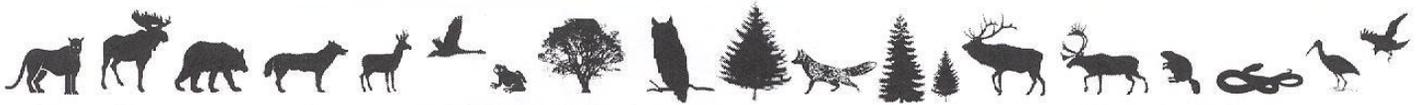

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Original Research

A Comparison of First-Year Growth in Wild and Captive Muskox Calves

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Abstract

We measured seasonal changes in body composition, including fatness and fill in the digestive tract, in 79 muskox (*Ovibos moschatus*) calves shot by Inuit hunters in April, May, July, August, September and November, 1989-1993, on Victoria Island in northern Canada. We compared their growth to that of 3 calves born in captivity near Saskatoon and 4 calves live-caught at about 2 weeks of age, then raised in captivity in 1993-1994. Muskox calves on Victoria Island grew from 15.9 ± 0.9 kg (mean \pm standard error) body mass in mid-late May, when they were about 2 weeks old, to peak fall mass in November of 82.9 ± 2.3 kg. These calves had an estimated 16.5 ± 1.1 kg fat in November but lost 80% of this fat by April. Muskox calves ingested plant material and detritus from their first day on and by summer the fill in calf digestive tract chambers was proportionately very similar to that of adults. The growth of 7 captive calves in Saskatoon initially was similar to that of the wild calves, but these calves were weaned at the end of July, and thereafter their growth was slower than in the wild. Over winter, however, the captive calves continued to grow slowly, while the wild calves lost mass and their linear growth nearly ceased. Serum insulin-like growth factor 1 (IGF-1), a hormone known to correlate closely with growth rate, was initially similar in the wild and captive calves, but dropped rapidly in the captive calves when they were weaned. Muskox calves benefit from a prolonged first growth season to become full ruminants in early summer, and they build substantial fat and protein reserves when entering their first winter.

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INTRODUCTION

The calves of muskoxen (*Ovibos moschatus*) are born very early in the year, usually on snow in the late winter in April or May (Tener 1965; Gray 1987; Flood and Tedesco 1997). Six to 8 weeks may elapse before the first green flush of spring brings readily digestible forage (Gray 1987; Thing *et al.* 1987). In the absence of high-quality forage, muskox cows must supply much of the cost of lactation from body reserves (Thing *et al.* 1987; Adamczewski *et al.* 1997). The newborn muskox calves can only gain limited nutrients from the senesced grasses, sedges and willows the adults subsist on in late winter (Raillard and Svoboda 1989; Klein and Bay 1990; Larter and Nagy 1997; Ihl and Klein 2001), although we have observed newborn calves in Saskatoon eating organic matter and detritus avidly from their first day on. A partial explanation for this early calving may lie in the slow metabolism (Nilssen *et al.* 1994), relatively slow growth of calves, and relatively slow recovery of maternal body reserves (Parker *et al.* 1990). Early muskox births extend the time available for the first year's growth, and extend the time available for lactating cows to recover body reserves. Despite the absence of high-quality forage in late winter, rapid development of ruminant capacity by summer could allow muskox calves to fully exploit the summer pulse of high-quality nutrients and gain substantial reserves of fat and protein entering their first winter.

In an earlier paper, we described seasonal patterns of body composition and reproduction in hunter-killed muskox cows on Victoria Island, Nunavut from 1989 to 1993 (Adamczewski *et al.* 1997). Muskoxen have an ability to fatten rarely seen in cervids, including caribou (Adamczewski *et al.* 1995). Muskox cows must be in very good condition to be pregnant in the fall (White *et al.* 1997; Adamczewski *et al.* 1998), retain much of their fat through winter, and deplete their reserves rapidly during late-winter lactation (Thing *et al.* 1987; White *et al.* 1989; Adamczewski *et al.* 1997). During the Victoria Island hunts, Inuit hunters also shot calves belonging to the cows, which provided us an opportunity to study calf growth, including changes in body composition, during their first year.

The caribou (*Rangifer tarandus*) that share many sub-arctic and arctic ranges with muskoxen (including Victoria Island) are faced with the same short summers when forage quality is high and long winters when forage quality and availability are reduced. There are differences between the 2 species in how they cope with these seasonal conditions. Caribou usually give birth much later than muskoxen, near

spring green-up in June (Klein 1992). Caribou calves grow at a faster rate than muskox calves (Parker *et al.* 1990), and are likely to be weaned earlier (White *et al.* 1989; Parker *et al.* 1990). Caribou calves are normally very lean through their first year (Huot 1989; Crête *et al.* 1993) while limited data from Victoria Island (Adamczewski *et al.* 1995) suggest that muskox calves can accumulate substantial fat reserves by early winter. The studies we describe in the current paper gave us an opportunity to gain additional comparative insights into how these 2 species cope with a strongly seasonal foraging environment.

Our main interest in this study was in quantifying the extent and nature of first-year muskox growth in the wild; published reports to date have been mostly limited to studies of growth in captive muskox calves and yearlings (Chaplin 1984; Frisby *et al.* 1984; Chaplin and Stevens 1989; Parker *et al.* 1990; Peltier and Barboza 2003; Knott *et al.* 2005), and limited body mass data from the wild (Latour 1987; Olesen *et al.* 1994). We were particularly interested in (1) the extent of muskox calf growth compared to growth of caribou in their first year, including the degree of fattening, (2) a comparison of growth in male and female calves, and (3) the rate at which muskox calves adapted to full ruminant capacity in their digestive tracts. We collected blood samples (serum) from the calves and assayed them for insulin-like growth factor-1 (IGF-1), a hormone sensitive to nutritional quality (Clemmons and Underwood 1991) and known to correlate with growth rate in ruminants (Roberts *et al.* 1990; Kerr *et al.* 1991). Our results for muskox calf condition and mass, together with equivalent data from cows, can be considered baseline values for a healthy, slowly increasing population.

In addition, we had an opportunity to compare the growth of these hunter-killed calves with the growth of 2 other groups of captive muskox calves. We live-captured 4 muskox calves in May 1993 on Victoria Island at about 2 weeks of age, then bottle-fed and raised them in Saskatoon (Adamczewski and Tedesco 1995). In the same year (1993-1994), 3 calves were born to the existing herd at the University of Saskatchewan, about a month later than the 4 wild-caught ones. Muskoxen at temperate latitudes tend to conceive a month or more later than at arctic latitudes (Flood and Tedesco 1997; Saskatoon 52° N, Cambridge Bay 69° N). The 2 groups of calves provided growth data from animals on controlled planes of nutrition and no limitations on forage intake in winter, to compare with data from free-ranging calves experiencing natural seasonal variation in nutritional quality and sometimes severe limitations on availability in

the winter. We recognize that the diets and environmental conditions, including restricted grazing and diets consumed by the captive calves, were very different from those experienced by wild muskoxen. We focused this comparison on 3 variables that could be measured readily in live and dead calves: total body mass, hind-foot length, and IGF-1 in serum.

MATERIALS AND METHODS

Field collections on Victoria Island

The study area and muskox population (Gunn 1990; Fournier and Gunn 1998; Gunn and Patterson 2012), along with hunting methods, field measurements, and values obtained by regression equations (Adamczewski *et al.* 1995; 1997) were described earlier, and a brief outline is given here. Muskox abundance on Victoria Island was very low in the early 1900s (Gunn 1990), as it was across much of the Canadian mainland and Arctic islands (Fournier and Gunn 1998). The population grew rapidly in the 1980s and by the early 1990s, 4 regional surveys between 1992 and 1994 indicated there were about 44,000 muskoxen on Victoria Island (Fournier and Gunn 1998). On southeast Victoria Island, the region of our studies, the muskox population was estimated in 1983 at $3,300 \pm 345$ (Standard Error, SE), in 1988 at $12,372 \pm 1,064$, in 1993 at $12,563 \pm 1,254$ and in 1999 at $18,290 \pm 1,100$ (Gunn and Patterson 2012) based on relatively consistent aerial fixed-wing strip-transect surveys and survey areas. Our studies between 1988 and 1993 are thus representative of a population increasing slowly. The muskox population on Victoria Island has declined substantially since the early 1990s with reduced productivity (L.-M. LeClerc, Government of Nunavut, unpublished data 2013-2014) and there is evidence from 2012 and other years of health-induced muskox die-offs on Victoria and Banks Islands (Kutz *et al.* 2015).

All the hunter-killed muskoxen were taken from southeastern Victoria Island, within about 100 km of the community of Cambridge Bay, also called Ekaluktutiak (then in the Northwest Territories, now in Nunavut) in northern Canada (69° – $69^{\circ} 45'$ N, 104 – 108° W), between 1989 and 1993. The primary years of study were 1989, 1990 and 1991, with further hunts in 1992 and 1993. Hunters avoided larger herds with many calves to reduce the likelihood of leaving orphaned calves; beyond this, selection of muskoxen was opportunistic and, we believe, relatively unbiased. A total of 79 calves (39 males, 40 females) were taken during 15 hunts (Table 1). Calves shot in April were considered to be 1 year old, although the actual peak of calving was in late April and early May. The meat from all study animals was taken to the meat-processing plant in Cambridge Bay after study.

Measurements made on calves were a sub-set of those recorded in cows and included the following:

Body mass: total body mass, ingesta-free body mass, and carcass mass. As with cows, ingesta-free body mass was measured after emptying the entire digestive tract during 1989 hunts, and thereafter was estimated from multiple regressions based either on carcass and liver masses or carcass and kidney masses, both with R^2 of 0.994 and $n=63$ or 65.

Chemical composition of the ingesta-free body: we used predictive equations (Adamczewski *et al.* 1995, 1997) to estimate masses of these components: fat, metabolizable protein, ash, water (by difference), and protein in the hair, hooves and horns. We found that the protein contained in the hair, horns and hooves was substantial in muskoxen. This protein (essentially keratin) could not be metabolized by the animal as protein in the muscles or gastrointestinal tract might be, so we identified and weighed it as a separate protein component (Adamczewski *et al.* 1995).

Indices of fatness: back fat thickness, kidney fat mass, and femur marrow fat.

