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DIGESTION AND BODY COMPOSITION IN MUSKOXEN

**A Thesis Submitted to the College of
Graduate Studies and Research
in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy
in the Department of Biology
University of Saskatchewan
Saskatoon**

By

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Spring 1995

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ABSTRACT

Muskoxen (*Ovibos moschatus*) are relatively large herbivores living in an arctic environment where forage is sparse and its availability during long winters is often much reduced by snow and ice. Muskoxen cope by obtaining energy and nutrients from the low-quality sedges and grasses they eat, and from body reserves accumulated in summer and autumn. The objectives of this study were to evaluate the physiological and energetic adaptation of muskoxen to digestion of graminoid forage, and to measure the extent and reproductive significance of seasonal changes in body composition of female muskoxen. The first objective was addressed using two studies with captive muskoxen in Saskatoon, and the second during a field study on Victoria Island, Northwest Territories.

In the first study, changes in body weight, intake, retention time and digestibility of a supplemented brome-alfalfa hay were measured in mature muskoxen during two seasonal cycles. Mean daily dry matter intake of breeding females was highest in July and August ($62 \pm 3.6 \text{ g/kg}^{0.75}$) then declined slowly to its lowest point in March and April ($41 \pm 0.7 \text{ g/kg}^{0.75}$). Mean retention time of hay, calculated from a chromium marker, declined ($P < 0.01$) from $114 \pm 4 \text{ h}$ in March to $95 \pm 4 \text{ h}$ in July. Apparent organic matter digestibility decreased ($P < 0.01$) from $74.7 \pm 0.8 \%$ in winter to $61.7 \pm 1.3 \%$ in summer. Compared with other ruminants, muskoxen are grazers exceptionally well-suited to slow, thorough digestion of graminoid forage.

In the second study, the voluntary intake and apparent digestibility of a low-protein grass hay, similar in composition to diets of wild muskoxen in winter, were measured in five mature muskoxen and three mature Hereford cows during late winter 1993. Both species maintained body weight on the experimental diet but daily dry matter intake of the muskoxen was only 1/3 that of the cattle (32 ± 2 vs. $96 \pm 3 \text{ g/kg}^{0.75}$; $P < 0.001$). Apparent digestibility of organic matter, measured using chromic oxide, was higher in the muskoxen than in the cattle (58 ± 2 [SE] vs. $50 \pm 3\%$; $P = 0.03$). Muskoxen are particularly well adapted to digesting low quality graminoid forage at exceptionally low rates of intake.

In the third study, the anatomical and chemical body composition of 22 muskoxen that varied widely in size, age and condition were analysed, and measures of body weight and condition were evaluated as predictors of body composition. The leanest muskoxen were four 5 to 15-day-old calves with $3.5 \pm 0.5 \%$ (mean \pm SE) fat in the IFBW, and the fattest were three females with $24.8 \pm 1.4 \%$ fat. Muscle weight was best predicted from weights of individual muscles, protein weight from IFBW, bone weight from the weights of individual limb bones, and ash weight from IFBW.

Combining kidney fat weight and a measure of body weight with up to three other measurements allowed dissectible and total fat weights to be estimated accurately. The extent of fattening in muskoxen exceeded that found in other wild ruminants with the exception of Svalbard reindeer (*Rangifer tarandus platyrhynchus*).

In the fourth study, the body weight, body composition and reproductive status of 202 muskox cows from Victoria Island were analysed during 16 seasonal collections from 1989 to 1993. Adult muskox cows were lightest and leanest in May, when the ingesta-free body weight (IFBW) of newly-lactating adult cows was 116 ± 2 kg (adjusted mean \pm SE) and a similar 112 ± 3 kg in nonlactating cows. Thereafter, the IFBW of lactating cows was virtually unchanged until July, increased rapidly during August, peaked in September at 166 ± 4 kg, then decreased to 148 ± 2 kg in November. In contrast, the IFBW of nonlactating cows increased throughout summer, reached a higher peak in September (176 ± 7 kg; $P < 0.01$) and changed little by November (164 ± 2.1 kg). Pregnancy rates in this population increased from 0 in females 1.5 years old in the autumn to 25 % in 2.5 year-olds and 62.5 % in cows at least 3.5 years old. Lactation did not appear to peak until at least two months after calving, and was sometimes extended to more than a year. Lactation in November did not preclude pregnancy, but pregnant females at this time were fatter and heavier than nonpregnant cows. These results indicate substantial flexibility in reproductive patterns of muskoxen and an unique ability to maintain condition through long arctic winters.

Based on these studies, the persistence of muskoxen through arctic winters can be ascribed in large part to exceptionally low maintenance requirements, along with an ability to thoroughly digest low-quality graminoid forage. Female muskoxen also deposit large quantities of fat in late summer and are able to conserve a large portion of them through early and mid- winter, and use them to support late-winter lactation. Muskox reproductive rates are strongly sensitive to nutritional influences. This suite of K-selected characters in muskoxen is consistent with a slow metabolism and a low rate of population growth.

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I was very fortunate to see something of the arctic tundra in all its beauty, vastness and unpredictability. For their help during 16 field trips, I thank Jack and Robert Ekpakohak, Jorgen Aitaok, Ronnie Akhok, David Amegainek, Duane Smith, David Nakashook, Joachim Obst, Luke Coady, Jimmy Haniliak, Bobby Klengenberg, Sam Angohiatok, Ted Leighton, and particularly Amos Wamikon and David Kaomayok. The co-operation and support of the Hunters and Trappers Association and community of Cambridge Bay and the support of John Stevenson of the Department of Renewable Resources in Coppermine, NWT are gratefully acknowledged. Special thanks are extended to Jim Schaefer, who shared field camps with me, helped with digestive trials in Saskatoon, provided samples of muskox winter forage, and reviewed several manuscripts.

I worked with the wonderful muskoxen at Goodale Farm for more than six years. For their patient help with many hours of muskox care, feeding and training, I thank Kim Romanufa, Sarah Parker, Richard Monseler, Tom Van Dyck, and many veterinary students. Goodale Farm manager Bill Kerr helped with many aspects of logistics at the farm and was instrumental in setting up the low-protein hay trials. For their help during various parts of sample collection and analysis, I am grateful to Charlotte Mayes, Rob Wagner, Gord Clark, Jay Thrush, Mike Bass, Barb Hanbidge, Glenna Miller, Bob Famulak, Richard Schaan, and Michelle Follensbee. My appreciation is extended to Todd Ree, Terry and Mirjana Fenton, Mick Price, Erasmus Okine, Eva Soskova and the Department of Animal Science at the University of Alberta for their help with muskox tissue grinding and chemical analyses, and with the

preparation and analysis of chromium-mordanted material. Technicians at the Department of Animal Science at the University of Saskatchewan ably carried out chemical analyses of samples from feed trials. Although the studies of metabolic hormones carried out with the tame muskoxen are not presented in this thesis, I am most thankful for the patience and help of Blair Goldade, Charlotte Hampton, Anita Lemke and summer students in Bernard Laarveld's lab in Saskatoon. My thanks are extended to Nic Larter, Department of Renewable Resources, Inuvik, NWT, for providing samples of winter forages, and to V. L. Harms, W. P. Fraser Herbarium, University of Saskatchewan, for identifying plant species in the low-protein hay. Juliane Deubner provided excellent help with figures and I thank Roger Pierson and Gregg Adams for ultrasounding muskox ovaries.

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DEDICATION

Amos Wamikon and Sue Tedesco are two friends who shared their time, hard work and bright, warm energy with me over the past few years. I salute them.

Amos is a hunter and guide in Cambridge Bay. We hunted and travelled together during all the seasons and moods of the tundra on Victoria Island. Amos has a million-dollar smile, particularly when the weather turns angry, the hour is late, and the task at hand seems impossible. He is a master craftsman, although he has no certificates or degrees, and like all true masters has no need of them. I could not have asked for a better partner in the field, and I learned more from Amos than he will ever know.

Sue was my comrade and office-mate for more than five years in Saskatoon. More importantly, we raised wooly babies together, watched over a special flock of long-haired sheep as best we could, and played idiotic games over mugs of coffee at many strange hours of the night. There are no commodities more valuable than enthusiasm, intelligence, and above all, caring. Of these, Sue has more than her share. Like Amos, Sue has a smile that lights up the room.

Much of the canvas between these covers is painted in the precise, dull pigments of science. They are an inadequate medium in which to portray the romance of the tundra and its remarkable inhabitants. Along with many other students of ecology, I owe a spiritual debt to Aldo Leopold, who showed so eloquently that an academic understanding of ecological processes should be just one facet of our awareness of nature. To keep my research, and all research, in perspective, it is useful sometimes to remember this question, asked by Leopold (1949):

"Is education possibly a process of trading awareness for things of lesser worth?"

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CHAPTER 1. THE CHALLENGE OF BEING A LARGE HERBIVORE ON THE ARCTIC TUNDRA.

The arctic environment poses formidable challenges to the animals and plants found there. The growing season for plants is short, the soil is sparse, nutrient-poor, and underlain by permafrost, and much of the arctic is arid or semi-arid (Bliss *et al.* 1973, Bliss 1977, Wielgolaski *et al.* 1982). Large portions of the arctic are essentially barren rock or "polar deserts" (Wielgolaski *et al.* 1982). The dominant season is winter, which may last 9-10 months at latitudes greater than 75° N (Gray 1987). Temperatures sometimes remain for extended periods at less than -40 °C, nearly 80°C below the normal internal temperature of mammals and birds. Few avian and mammalian species currently persist on the tundra year-round. Historical evidence from Greenland also indicates that the abundance of many arctic species has varied greatly and has been strongly influenced by winter weather (Vibe 1967, Meldgaard 1986, Forchhammer and Boertmann 1993).

Mammalian species which do exist on the tundra throughout the seasons deal with the long arctic winter in different ways. For predators such as wolves (*Canis lupus*) and polar bears (*Ursus maritimus*), large body size and ample insulation hold the cold at bay, while nutrients are intermittently but richly supplied by prey. For a few species of small mammals, the snow provides insulation and cover from predators, and their diminutiveness makes absolute food requirements small. Caribou (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*), the only large arctic herbivores, survive by lowering their nutrient requirements, continuing to forage, and making use of body reserves stored during the short snow-free season (Tyler and Blix 1990). Their large body size and excellent insulation reduce heat loss to a minimum.

These two ruminant species face unique problems during winter. The maintenance of homeothermy requires an abundant supply of metabolic fuels. As a group, ruminants do not deposit large quantities of fat (Pond and Mattacks 1985, Tyler and Blix 1990) and body reserves can only supply a small proportion of winter needs even in exceptionally fat Svalbard reindeer (*R. t. platyrhynchus*; Tyler 1987). Because they are ruminants dependent on a near-continuous fermentation of plant matter, caribou and muskoxen must eat forage regularly. The arctic is at best sparsely vegetated when compared to temperate and tropical biomes (Bliss *et al.* 1973). To compound the problem, vascular plants in the arctic withdraw most nutrients below ground by the end of the brief growing season (Chapin *et al.* 1975, Wielgolaski *et al.* 1982, Stoner *et al.* 1982). The forage then available to herbivores is low in nutrients

and high in structural carbohydrates (Staal and Olesen 1992). To further exacerbate the problem, the availability of this scarce, low-quality forage is often further reduced by snow and ice (Jingfors 1981, Tyler 1987, Schaefer and Messier 1995). Muskoxen are 2-3 times heavier than caribou and should require proportionately more food. Yet on some arctic islands, Peary caribou (*R. t. pearyi*) suffered greater mortality than muskoxen during severe winters (Miller *et al.* 1977), muskox numbers grew exponentially on Banks Island while caribou declined (Gunn *et al.* 1991), and muskoxen persisted in northeast Greenland when caribou populations were intermittent (Klein and Bay 1990). Muskoxen have been reported with substantial fat reserves at the end of harsh winters in Greenland (Thing *et al.* 1987) and on Banks Island (Rowell 1991). The genus *Ovibos* survived several glaciations and unlike related genera and other large herbivores once common in northern biomes, did not disappear during the Peistocene or at the end of the last glaciation some 10,000 years ago (Rowell 1990). Thus, an environment which to southern eyes seems utterly inhospitable has in fact not only allowed muskoxen to persist, but has at times allowed them to thrive. The research described on these pages was driven by a sense of wonder at the ability of muskoxen to persist under such apparently extreme and variable conditions.

My goal in this research was to provide insight into the means by which muskoxen have "solved" the problems of maintaining homeothermy and a grazing ruminant existence under unkind conditions. The objectives were (1) to identify the physiological and energetic adaptations of muskoxen to subsistence on scarce graminoid forage, and (2) to measure the extent and reproductive significance of seasonal changes in body composition of female muskoxen. The first objective was addressed using studies of digestion and nutrition in captive muskoxen in Saskatoon, and the second through a field study of seasonal changes in body composition of female muskoxen on Victoria Island, Northwest Territories.

The approach taken in this work was largely observational, to some extent comparative, and to a small extent experimental. This approach reflects the very limited number of studies of muskox nutrition and physiology, much smaller than that for caribou and reindeer, and tiny compared to that for domestic ruminants. Hypothesis-testing and experiments are powerful tools, but they are most appropriate to research where sufficient baseline knowledge exists to formulate specific, testable hypotheses, and where the means exist to conduct suitable experiments. In the body of work presented, these conditions were met in the work described in Chapters 2 and 3, where baseline data on muskox digestion and feed intake of a medium-quality diet

(Chapter 2) were used to formulate hypotheses tested in Chapter 3, in comparing intake and digestion of a poor-quality diet by muskoxen and cattle. The remaining work was largely descriptive. The controlled studies with tame muskoxen were intended to complement field studies, and by the marriage of these partners, provide a greater understanding of muskox ecology. In rationalizing this approach, I close the introduction with a quote from Mayr (1982: 32), who discussed the variety, validity and history of various approaches in biology.

"It is important to emphasize the scientific legitimacy of the observational-comparative method because the experimental method is inapplicable to many scientific problems... As a wise scientist, E. B. Wilson, expressed a long time ago, "The experiments performed in our laboratories but supplement those that have taken place and are always taking place in nature, and their results must be wrought into the same fabric."... Observation led to the discovery of foreign faunas and floras and became the basis of biogeography; observation revealed the diversity of organic nature and led to the establishment of the Linnaean hierarchy and to the theory of common descent; observation led to the foundations of ethology and ecology. Observation in biology has probably produced more insights than all experiments combined."

