.0–76.9	n/a	R. Kacyon, unpubl. data
Nunivak Island, Alaska	1994–96	43.1–50.5	21.6–35.7	R. Kacyon, unpubl. data

¹ Mean yearlings per 100 females for the period are reported.

² For this area, only females aged 3 years or more were considered adults.

al., 1987). Prior to this study, anecdotal evidence had linked the low percentage of yearling muskoxen and the small proportion of calves in the Banks Island population to particular weather events (Gunn et al., 1991). Severe winter weather events (in this case deep late-winter snow and late snow disappearance) have been correlated with low calf production and reduced overwinter survival of calves in Alaska (Reynolds, 1998). However, since three of the four winters with deep, late-winter snows occurred while the population was stabilizing or declining, weather and population density factors may be confounded in this study. Overwinter survival of calves did not decline during the stable or declining phase of the population in Alaska (Reynolds, 1998). Larter and Nagy (2001a) documented higher cortisol levels in snow urine of muskoxen collected during winter 1993–94 than in samples from winter 1995–96. Increased cortisol levels are associated with increased nutritional deprivation. Winter 1995–96 was much less severe than 1993–94, when freezing rains occurred, but again muskox densities were lower in 1995–96 than in 1993–94.

We found that late-winter snow depth on Banks Island explained little variation in calf production or calf survival. Where late-winter snow depth did explain significant variation in recruitment, the effect was positive, not negative as expected. (Recruitment would be lower if severe weather had a negative impact on demographic parameters.) In contrast, we found that animal density explained considerable variation in calf survival and recruitment. Possibly late-winter snow depth is not an appropriate measure of winter severity for muskoxen on High Arctic Islands.

Schaefer and Messier (1995) found that muskox feeding sites were similar between years when peak snow cover was 59% greater in one year than in the other. Late-winter snow depth and snow disappearance may create more of a hardship for movement and foraging on mainland areas, where accumulation of especially wet snow likely impedes travel. On High Arctic Islands, with the constant buffeting of the wind, snow depth alone may not be an important factor affecting foraging or forage availability. The ability of the animals to penetrate the snow pack may be more important, and that depends on such

factors as snow hardness, the presence of ice layers, and ground-fast ice, as well as snow depth. Larter and Nagy (2000) reported that calf production and survival were lower following a winter when snow was deepest, densest, and most resistant, but the relationship with snow conditions did not hold for other years. Reduced calf survival and recruitment on Banks Island seem to be responses to muskox density more than to severe winter weather.

Possibly our more conservative estimates of calf production and recruitment, which include two-year-old females in the denominator of the proportion, affected our results and interpretation. However, our estimates of calf production, recruitment, and calf survival are similar to estimates reported from muskox populations elsewhere (Table 2). One-year-old females have also been reported to conceive in Greenland (Olesen, 1993). During the 1930s and 1940s, the Nunivak Island founder population was less than 150 animals, and there is some indication that females bred in alternate years. Alternate-year breeding is likely responsible for this population's having the greatest range in the ratio of calves to 100 adult females (R. Kacyon, pers. comm. 1997). The values for Banks Island are realistic, given the rate of population increase. Although high, our estimates of calf survival are similar to those reported for rapidly increasing populations elsewhere (Jingfors and Klein, 1982; Le Hénaff and Crête, 1989).

It is unlikely that commercial or subsistence harvesting has had much impact on our results. Although commercial harvesting is conducted within the areas where sex and age classification surveys are conducted, harvesting is not selective by sex or age class; occasionally older bulls are released, but in general all animals are captured, corralled, and herded to slaughter. Subsistence harvesting may be more sex- and age-selective, as it is usually aimed at younger animals. This fact could also mean that our estimates are somewhat conservative. However, the number of animals harvested for subsistence is fewer than 300 animals annually, and most are harvested in the vicinity of Sachs Harbour. Few animals are harvested from areas where sex and age classification surveys were conducted.

The two consecutive severe winters (1987–88 and 1988–89) definitely affected calf survival and recruitment, but the data over 14 years are more consistent with

an underlying density-dependent response than with severe winter weather as the explanation of population fluctuations in Banks Island muskoxen. Whether this response is food-related, as some of the data imply, remains to be further elucidated. Recruitment has been slow to rebound after peak density, even though two of the mildest winters and two years when higher-quality winter sedge was available occurred during this population decline (Larter and Nagy, 2000, 2001a). A higher incidence of disease and parasites or increased predation (or both), occurring alone or in combination with a decrease in food resources, could reduce survival and recruitment after peak densities, preventing them from reaching the levels reported before the peak. Wolves have increased in number since 1994, and their diet is predominantly muskox (Nagy and Larter, 2000; unpubl. data). The prevalence of abomasal parasites in different sex and age classes of muskox is currently being investigated.

CONCLUSION

On Banks Island, recruitment and calf survival (1) were higher during the period of population increase than during the period of population decline, (2) showed interannual variability that was better explained by animal density than by late-winter snow depth, and (3) showed a relationship with animal density that was consistent with a density-dependent model. Calf production was similar regardless of animal density and showed no relationship with late-winter snow depth. Even though a period of two consecutive severe winters affected demography during the period of population increase, the population continued to increase. Severe weather alone cannot explain the fluctuations in population dynamics of the Banks Island muskox population over the past 14 years. An underlying density-dependent response, possibly related to food, has been a more important factor.

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