Indices of lean body tissues: gastrocnemius muscle mass and femur mass.

Kidney and liver masses.

Digestive tract contents and tissues: mass of the ruminoreticulum contents and ruminoreticulum tissues. In 1989, masses of ingesta and tissues were also recorded for the omasum, abomasum, small intestine, caecum and large intestine.

Linear measurements: Horn length, femur length, and hind-foot length (hoof-tip to end of the calcaneum).

Management and measurements from captive muskox calves in 1993-1994

Two groups of calves were studied in their first year in 1993-1994. The first group consisted of 4 calves, 1 male and 3 females, live-captured on southeast Victoria Island on May 18 and 19, 1993, to add unrelated genetic stock to the existing research herd at the University of Saskatchewan. The muskoxen in the existing herd in 1993-1994 were either live-captured on Banks Island in 1982 (Flood *et al.* 1984) or descended from them.

The calves captured in 1993 were caught by hunters on snowmobiles, who trailed small herds with few calves until the young calves, an estimated 2 weeks old, fell behind and could be picked up by hand. The calves were held in a small pen of snow fencing and burlap in a field camp for 6 d and bottle-fed 4-5 times daily with a commercial lamb milk replacer. The milk replacer was fed at a slightly diluted concentration to reduce the probability of bloating. On May 26 the calves were transported in wooden crates on sleds

Table 1. Numbers of muskox calves studied on southeast Victoria Island, Nunavut, 1989-1993, during 15 seasonal hunts. There was 1 further hunt in April 1992, but no calves were taken.

Dates	Male s	Female s	Total	Dates	Males	Females	Total
1989				1991			
April 4-8	2	2	4	April 5-8	2	2	4
May 19-22	5	2	7	May 17-20	1	5	6
Aug. 10-15	5	2	7	Aug. 12-15	1	2	3
Nov. 18-22	1	3	4	Nov. 7-11	4	3	7
1990				1992			
April 9-10	2	2	4	Nov. 6-9	1	1	2
May 16-18	3	5	8	1993			
July 10-15	4	4	8	May 18-21	4	0	4
Sept. 2-7	2	5	7	Overall			
Nov. 9-12	2	1	3	Totals			
					39	40	79

pulled behind snowmobiles to Cambridge Bay, flown to Yellowknife, then to Edmonton, and driven by truck to Saskatoon the same evening. We monitored and bottle-fed the calves opportunistically en route. The calves were initially kept in an air-conditioned indoor pen at the Veterinary College, University of Saskatchewan to prevent heat stress from unaccustomed warmer southern temperatures, then moved to an outdoor pen of about 30m x 40m on the university campus in mid-June.

Details of management and diets offered the calves are listed in Tables 2A and 2B. In general, the calves were kept on a medium or medium-high plane of nutrition to achieve consistent, though not necessarily maximal, growth. They were weaned at the end of July to improve tractability and because of concerns over ruminal bloating. During the summer the calves were offered a mixture of limited grazing, brome hay, "green feed" (whole oats cut early) and 2 pelleted supplements. The pelleted rations were always consumed fully, while the hay and green feed were eaten free-choice. During the fall and early winter their diet was gradually shifted to match the medium-quality diet the research herd was fed for much of the year: free-choice brome-alfalfa hay with 9-12 % crude protein and a daily pellet ration of 540 g/animal (Adamczewski *et al.* 1994).

The second group of calves consisted of 3 females born to cows of the existing research herd in Saskatoon in 1993. These calves were the only ones born in the herd that year, on May 31, June 8 and June 9, about 1 month later than the 4 wild-caught calves. These 3 calves were left with their mothers until July 26, when they were moved in with the 4 wild-caught calves and bottle-fed until the end of July. At

the end of July, all 7 captive calves were weaned, and thereafter all the captive calves were managed as 1 group, with the same diet. At the end of the winter, the 7 calves were moved from a relatively small pen on the university campus to a new, previously ungrazed rye-grass pasture of ca. 3 ha at Goodale Farm outside the city of Saskatoon, where the main muskox research herd had been kept for several years.

Measurements recorded from the 2 groups of calves were limited to 3 that could be compared with the same measurements in hunter-killed calves from Victoria Island: body mass was measured on an approximately weekly basis, a hind-foot measurement was recorded once a month, and a blood sample was taken once a month and the serum assayed for IGF-1. Hindfoot length has been used as an indicator of growth in a number of species, including red deer (*Cervus elaphus*; Suttie and Mitchell 1983) and roe deer (*Capreolus capreolus*; Zannèse *et al.* 2006). We used it here as a proxy for growth in long bones in live muskoxen, where measuring long bones directly was not feasible; this was also a measurement that we recorded in dead muskoxen. The hind-foot measurement depends in part on hoof growth and varies slightly with the calf's posture. We sought to minimize these sources of variability by having 1 person (JA) record all the hind-foot measurements, both in the field on dead calves on Victoria Island, and on live calves in Saskatoon. In our experience the hoof growth of the captive calves was normal and similar to that of wild calves.

IGF-1 assay

IGF-1 was assayed in serum samples by a radioimmunoassay developed in Bernard Laarveld's lab

Table 2A. Management and diets of 2 captive groups of muskox calves in Saskatoon, Saskatchewan, 1993-1994.

Date(s)	4 calves (3F, 1M) live-captured on Victoria Island and raised in Saskatoon, Saskatchewan, 1993-1994	3 calves (all F) born to research herd in Saskatoon, Saskatchewan, 1993-1994
May 18-19	4 live-captured calves on Victoria Island, likely born 1 st week of May.	
May 18-26	4 calves held in pen on snow, fed lamb milk replacer (A) 4-5 times/day, total 1.2-2 litres/calf/day; local soil and sedges offered and eaten.	
May 26	4 calves travel by snowmobile, air and truck to Saskatoon; bottle-fed en route.	
May 26- June 12	4 calves kept in air-conditioned indoor pen with brome hay (B) and straw (to avoid sudden change in temperature); 3-4 bottles (total ca. 2l/day/calf/day) lamb milk replacer (A).	3 calves born May 31, June 8 and 9 to cows in research herd, Saskatoon; left with mothers. Herd with limited grazing, medium-quality brome-alfalfa hay (C) and daily pellet supplement (D) of 540g/animal.
June 12	4 calves moved to small outdoor pen (ca. 30x40m) on university campus, Saskatoon.	3 calves remain with mothers on farm near Saskatoon.
June 12- July 26	4 calves bottle-fed 3 times/day, total 2-2.4l/calf/day (A); brome hay (B), soil, limited grazing on grass available.	3 calves remain with mothers.
July 26	4 calves joined by 3 calves born in Saskatoon.	3 calves taken from mothers, joined with 4 wild-caught calves.
July 26-31	7 calves (6F, 1M) get 3 bottles lamb milk replacer (total 2-2.4l/calf/day, A); in small outdoor pen with limited grazing, free-choice brome hay (B).	
July 31	All 7 calves weaned to increase tractability and due to concerns over bloating.	
Aug. 1- Sept. 15	7 calves fed 300-350g/day commercial starter-grower pellets (E), free-choice brome hay (B), limited grazing.	
Sept. 15- Oct. 15	7 calves offered "green feed" (F) mixed 40-50% with brome hay (B), and 210g each of starter-grower pellets (E) and muskox pellets (D; total 420g).	
Sept. 15- Oct 30	2 calves born in Saskatoon treated for recurrent abscesses in facial area; otherwise, all calves in good health.	
Oct. 16- Dec. 25	7 calves offered green feed (F), brome hay (B) as above; 420g/calf/day muskox pellets (D).	
Dec. 25- Feb. 14	7 calves offered free-choice brome-alfalfa hay (C) and 420g/day muskox pellets (D).	
Feb. 14- April 3	Diet of free-choice brome-alfalfa hay (C) and 540g/day muskox pellets (D) - diet of adult muskoxen.	
April 3	7 calves moved to new 3-hectare ryegrass pasture; 540g/day muskox pellets daily ration (D) & grazing.	

Table 2B. Composition of diet components of 2 captive groups of muskox calves in Saskatoon, Saskatchewan, 1993-1994. Pelleted rations were always consumed fully; hay or green feed was eaten free-choice.

Diet Type	Measured Component	Values Estimated	
(A) Commercial Lamb Milk Replacer (Dry Matter)	Crude Protein	Min. 21.0%	
	Crude Fat	Max. 25.0%	
	Crude Fat	Min. 24.0%	
	Calcium	Actual 0.90%	
	Phosphorus	Actual 0.70%	
	Vitamin A, IU/kg	Min. 44,000	
	Vitamin D3, IU/kg	Min. 5,500	
	Vitamin E, IU/kg	Min. 44	
	Selenium, mg/tonne	300	
(B) Brome Hay (Dry Matter)	Crude Protein	14.0%	
	Acid Detergent Fiber	38.2%	
	Phosphorus	0.17%	
	Calcium	1.36%	
	Potassium	2.13%	
	Crude Protein	9-14%	
(C) Brome-Alfalfa Hay (Dry Matter; various batches); see Adamczewski <i>et al.</i> (1994)	Acid Detergent Fiber	36-45%	
	Crude Protein	14.18%	
(D) Muskox Pellets (Adamczewski <i>et al.</i> 1994). Composed of (Dry Matter):	Acid Detergent Fiber	19.11%	
	Oats 51.5%	Phosphorus	1.32%
	Hay 38.0%	Calcium	1.16%
	Molasses 4.0%		
	Phosphate 2.0%		
Mineral-vitamin mix 2.0%			
Vitamin A and D mix 1.5%			
Salt (Na Cl) 1.0%			
(E) Commercial Starter-Grower Pellets (Dry Matter)	Crude Protein	16.5%	
(F) Green Feed (Whole Oats Cut Early; Dry Matter)	Crude Protein	14.0%	
Digestibility (Organic Matter) of Brome-Alfalfa Hay (C) and Muskox Pellets (D) in adult muskoxen (Adamczewski <i>et al.</i> 1994)	March	73.8%	
	July	60.8%	

(Department of Animal and Poultry Science, University of Saskatchewan) for ovine IGF-1 in domestic sheep (*Ovis aries*) and used for other domesticated species. The assay was described in detail by Van Kessel (1992) and Kerr *et al.* (1990, 1991). The assay was validated for muskox serum by demonstrating parallelism to the standard curve in a serial dilution of a concentrated sample. IGF-1 assays were carried out in January 1992, June 1993, August 1994, September 1995 and September 1996. Sheep and muskox pooled sera were used repeatedly in each assay, to assess variability within and among assays. The inter-assay coefficient of variation (standard deviation/mean, times 100) was 4.3%, and the intra-assay coefficient of variation averaged 4.3% (range 1.2-7.6%). IGF-1 was assayed in serum samples from the 2 groups of calves raised in Saskatoon, and

in serum from hunter-killed calves from Victoria Island from 1989, 1990, and 1991.