CHAPTER 2. SEASONAL VARIATION IN INTAKE AND DIGESTION OF A HIGH-ROUGHAGE DIET BY MUSKOXEN¹

2.1 Abstract

We studied changes in body weight, intake, retention time and digestibility of a supplemented brome-alfalfa hay by mature muskoxen held near Saskatoon, Saskatchewan during two seasonal cycles. Body weights and voluntary intake were monitored during 16 trials from late March 1990 to December 1991, in four annually-breeding females and in three hysterectomized females. Retention time of the hay and apparent digestibility of the diet were estimated in winter and summer 1991 from fecal excretion of chromium (Cr) after a pulse dose of Cr-mordanted hay, and from forage/fecal concentrations of chromic oxide, respectively, in six non-breeding muskoxen. Mean (\pm SE) body weights of breeding females were greatest in February and March (248 ± 5 kg) and lowest following calving in late May or early June (216 ± 6 kg), while mean weight of hysterectomized females declined little from a peak of 228 ± 21 kg in February-March to a low of 213 ± 21 kg in July. Mean daily dry matter intake of breeding females was highest in July and August (62 ± 3.6 g/kg^{0.75}) then declined slowly to its lowest point in March and April (41 ± 0.7 g/kg^{0.75}). Daily dry matter intake of hysterectomized cows was less clearly seasonal but averaged 42 ± 1.7 g/kg^{0.75} in late winter and 50 ± 4.9 g/kg^{0.75} in mid-summer. Mean retention time of hay, calculated using a noncompartmental model, declined ($P < 0.01$) from 114 ± 4 hours in March to 95 ± 4 hours in July. Apparent organic matter digestibility decreased ($P < 0.01$) from 74.7 ± 0.8 % in winter to 61.7 ± 1.3 % in summer. Compared with other ruminants, muskoxen are grazers exceptionally well-suited to digesting graminoid forage, with relatively low maintenance requirements and prolonged retention times. Most of the seasonal changes in weight and intake of breeding females could be ascribed to reproductive cost, but there also appeared to be seasonal effects on intake, retention time and body weight in non-breeding muskoxen.

2.2 Introduction

Muskoxen are arctic-adapted ruminants with the large rumen, large omasum and relatively small cecum typical of grazers (Staal and Thing 1991) and their diet is usually dominated by grasses and sedges (Thing *et al.* 1987; Klein and Bay 1990; Oakes *et al.* 1992). High-quality forage is only briefly available in summer (Thing *et al.* 1987;

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Klein and Bay 1990), and access to nearly all forage may be severely restricted by snow for 8-10 months annually (Jingfors 1981). The ability of muskoxen to subsist on sparse winter forage is essential to their survival and reproduction but relatively little is known of their digestive characteristics and nutritional requirements. Hubert (1977) measured digestibility of diets fed to captive muskoxen in Alaska at 62 to 65 %, and estimated dry matter (DM) digestibility in free-ranging muskoxen on Devon Island at 65 % in early winter and at least 75 % in summer. White *et al.* (1984b) measured a high digestibility (74 %) for brome hay, and up to 81 % for mixed high-quality diets in young muskoxen; daily voluntary intake in winter was a relatively low $38 \text{ g/kg}^{0.75}$. Chaplin (1984) showed that 6 month-old muskox calves digested a timothy-brome hay better than domestic lambs of similar weight.

Our objective was to evaluate the seasonal use of a high-roughage diet by mature muskoxen, by measuring seasonal patterns in body weight and feed consumption of mature muskox females, and by comparing retention time, digestibility and maintenance requirements of muskoxen on the same high-roughage diet between winter and summer. Data from breeding females and non-breeding females were compared to determine whether patterns in body weight, intake and digestion are affected by season as well as by the demands of reproduction. A preliminary summary of this material has been published previously (Adamczewski *et al.* 1993).

2.3 Materials and methods

2.3.1 Research Herd

The establishment of a small herd of captive muskoxen by the University of Saskatchewan was described by Flood *et al.* (1984) and Rowell (1991). In 1990 and 1991 the muskox herd numbered approximately 20 and included seven of the original animals captured in 1982. Most of these muskoxen were bottle-raised and halter-trained; all were handled daily during feeding and were thoroughly habituated to humans. The facility included a 1.3 ha pasture with a small grove of aspens, a 2.0 ha pasture, and a handling facility of smaller paddocks and chutes. Individual pens used to monitor intake and digestion were constructed within one of these paddocks. Owing to the high stocking density and lack of preferred grasses in both pastures, supplemental brome-alfalfa hay was offered in summer to muskoxen during the study period, and was their primary diet during autumn, winter and spring. The muskoxen were brought into individual stalls daily and fed a ration (550 g) of pelleted supplement (Table 2.1) to ensure a balanced diet and to maintain tractability.

Table 2.1. Composition of pelleted concentrate fed to muskoxen during 1990 and 1991.

Component	% (as fed)
Oats	51.5
Hay ^z	38.0
Molasses	4.0
Phosphate (NaHPO ₄)	2.0
Mineral - vitamin mix ^y	2.0
Vitamin A and D mix ^x	1.5
Salt (NaCl)	1.0

z - Hay was medium-quality brome-alfalfa.

y - Contained (%) calcium, 18; phosphorus, 18; (mg/kg zinc 10.1; iodine, 185; iron, 10.1; manganese, 5.25; copper, 3.15; cobalt, 75; fluorine, 3.00; and vitamins (IU/kg) A, 500; D, 50; and E, 500.

x - Vitamins A and D₃ (440,000 IU/kg each) were mixed with barley.

2.3.2 Voluntary Intake and Body Weight

Sixteen feed intake trials were conducted approximately every 4 to 6 weeks from March 1990 to December 1991. Muskoxen were kept in adjacent individual 3 m x 9 m outdoor shaded pens. Water or snow was freely available. Seven mature (≥ 4 years old) muskox females were used; four bred annually during the study period, and three had intact ovaries but had been partially hysterectomized following failed pregnancies several years earlier. One of the hysterectomized females had recurrent respiratory problems in 1990 and we used intake data only from her 1991 trials. We did not pen breeding females around calving time (late May or early June) to avoid risks to newborn calves, and we did not pen breeding females during the height of the breeding season (late August - early September). Lactating females were given double-sized pens, with a separate "creep" area for the calf. Calves were separated from their mothers and weaned in early August, to improve calf tractability.

During autumn, winter and spring, when the muskoxen made minimal use of pasture, animals were given 2 to 3 days to habituate to individual pens before trials. During summer, when there was some use of pasture, muskoxen were group-penned for 5 to 7 days without access to pasture prior to the habituation period. Voluntary intake was measured by monitoring daily consumption of hay (adjusted so the animals left 1 to 1.5 kg of the offered hay daily) for 5 successive days. The daily supplement of pellets described earlier was continued throughout the trials.

The hay used was locally-grown brome grass, with a small alfalfa component. To minimize changes in diet quality, all hay used during March to June 1990, July 1990 to July 1991, and August to December 1991 was from a single field cut in July of 1989, 1990 and 1991, respectively. We monitored acid detergent fiber (ADF) and crude protein (CP) content of the hay periodically to ensure a relatively consistent quality. Muskoxen were weighed weekly and the mean weights for each month calculated.

Daily dry matter intake of the muskoxen was scaled to metabolic body weight ($\text{g/kg}^{0.75}$). Mean intake and body weights of the four breeding cows were compared over the 2 years of trials using repeated measures ANOVA. Seasonal patterns in intake and body weights were analysed individually for each hysterectomized female using Kolmogorov-Smirnov one sample tests and change-point tests (Siegel and Castellan 1988) because of substantial individual variation among the three individuals and reduced data from two of them.

2.3.3 Retention Time

Retention time of the hay was measured using a pulse dose of chromium (Cr)-mordanted hay in winter (late February/early March 1991) and summer (July 1991). In winter the animals had been consuming the same hay and pellets for several months and in summer the animals were given a 2-week habituation period. Three hysterectomized females and three castrated males (all 9 years old) were used during both retention-time trials and subsequent digestibility trials. Hay used during all retention time and digestibility trials was from a single brome-alfalfa field cut in July 1990.

Long hay from a square bale was mordanted with Cr by the method of Udén *et al.* (1980) and 80 to 90 g portions of this material were fed to each muskox by mixing with successive small quantities of normal hay until all had been consumed. This took on average about 15 minutes per animal. Fecal samples were collected for the next 7 to 8 days, at 2 to 3 hour intervals for the first 80 hours and 10 to 14 hour intervals thereafter. These samples and a sample of the mordanted hay were freeze-dried, oven-dried to determine moisture content, ground through a 1-mm mesh in a Wiley mill, and analysed as described by Okine and Mathison (1991b). During the July trial, fecal samples were also collected from each muskox prior to consumption of the Cr-mordanted hay to obtain background values for Cr. These background values were used for both trials. Chromium in the mordanted hay was 3.61% in March and 3.95 % in July.

Fecal Cr values were expressed as $\mu\text{g/g}$ (DM) and plotted as natural logs against time after dose (time 0). Because such data have been variably interpreted by different researchers, Cr-excretion curves were interpreted using the following three approaches: (1) Holleman *et al.* (1984) used ruthenium-103 chloride to measure particulate rate of passage in muskoxen; following Grovum and Phillips (1973), they defined the reciprocal of the slope of the declining portion of marker excretion as rumen turnover time (RTT), transit time (TT) as the time of first appearance of marker in feces, the reciprocal of the slope of the difference line ($1/k_2$) as retention time in the lower part of the gut and total mean retention time (TMRT) as the sum of RTT, TT, and $1/k_2$. Following correction for background Cr in the feces, we followed these calculations but estimated TT as the point at which Cr first exceeded background levels. (2) Okine and Mathison (1991a, b) conducted trials with Cr-mordanted hay in mature cattle and defined the slope of the declining part of the excretion curve as total tract passage rate (K_{pt}), and the reciprocal of K_{pt} as mean retention time for the total tract (MRT, identified as RTT above). (3) Holleman and White (1989) validated the use of the Stewart-Hamilton Principle to measure retention time in sheep using cerium-141 chloride, and used this noncompartmental model to estimate total mean retention time (TMRT), total DM

indigestible fill (V_N) and total DM digesta fill (V) (Holleman and White 1989: equations 4, 5 and 6). We followed these methods after extrapolating the terminal portion of the Cr excretion curve (natural logs) to a background Cr of 31.0 $\mu\text{g/g}$, included an estimate of DM fecal output (F) and fractional digestibility derived from the trials described below, and converted estimated DM fill to total digesta fill assuming DM of fill was 17.8 % (Staal and Thing 1991, Table 2).

We discarded the results from two animals in March: one castrate apparently did not consume all the marked hay, and we obtained only four fecal samples during the declining part of the marker excretion from one cow. We used only results from the other four muskoxen in comparing winter and summer results, using paired two-tailed t -tests.

2.3.4 Apparent Digestibility and Energy Intake

Apparent digestibility was measured by reference to chromic oxide (Cr_2O_3) in winter (March) and summer (July) commencing 3 to 4 days after the retention time trials. At those times the muskoxen had been consuming the supplemented hay diet for at least 4 weeks. A sample of the pellets normally fed to the muskoxen was re-ground, mixed with Cr_2O_3 at approximately 1.8 % by weight, and re-pelleted. For 10 days, 270 g portions of marked pellets (260 g in July) were fed to each muskox in the morning (8:00 to 10:00) and afternoon (16:00 to 17:00), and fecal samples were collected twice daily during the last 5 days. Hay intake was measured during the last 7 days of the trial as described earlier. We assumed that a steady-state flow of Cr_2O_3 had been achieved by day 6: day-to-day variation in intake was small. We collected representative samples of hay and pellets offered and of refused hay for each animal.

Because Cr_2O_3 may not be fully equilibrated in the gastrointestinal contents of ruminants for eight to nine days after commencement of use (Schneider and Flatt 1975), two pooled samples of feces were made up from each muskox and analysed for Cr_2O_3 , one for the last 5 days of each trial and one for the last 2 days.

Samples of feed and feces were freeze-dried, ground through a 1-mm mesh on a Wiley mill, and analysed for DM, CP, neutral-detergent fiber (NDF), ADF, lignin (using sulfuric acid), ash [to derive organic matter (OM)] and gross energy (GE) (Van Soest 1982; Association of Official Analytical Chemists 1984). Hemicellulose was calculated as NDF - ADF, and cellulose as ADF - lignin (Van Soest 1982). Samples of hay and pellets were analysed separately for DM by drying to constant weight at 60 °C. Pellets and feces were analysed for Cr_2O_3 following Method A of Fenton and Fenton (1979), using 3 to 4 g of feces per sample analysed.

Because the muskoxen consistently selected the leafier portions of the hay, we suspected that the consumed hay would be of higher quality than the hay offered. We therefore calculated the characteristics of the hay actually consumed by each animal, by difference, using mean weight and composition of the offered hay and of the refused hay. No correction was necessary for the pellets as they were always fully consumed. An overall composition of daily intake was calculated using weighted values for hay and pellets.

Apparent digestibilities of organic matter (OM), DM, crude protein (CP), gross energy (GE), neutral-detergent fiber (NDF), acid-detergent fiber (ADF), lignin, hemicellulose and cellulose were calculated by reference to Cr₂O₃ concentration in feed and feces following Schneider and Flatt (1975). Daily digestible energy (DE) intake in MJ was calculated from digestibility of GE and the quantity of feed consumed. Because mean body weights were stable throughout these trials, daily metabolizable energy intake (ME) for maintenance, in MJ, was estimated as 0.82 times DE intake (Agricultural Research Council 1980) and expressed as MJ/kg^{0.75}. Digestibility, energy intake, and body weight were compared between March and July using paired two-tailed *t*-tests.

2.4 Results

2.4.1 Voluntary Intake and Body Weight

There was a strong seasonal pattern in feed intake of breeding muskox females ($P < 0.001$), and the patterns were similar between years (Figs. 2.1 and 2.2). Peak intake occurred during July in 1990 ($66.0 \pm 3.6 \text{ g/kg}^{0.75}$) and during August in 1991 ($59.1 \pm 3.7 \text{ g/kg}^{0.75}$) and was followed by a slow decline through autumn and early winter to a low point during March in 1990 ($42.1 \pm 0.6 \text{ g/kg}^{0.75}$) and during April in 1991 ($40.9 \pm 0.7 \text{ g/kg}^{0.75}$). There were small but significant differences in overall mean intake among the four individual females ($P = 0.002$): Kerrlie 56.4 ± 2.9 , Annie 50.6 ± 2.5 , Kathy 50.6 ± 2.0 , and Woodstock 52.9 ± 2.3 . The highest intakes in June and July were recorded in lactating females; during these 2 months mean intake of lactating cows was $66.9 \pm 2.2 \text{ g/kg}^{0.75}$ ($n = 5$) compared to $56.8 \pm 2.2 \text{ g/kg}^{0.75}$ ($n = 6$) in non-lactating females. During both August feed trials, none of the females were lactating but their mean intake was about as high as in July.

Body weight of the four breeding females varied significantly with season ($P = 0.001$), with decreasing weights during late pregnancy and lowest weights following calving in late May or early June (Figs. 2.1 and 2.2). Lactating females typically either maintained or lost weight in the initial 6 to 8 weeks following calving, while cows which lost their calves early initiated weight gains much earlier. All four females gained weight

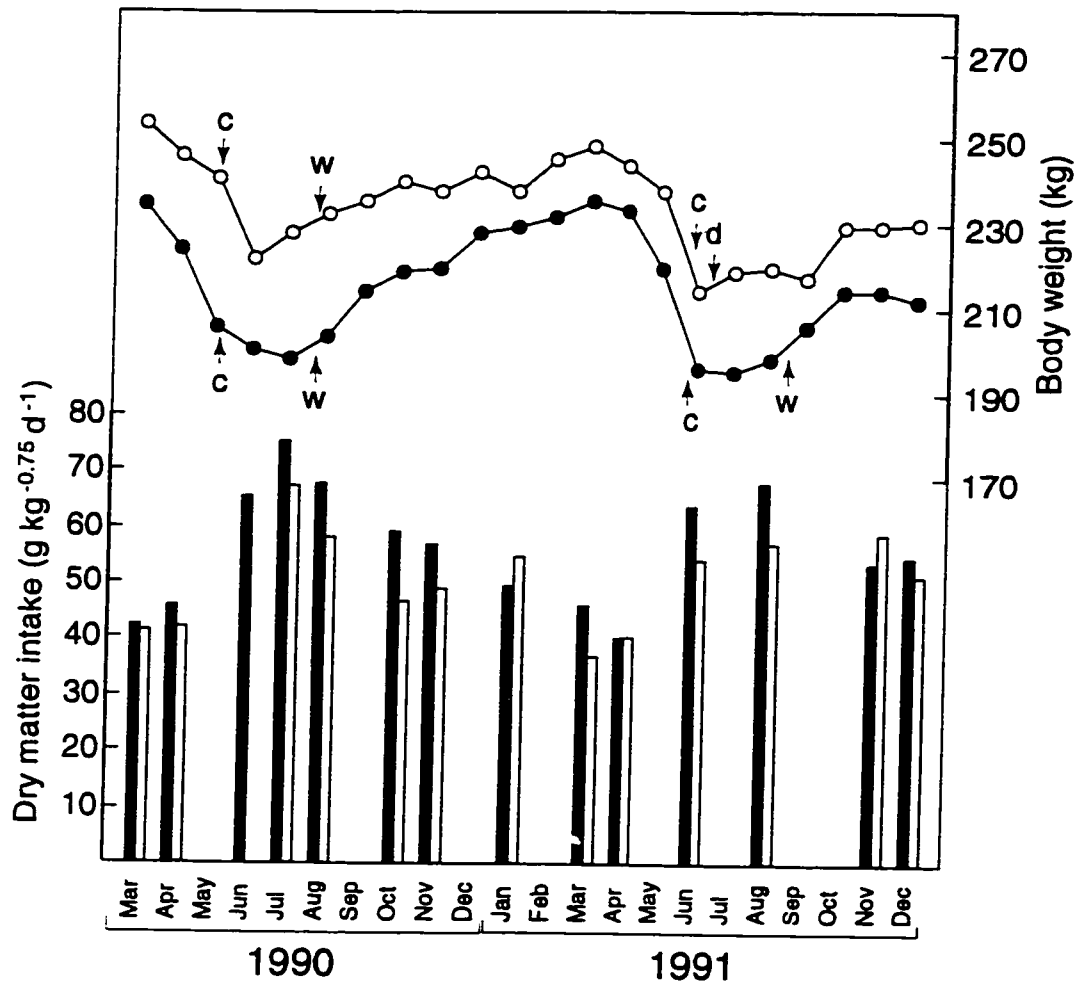


Fig. 2.1. Seasonal changes in dry matter intake and body weight of two breeding muskox cows [Kathy (\circ) and Annie (\bullet)] in 1990 and 1991. (c - calved, d - calf died, w - calf weaned, a - aborted).

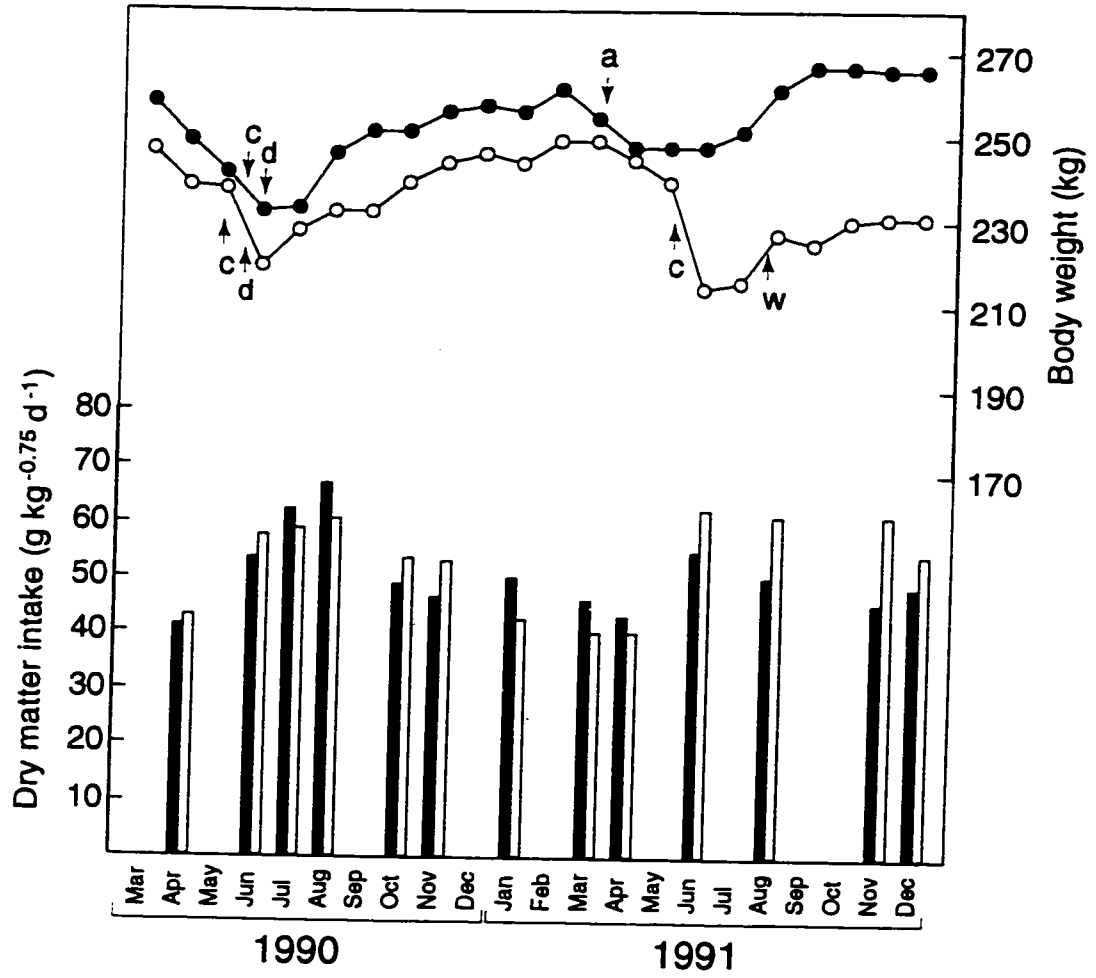


Fig. 2.2. Seasonal changes in dry matter intake and body weight of two breeding muskox cows [Kerlie (●) and Woodstock (○)] in 1990 and 1991. (c - calved, d - calf died, w - calf weaned, a - aborted).

during autumn and much of winter. Females which nursed calves for at least 2 months tended not to reach the previous winter's maximal weight during the following winter. In one individual (Annie, Fig. 2.1) the decreased weight gain appeared to carry over from successive lactations in 1990 and 1991, and she was not pregnant at the end of the breeding season in 1991. A second individual (Kathy) nursed a calf successfully in 1990, lost her calf early in 1991, nursed a calf successfully in 1992 (not shown in Fig. 2.1), and reached lower peak weights during each successive winter. She was not pregnant at the end of the breeding season in 1992. In contrast, a third female (Kerrlie, Fig. 2.2) aborted early in March 1991 and thereafter achieved a body weight she had not previously attained; she was pregnant at the end of each breeding season.

There was a much less pronounced seasonal pattern in feed intake and body weight in the three hysterectomized females (Fig. 2.3) and none of the seasonal changes were significant. However, as in breeding cows, daily DM intake was lowest in March and April ($41.6 \pm 1.7 \text{ g/kg}^{0.75}$) and highest in summer and autumn ($49.9 \pm 4.9 \text{ g/kg}^{0.75}$) while body weight tended to be lowest in early summer ($213 \pm 21 \text{ kg}$) and maximal in mid-winter ($228 \pm 21 \text{ kg}$). Intake was consistently lower in one female (Eeyore; 30 to 42 $\text{g/kg}^{0.75}$) than in any other muskox studied.

Hay used during feed trials ranged in % CP from 10 to 14, 9 to 13 and 10 to 11, and in % ADF from 39 to 41, 41 to 45, and 36 to 40, from fields cut in July 1989, 1990, and 1991, respectively.

2.4.2 Retention Time

Patterns of Cr-excretion by muskoxen were generally similar in winter and summer with a steep ascending curve which slowed to reach a plateau, followed by a slow decline (Fig. 2.4). A distinct peak was often difficult to distinguish but typically occurred between 60 and 80 hours after the dose. All measures of retention time were significantly greater ($P < 0.01$) in March than in July, with the exception of transit time which changed little between the two sets of trials (Table 2.2). The longest estimates of mean retention time were those based on the Grovum and Phillips (1973) compartmental model (140.5 ± 6.9 hours in winter), the shortest (104.9 ± 5.9 hours in winter) based on the model of Okine and Mathison (1991b), while those calculated from the noncompartmental model were of intermediate length. Estimated retention in the lower part of the gastrointestinal tract ($1/k_2$) declined 30.2% from 21.0 hours in March to 14.7 hours in July. Total gut fill estimated from the noncompartmental model was very similar in winter and summer (17 to 17.5 % of body weight).

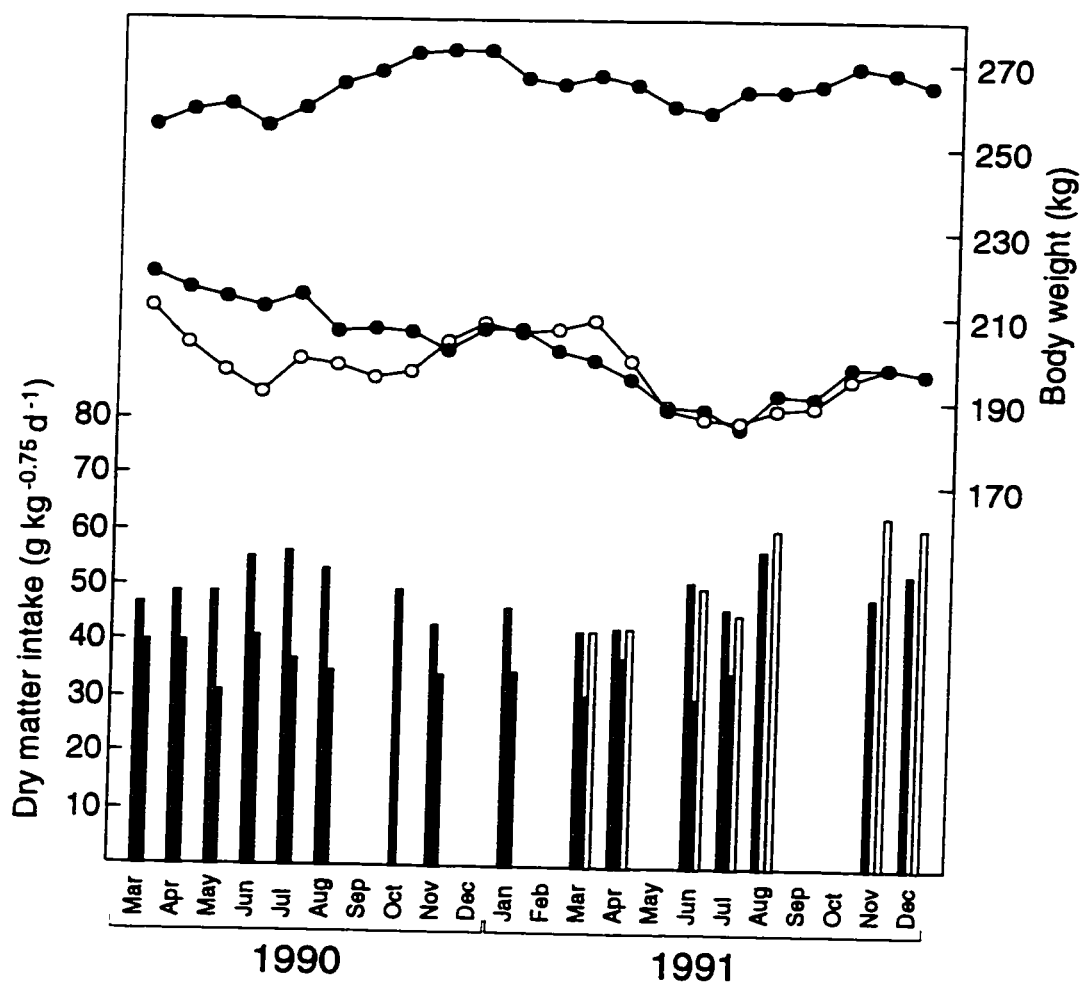


Fig. 2.3. Seasonal changes in dry matter intake and body weight of three hysterectomized muskox cows

[Eeyore (●), Peggy (○) and Athabasca (●)] in 1990 and 1991.