Statistical analyses

Body composition and IGF-1 data from seasonal hunts on Victoria Island were analyzed by 3-way analysis of variance (ANOVA) with season (April, May, July, August, September and November), sex, and year as main factors, along with possible 2- and 3-way interactions among the main factors. Where these ANOVA's showed a significant seasonal effect ($P < 0.05$), individual seasonal means were compared pair-wise by Student-Newman-Keuls (SNK) post-hoc comparisons, with significance at $P < 0.05$. Comparisons among years were somewhat limited because there was only 1 hunt in July and September (both in 1990), 2 in August (1989 and 1991), 3 in April, and 4 in each of May and

November (Table 1). Statistical analyses were carried out using primarily the paired programs Statview SE+ Graphics and Superanova (Abacus Concepts 1991, Berkeley, California) and secondarily with the program Kaleidagraph (version 4.0, 2006, Synergy Software, Reading, Pennsylvania).

Body mass, hind-foot and IGF-1 data from the 2 groups of calves raised in captivity were analyzed by repeated-measures ANOVA. Initially we carried out 1-way repeated measures ANOVA separately with the data from the 4 wild-caught calves, and with data from the 3 captive-born calves, because the latter calves were born about a month later than the former, thus the data sets were of unequal length. Thereafter, we carried out 2-way repeated-measures ANOVA and compared changes over time in mass, hind-foot length and IGF-1 between the 2 groups, for the dates when we had data from all 7 calves, as initial review of the data suggested that their growth patterns differed.

We carried out further evaluation of IGF-1 data in relation to body mass and condition in the hunter-killed calves and in the captive calves, as studies in growing sheep showed a positive correlation between body mass and IGF-1 (Roberts *et al.* 1990). Using data from the hunter-killed calves, we looked for correlation between body mass and gastrocnemius muscle mass as independent variables, and IGF-1 as the dependent variable, for each of the 6 monthly periods. We also carried out analysis of covariance using month as a factor and evaluating body mass and gastrocnemius mass as covariates for IGF-1, to use the full data set at one time. We evaluated mean IGF-1 for the 7 captive calves in relation to body mass over their first year, and ranked their body mass and hind-foot length at the end of the year (from 1 to 7) as well as their mean IGF-1 over the year, to assess association between the 2 measures of growth with serum IGF-1.

RESULTS

Body mass, composition and linear size in hunter-killed calves: seasonal patterns

All the body mass, body composition, and linear variables we measured varied significantly ($P < 0.001$) with season, not surprisingly, since we were measuring growing calves. For nearly all these variables, there was no significant difference due to sex ($P > 0.1$) but for a few measurements there was a significant ($P < 0.05$) or near-significant month-sex interaction term. Males tended to be bigger and heavier, although the differences were generally small. Year was not significant in the ANOVA's as a main factor for any variable. We have presented the patterns primarily as seasonal progressions graphically for males and females, using data from all years. Seasonal values as means are included in

Appendix 1A (body mass, condition and composition), 1B (chemical composition), and 1C (1989 gastrointestinal tract fill and tissue masses) for readers interested in the exact values. We used the May data from the youngest calves as our starting point, with April data treated as the end of the first year of growth.

Body mass measurements

Total body mass increased from 15.9 ± 0.9 kg (mean \pm standard error) in young calves in May to peak mass of 82.9 ± 2.3 kg in November, then declined significantly ($P < 0.05$) by 10.0 kg to April (Figure 1). The patterns in carcass mass and IFBM were similar, and also showed a significant decline ($P < 0.05$) from peak mass over winter from November to April. All 3 measurements showed similar means in the 2 August hunts and 1 September hunt, which was made just 3 weeks later, and means for all 3 body mass variables increased significantly ($P < 0.05$) from August/September to November. The 3 body mass measurements were not significantly greater in males than females ($P = 0.2-0.4$), although males tended to be slightly heavier.

Using averaged median dates of May 18, July 12, August 25 (for the 2 August and 1 September hunts), November 12 and April 8, the daily rates of overall body mass change were: $+463$ g/day (May-July), $+568$ g/day (July-August), $+209$ g/day (August-November) and -68 g/day (November-April). If the September data are set aside, then the daily mass gain from July 12 to August 12 (average of the median dates for the 2 August hunts) was $+806$ g/day, by far the most rapid period of mass gain during the year.

Fat indices

Peak values for back fat thickness of 2.0 ± 0.1 cm and kidney fat mass of 284.6 ± 19.6 g were recorded in November. Both indices declined significantly and substantially over winter to 0.4 ± 0.1 cm and 47.8 ± 6.1 g in April ($P < 0.05$), similar to the values initially found in very young calves in May. Femur marrow fat showed a less extreme seasonal cycle, with the lowest values in May (54.3 ± 5.5 %) and the highest in September (88.4 ± 1.3 %) and November (87.8 ± 1.6 %), and a significant decline ($P < 0.05$) to 62.5 ± 4.0 % in April.

Indices of lean body mass

Mass of the gastrocnemius muscle increased rapidly from May to a peak of 285.7 ± 10.0 g in November, then declined significantly ($P < 0.05$) to 234.4 ± 8.5 g in April, a loss of 17.9%. Femur mass also increased through the summer and fall but was virtually unchanged from November (mean 340.8 ± 7.4 g) to April (346.0 ± 10.7 g). Femur mass was 1 of the few measurements that showed a significant overall effect of sex ($P = 0.05$), with slightly higher values for males in all 6 monthly periods.

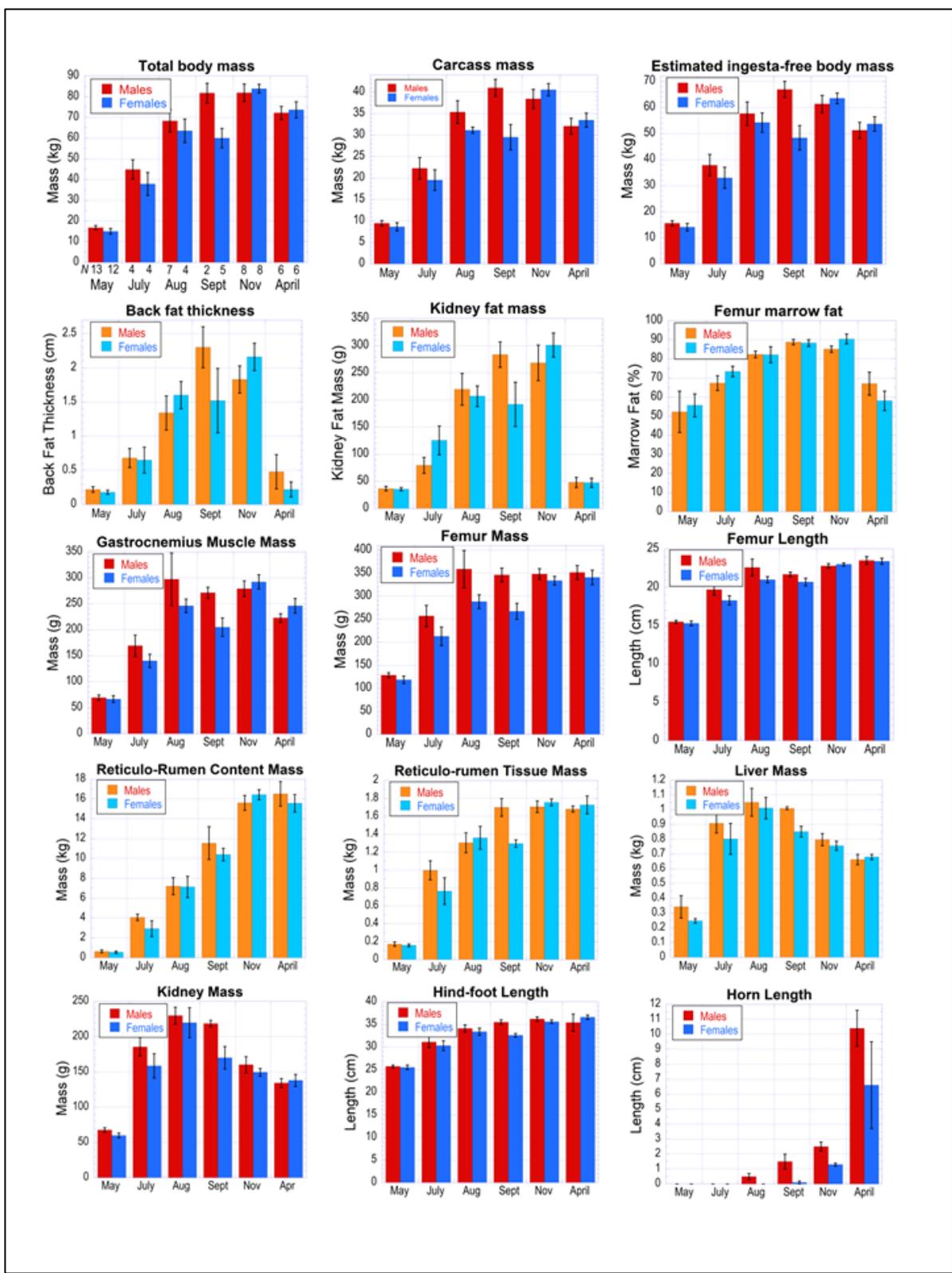


Figure 1. Seasonal changes in mass, body condition and size of Victoria Island muskox calves, Nunavut, 1989-1993.

Liver and kidneys

Liver and kidney masses showed a different seasonal progression from most other tissues and body mass measurements. Kidney mass was greatest in August (mean 226.3 ± 10.0 g), with significantly lower ($P < 0.05$) values in July (172.0 ± 11.2 g) and September (183.9 ± 14.2 g), and further decreases to November (154.4 ± 6.0 g) and April (135.9 ± 5.0 g). The mass of the liver showed a similar seasonal progression with a peak in August.