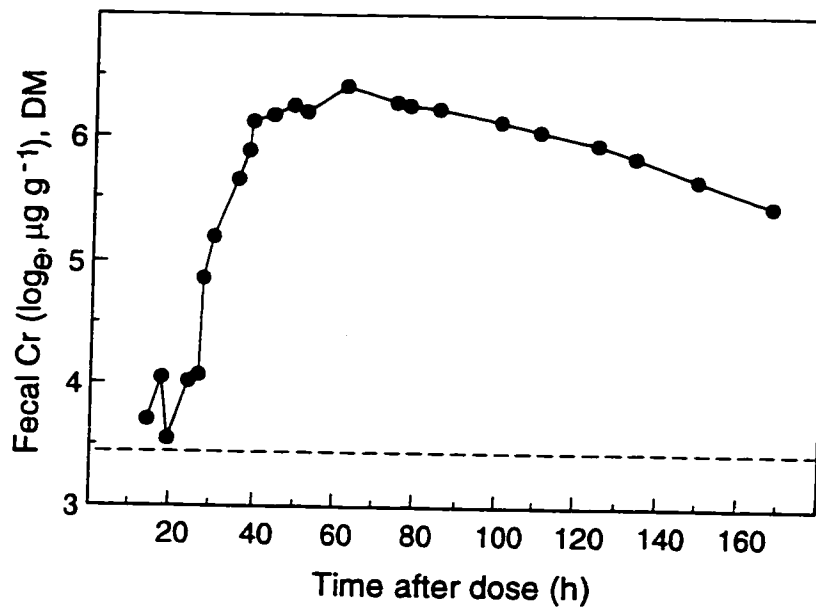


Fig. 2.4. Typical chromium excretion in feces of a castrated muskox in winter 1991, following a pulse dose of Cr-mordanted hay. Dotted line indicates mean background value of Cr from July trial.

Table 2.2. Mean estimates of retention time of hay by six non-breeding muskoxen in March and July 1991, based on fecal chromium excretion curves ($n = 4$).

Item	March		July		P
	Mean	SE	Mean	SE	
Estimate A ^Z					
Rumen turnover time (hours)	104.9	5.9	71.0	3.8	0.001
Transit time (hours)	14.6	3.5	17.9	2.1	0.32
Lower tract turnover time (hours)	21.0	1.1	14.7	0.5	0.004
Total mean retention time (hours)	140.5	6.9	103.8	5.2	0.003
Estimate B ^Y					
Mean retention time (hours)	104.9	5.9	71.0	3.8	0.001
Estimate C ^X					
Total mean retention time (hours)	114.6	3.8	95.1	4.4	0.001
Indigestible DM gut fill (kg)	3.34	0.20	2.98	0.84	0.023
Total DM gut fill (kg)	8.36	0.55	8.25	0.56	0.55
Total "wet" gut fill (kg)	47.0	3.6	46.4	3.8	0.55
Wet gut fill (% of body weight)	17.0	1.1	17.5	1.4	0.088

z - Calculated following Holleman et al. (1984), using model of Grovum and Phillips (1973).

y - Calculated following Okine and Mathison (1991b).

x - Calculated following Holleman and White (1989), using Stewart-Hamilton non-compartmental model.

The muskoxen showed strongly individual patterns in Cr-excretion, but those which had the longer retention times in March also had the longer times in July. Estimated MRT (based on Okine and Mathison 1991b) for one female, Eeyore, was 140 hours in July, nearly double the mean for the other muskoxen. Results for this female were not included in calculations because of inadequate fecal sampling in March.

2.4.3 Digestibility and Energy Intake

Mean Cr₂O₃ concentration in feces was nearly identical between the 5-day pools and the 2-day pools in each trial (March: 5-day pool 1.98 %, 2-day pool 1.94 %; July: 5-day pool 1.22 %, 2-day pool 1.21 %) so we used the 5-day pooled fecal samples in calculating digestibility from Cr₂O₃.

Overall diet quality was very similar in March and July, although CP and most fiber and lignin fractions were slightly higher in March (Table 2.3). The hay eaten was consistently higher in protein and lower in fiber and lignin than the hay offered. Apparent OM digestibility was significantly greater ($P < 0.001$) in March (73.8 %) than in July (60.8 %) and similarly CP and most fiber fractions were more digestible during the winter trial (Table 2.4). Lignin digestibility was estimated to be 3.9 % in July compared to 47.9 % in March. The muskoxen consumed 12.6 % more daily DM in July than in March (44.6 vs. 39.0 g/kg^{0.75}, $P = 0.006$), but owing to the lower digestibility in July, estimated maintenance ME intake was similar during the two trials (0.441 vs. 0.413 MJ kg^{-0.75}, $P = 0.344$). The body weights of the muskoxen were stable during each trial but the mean body weight was significantly higher ($P = 0.007$) in March (266 ± 20) than in July (253 ± 22). The decrease in weight of the six animals occurred in April and May.

2.5 Discussion

2.5.1 Energy Costs of Reproduction in Female Muskoxen

Breeding muskox cows ate about as much in winter as non-breeding females and castrate males, but substantially more in summer; peak intake of lactating females was about 48 % higher than in non-breeding muskoxen. This value gives an indication of the energy costs of lactation but may not reveal their full extent. Body weights of lactating females changed little during early summer, as found in captive muskoxen in Alaska by White *et al.* (1989). However, free-ranging lactating muskoxen on Victoria Island catabolized body fat rapidly in early lactation (Adamczewski *et al.* 1992), although this was masked in whole body weights by large and variable gut fill (see Chapter 4). Sheep and cattle are hormonally predisposed to catabolizing body fat in early lactation even if well-fed (Vernon 1980). The same may be true of lactating muskoxen (White *et al.*

Table 2.3. Dry matter composition (%) of feed offered, refused, and eaten by six non-breeding muskoxen in March and July 1991.

Component	Hay			Pellets	Overall Intake
	Offered	Refused	Eaten		
March					
Organic matter	93.7	93.7	93.7	87.2	92.6
Crude protein	12.8	8.2	15.4	12.0	14.8
NDF ^z	68.6	73.4	65.6	32.0	59.2
ADFY	45.6	46.4	45.0	16.1	39.5
Lignin	7.5	9.7	6.3	1.8	5.5
Hemicellulose	22.9	26.9	21.7	15.9	20.6
Cellulose	38.0	36.8	38.5	14.3	33.9
GE ^x (MJ/kg)	18.9	18.5	19.1	19.9	19.3
Daily quantity (kg)	3.41	1.35	2.06	0.52	2.58
July					
Organic matter	93.4	92.5	94.1	88.0	93.1
Crude protein	11.2	8.5	13.2	11.4	12.9
NDF ^z	69.6	70.6	68.8	29.0	58.6
ADFY	40.1	46.3	35.3	14.4	32.3
Lignin	6.5	8.7	4.9	1.5	4.3
Hemicellulose	29.5	24.3	33.6	14.6	30.4
Cellulose	33.6	37.6	30.4	12.9	27.5
GE ^x (MJ/kg)	18.7	18.2	19.1	18.2	18.9
Daily quantity (kg)	4.32	1.97	2.35	0.50	2.84

z - Neutral detergent fiber; y - Acid detergent fiber; x - Gross energy

Table 2.4. Mean apparent digestibility and intake of hay and pellet diet by muskoxen in March and July 1991 ($n = 6$).

Component	March		July		P
	Mean	SE	Mean	SE	
Digestibility (%)					
Dry matter	70.8	1.1	56.4	1.3	<0.001
Organic matter	73.8	1.0	60.8	1.6	<0.001
Crude protein	75.9	1.2	54.6	1.0	<0.001
NDF ^z	74.5	1.2	62.9	1.7	0.01
ADF ^y	76.0	1.5	54.2	2.7	0.004
Lignin	47.9	3.3	3.9	3.9	0.009
Hemicellulose	68.5	1.2	71.9	1.7	0.06
Cellulose	79.2	2.6	56.6	1.5	0.004
Intake					
DE ^x (MJ/d)	35.5	2.8	32.5	2.9	0.04
ME ^w (MJ/d)	29.1	2.3	26.7	2.4	0.04
DM (kg/day)	2.58	0.22	2.84	0.27	0.06
DM (g/kg ^{0.75})	39.0	1.79	44.6	1.97	0.006
ME (MJ/kg ^{0.75})	0.441	0.02	0.413	0.02	0.344
Body Weight (kg)	266	20	253	22	0.007

z - Neutral detergent fiber; y - Acid detergent fiber; x - Digestible energy
w - Metabolizable energy.

1989), which often nurse calves for 6 to 8 weeks in the wild before the emergence of green forage.

Pregnancy and lactation in successive years apparently carry a substantial energetic cost in muskoxen. Our data are sparse but we suggest that, on the diet used, some muskox cows may have had difficulty fully recovering body reserves during late summer and autumn, and their ability to conceive or maintain pregnancy may then have been adversely affected. This pattern is more pronounced in wild muskoxen on Victoria Island (Adamczewski *et al.* 1992). White *et al.* (1989) noted considerable between-year differences in recovery of body weight by lactating muskoxen, although pregnancy rate was not affected. The recovery of body reserves in autumn may depend on the quality of nutrition available. Before 1989 muskoxen at the University of Saskatchewan were fed a larger daily pellet supplement of lower fiber content than presently (1200 to 1600 vs. 550 g/day; Rowell 1991). During this period several mature muskoxen maintained a higher body weight than they have since 1989, mature females recovered their maximal weight each winter, and all breeding cows were pregnant annually.

2.5.2 The Effect of Season on Body Weight, Digestion and Energy Requirements

In strongly seasonal ungulates, photoperiod and melatonin have been shown to affect food intake (Simpson *et al.* 1984), growth (Suttie *et al.* 1992) and digestive function (Milne *et al.* 1978; Domingue *et al.* 1992). The increased food intake and reduced retention in summer noted here in castrated males and hysterectomized females may well reflect photoperiodic influences, as they occurred in the absence of a significant change in diet, and clearly were not due to reproductive costs. A similar pattern of decreased retention and decreased digestibility in summer, on a standard diet, was found in Soay sheep by Argo (1986). Wild muskoxen would normally have access to highly digestible green forage in mid-summer (Thing *et al.* 1987; Klein and Bay 1990) and increased intake and reduced retention of forage might then be expected.

Although body weight and feed intake of non-breeding muskoxen were less clearly seasonal than in breeding females, they showed some evidence of a photoperiodic effect. Both breeding and non-breeding muskoxen tended to lose weight in late winter and spring, and to re-gain it during autumn and early winter. The winter-summer weight loss of the three hysterectomized females and the three castrate males was small (5 to 6 %) but significant and apparently not due to altered gut fill. Serum levels of insulin-like growth factor 1 (IGF-1) are strongly correlated with lean weight gain in many species (Clemmons and Underwood 1991) and are known to be affected by photoperiod in cervids (Suttie *et al.* 1991; 1992). An autumn surge in IGF-1 of breeding and hysterectomized muskox

cows fed a constant diet quality has been reported (Adamczewski *et al.* 1992) and may in part explain the tendency of muskox females to gain weight in autumn and early winter. Muskox cows at the University of Alaska also consistently show a weight surge in the autumn (White *et al.* 1989) and castrated muskoxen in Palmer, Alaska gain and lose weight in a similar seasonal manner (Groves 1992). Wild muskoxen usually have a more compressed period of compensatory weight gain in autumn, and winter weight losses usually begin earlier (Thing *et al.* 1987; Adamczewski *et al.* 1992).

Whether basal metabolic rates of wild ruminants in Arctic and temperate environments change with season is not entirely clear; possible seasonal effects are often confounded by increased intake and an associated increase in energy metabolism in summer (Tyler and Blix 1990; Mautz *et al.* 1992). Maintenance energy requirements of muskoxen estimated here were similar in summer and winter, but estimated as 26 % higher in summer than in winter by White *et al.* (1984b). The apparent contradiction may reflect different patterns of feeding. A lower level of nutrition can result in substantially decreased weights of liver and gut tissues in sheep, and an associated decrease in oxygen consumption (Koong *et al.* 1985; Burrin *et al.* 1989, 1990). Several weeks of maintenance feeding may be necessary to eliminate the shorter and longer-term effects of altered food intake on metabolic rates (Hudson and Christopherson 1985). These conditions were met in our summer-winter comparison. Our estimates are therefore not necessarily at odds with those of White *et al.* (1984b), whose well-fed young muskoxen were in weight stasis during winter but growing during summer.

2.5.3 Evaluation of Markers

Chromic oxide is one of the most widely used food digestibility markers as it is minimally absorbed and experimental recovery has been very high (Schneider and Flatt 1975; Van Soest 1982). Feeding the marker for 5 days prior to fecal collections appeared to be a sufficient time for equilibration within the gut contents of muskoxen despite their slow rate of passage. Lignin has been used as an internal indigestible marker for assessment of digestibility (Van Soest 1982; Renecker and Hudson 1990) but, with an apparent digestibility of 48 % in March, would clearly not have been suitable here. Because the lignin from immature forages may be partially digestible (20 to 40 %, Van Soest 1982), the prolonged retention measured in winter in our muskoxen may have increased breakdown of the digestible portions of the "lignin" to a degree not usually encountered in ruminants.

The markers used to measure rate of passage in ruminants have differed considerably, as have interpretations of the results (Faichney 1975; Warner 1981;

Lechner-Doll *et al.* 1991). The calculations used by Holleman *et al.* (1984) were based on the models and equations of Grovum and Phillips (1973) and validated for pulse doses of rare-earth markers in sheep. These calculations have been widely used but the model and equations may not apply to all species, markers and diets (Warner 1981; Lechner-Doll *et al.* 1991). Cr-mordanted particles tend to move with the indigestible portion of gut fill and produce slower estimates of retention time in ruminants than rare-earth markers, which move with the more digestible material (Mader *et al.* 1984). For cattle pulse-dosed with Cr-mordanted hay (Okine and Mathison 1991b), the slope of the declining portion of the fecal Cr-excretion curve best approximated passage from the whole tract, not from the rumen alone (E.K. Okine, pers. comm.). In species and studies where marker kinetics are unknown, Warner (1981) recommended a noncompartmental estimate of mean retention time such as that of Faichney (1975, equations 8 or 9). The Stewart-Hamilton noncompartmental model validated by Holleman and White (1989) is quite similar to the noncompartmental model of Faichney (1975, equation 9). These noncompartmental estimates of mean retention time may thus be the most appropriate for our data, since we cannot assume that the digestive physiology of the muskox matches those of the domestic ruminants, and the noncompartmental estimates of mean retention time did not match those of either of the other models.

2.5.4 Digestive Characteristics of Muskoxen

The digestive anatomy (Staal and Thing 1991) and graminoid-dominated diets (Klein and Bay 1990; Klein 1992; Oakes *et al.* 1992) of muskoxen clearly identify them as "grazers" (Hofmann 1989). The very high digestibility of a medium-quality hay and slow retention times reported here further support this classification. Mean retention times estimated in our March trial are among the longest reported for ruminants (see Warner 1981). In mature cattle fed four levels of a medium-quality hay, MRT using Cr-mordanted hay ranged from 52 to 63 hours (Okine and Mathison 1991b) compared with a winter mean of 105 hours in muskoxen fed a similar diet. MRT of a cow fed a maintenance level of low-protein timothy hay (calculated from Udén *et al.* 1980) was 98 hours using the same marker. Retention times measured by Holleman *et al.* (1984) using a rare-earth marker in muskoxen were substantially shorter, but occurred in young animals fed a high-protein, low-roughage diet. Because retention times tend to increase in grazers as diet quality decreases (Van Soest 1982), the retention times reported here are probably not the extreme possible in muskoxen. The feed used in this study was of much better quality than is commonly available to wild muskoxen in winter (Thing *et al.* 1987). An apparent OM digestibility of 74 % for the diet used here would have been improbable

in most ruminants but is consistent with exceptionally prolonged food retention. The pelleted supplement may have been slightly more digestible than the hay, but the effect on overall digestibility was likely small since the supplement contained 38 % hay and was lower in protein than the hay eaten.

Although muskoxen show many of the attributes of grazers, they can be quite selective in their feeding in the wild (Oakes *et al.* 1992) and in captivity (Rowell 1991), as our intake and digestibility trials confirmed. The penned muskoxen never ate all the hay offered over a 24-hour period, even when offered less than they normally consumed, and despite their relatively wide muzzles were remarkably adept at taking the leafier portions of hay and rejecting larger stems. These results suggest that muskoxen are quite selective in their natural foraging, and such selectivity may contribute substantially to increasing the digestibility of low-quality diets.

Maintenance energy requirements of muskoxen are relatively low in winter compared with those of most ruminants (see Hudson and Christopherson 1985). Our estimates of their maintenance ME and DM intake in winter are comparable to those of White *et al.* (1984b): 0.425 vs. 0.441 MJ/kg^{0.75}, 38 vs. 39 g/kg^{0.75}, although the diets were quite different. Daily food intake suggested for wintering muskox cows by Groves (1992) was also similar. Fasting metabolic rates of muskoxen are similar to those of domestic sheep (White *et al.* 1984b; Nilssen *et al.* 1994) which are relatively low compared with those of cattle and most cervids (Tyler and Blix 1990). Muskoxen, however, are much larger than most sheep. If fasting metabolic rates of 0.205, 0.203, and 0.318 MJ/kg^{0.75} (Nilssen *et al.* 1994) are expressed as MJ/kg for a 200-kg muskox, a 70-kg sheep and a 700-kg cow, respectively, then metabolic rates are lower in muskoxen (0.0545) than in cattle (0.0618) or sheep (0.070). This low relative energy requirement, combined with a large gut fill and very slow rate of food passage, allows muskoxen to thrive on low-quality forage. Muskoxen may be comparable to some of the more "primitive" breeds of sheep (Weyreter *et al.* 1987) and Bangali cattle (Mould *et al.* 1982), which can subsist on high-straw diets owing to very slow retention times and exceptionally high gut fill.

CHAPTER 3. DIGESTION OF LOW-PROTEIN GRASS HAY BY MUSKOXEN AND CATTLE¹

3.1. Abstract

Because nutritional requirements of muskoxen (*Ovibos moschatus*) in winter are poorly understood, we compared the voluntary intake and apparent digestibility of low-protein grass hay by five mature muskoxen and three mature Hereford cows during late winter 1993. We hypothesized that muskoxen would digest poor quality graminoid forage more completely and maintain weight at lower rates of intake than cattle, based on evidence of relatively low intake and relatively complete digestion of high- and medium-quality diets by captive muskoxen during winter. The hay averaged 6 % crude protein and 74 % neutral-detergent fiber, and was similar in composition to samples of sedge (*Carex* spp.) and grass (e.g., *Kobresia* spp.) from feeding craters of muskoxen on Banks and Victoria Islands, Northwest Territories (NWT). Both species maintained body weight on the experimental diet but daily dry matter intake of the muskoxen was only 1/3 that of the cattle (32 ± 2 vs. 96 ± 3 g/kg^{0.75}; $P < 0.001$). Apparent digestibility of organic matter, measured using chromic oxide, was higher in the muskoxen than in the cattle (58 ± 2 vs. 50 ± 3 %; $P = 0.03$). Muskoxen are well adapted to digesting low quality graminoid forage and maintaining weight at exceptionally low rates of intake, and these traits likely contribute to their success in surviving long arctic winters.

3.2 Introduction

On many arctic islands and in Greenland, muskoxen share range with caribou (*Rangifer tarandus*). There has been much interest in the possible role of competition between these species (Wilkinson *et al.* 1976; Vincent and Gunn 1981; Staal and Olesen 1992), particularly because muskox numbers grew exponentially on Banks Island, NWT, while caribou numbers declined (Gunn *et al.* 1991). A better understanding of foraging adaptations in muskoxen may be useful in evaluating possible competition with caribou.

Although caribou foraging ecology has been comparatively well studied, foraging adaptations of muskoxen are less understood. Caribou are small- to medium-sized "intermediate feeders" (Hofmann 1989) best adapted to medium or high quality diets (Syrjälä-Qvist 1985). The minimum daily voluntary intake of a high quality diet

¹ A version of this chapter was published in 1994 in the Journal of Wildlife Management (Adamczewski *et al.* 1994b).

by captive caribou in winter was $70 \text{ g/kg}^{0.75}$ (Crête et al. 1993). Muskoxen, by contrast, weigh two to three times as much as caribou, and their digestive anatomy and graminoid-dominated diets identify them as "grazers" (Staal and Thing 1991). Winter imposes unique foraging constraints on these relatively large grazers, because their forage is of low quality (Staal and Olesen 1992) and its availability is often reduced by snow (Jingfors 1981; Raillard 1992; Schaefer and Messier 1995). In captive muskoxen offered good quality diets during winter, the daily intake of dry matter (DM) was $38\text{-}39 \text{ g/kg}^{0.75}$ and the DM digestibility of hay was 70-74% (White et al. 1984b; Adamczewski et al. 1994). Based on these results, we speculated that muskoxen have adapted to the foraging constraints of arctic winters by digesting low quality graminoid forage more completely than other grazers and by maintaining body weight at lower rates of intake. To test these hypotheses, we compared the voluntary intake and digestibility of a low-protein grass hay by mature muskoxen and cattle, a classic grazer (Hofmann 1989). To determine whether the nutrient characteristics of the experimental diet were comparable with those of wild muskox forages, we compared the protein and fiber composition of the experimental diet with that of grasses and sedges commonly eaten in winter by wild muskoxen on Banks and Victoria Islands, NWT. The trials were carried out in accordance with Guides to the Care and Use of Experimental Animals (Canadian Council on Animal Care 1980, 1984).

3.3 Materials and Methods

We conducted separate feeding trials with muskoxen and cattle at the University of Saskatchewan's Goodale Research Station, 20 km southeast of Saskatoon, Saskatchewan, in late winter 1993. Five mature muskoxen were used during a trial in early March 1993, including a 10-year-old castrate male, a 10-year-old hysterectomized female with intact ovaries, a 6-year-old pregnant female, a 10-year-old pregnant female, and a 10-year-old non-pregnant female. The two pregnant females were in mid-gestation and calved in late May and early June. We used three mature non-pregnant, non-lactating Hereford cows four, five, and seven years old during a trial in early April 1993. The digestion trial with the Herefords was carried out a month later than the muskox trial to ensure that cold temperatures would not increase forage intake by the cattle (Christopherson *et al.* 1978) and confound effects of temperature with intrinsic differences between species. In cattle, the seasonal variation in intake associated with day length is minimal ($< 3\%$; Ingvarsen *et al.* 1991) and should not have measurably affected our results.

The hay fed during these trials was cut late in the growing season, 1992, at a farm near Perdue, Saskatchewan. We chose this hay because its protein and fiber composition was similar to that of sedges and grasses often found in the diets of free-ranging muskoxen in winter (Klein and Bay 1990; Staal and Olesen 1992). A composite sample of the hay was identified as predominantly (75-85 %) Kentucky bluegrass (*Poa pratensis*) with smaller components of timothy (*Phleum pratense*), smooth brome (*Bromus inermis*), foxtail barley (*Hordeum jubatum*), marsh muhly (*Muhlenbergia racemosa*), alkali grass (*Distichlis stricta*), sedge (*Carex* sp.), plains rough fescue (*Festuca hallii*) and occasional forbs (Looman and Best 1987).

We gave the muskoxen and the cattle 3-week adjustment periods, with free access to hay before their respective 10-day digestibility trials. The muskoxen had been eating a brome-alfalfa hay and a daily pelleted supplement of 550 g/animal before the adjustment period. The pellets consisted of oats (50 %), a medium quality hay (38 %), and a mixture of molasses, minerals, and vitamins (Adamczewski *et al.* 1994a). This supplement was reduced to 300 g/animal at the start of the adjustment period. The cattle had been fed a mixed, medium quality hay and a daily barley supplement of about 3 kg/animal prior to the adjustment period. From the start of the adjustment period, the cattle were each given 940 g/day of the pellets previously fed only to the muskoxen.

During the adjustment period, we kept the muskoxen together and provided them with hay and water in three connected outdoor paddocks, each approximately 15 x 20 m. During the trial they were held in adjacent individual 3 x 9-m outdoor shaded pens, constructed within one of the paddocks, with access to water. All the muskoxen had been kept in these pens during several previous trials and were given two days to habituate to them. We kept the cattle in a 15 x 20-m outdoor corral during the adjustment period. This corral was divided into three pens of approximately equal area for the feeding trials, each with shade and access to water. The cattle were also given a 2-day habituation period. We weighed all the animals to ± 1 kg weekly during the adjustment periods, and at the beginning, mid point, and end of the digestibility trials. Mean 24-hour temperatures from Environment Canada in Saskatoon were -2.1 °C (range -10 to 2 °C) during the muskox trial in early March and 3.2 °C (range -1 to 10 °C) during the cattle trial in early April.

Apparent digestibility was measured using chromic oxide (Cr_2O_3) as a marker. A sample of the pellets normally fed to the muskoxen was ground, mixed with Cr_2O_3 (2.0 % for muskoxen, 2.9 % for cattle), and re-pelleted. For 10 days, weighed portions of the marked pellets (muskoxen 150 g; cattle 470 g) were fed to each animal at varying times between 0800 and 1100 and between 1600 and 1900. We collected fecal samples

twice daily when the pellet rations were fed, during the last 4 days and on the morning of the 11th day. Voluntary intake of the hay was measured during the last eight days of each trial; we adjusted the amount of long hay offered in the morning so that each animal left 1-2 kg daily. We collected a sample of pellets and pooled samples of hay offered and refused each day during the trials.

Three samples of native graminoid forage were obtained next to muskox feeding craters in the NWT. The samples included *Carex aquatilis* collected during snowmelt in June 1992 near Wellington Bay, Victoria Island by J. A. Schaefer, a composite of sedges and grasses collected in May 1993 north of Ferguson Lake, Victoria Island by the authors, and a composite of sedges collected in March 1993 near Deep Creek on Banks Island by N. Larter.

We oven-dried the hay, pellets, and native forage samples to constant weight at 60 °C to determine DM, while fecal samples were first freeze-dried and then oven-dried. The samples of feed and feces were ground through a 1-mm mesh on a Wiley mill, and a composite fecal sample was then prepared from equal amounts of the nine collections for each animal. Crude protein, neutral-detergent fiber, acid-detergent fiber, lignin, cellulose, hemicellulose, ash, and gross energy contents of the hay, native forage, pellets, and fecal samples were determined using standard methods (Van Soest 1982; Association of Official Analytical Chemists 1984). The samples of marked pellets and composited fecal samples were analysed for Cr₂O₃ content following method A of Fenton and Fenton (1979), using 3-4 g DM of feces and centrifugation prior to optical density readings.

We calculated apparent digestibilities of DM, organic matter, crude protein, gross energy, neutral-detergent fiber, acid-detergent fiber, lignin, hemicellulose, and cellulose from concentrations of Cr₂O₃ in feed and feces following Schneider and Flatt (1975). Although diurnal variation in Cr₂O₃ excretion may bias digestibility estimates in ruminants (Schneider and Flatt 1975), we believe that our practice of feeding the marked pellets and collecting feces at variable times over several days minimized biases, and permitted valid comparisons of digestibility between the two species. Daily intake of digestible energy was calculated from digestibility of gross energy and feed consumption, and daily intake of metabolizable energy (ME) was estimated as 82 % of digestible energy (Agricultural Research Council 1980). Daily intakes of DM, ME, and digestible energy were expressed as absolute quantities, and scaled to metabolic body weight (kg^{0.75}). We also scaled intake of DM to body weight (kg^{1.0}). The mean values for cattle and muskoxen were compared using 2-tailed *t*-tests.

3.4 Results

Both the muskoxen and the cattle maintained nearly constant body weight throughout the adjustment periods and digestibility trials, although weights tended to fluctuate more in the cattle (Table 3.1). Diet composition was similar for both species (Table 3.2) although the hay made up slightly less of the muskox diet (86.4 %) than of the cattle diet (93.3 %) (Table 3.3). The samples of refused hay were nearly identical in composition to the hay offered to the muskoxen and the cattle. Protein content of the composite diets was slightly higher and fiber content slightly lower than in the hay alone, due to the pelleted supplement. The hay offered during these trials was similar in crude protein (6.0 vs. 5.3 % of DM) and fiber (neutral-detergent fiber of 73 vs. 72 %) to the mean of three samples of graminoid forage from Victoria and Banks Islands (Table 3.2).

Apparent digestibility of organic matter was higher in the muskoxen than in the cattle, as were digestibilities of DM, crude protein and most fiber fractions (Table 3.3). Daily intake of DM scaled to metabolic weight was three times higher in the cattle than in the muskoxen and more than twice as high when scaled to body weight. Intake of ME was also much lower in the muskoxen than in the cattle.

3.5 Discussion

This study provided evidence that muskoxen are well adapted to winter foraging conditions in the arctic, where access to forage is frequently restricted by snow (Jingfors 1981; Gray 1987). A combination of efficient digestion of low quality graminoid forage and relatively low metabolic requirements enabled the captive muskoxen to maintain body weight at remarkably low rates of intake, characteristics that help explain why wild muskoxen can maintain substantial body fat through the long arctic winter (Thing *et al.* 1987).