Ruminoreticulum contents and tissues

Ingesta mass in the ruminoreticulum increased in a nearly linear manner from May to November, with each increase between periods significant ($P < 0.05$), and nearly identical means of 16.0 ± 0.5 kg in November and April. Ruminoreticulum tissue mass showed a similar seasonal pattern, but the greatest increases occurred earlier, from May to July and July to August, and there was little change in the fall or winter.

Linear measures

Horn length was 0 in May and July, began to be measurable in August, and increased most from November to April. There was no significant difference between males and females ($P = 0.10$), although we suspect this reflects high variance, small samples and the initial horn lengths of 0 in May and July. Horn length was numerically greater in males than in females in August, September, November and April, the 4 periods when the horns were measurable, and the difference increased over time. The overall increase in horn length (all calves) from November (1.9 ± 0.2 cm) to April (8.5 ± 1.6 cm) was significant ($P < 0.05$). Length of the femur and hind-foot showed similar trends from May to April, with rapid increases early (May to July and July to August), tapering to peak values in November. Both femur length (22.0 ± 0.8 cm vs. 21.0 ± 0.4 cm) and hind-foot length (33.8 ± 0.6 cm vs. 33.4 ± 0.6 cm) decreased numerically, but not significantly, from August to September. Hind-foot length was identical in November (36.0 ± 0.3 cm, $n = 16$) and April (36.0 ± 1.0 cm, $n = 12$) and femur length was very similar in November (22.9 ± 0.2 cm) and April (23.4 ± 0.3 cm).

Chemical composition of the ingesta-free body mass

Estimated masses of fat, metabolizable protein, protein in the hair, horns, and hooves, ash and water in the ingesta-free body mass paralleled seasonal changes in body mass, with fat showing the greatest seasonal increase and loss (Figure 2). The very young calves we examined in May had little fat and the calves in July had mostly gained lean tissue mass, but by November the mean estimated fat mass per calf was 16.5 ± 1.1 kg, or 26.5% of IFBM. This declined over winter to 3.33 ± 0.4 kg in April, or 6.35% of IFBM, and represented a loss of 80% of the November peak fat mass. Using the same median dates as above, the mean daily rates of fat gained or

lost were +73 g/day (May-July), +181 g/day (July-August), +45 g/day (August-November), and -90 g/day (November-April). The comparable rates of daily gain or loss of protein, combining the metabolizable and hair/horn/hooves portions, were +93g/day (May-July), +97g/day (July-August), +26g/day (August-November), and -17g/day (November-April).

Ingesta and gastrointestinal tissue masses in 1989

Ingesta mass data of muskox calves in the 6 gastrointestinal chambers in 1989 are presented as proportions (%) of the total ingesta, along with the proportion of ingesta in total body mass, of calves and adult cows in 1989 (Figure 3). Changes in tissue mass of gastrointestinal chambers are similarly presented as proportions of the total. Data from cows were previously presented in Adamczewski *et al.* (1997); proportionate values from adult cows are included for comparison with calves.

Initial evaluation of data from 6 young calves in May showed that the values from the youngest calf (body mass 13.0 kg, estimated 1-2 days old) were distinct from those of the other 5 calves (body mass 17.5 - 24.5 kg, estimated 2 weeks old), so are presented separately. Overall, ingesta were 4.5% of body mass in the youngest calf, 8.8 ± 0.6 % in the other calves, and 24.6 ± 1.1 % in the cows in May. The largest proportions of the ingesta (mostly milk curds) in the youngest calf were in the abomasum (46.0%) and small intestine (27.5%), while 73.9 ± 1.2 % of the ingesta in the cows were in the ruminoreticulum. The other calves in May had 65.6 ± 3.3 % of their ingesta in the ruminoreticulum, with substantially more in the abomasum (13.2 ± 1.4 % vs. 1.2 ± 0.2 %) than in the cows, and substantially less (1.1 ± 0.3 % vs. 8.0 ± 0.5 %) in the omasum. Ruminoreticulum contents in the calves in May were a mix of hair, soil, gravel, and plant parts; the fermentation typical of adult ruminoreticula appeared nearly absent.

The distribution of ingesta in the calves' digestive tract chambers in August was similar to that of the cows. The August patterns differed from the November and April patterns in the slightly higher proportion of ingesta in the abomasum (August calves 3.3 ± 0.5 %, cows 2.3 ± 0.3 %) and in the small intestine (August calves 16.2 ± 0.7 %, cows 14.0 ± 0.9 %; November calves 6.2 ± 1.4 %, cows 5.9 ± 0.3 %). In November and April the distribution of ingesta mass was nearly the same in calves as in adult muskoxen, with 75-80% of the ingesta in the ruminoreticulum and 24-27% of body mass in the ingesta.

Distribution of mass in the tissues of the digestive tract was also most different between calves and adults in May (Figure 4). The youngest calf in May had 57.1% of digestive tract tissue mass in the small intestine, compared to 41.6 ± 2.5 %

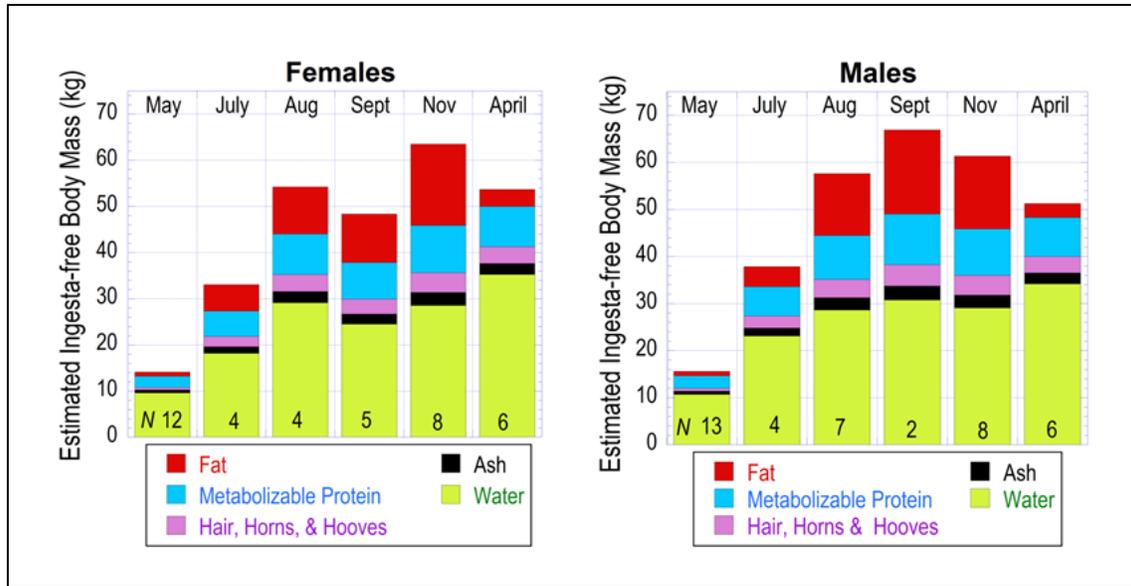


Figure 2. Seasonal changes in chemical composition of Victoria Island muskox calves, Nunavut, 1989-1993.

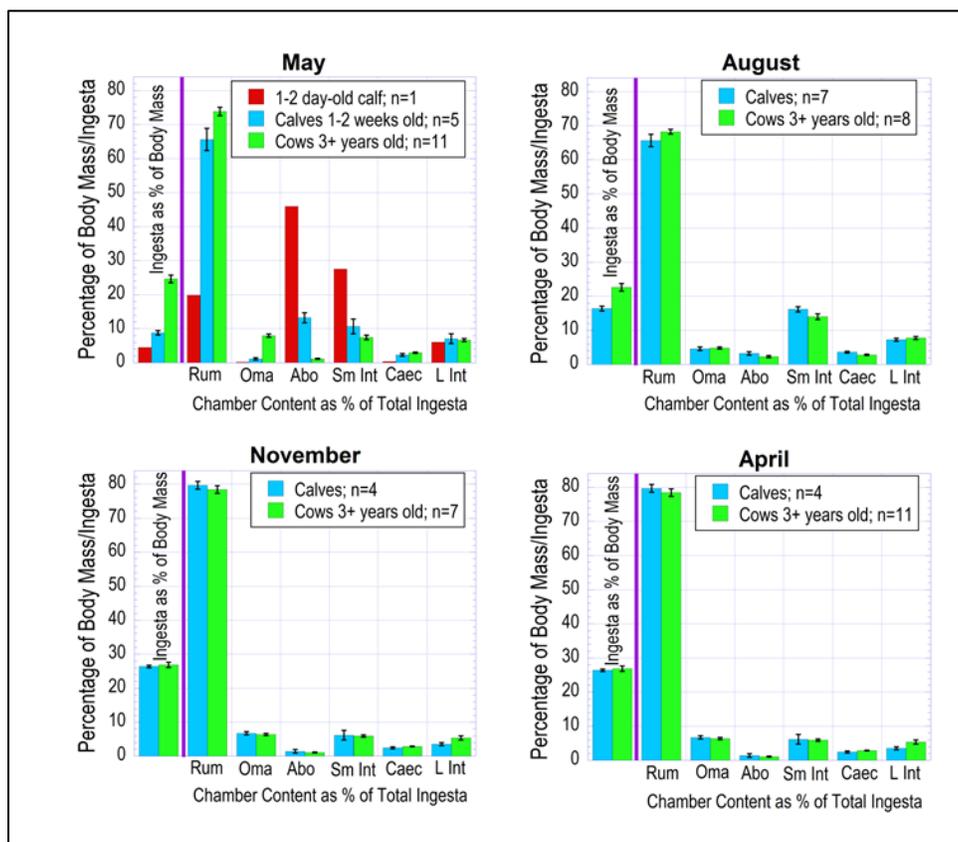


Figure 3. Seasonal changes in proportionate ingesta in digestive tract chambers of Victoria Island muskox calves and adult cows, Nunavut, 1989 (Rum = Ruminoreticulum, Oma = Omasum, Abo = Abomasum, Sm Int = Small Intestine, Caec = Caecum, L Int = Large Intestine).