Muskoxen share several digestive features with goats and sheep that also subsist on low-protein, high-fiber diets, notably a relatively large rumen (Staland and Thing 1991), a slow rate of passage when eating high-roughage diets (Adamczewski *et al.* 1994a), and relatively low rates of intake. Greater digestibility of the experimental diet in the muskoxen than in the cattle was most likely due to slower passage, because digestibility of high-roughage diets depends to a large extent on the duration of rumen fermentation (Flachowsky and Tiroke 1993). Similar physiological features have been shown in indigenous Heidschnucken sheep (Weyreter *et al.* 1987). The daily voluntary intake of Nubian ibex (*Capra ibex nubiana*) and Bedouin goats fed a 5.0 % protein straw diet (29-30 g/kg^{0.75}, Choshniak *et al.* 1984) was also similar to that of the

Table 3.1. Mean body weight of muskoxen and Hereford cows fed a marginally supplemented low-protein grass hay in late winter 1993.

Period	Muskoxen (<i>n</i> = 5)			Cattle (<i>n</i> = 3)		
	Date	Weight (kg)		Date	Weight (kg)	
		Mean	SE		Mean	SE
Adjustment	9 Feb	255	16	19 Mar	711	32
	16 Feb	254	16	26 Mar	699	37
				2 Apr	733	44
Digestibility trial	2 Mar	257	17	8 Apr	710	42
	9 Mar	255	17	12 Apr	713	39
	13 Mar	254	18	17 Apr	702	42

Table 3.2. Composition of feeds (% of dry matter) offered and eaten by cattle and muskoxen during digestibility trials in 1993, and of native forages ($n = 3$) from Banks and Victoria Islands, NWT.

Component ^a	Feeds offered			Composite diet		Native forages	
	Hay (muskoxen)	Hay (cattle)	Pellets	Muskoxen	Cattle	Mean	SE
DM	87.2	88.1	92.7	87.9	88.8	88.5	1.1
OM	89.6	90.27	88.4	89.4	89.2	93.5	1.7
CP	6.1	6.0	13.5	7.1	6.5	5.3	0.4
NDF	73.2	73.0	33.1	67.7	71.2	71.9	2.7
ADF	44.3	45.0	19.5	40.9	42.2	43.5	1.8
Lignin	4.1	4.3	3.2	4.0	3.7	8.1	2.3
Hemicellulose	28.9	28.0	13.6	26.8	29.0	28.5	2.9
Cellulose	40.2	40.6	16.3	36.9	38.5	35.4	1.3
GE (MJ/kg)	17.6	17.6	18.5	17.8	17.8	18.4	0.5

^a DM = dry matter, OM = organic matter, CP = crude protein, NDF = neutral-detergent fiber, ADF = acid-detergent fiber, GE = gross energy.

Table 3.3. Mean apparent digestibility and daily intake of hay and pellet diet by muskoxen and cattle, March-April 1993.

Measurement a, b	Muskoxen (n = 5)		Cattle (n = 3)		p ^c
	Mean	SE	Mean	SE	
Apparent digestibility (%)					
DM	52.5	1.3	45.0	2.6	0.03
OM	57.8	1.1	50.0	3.1	0.03
CP	43.2	1.9	36.1	1.8	0.04
NDF	56.7	1.1	49.4	3.4	0.04
ADF	48.9	1.6	41.0	2.6	0.03
Hemicellulose	68.6	1.3	61.1	4.1	0.07
Cellulose	59.5	1.2	47.9	3.1	0.01
Daily intake (DM)					
Hay (kg)	1.76	0.22	12.18	0.33	
Pellets (kg)	0.28	0	0.87	0	
DM (kg)	2.04	0.22	13.05	0.58	
DM (g/kg ^{1.0})	7.85	0.39	18.14	1.16	<0.001
DM (g/kg ^{0.75})	31.5	2.0	95.5	4.8	<0.001
DE (MJ)	19.3	2.2	105.7	7.1	
ME (MJ)	15.9	1.8	86.6	5.8	
ME (MJ/kg ^{0.75})	0.245	0.017	0.636	0.065	<0.001

^a DM = dry matter, OM = organic matter, CP = crude protein,
 NDF = neutral-detergent fiber, ADF = acid-detergent fiber,
 DE = digestible energy, ME = metabolizable energy.

^b Apparent digestibilities of lignin were negative and omitted from the table.

^c Probability value for *t*-test.

muskoxen in this study. Muskoxen are ecologically comparable with these ibex and goats, because all three species are adapted to desert environments where food is often scarce and of poor quality.

Although digestive adaptation may have enabled the muskoxen to extract more energy from the experimental diet than the cattle did, the much lower intake of ME in the muskoxen was consistent with their relatively low fasting metabolic rate (FMR) ($0.205 \text{ MJ/kg}^{0.75}$, Nilssen *et al.* 1994). Low FMR in muskoxen has been corroborated by the relatively low intakes of DM and ME for winter maintenance estimated by White *et al.* (1984b; $38 \text{ g/kg}^{0.75}$ and $0.425 \text{ MJ/kg}^{0.75}$) and Adamczewski *et al.* (1994a; $39 \text{ g/kg}^{0.75}$ and $0.441 \text{ MJ/kg}^{0.75}$) for muskoxen fed high and medium quality diets, respectively. Our estimates of DM and ME intake for maintenance ($32 \text{ g/kg}^{0.75}$ and $0.245 \text{ MJ/kg}^{0.75}$) for muskoxen were even lower. The low levels of DM and ME intake we observed might be due in part to reduced physical activity and a greater gut fill associated with low quality feeds, but more likely reflect the lower oxygen consumption and energy needs of ruminants adapted to low planes of nutrition (Burrin *et al.* 1989). On restricted diets, oxygen consumption, the weights of the liver and gut, and the heat increment of feeding are all reduced in sheep (Burrin *et al.* 1990). Similarly, the oxygen consumption rates of resting Nubian ibex fed wheat straw were 33% lower than when they were fed high-protein alfalfa hay (Choshniak *et al.* 1984). Our estimate of daily intake of maintenance ME in muskoxen was only 16 % higher than the estimated FMR of muskoxen (Nilssen *et al.* 1994). Because daily ME intake for maintenance generally exceeds FMR by $\geq 30 \%$ in domestic ruminants (Hudson and Christopherson 1985), we hypothesize that muskoxen accustomed to a low quality graminoid diet may have a FMR lower than $0.205 \text{ MJ/kg}^{0.75}$, already among the lowest known in ruminants (Hudson and Christopherson 1985).

Like muskoxen, the cattle were able to maintain body weight on low quality graminoid forages, but they required a substantially higher daily intake of DM and ME than did the muskoxen. Similar to muskoxen and the small ovine and caprine grazers, large bovine grazers adapted to low quality diets tend to have relatively large rumens and slow rates of passage (Schaefer *et al.* 1978; Mould *et al.* 1982; Saadullah *et al.* 1982). The cattle in this study appeared to compensate for low food quality by maintaining a high rate of forage intake; their daily intake of DM and ME exceeded the maintenance levels of feeding recommended by the National Research Council (1976) for a 700-kg beef cow (96 vs. $70 \text{ g/kg}^{0.75}$, and 0.636 vs. $0.565 \text{ MJ/kg}^{0.75}$, respectively). In contrast to muskoxen and sheep, whose FMRs are below the interspecific mean for eutherian mammals, the FMR of cattle is slightly higher than the

interspecific mean (Tyler and Blix 1990), indicating a higher maintenance food requirement. These energetic and digestive characteristics of cattle, similar to those of other large bovine grazers such as bison (*Bison bison*) and yak (*Bos grunniens*) (Christopherson *et al.* 1978; Schaefer *et al.* 1978) are consistent with the adaptation of these species to lower latitude grasslands where forage densities are much higher than in the arctic.

3.6 Conclusion

Our results confirm that muskoxen are well adapted for the efficient digestion of low quality forage at low rates of intake. In contrast to muskoxen, caribou are smaller and have relatively high metabolic rates (Fancy 1986), with higher food requirements relative to their size (Crête *et al.* 1993). Caribou also have relatively small rumens (Hofmann 1989), relatively rapid rates of passage (Valtonen *et al.* 1983), and have difficulty with highly fibrous diets (Syrjälä-Qvist 1985). Where highly digestible forage such as lichens is scarce or unavailable and low-quality grasses and sedges are the primary winter forage, muskoxen are likely to fare better nutritionally than caribou. This has been shown in western Greenland (Staal and Olesen 1992). Differences in foraging adaptations between muskoxen and caribou may also help explain the exponential growth of the muskox population during a large decrease of caribou on Banks Island, NWT (Gunn *et al.* 1991), and the persistence of muskoxen where caribou populations have been intermittent in northernmost Greenland (Klein and Bay 1990).

CHAPTER 4. BODY COMPOSITION OF MUSKOXEN AND ITS ESTIMATION FROM CONDITION INDEX AND WEIGHT MEASUREMENTS¹

4.1 Abstract

As part of a study of seasonal changes in body composition of muskoxen on Victoria Island, Northwest Territories, we analysed the anatomical and chemical body composition of 22 muskoxen (7 adult females, 6 sub-adult females, 2 yearlings, 5 calves, and 2 near-term fetuses) that varied widely in size and condition. Distribution of dissectible fat among the major depots and weights of muscle, fat, bone and hair were determined by dissection. The dissected tissues were ground and analysed for lipid, water, protein and ash. Lipid extracts were further analysed for major lipid classes by thin-layer chromatography to determine the proportion of lipids usable as energy reserves. We evaluated physical indices of condition, as well as weights of the body, carcass and ingesta-free body (IFBW), either alone or in combinations, as predictors of body composition. Among the fatter females, about 33 % of the fat was intermuscular, 27 % subcutaneous, 20 % abdominal and 13 % intramuscular. The leanest muskoxen were four 5 to 15-day-old calves with 3.5 ± 0.5 % (mean \pm SE) fat in the IFBW, and the fattest were 3 females with 24.8 ± 1.4 % fat. The proportion of fat increased most rapidly in muskoxen with an IFBW greater than 100 kg, while the fat-free proportions of protein, water and ash were consistent within age-class. Muscle weight was best predicted from weights of individual muscles, while protein weight was best predicted from IFBW. Bone weight was readily estimated from the weights of individual limb bones, and ash weight was best estimated from IFBW. Dissectible and total fat weights were more difficult to estimate than other components, but combining kidney fat weight and a measure of body weight with up to three other measurements allowed both these fat weights to be estimated accurately. Accurate estimates of protein and ash weight could also be made by assuming constant fat-free composition of the IFBW after subtraction of estimated fat weight. Patterns of body composition and fat distribution in muskoxen were similar to those in cattle and sheep, and the extent of fattening exceeded that found in other wild ruminants with the exception of Svalbard reindeer (*Rangifer tarandus platyrhynchus*).

¹ A version of this chapter was submitted to the Canadian Journal of Zoology in September 1994 (Adamczewski *et al.* 1995).

4.2 Introduction

Muskoxen (*Ovibos moschatus*) and caribou (*Rangifer tarandus*) normally endure extreme seasonal fluctuation in the quality and availability of forage on their arctic ranges (Klein 1992). To cope during winter, caribou curtail energy and nutrient needs by means of conservative behaviour, reduced metabolic rate (Ringberg 1979; Fancy 1986) and digestive adaptation to low-quality forage (Staal and White 1991). Body fat and protein accumulated during summer and autumn also provide a small but important buffer against winter scarcity (Tyler 1987; Adamczewski *et al.* 1993). There have been several studies of seasonal patterns in body weight and reserves of caribou and reindeer (Dauphine 1976; Adamczewski *et al.* 1987a; Tyler 1987, Huot 1989), but few opportunities to evaluate such changes in muskoxen. Muskox cows can become very fat and can retain much of this fat until late winter (Thing *et al.* 1987). Such reserves may be particularly important because they help sustain several energetically costly weeks of lactation before high-quality spring forage becomes available. Given the relatively slow metabolism of muskoxen (Nilssen *et al.* 1994) and their sedentary lifestyle in winter (Jingfors 1981), body reserves might also contribute a substantial proportion of their over-winter energy needs. To evaluate the extent and reproductive significance of seasonal changes in body composition of female muskoxen, a field study was carried out from 1989 to 1993 on Victoria Island, Northwest Territories (NWT), in cooperation with Inuit hunters from Cambridge Bay, NWT.

The number of muskoxen on Victoria Island has fluctuated widely in the past but has steadily increased since 1970 (Gunn 1990). By 1993 the population had grown to an estimated 45,000 muskoxen, (A. Gunn, unpubl. data). Muskoxen in the NWT are hunted under a quota system for subsistence, commercial use, and sports hunts (Gunn *et al.* 1991). The 302 muskoxen studied were part of the commercial quota for Cambridge Bay. Because the carcasses were primarily intended for commercial use, their body composition could not be measured directly. We relied instead on measures of condition and weight that could be used in the field, an approach that has been used in reindeer and caribou (Ringberg *et al.* 1981; Tyler 1987; Adamczewski *et al.* 1987b). To validate this approach, 22 representative individuals differing widely in age, size and condition, were studied in detail. They are the subject of this paper. Our main objectives were (1) to determine the anatomical and chemical composition of the representative muskoxen for comparison with other ruminants, and (2) to identify condition index or weight measurements, or combinations of measurements, that could be used to accurately estimate body composition in the larger sample of muskoxen.

4.3 Materials and Methods

4.3.1 Field collections

The 22 representative muskoxen were chosen from those shot near Wellington Bay, Victoria Island (Fig. 4.1) in November (7), when the muskoxen were fattest, May (6), when the animals were leanest, and April (9), when the muskoxen were of intermediate condition. The sample included 2 near-term fetuses, 5 calves, 2 yearlings, 6 sub-adult females (2 or 3 years old), and 7 adult females (≥ 4 years old). Weights measured on each animal in the field included the total body and the dressed carcass (Langvatn 1977), while condition indices included the weight of the gastrocnemius muscle, the weight and length of the femur, maximum depth of back fat measured near the base of the tail (DBF; Langvatn 1977) and kidney fat weight, trimmed following Riney's (1955) method. We did not use the kidney fat index (kidney fat weight divided by the weight of the kidneys) because kidney weight varied widely with season and was a poor correlate of size. We also collected a sample of marrow from the mid-section of the femur and determined its fat content by drying. Muskox ages were estimated up to 5 or more years of age by tooth eruption and wear patterns (Henrichsen and Grue 1980). Each carcass was bisected in the median plane with a meat saw and one side was cut into 2-4 pieces, wrapped in two layers of thick plastic, and frozen. The emptied rumen, half the hide, half the head, and a fore and hind foot were treated likewise. The remaining gastrointestinal tract was either weighed full and empty in the field, or frozen full with the rest of the viscera. These specimens were flown to the University of Saskatchewan and stored at -20°C until dissected further.

4.3.2 Dissections

Each carcass side was thawed and separated into muscle, fat, bone and other tissue (large tendons, lymph nodes, neural tissue and connective tissue) and these components were weighed to ± 10 g. Muscles weighed individually, after removal of extraneous fat and large tendons, included the gluteobiceps, semitendinosus, semimembranosus, gastrocnemius (Fig. 4.2) and extensor carpi radialis (Fig. 4.3). The gastrocnemius has been used as an index of muscle weight in reindeer (Ringberg *et al.* 1981). The extensor carpi radialis was chosen as an alternative muscle whose removal would not require dissection of the hind quarter. Bone weight included articular and costal cartilage. The femur, tibia, humerus, and radius-ulna were weighed individually and their lengths recorded. Dissectible fat was identified as subcutaneous or intermuscular, while fat remaining within the body cavity was considered part of the abdominal fat (see below).

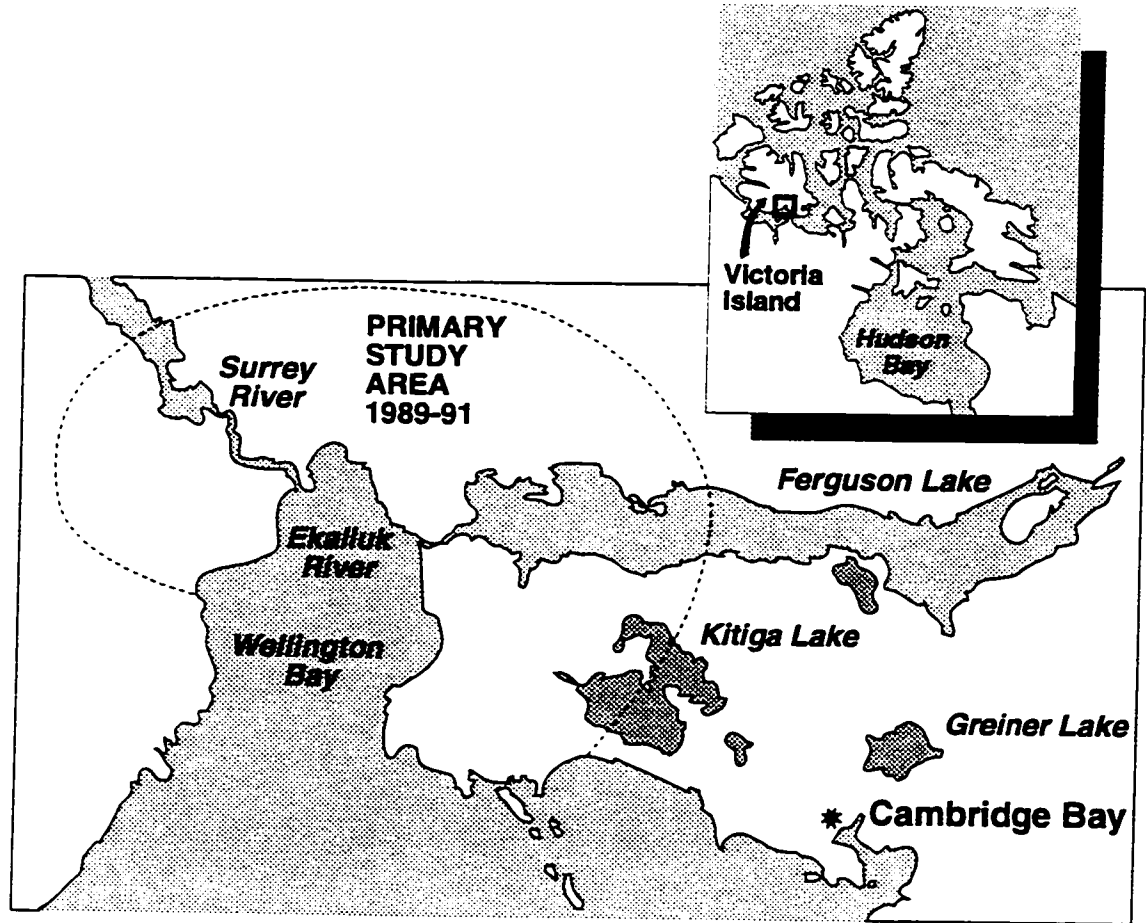


Fig. 4.1. The study area in the vicinity of Wellington Bay, Victoria Island, Northwest Territories, Canada.

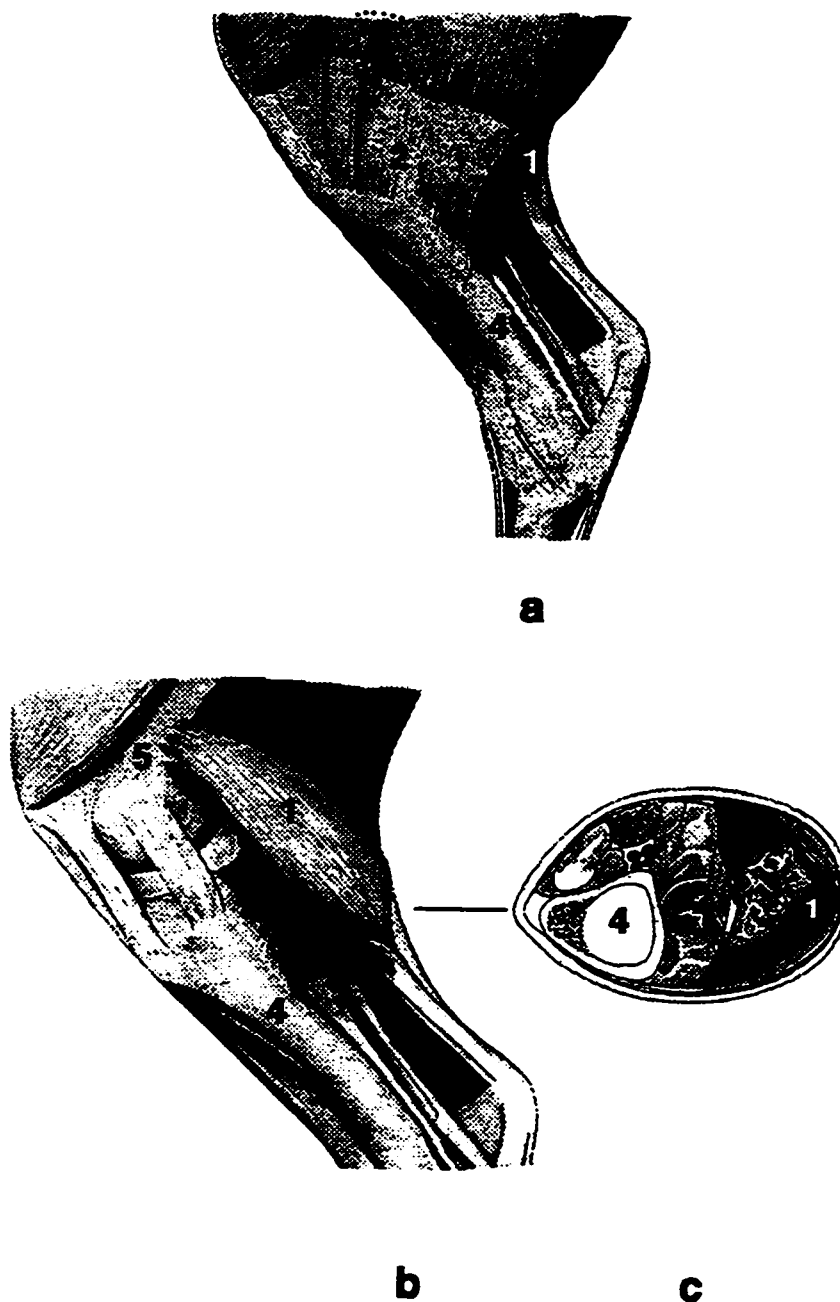


Fig. 4.2. Identification of the gastrocnemius in the bovine hind limb; modified from Popesko (1979).
 1 - gastrocnemius; 2 - gluteobiceps; 3 - flexor digitorum superficialis; 4 - tibia; 5 - femur.
 (a). Medial view of the hind limb, with superficial fat and fascia removed. The gastrocnemius, indicated by dotted line, is largely covered by the gluteobiceps.
 (b). Medial view of the hind limb, with the distal portion of the gluteobiceps removed.
 (c). Transverse section of the hind-limb near the proximal end of the tibia; the gastrocnemius, indicated by dark shading, "surrounds" the flexor digitorum superficialis, a smaller muscle continuous with the large common calcaneal tendon.

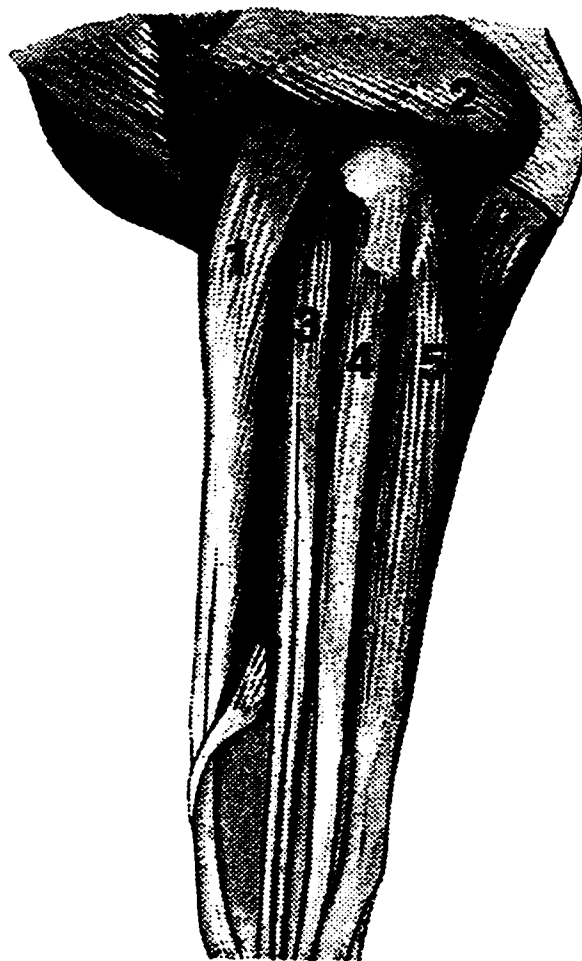


Fig. 4.3. Identification of the extensor carpi radialis in the bovine forelimb, lateral view; modified from Popesko (1979). 1 - extensor carpi radialis; 2 - triceps brachii; 3 - extensor digitorum communis; 4 - extensor digitalis; 5 - extensor carpi ulnaris.

The fore and hind feet were separated into bone, hoof and other tissue (mostly tendon); the metacarpus and metatarsus were weighed and measured individually and the hooves weighed. Muscle, fat (considered intermuscular), bone and other tissues of the half-head were separated and weighed. The horn was cut near the head and weighed. In some cases the mandible had been removed for aging and a small correction was applied to account for this.

The viscera were thawed and the chambers of the gastrointestinal tract were weighed with and without their contents, and the abdominal fat (including kidney fat) and fat associated with the heart and lungs were separated and weighed. Ingesta-free body weight (IFBW) was defined as the weight of the whole body, less the weight of the ingesta and the gravid uterus. Total muscle, bone and dissectible fat included both carcass and non-carcass portions.

The half-hides and skin from the half-head and a fore and hind foot were thawed, allowed to dry in a cold-room for 36 hours, then clipped to within 5-6 mm of the skin using sheep shears to determine weight of the hair. The hair weight was corrected for the coat remaining on the skin using a factor determined by clipping a known area to within 1 mm of the skin with a fine clipper.

4.3.3 Chemical analysis

Before analysis, frozen tissues from 20 of the 22 muskoxen were ground three times in a whole-body grinder, with mixing between successive grindings. In 13 cases, all tissues, including half the previously ground viscera, were treated as one pool. For the remaining seven, separate pools were made up from the skeletal muscle and from all the other tissues combined. Representative samples of the 27 ground tissue pools, each weighing 80-120 g, were stored at -20 °C, then freeze-dried. The non-metabolizable protein of the pelage, hooves and horns was not ground.

The water content of the ground tissue samples was determined by freeze-drying, and corrected for residual moisture by oven-drying sub-samples to constant weight at 110 °C. Corrections were also made for water loss during thawing and dissection by weighing the tissues before thawing and following dissection. No correction was made for blood loss at death. Ash was measured by overnight combustion in a muffle furnace at 500 °C. Lipid content was determined by extraction with chloroform-methanol-water following Atkinson *et al.* (1972), except that the samples were shaken with solvent overnight, not homogenized. Protein was calculated by subtraction of the lipid and ash from the total dry matter. To verify this estimate,

crude protein was also measured in 13 samples as Kjeldahl nitrogen x 6.25; agreement between the two methods was within 2 %.

To determine the proportion of the total lipids usable as energy reserves, representative lipid extracts from each tissue pool sample were analysed by thin-layer chromatography. S-III Chromarods were used on an Iatroscan TH-10 Mk IV analyser (Iatron Labs, Tokyo, Japan) to determine proportions of cholesterol esters, triglycerides, free fatty acids, diglycerides, monoglycerides, cholesterol and phospholipids (Ackman and Ratnayake 1989; Cherian and Sim 1992; Fig. 4.4). The solvent was composed of benzene:chloroform:acetic acid:methanol in the ratio 500:100:2:1. Only the glycerides and free fatty acids were included as fat; we excluded cholesterol, cholesterol esters and phospholipids, which are not energy reserves.

4.3.4 Data analysis

Overall patterns in weight of dissectible tissues, organs and weights of chemically analysed components were evaluated by regressing their weight against IFBW, using primarily the natural log form of Huxley's (1932) equation $y = ax^b$, where y is the weight of the organ or part, a is a constant, x is the weight of the rest of the body, and b is the growth coefficient of the organ or part, following Berg and Butterfield (1976). In a few cases the fit produced by this equation was statistically significant but biologically inappropriate, and a quadratic equation was fitted instead. The weights of dissectible fat, muscle and bone were evaluated by regression against weights of chemically determined fat, protein and ash, respectively, using natural log-transformed or untransformed data. Fat distribution among the major depots was evaluated by regression of the weights of individual fat depots against total dissectible fat following log-transformation.