Table 3. Year-to-year variation in body mass, back fat and femur length of muskox calves on Victoria Island, Nunavut, 1989-1993. SE = Standard Error.

Month & Year	Sample Size	Total Body Mass (kg)		Back Fat (cm)		Femur Length (cm)	
		Mean	SE	Mean	SE	Mean	SE
May							
1989	7	20.90	1.70	0.16	0.04	16.40	0.40
1990	8	14.50	0.80	0.20	0.04	15.00	0.20
1991	6	12.00	1.00	0.13	0.03	14.80	0.30
1993	4	15.90	0.30	0.38	0.06	15.30	0.10
November							
1989	4	76.50	6.50	1.68	0.39	22.50	0.40
1990	3	80.80	5.70	1.77	0.19	22.70	0.50
1991	7	85.20	2.40	2.11	0.18	23.10	0.20
1992	2	90.50	1.50	2.56	0.35	23.40	0.40
April							
1989	4	78.90	2.70	0.80	0.31	24.10	0.30
1990	4	70.90	2.40	0.13	0.03	23.10	0.40
1991	4	69.00	5.70	0.13	0.05	23.00	0.60

Table 4. Comparison of body mass, hind-foot length, and mean IGF-1 in 7 captive-raised muskox calves in Saskatoon, Saskatchewan, 1993-1994, at the end of the first year. F = Female, M = Male, SE = Standard Error.

Calf name	Born in Victoria Island or Saskatoon	Body mass April 12, 1994 (kg)	Rank in body mass	Hind-foot length April 12, 1994 (cm)	Rank in hind-foot length	Mean IGF-1 for the year: Mean +/- SE (sample #), ng/ml	Rank in mean IGF-1
Victoria (F)	Victoria	110	1	40.0	2	117.6 +/- 36.9 (14)	1
GW (M)	Victoria	105	2	40.5	1	101.0 +/- 26.1 (14)	2
Mikiok (F)	Victoria	102	3	39.8	3	56.4 +/- 13.2 (14)	5
Kim (F)	Saskatoon	88	4	38	5	72.7 +/- 25.9 (13)	3
Sarah (F)	Victoria	84	5	38.4	4	38.1 +/- 8.1 (13)	7
Jan (F)	Saskatoon	83	6	37.0	6	62.7 +/- 20.9 (11)	4
Colleen (F)	Saskatoon	69	7	34.6	7	42.6 +/- 13.2 (10)	6

in the other calves and 21.6 ± 1.2 % in cows. The ruminoreticulum had just 14.3% of tissue mass in the youngest calf, but it was 31.6 ± 2.7 % in the other calves, similar to the 35.7 ± 1.2 % in adults. Distribution of tissue mass in the digestive tract in August, November and April was generally similar between calves and adults. A slightly greater proportion of the calves' tissue mass was in the small intestine, and less in the large intestine, than in the cows, in August and November.

Year-to-year variation in calf body composition

Because year-to-year variation in calf mass and condition was limited and the sample numbers were low, we present a representative selection of trends in body mass, back fat thickness and femur length for the 3 seasonal hunts where we

had 3 or more years of data: May (4 years), November (4 years) and April (3 years) (Table 3). None of the study years between 1989 and 1993 stood out as having calves of exceptional size, condition or mass. Body mass ($P=0.45$), back fat thickness ($P=0.14$) and femur length ($P=0.45$) did not vary significantly with year.

Growth of captive-raised calves relative to hunter-killed calves from Victoria Island

Growth in body mass was significant for all 3 groups of calves over the first year ($P<0.001$) but was distinct for each group (Figure 5). The 4 calves wild-caught on Victoria Island initially had body mass means very similar to those in hunter-killed calves (May and July). The gain in body mass of these 4 calves averaged 457 g/day from May 19 to July 12,

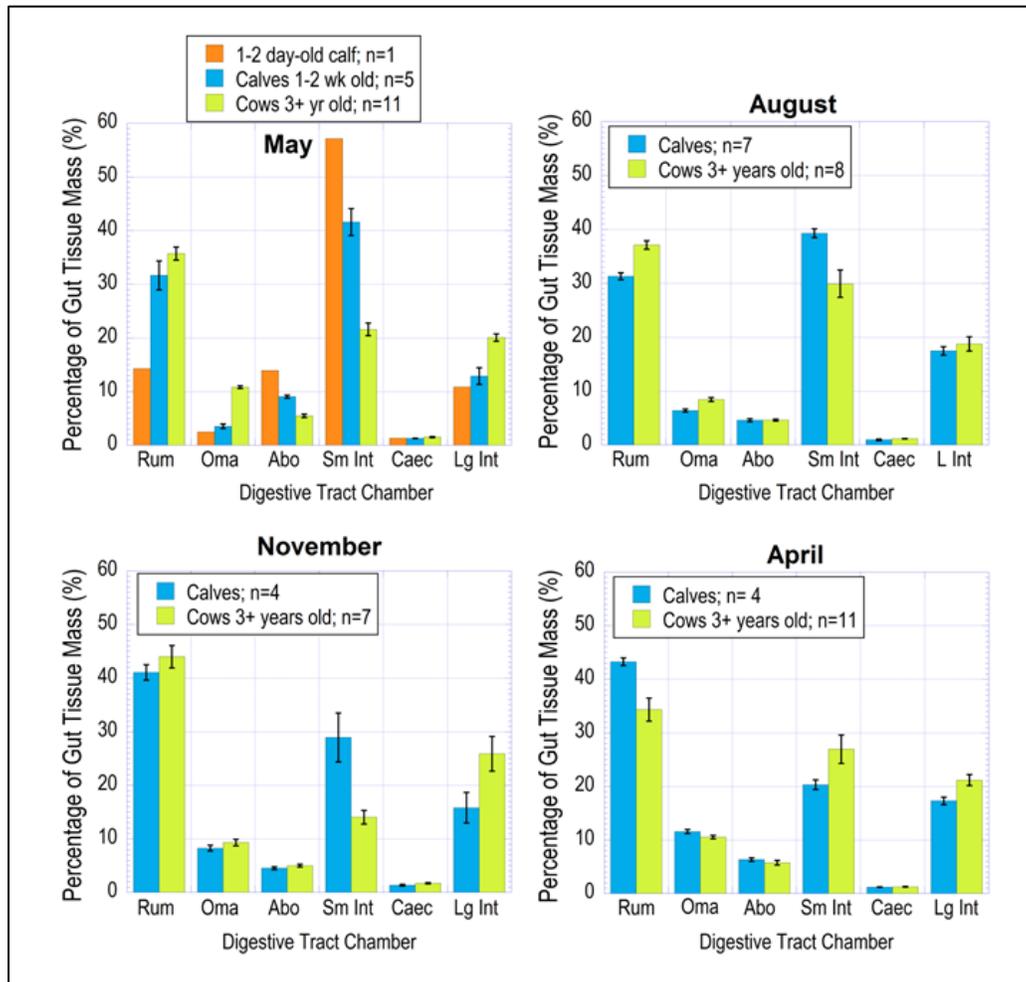


Figure 4. Seasonal changes in proportionate digestive chamber tissue mass of Victoria Island muskox calves and adult cows, Nunavut, 1989 (Rum = Ruminoreticulum, Oma = Omasum, Abo = Abomasum, Sm Int = Small Intestine, Caec = Caecum, L Int = Large Intestine).

nearly identical to the 463 g/day noted earlier for the hunter-killed calves for the same period. However, after the end of July, when the 4 wild-caught calves were weaned, their body mass lagged behind that of the hunter-killed calves in August, September and November. After November, body mass in the wild-caught calves continued to increase slowly to April (April 12, mean 100.3 ± 5.7 kg), while it declined in the hunter-killed calves to a mean of 72.9 ± 2.4 kg.

The 3 captive-born calves were born later and maintained a growth trajectory that closely paralleled that of the 4 wild-caught calves, but their body mass remained significantly lower ($P=0.04$) throughout the first year; they had not caught up by May 1994. While still with their mothers, their average mass gain was 461 g/day from June 14 to July 26, nearly identical to the growth rates of the 4 wild-caught calves and the hunter-killed calves. Like the wild-caught calves, growth

continued in these 3 calves through the winter. By April, the mean body mass of the 3 captive-born calves exceeded the body mass of the hunter-killed calves (April 12, mean 80.0 ± 5.7 kg vs. 72.9 ± 2.4 kg).

The 3 captive-born calves, like the 4 wild-caught ones, had a period of weight stasis when they were weaned at the end of July, and both groups thereafter gained mass more slowly than in June and July. Both groups of captive calves also had a period of stasis or slow increase in January and February, although there was no change of diet at the beginning and end of this period.

Changes in hind-foot length in the 3 groups of calves were significant through their first year ($P<0.001$) and generally paralleled the patterns in body mass (Figure 6). The most

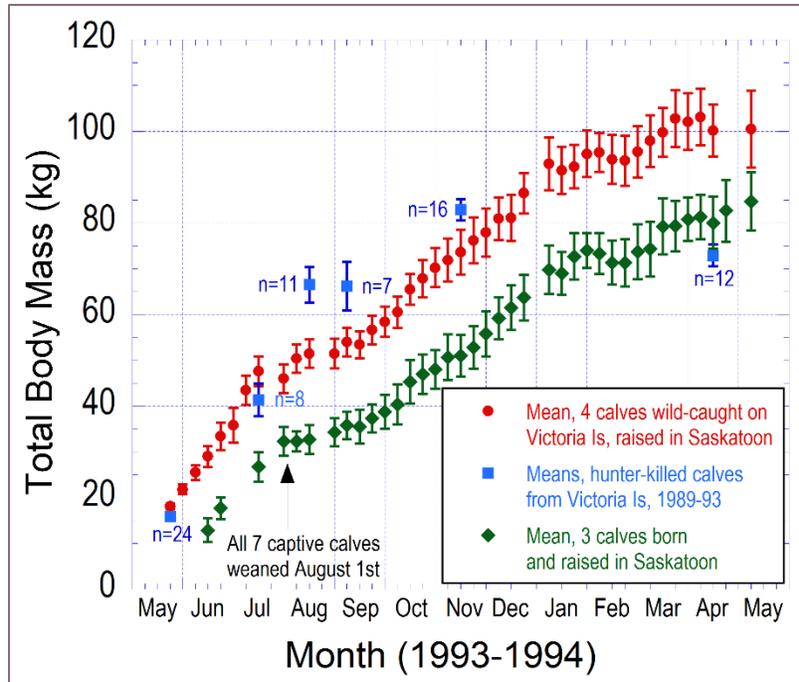


Figure 5. Increase in body mass of Victoria Island muskox calves 1989-1993, and 2 groups of captive calves in Saskatoon, Saskatchewan, 1993-1994.

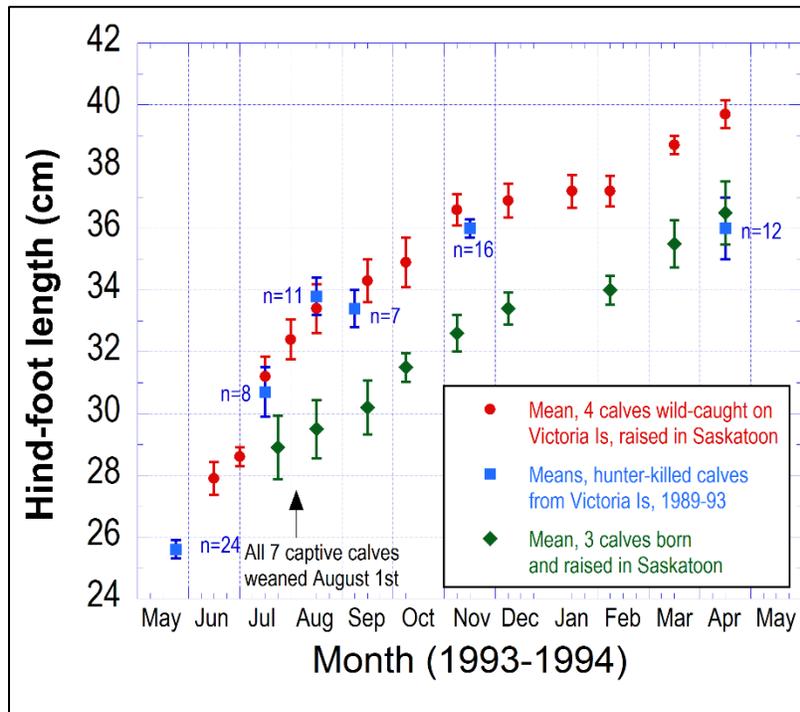


Figure 6. Increase in hind-foot length of Victoria Island muskox calves, Nunavut 1989-1993, and 2 groups of captive calves in Saskatoon, Saskatchewan 1993-1994.

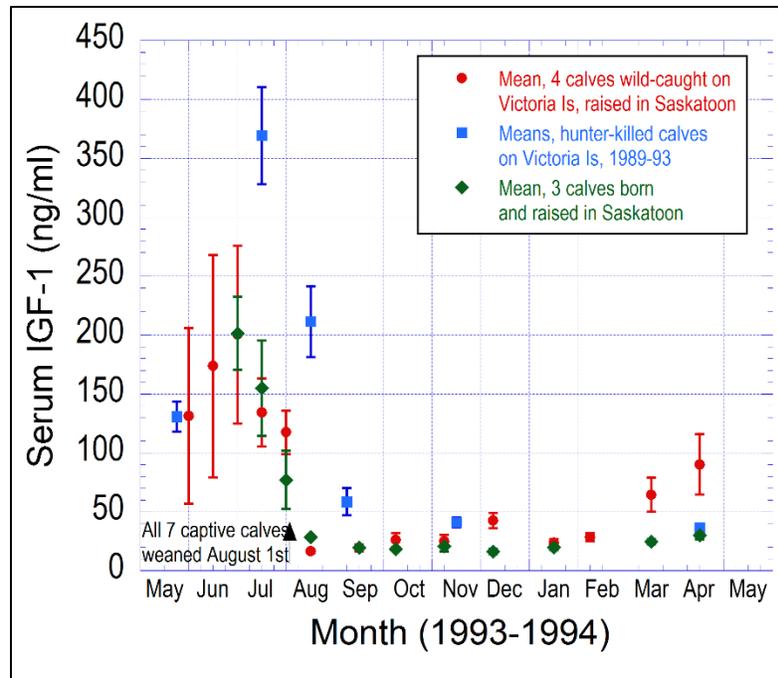


Figure 7. Changes in serum IGF-1 in Victoria Island muskox calves, Nunavut 1989-1993, and 2 groups of captive calves in Saskatoon, Saskatchewan 1993-1994.

rapid increases occurred early in the year. Hind-foot length remained very similar in the hunter-killed and 4 wild-caught calves from May to November. Thereafter, this measurement continued to increase in the wild-caught calves (November 7, mean 36.6 ± 0.5 cm; April 12, mean 39.7 ± 0.5 cm; a significant increase, $P < 0.001$) but remained the same (November, 36.0 ± 0.3 cm; April, 36.0 ± 0.1 cm) over winter in the hunter-killed calves. Hind-foot length in the 3 captive-born calves again paralleled length in the 4 wild-caught calves but remained consistently lower ($P = 0.02$) through the first year. Hind-foot length was similar in April in the 3 captive-born calves (mean 36.5 ± 1.0 cm) and in the hunter-killed calves (36.0 ± 0.1 cm).

IGF-1 in the hunter-killed calves varied significantly with season ($P < 0.001$) but did not differ with sex ($P = 0.20$) or year ($P = 0.10$), although there was high variance, particularly during the summer (Figure 7). The highest mean IGF-1 occurred in July (369 ± 41.2 ng/ml), a significant increase ($P < 0.05$) over May (130.7 ± 12.8 ng/ml), followed by significant decreases ($P < 0.05$) to August (211.4 ± 30.1 ng/ml), and September (58.5 ± 11.4 ng/ml). IGF-1 in the hunter-killed calves was lower (though not significantly) in November and April ($36-41$ ng/ml), than in September. We found no significant or near-significant correlations between body mass or gastrocnemius muscle mass and IGF-1 in the

hunter-killed calves, for any of the 6 monthly periods individually, or for all months in the analysis of covariance.

IGF-1 showed a strong seasonal progression ($P < 0.001$) in the 2 groups of captive-raised calves but did not differ significantly between them ($P = 0.13$). IGF-1 was lower in the 4 wild-caught and 3 captive-born calves than in the hunter-killed calves in July, August and September. From August, after they were weaned, IGF-1 in both the captive groups of calves remained at a fairly constant level until March (20-50 ng/ml). IGF-1 began to increase in the wild-caught calves in March and April, near the end of our data collection. IGF-1 values in hunter-killed calves and in the 2 groups of captive calves were similar over the winter (20-50 ng/ml) although the 7 captive calves continued to grow, while the hunter-killed calves lost mass and their linear growth nearly stopped.

There was a fairly strong positive association between body mass and hind-foot length among the 7 captive muskox calves, but a weaker association between mean IGF-1 and body mass or hind-foot length (Table 4). The 2 heaviest calves were a female and the 1 male, and these 2 individuals also had the 2 greatest hind-foot lengths and the 2 highest mean IGF-1 values. In the other 5 calves, though, higher mean IGF-1 was only loosely related to body mass or hind-foot length. We noted high individual variance in IGF-1 in

the 7 calves, particularly in summer. For example, the largest female had the following 4 IGF-1 values on successive sampling dates: May 31: 50.3 ng/ml; June 14: 456.0 ng/ml; June 26: 387 ng/ml; July 12: 174 ng/ml. The diet of lamb milk replacer and forage did not vary much over this period (Table 2A).

DISCUSSION

Growth of Victoria Island muskox calves compared to other populations and species

Body mass data from other studies suggest that the muskox calf growth we documented on Victoria Island in the 1990s was moderate and well below the maximum possible. Latour (1987) recorded body mass means for males and females about 1 year of age of 86 and 84 kg, respectively, on Banks Island in a population increasing rapidly (Gunn *et al.* 1991); the most comparable body masses on Victoria Island in the 1990s were means in April of 72.2 kg in males and 73.7 in females (this paper). Olesen *et al.* (1994) found average body mass of 1-year-old male muskoxen of 130 kg in an introduced muskox population growing exponentially in West Greenland (Olesen 1993), indicating a much higher calf growth rate and better feeding conditions, including limited snow cover (Olesen 1993) in that population in those years.

The information from our studies, combined with data on mass, condition and pregnancy rate of cows of various ages (Adamczewski *et al.* 1997), provides a benchmark for a healthy muskox population growing slowly, for comparison with other muskox populations that may be in a different demographic phase and will likely have poorer or better mass and condition.

The lack of significant variation among years in muskox calf size, mass and condition (Table 3) suggests that the seasonal patterns and values we documented were representative of the population in the early 1990s on southeast Victoria Island. It did not appear that hunters chose larger or smaller calves; rather, they shot cows and calves associated with those cows. The apparent slight decline in calf mass and size from August to September most likely reflects a sampling, by chance, of 7 relatively small calves (including 5 females) in the 1 September hunt.

Caribou and reindeer calves grow quickly during their first summers (Parker *et al.* 1990), but they generally remain much leaner than the muskox calves we studied. Calf and yearling caribou from the George River herd had 3.44% and 7.76% fat in the IFBM during early and late-winter hunts in 1984 (Huot 1989); well-fed captive-raised George River caribou calves and yearlings had similar values of 6.6% and 6.9% fat in the IFBM (Crête *et al.* 1993). Growing reindeer studied between birth and sexual maturity by Ringberg *et al.*

(1981a, b) rarely exceeded 10% extractable fat in the carcass. The only young reindeer or caribou that achieve fatness similar to that of our muskox calves are Svalbard reindeer (*R. t. platyrhynchus*). Reimers and Ringberg (1983) estimated dissectible fat of 14-17% of whole body mass in calf and yearling Svalbard reindeer, Reimers *et al.* (1982) recorded 27.8% fat in the IFBM of a yearling Svalbard reindeer, and fatness as high as 16.8 to 28.7% of whole body mass was reported in adults by Tyler and Blix (1990). Domestic sheep and cattle (*Bos taurus*), however, often achieve fatness matching or exceeding the levels we found in muskox calves and adults (e.g. cattle: Koch *et al.* 1979; sheep: Blaxter *et al.* 1982).

Although muskox calves are small at birth relative to maternal body mass (Robbins and Robbins 1979), their first year's growth stretches from birth in late April or early May to November, and they achieve by fall a size and fatness (26% of IFBM) that serve them well as they begin their first winter. On Victoria Island, full-grown adult caribou cows commonly weighed 70-75 kg in November at the time of our studies (A. Gunn, unpublished data), while 6-month-old muskox calves weighed 82-84 kg. The muskox yearlings studied by Olesen *et al.* (1994) in West Greenland may well have had greater fat reserves than the calves we measured on Victoria Island.

Growth in male and female muskox calves

Male and female muskox calves in our studies generally grew at a very similar pace through their first year, although males tended to be bigger and heavier, with significantly greater bone mass and greater horn growth. Latour (1987) recorded similar mean body masses for 1-year-old female (84 kg) and male (86 kg) muskoxen on Banks Island, then progressively greater divergence between older males and females. Chaplin and Stevens (1989) found essentially identical growth in captive male and female calves in Saskatoon in their first year, with increasing divergence in the second year. Captive-raised male and female muskox calves in Fairbanks, Alaska showed very similar mass gains through the first year (Frisby *et al.* 1984). Peltier and Barboza (2003) found slightly higher first-year mean body mass in captive Alaskan males than in females, and greater differences in the second year.

We suspect that a larger data set from Victoria Island might have resulted in a greater number of small but significant differences in body composition between males and females. Given the massive horns, head and neck bones muskox bulls develop later, the early difference we found in bone mass likely accelerates as the sexes mature. The limited horn length data suggest that horn growth begins at about the same time in summer in males and females but diverges increasingly before the end of the first year.

Early development of ruminant function in muskox calves

Muskox calves on Victoria Island appeared predisposed to early development of the ruminoreticulum and ruminant digestion. The youngest calf we studied in May 1989, estimated 1-2 days old, had significant ingesta in the ruminoreticulum, and the 2-week-old calves in May had more than 8% of their body mass in ingesta, the bulk of it in the ruminoreticulum. We have observed newborn 1-2-day-old calves taking in gravel, soil, and bits of vegetation in Saskatoon, as did the 2-week-old calves live-captured in 1993. Ingestion of soil and hair in very young muskoxen was also noted by Knott *et al.* (2004) in captive Alaskan muskoxen. The presence of these ingesta in the ruminoreticulum appeared to stimulate rapid growth of the ruminoreticulum tissue, as seen from the much greater ruminoreticulum tissue mass in the 2-week-old calves than in the 1-2-day-old calf. Chaplin (1984) observed live-captured calves from Banks Island ruminating at about 3 weeks of age.

Calf ruminoreticulum contents in May on Victoria Island had little evidence of the fermentation typical of adult ruminoreticula, however, and development of full ruminant capacity requires more than the presence of plant material in the ruminoreticulum. Knott *et al.* (2004, 2005) documented the changes of ingesta and maturation of digestive tract tissues and organs in detail in the first 30- and 60-day-periods after birth in captive muskoxen and reindeer; they commented that "Successful ruminal development allows young muskoxen and reindeer to consume plants at early phenological stages in July". On Victoria Island, forage quality was highest in July of the periods sampled (Adamczewski *et al.* 1997), with many plants flowering; by that time the calves were more than 2 months old. By August, Victoria Island calves had tissue and ingesta masses and proportions that differed little from those of adults, and their ruminoreticulum contents in July and August appeared identical to those of adults in terms of consistency and gas production.

Patterns in mass of ingesta and digestive tract tissues in Victoria Island muskox calves confirm earlier studies that identify muskoxen as grazers (as defined by Hofmann 1989) primarily adapted to slow digestion of graminoids. Studies by Staal and Thing (1991), Hofmann (2000), Knott *et al.* (2004; 2005), Barboza *et al.* (2006), and Clauss *et al.* (2007) are all consistent with the current results showing that muskoxen have the high ingesta masses, predominantly in the ruminoreticulum, and ruminal and omasal morphology typical of bovid grazers. Although relative distribution of tissue and ingesta among digestive tract chambers was similar in the wild muskox calves and adults we studied and

those measured by Knott *et al.* (2005), the wild muskoxen tended to have a higher proportion of ingesta overall (17-23% of body mass in August and 25-27% in November and April) while 60-day-old muskoxen studied by Knott *et al.* (2005) had 10.9% of body mass in ingesta and adults had 14.3%. Barboza *et al.* (2006) also noted the lower overall ingesta fill of Alaskan captive muskoxen (ca. 16%) than in the wild. The differences may reflect differences in diets and condition between wild and captive muskoxen.

Summer peak in muskox calf growth

Our data from Victoria Island muskox calves indicate that calf growth is moderate from May to July, most rapid in July and August, and much slower in the fall. This likely reflects in part the highly seasonal forage quality available to both calves and cows on Victoria Island: highest in July (dry matter nitrogen in ruminoreticulum contents = 5.41%), then decreasing significantly ($P < 0.05$) to August (4.26%) and September (3.48%), with poorer quality in November (2.64%), April (2.54%) and May (2.39%; Adamczewski *et al.* 1992). However, calf liver and kidney mass peaked in August, not in July; masses of these organs are highly responsive to recent nutrition in domestic ruminants (O'Donovan 1984; Burrin *et al.* 1989, 1990). The slower calf growth from May to July may also reflect a summer peak in the wild in muskox milk production. Milk production was highest in well-fed captive muskox cows in Alaska 3 weeks after birth (White *et al.* 1989). However, mammary gland masses or volumes, measured as an index of milk production in goats (*Capra aegagrus hircus*; Linzell 1966, 1972; Knight and Peaker 1984) were greater in August than in May or July in hunter-killed muskox cows on Victoria Island (Adamczewski *et al.* 1997). Lactation in domestic cattle often does not peak until 2-3 months after birth (Walker and Pos 1963), and the level of early milk production in sheep is strongly influenced by maternal nutrient intake (Peart 1970; Wood 1976; Loudon *et al.* 1984). Early milk production in late winter in muskox cows in the wild may well be similarly dampened by the lack of high-quality forage. The fastest growth of the calves in July and August may reflect a combination of high forage quality, development of a fully functional ruminant system, and a relatively late peak in milk production in the summer.

The importance of milk to first year muskox calf growth

From May to July (June to July in the 3 late-born captive calves) the body mass gains of the hunter-killed, wild-caught and captive born muskoxen were a remarkably similar 457-463 g/day. The hunter-killed calves were nursing from their mothers, as were the 3 captive-born calves, while the 4 wild-caught calves were fed a lamb milk-replacer that resulted in similar growth rates. After the 2 groups of captive calves were weaned at the end of July, however, their mass gains

lagged behind those of the wild calves until November; IGF-1 levels, particularly, remained substantially higher in the wild calves than in the 2 groups of captive calves. By this time, their ability to function as full ruminants should have been well established. The critical importance of milk to muskox calf growth in the 6-8 weeks before spring has been recognized (Thing *et al.* 1987; Adamczewski *et al.* 1997). The slowed growth of the captive calves after weaning suggests that lactation in the summer and fall may still be important in allowing muskox calves to achieve continuing growth toward adequate size and body reserves entering their first winter. Muskox cows may extend lactation through the first winter (White *et al.* 1989; Adamczewski *et al.* 1997) and even past the first year (Adamczewski *et al.* 1997). However, the slow growth of the captive calves after weaning may also reflect factors in the diets and environmental conditions experienced by the captive herd in Saskatoon. Trace minerals, particularly low copper, have been shown to affect growth rates and health of captive muskox calves in Alaska (Rombach *et al.* 2002) and in muskoxen in Saskatoon (Blakley *et al.* 1998).

Growth stasis in winter

In barren-ground caribou, linear growth usually ceases in the fall and animal condition declines over winter, as plant senescence and snow cover restrict nutrient availability (Dauphiné 1976). In a similar way, in the wild muskox calves we studied on Victoria Island, linear measures (hindfoot length and femur length) were nearly identical in November and April, and body mass and condition declined significantly over winter. Horns continued to grow slowly over the winter, however, despite the losses in body mass and condition. Growth stasis in the winter is clearly not obligatory in muskoxen as well-fed captive calves in Saskatoon (Chaplin 1984; Chaplin and Stevens 1989; this study) and in Fairbanks (Frisby *et al.* 1984; Peltier and Barboza 2003) continued to grow steadily through their first winters. We noted an apparent growth stasis in January and February in the 7 captive calves we studied, which we were not able to connect to any change of diet, but no such stasis was noted in other studies of captive calves.

Growth patterns through the year, including hormones like IGF-1 that regulate growth, are also influenced by photoperiod in ungulates that live in strongly seasonal environments (Suttie *et al.* 1991; Webster *et al.* 1999). In an earlier study, we found that IGF-1 showed a strong seasonal pattern in captive muskox cows in Saskatoon fed a nearly constant medium-quality diet, with a peak in the fall suggesting a predisposition to weight gain at that time (Adamczewski *et al.* 1992). In the wild cows, IGF-1 remained similar at about 100 ng/ml from July to September, even though forage quality declined substantially over that

time period, suggesting that diet quality and photoperiod both influenced serum levels of this hormone.

IGF-1 levels in the hunter-killed muskox calves showed a greater amplitude seasonally than in cows shot at the same times (Adamczewski *et al.* 1992). In the winter the IGF-1 values of about 50 ng/ml were similar in wild calves and cows, while in summer IGF-1 in the wild cows increased to about 100 ng/ml but did not reach the 200-350 ng/ml found in the wild calves in early summer. IGF-1 levels in the 2 groups of captive calves were approximately similar to those in the wild until the captive calves were weaned; thereafter the calf IGF-1 levels averaged 20-30 ng/ml through the winter, below the levels found in captive cows of 70-100 ng/ml in winter. The relatively low levels of IGF-1 in the captive calves were apparently still sufficient to allow for the slow continued growth in body mass and hindfoot length they achieved.

For captive muskoxen with abundant food, slower growth in late summer and fall could be compensated for by continuing growth in winter. In the wild, though, November appeared to mark the beginning of negative energy balance for the calves on Victoria Island. Although they have fully functional ruminant systems, young muskoxen have higher relative energy needs than adults (Munn and Barboza 2008), which may account for the larger relative losses of fat and mass over winter of Victoria Island calves compared to adult cows (Adamczewski *et al.* 1997).

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Jan Adamczewski has a BSc in Wildlife Biology from the University of Guelph, an MSc from the University of Alberta in wildlife productivity, and a PhD from the University of Saskatchewan in biology. He has worked as a biologist for the Government of Newfoundland, as a biologist for the Sahtú Renewable Resources Board in Norman Wells, NWT, as a regional biologist for the Yukon Government in Watson Lake, and as an ungulate biologist with the Government of the Northwest Territories in Yellowknife. Most of his time since 2007 with the GNWT has been focused on barren-ground caribou, but his first love among all wildlife remains muskoxen, which have the cutest babies on the planet.



Peter Flood was born in Manchester at the outbreak of WWII and scrupulously educated in the sciences at an old-fashioned grammar school where the seeds of a career in biology began to germinate. Having taken a degree in Veterinary Science at Liverpool, he worked for some years in farm animal practice. This led to an interest in reproductive physiology and eventually to an MSc in mammalian reproduction at the University of Wales. What followed was a faculty position at the University of Bristol, extensive experience in teaching comparative anatomy, and a PhD. After 10 years in Bristol, it was time for change and Peter has been associated with the University of Saskatchewan ever since.



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Appendix 1A. Changes in body mass, composition and condition of hunter-killed muskox calves on Victoria Island 1989-1993. IFBM = Ingesta-Free Body Mass; M = Male; F = Female; SE = Standard Error.

Sample Size	Month	Total Body Mass (kg)				IFBM (Estimated; kg)				Carcass Mass (kg)				
		M		F		M		F		M		F		
M	F	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
13	1	May	16.79	1.06	14.99	1.42	15.61	1.01	14.10	1.43	9.45	0.63	8.64	0.95
4	4	July	44.88	4.62	37.88	5.54	37.86	4.14	33.05	4.04	22.25	2.52	19.50	2.40
7	4	Aug.	68.29	5.38	63.50	5.68	57.66	4.43	54.22	3.71	35.36	2.64	31.12	0.72
2	5	Sept.	81.75	4.75	60.00	4.70	66.90	3.09	48.36	4.69	41.00	2.00	29.50	2.94
8	8	Nov.	81.88	4.23	83.88	2.12	61.33	3.34	63.51	2.06	38.42	2.21	40.56	1.44
6	6	April	72.17	3.19	73.67	3.91	51.26	3.05	53.67	2.78	32.07	1.84	33.50	1.63
Month	Back Fat (cm)				Kidney Fat (g)				Femur Marrow Fat (%)					
	M		F		M		F		M		F			
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE		
May	0.22	0.04	0.18	0.03	36.6	4.3	35.5	3.0	52.3	10.8	55.7	6.0		
July	0.68	0.14	0.65	0.19	79.5	14.8	125.5	26.7	67.3	3.9	73.4	2.7		
Aug.	1.34	0.25	1.60	0.20	219.5	29.2	207.0	19.0	82.3	1.7	82.2	4.2		
Sept.	2.30	0.30	1.52	0.47	283.5	23.5	192.0	40.6	88.8	1.4	88.3	1.8		
Nov.	1.83	0.20	2.16	0.20	268.2	32.7	301.0	22.3	85.1	1.7	90.4	2.6		
April	0.48	0.25	0.22	0.11	48.2	9.4	47.4	8.6	67.1	6.1	58.1	5.1		
Month	Gastrocnemius Mass (g)				Femur Mass (g)				Kidney Mass (both; g)					
	M		F		M		F		M		F			
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE		
May	69.4	5.0	66.6	6.6	128.4	5.3	118.3	8.0	67.7	3.2	59.9	3.4		
July	169.3	20.6	140.3	12.7	257.0	23.1	212.8	20.2	185.5	13.1	158.5	17.3		
Aug.	297.3	50.4	246.0	13.0	358.9	40.4	288.0	15.1	229.7	11.9	219.7	21.3		
Sept.	271.5	10.5	205.0	17.8	346.0	15.0	267.0	17.4	218.5	4.5	170.0	15.9		
Nov.	279.0	15.4	292.3	13.5	348.0	11.6	333.6	9.2	160.1	11.5	149.4	5.5		
April	222.8	8.1	246.0	14.2	351.5	15.4	340.5	15.8	134.2	6.4	138.0	8.6		
Month	Liver Mass (kg)				Ruminoreticulum Content Mass (kg)				Ruminoreticulum Tissue Mass (kg)					
	M		F		M		F		M		F			
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE		
May	0.342	0.076	0.247	0.015	0.64	0.15	0.56	0.11	0.173	0.024	0.159	0.015		
July	0.908	0.065	0.803	0.105	4.07	0.32	2.93	0.81	0.997	0.106	0.765	0.150		
Aug.	1.050	0.094	1.012	0.073	7.21	0.86	7.14	1.07	1.305	0.112	1.360	0.127		
Sept.	1.010	0.010	0.852	0.036	11.55	1.65	10.40	0.63	1.700	0.100	1.296	0.041		
Nov.	0.798	0.041	0.756	0.032	15.61	0.75	16.43	0.51	1.707	0.066	1.756	0.039		
April	0.663	0.035	0.680	0.017	16.52	1.24	15.57	0.88	1.682	0.034	1.728	0.100		
Month	Femur Length (cm)				Hind-Foot Length (cm)				Horn Length (cm)					
	M		F		M		F		M		F			
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE		
May	15.5	0.2	15.3	0.3	25.7	0.3	25.5	0.5	0.0	0.0	0.0	0.0		
July	19.7	0.7	18.3	0.6	31.1	1.2	30.3	1.1	0.0	0.0	0.0	0.0		
Aug.	22.6	1.1	21.0	0.4	34.1	0.8	33.4	0.8	0.5	0.2	0.0	0.0		
Sept.	21.7	0.3	20.7	0.5	35.5	0.5	32.6	0.4	1.5	0.5	0.1	0.1		
Nov.	22.8	0.3	23.0	0.2	36.2	0.5	35.6	0.4	2.5	0.3	1.3	0.1		
April	23.5	0.5	23.4	0.4	35.4	1.9	36.6	0.5	10.4	1.2	6.6	2.9		

Appendix 1B. Changes in estimated chemical composition of ingesta-free body mass in hunter-killed muskox calves on Victoria Island 1989-1993. All measurements are in kg. IFBM = Ingesta-Free Body Mass; M = Male; F = Female; SE = Standard Error. Sample Sizes as in table above.

Month	IFBM (Estimated)				Fat (Estimated)				Ash (Estimated)			
	M		F		M		F		M		F	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
May	15.61	1.01	14.1	1.43	0.938	0.206	0.896	0.149	0.697	0.045	0.63	0.064
July	37.86	4.14	33.05	4.04	4.257	1.154	5.720	1.227	1.693	0.185	1.478	0.181
Aug.	57.66	4.43	54.22	3.71	13.201	1.331	10.204	1.536	2.580	0.198	2.425	0.166
Sept.	66.9	3.09	48.36	4.69	17.872	1.554	10.548	2.576	2.994	0.139	2.163	0.210
Nov.	61.33	3.34	63.51	2.06	15.461	1.884	17.628	1.262	2.743	0.149	2.842	0.093
April	51.26	3.05	53.67	2.78	2.962	0.577	3.692	0.693	2.293	0.137	2.401	0.124
Month	Metabolizable Protein (Estimated)				Protein in Hair, Horns & Hooves (Estimated)				Water (Estimated)			
	M		F		M		F		M		F	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
May	2.672	0.165	2.422	0.235	0.609	0.039	0.550	0.056	10.694	0.655	9.602	0.942
July	6.231	0.652	5.473	0.638	2.574	0.281	2.247	0.274	23.105	2.020	18.132	2.677
Aug.	9.312	0.687	8.785	0.731	3.921	0.301	3.687	0.252	28.646	2.256	29.119	3.510
Sept.	10.742	0.474	7.872	0.731	4.549	0.210	3.288	0.319	30.743	0.979	24.489	1.482
Nov.	9.88	0.515	10.219	0.318	4.170	0.227	4.319	0.140	29.076	1.082	28.502	0.633
April	8.326	0.474	8.700	0.431	3.486	0.207	3.650	0.189	34.193	1.731	35.227	1.625

Appendix 1C. Changes in mass of gastrointestinal chambers and ingesta in muskox calves in 1989 on Victoria Island. All measurements are in kg. SE = Standard Error; C = Content; T = Tissues.

Month	Sample Size	May		August		November		April		
		1 (est. 1-2 days old)	5 (estimated 2 weeks old)	7	7	4	4	4	4	
	Mass	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
Body		13.00	21.900	1.528	67.64	5.69	76.50	6.47	78.88	2.73
Ingesta		0.581	1.901	0.111	11.243	1.202	20.224	1.820	20.331	1.618
Ruminoreticulum C		0.115	1.251	0.101	7.466	0.884	16.107	1.442	15.85	1.040
Omasum C		0.001	0.021	0.005	0.453	0.100	1.364	0.158	1.628	0.165
Abomasum C		0.267	0.249	0.026	0.343	0.040	0.263	0.070	0.205	0.030
Sm Intestine C		0.160	0.200	0.035	1.789	0.178	1.265	0.332	1.082	0.390
Caecum C		0.002	0.042	0.005	0.397	0.040	0.495	0.077	0.476	0.099
Lg Intestine C		0.034	0.138	0.036	0.796	0.072	0.730	0.137	1.090	0.102
All Gut T		0.525	0.838	0.054	4.317	0.313	4.310	0.236	4.349	0.267
Ruminoreticulum T		0.075	0.261	0.017	1.334	0.117	1.768	0.103	1.775	0.103
Omasum T		0.013	0.029	0.003	0.340	0.077	0.359	0.039	0.478	0.039
Abomasum T		0.073	0.076	0.007	0.193	0.016	0.195	0.013	0.260	0.022
Sm Intestine T		0.300	0.354	0.041	1.661	0.118	1.242	0.196	1.077	0.248
Caecum T		0.007	0.011	0.001	0.039	0.004	0.058	0.005	0.049	0.004
Large Intestine T		0.057	0.107	0.014	0.750	0.083	0.699	0.145	0.71	0.047