The weights of the five individual muscles were evaluated as predictors of the weights of dissectible muscle and protein in the IFBW by regression analysis, following natural log-transformation. The weights of individual bones were similarly assessed as estimators of total bone and ash weights. We also calculated growth coefficients (Berg and Butterfield 1976) for these muscles and bones, by using total muscle and bone weight as estimators of the individual bone or muscle weights. We tested whether these coefficients, and those for the individual fat depots above, differed significantly from 1.0 using t -tests. The fat indices, DBF and kidney fat weight, were similarly assessed as untransformed individual or paired predictors of dissectible and total fat weight. Because femur marrow fat varied little except in a few young calves (Fig. 4.5), it was not analysed further. Body weight, carcass weight and IFBW were also evaluated as

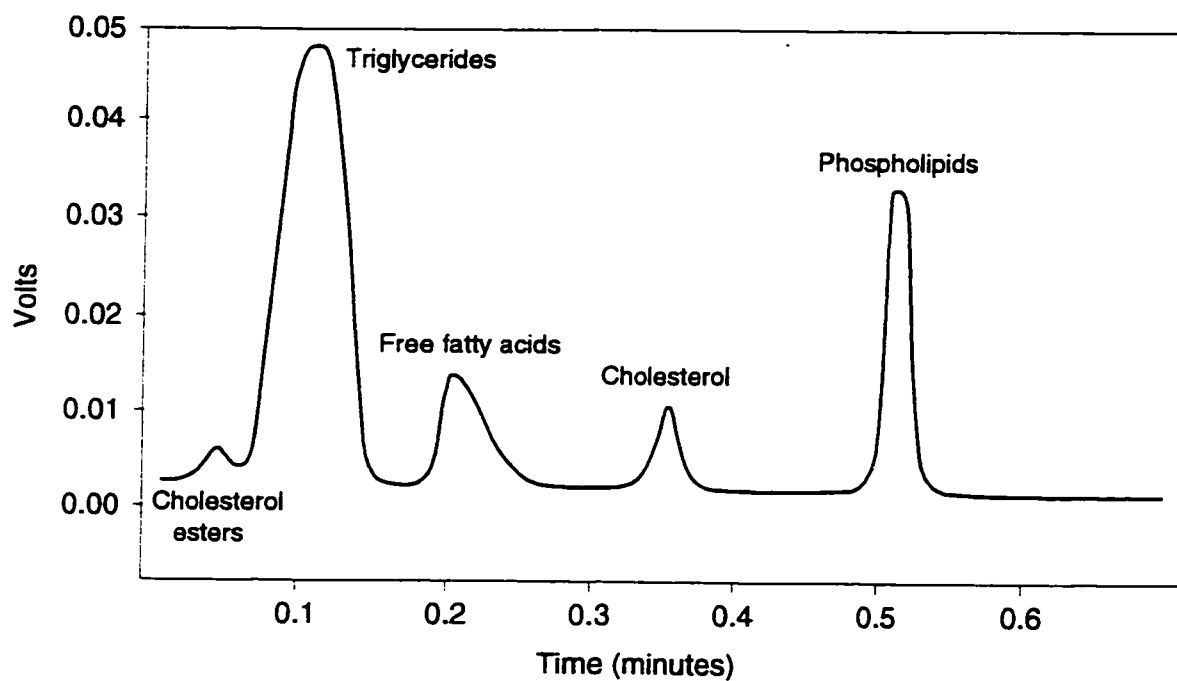


Fig. 4.4. An example of a chromatogram of lipid classes from a muskox calf. The proportion of each lipid class is indicated by the area under the curve. The sample did not contain detectable levels of diglycerides or monoglycerides.

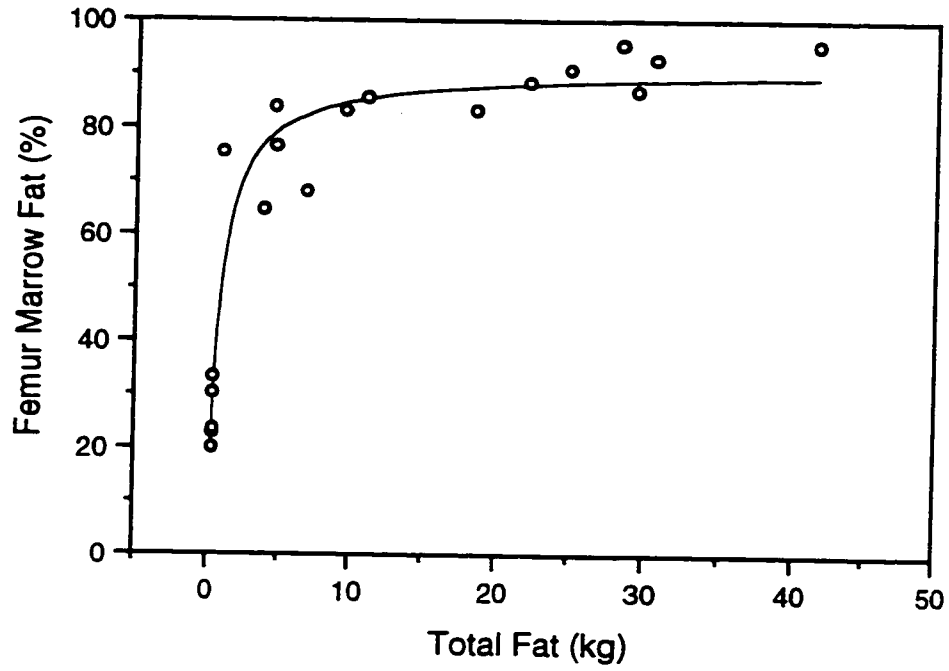


Fig. 4.5. Changes in femur marrow fat in relation to fat weight in muskoxen. Equation: $y = (90.8 x)/(0.69 + x)$, $r^2 = 0.895$, $SEE = 8.73$, $n = 19$, where y is marrow fat (%), x is total fat weight (kg).

estimators of anatomical and chemical body components. We determined whether we could improve on simple equations by combining weight and index measurements, using stepwise regression analysis where the partial F -to-enter for each added independent variable was significant at $P < 0.05$. We also tested a hybrid method of estimating composition of the IFBW, by: (1) estimating fat weight using a multiple regression with independent variables kidney fat weight, carcass weight, DBF, femur length and gastrocnemius weight (described below) and subtracting this from IFBW, (2) subtracting from IFBW an age-specific weight for hair, horn and hoof weight, (3) dividing the remaining IFBW into protein, ash and water weights according to the age-specific proportions of these components established by chemical analysis.

In presenting predictive equations, we listed the adjusted coefficient of determination (r^2 or R^2) as a measure of the fit of the line and the standard error of the estimate (SEE) as a measure of the predictive strength of the equations. However, the SEE from a ln-transformed regression cannot properly be anti-logged and appears deceptively small compared to the SEE of other regressions. We therefore also included the coefficient of variation [CV; $CV = (SEE / \bar{Y}) \cdot 100$]; Reid *et al.* 1968] because this CV allowed an unbiased comparison of the predictive strength of all equations. We could not calculate these statistics for the hybrid method described above, but we were able to approximate the SEE and CV for this method by comparing the residual sums of squares (estimated-true value, with one degree of freedom lost for each calculation) from this method to those established by regression analysis for other predictor variables. Because initial scatter-plots suggested that the residual variance around regression lines was greatest in adult females, each regression was re-calculated using only data from cows at least 3 years old ($n = 11$), and the r^2 (or R^2), SEE and CV for these equations were included to evaluate the utility of these regressions for larger animals.

Lipid compositions of the four very young calves (estimated as 5-15 days old) and the two fetuses were compared using two-tailed t -tests. Statistical comparisons were carried out using Statview SE+Graphics (Abacus Concepts 1991, Calabasas, Ca.), except for the Michaelis-Menten equation fitted to marrow fat data, which was calculated using Sigmastat (Jandel Scientific Software 1994, San Rafael, Ca).

4.4 Results

4.4.1 Overall patterns in body composition

Body weights of the muskoxen ranged from 9.26 to 9.52 kg in the two fetuses, to just over 200 kg in the largest female (Appendix 7.1a). The relative weight of ingesta was lowest in the two fetuses (3.2 ± 0.6 % of whole body weight; mean \pm SE), relatively low (9.1 ± 1.3 %) in four young calves, and substantially greater in the 16 larger muskoxen (26.3 ± 1.1 %, range 19.4 to 31.9 %).

The proportions of muscle and bone slowly declined with increasing IFBW, while dissectible fat increased most rapidly at IFBW over 100 kg (Fig. 4.6a). There were comparable increases in protein, ash and total fat (Fig. 4.6b) as there was a strong linear or near-linear relationship between the weight of each tissue and its chemical counterpart (Fig. 4.7). Dissectible fat was about 80 % of total fat, and just over half the protein in the IFBW was located in the skeletal muscle², with the remainder primarily concentrated in the viscera.

A muskox cow with 20 kg protein in the IFBW had an additional 5 to 5.5 kg protein in the hair and 1.5 kg in the horns and hooves³. The weight of hair was correlated with IFBW (Fig. 4.8), but changed little above an IFBW of 100 kg. About 70 % of the bone was found in the carcass, 21 % in the head and the remainder in the metapodials and smaller bones of the lower legs.

Expressed on a fat-free basis, proportions of water, ash and protein were relatively constant in the muskoxen but ash tended to increase with age, from 4.75 ± 0.20 % (mean \pm SE) in the fetuses to 5.99 ± 0.20 % in mature females (Table 4.1). Water content tended to be highest, and protein lowest, in fetuses and young calves. Proportions of fat and water in the IFBW were strongly but inversely correlated (Fig. 4.9). Fat content varied from 3.5 ± 0.5 of IFBW in four young calves to 24.8 ± 1.4 % in the three fattest females.

4.4.2 Distribution and composition of fat

The intermuscular fat depot was the largest in muskoxen, followed by the subcutaneous, abdominal, and heart-lung depots (Fig. 4.10). The growth coefficients for these depots, from highest to lowest were the subcutaneous (1.336), abdominal (1.055), intermuscular (0.952), and heart-lung (0.759). The first and last of these coefficients differed significantly from 1.0 ($P < 0.05$). Intramuscular fat accounted for

² The estimate of muscle protein is based on the mean protein content of 18 % in muscle of the 7 muskoxen where muscle was analysed separately.

³ We have assumed here that the muskox hair and hooves, which were quite dry, contained no more than 10 % moisture, and that they were 100 % keratin.

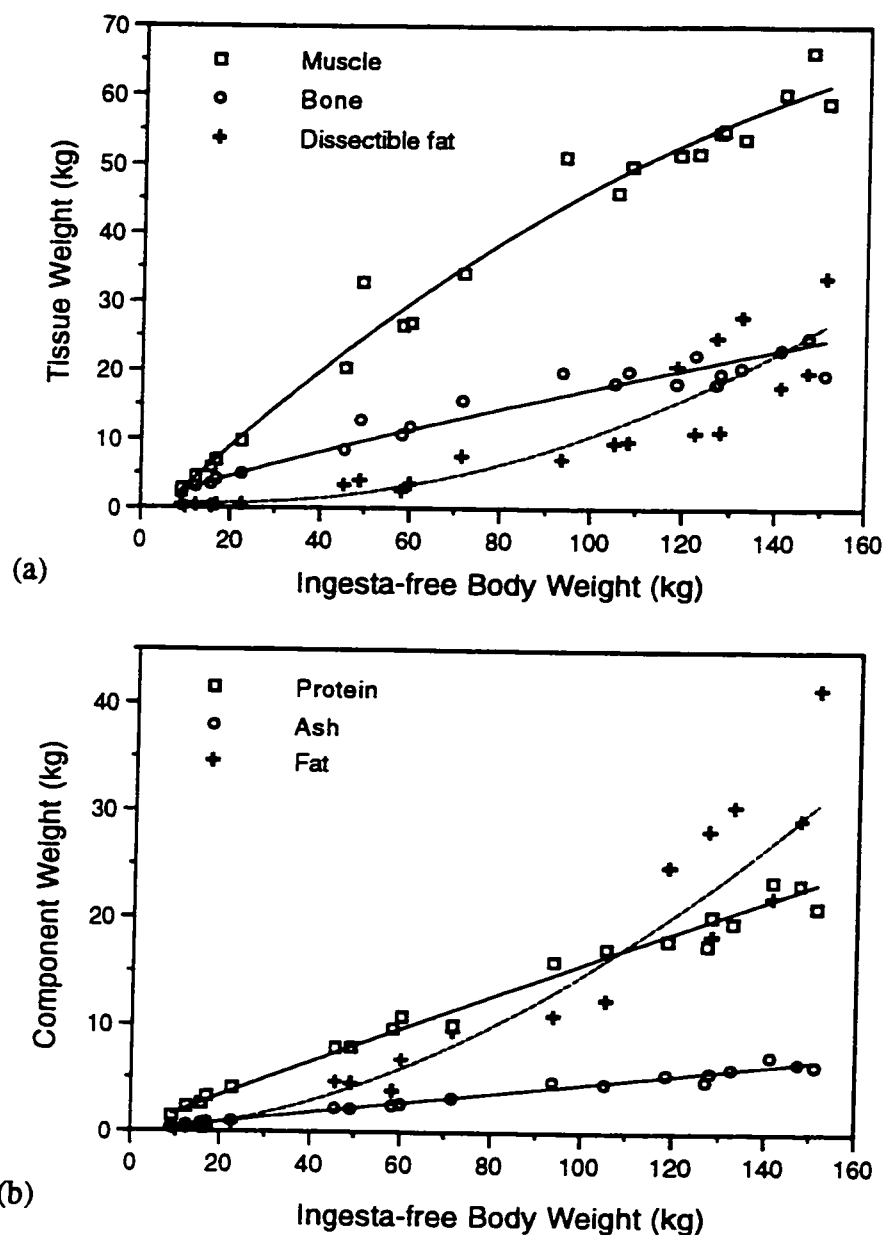


Fig. 4.6 (a) Changes in dissectible muscle, fat and bone in relation to ingesta-free body weight in muskoxen ($n = 22$). Equations: Muscle: $y = 0.632x - 0.001x^2 - 3.182$, $r^2 = 0.978$, $SEE = 3.27$, where y is muscle wt., x is IFBW; Bone: $\ln(y) = 1.141 \ln(x) - 4.266$, $r^2 = 0.988$, $SEE = 0.09$, where y is bone wt., x is IFBW; Dissectible fat: $y = -0.054x - 0.001x^2 + 1.194$, $r^2 = 0.815$, $SEE = 4.32$, where y is dissectible fat wt., x is IFBW (all in kg).

(b) Changes in total fat, protein and ash in relation to ingesta-free body weight in muskoxen ($n = 20$). Equations: Protein: $\ln(y) = 0.955 \ln(x) - 1.64$, $r^2 = 0.992$, $SEE = 0.084$, where y is protein wt., x is IFBW; Ash: $\ln(y) = 1.001 \ln(x) - 3.111$, $r^2 = 0.995$, $SEE = 0.072$, where y is ash wt., x is IFBW; Fat: $\ln(y) = 1.787 \ln(x) - 5.535$, $r^2 = 0.969$, $SEE = 0.318$, where y is fat wt., x is IFBW (all in kg).

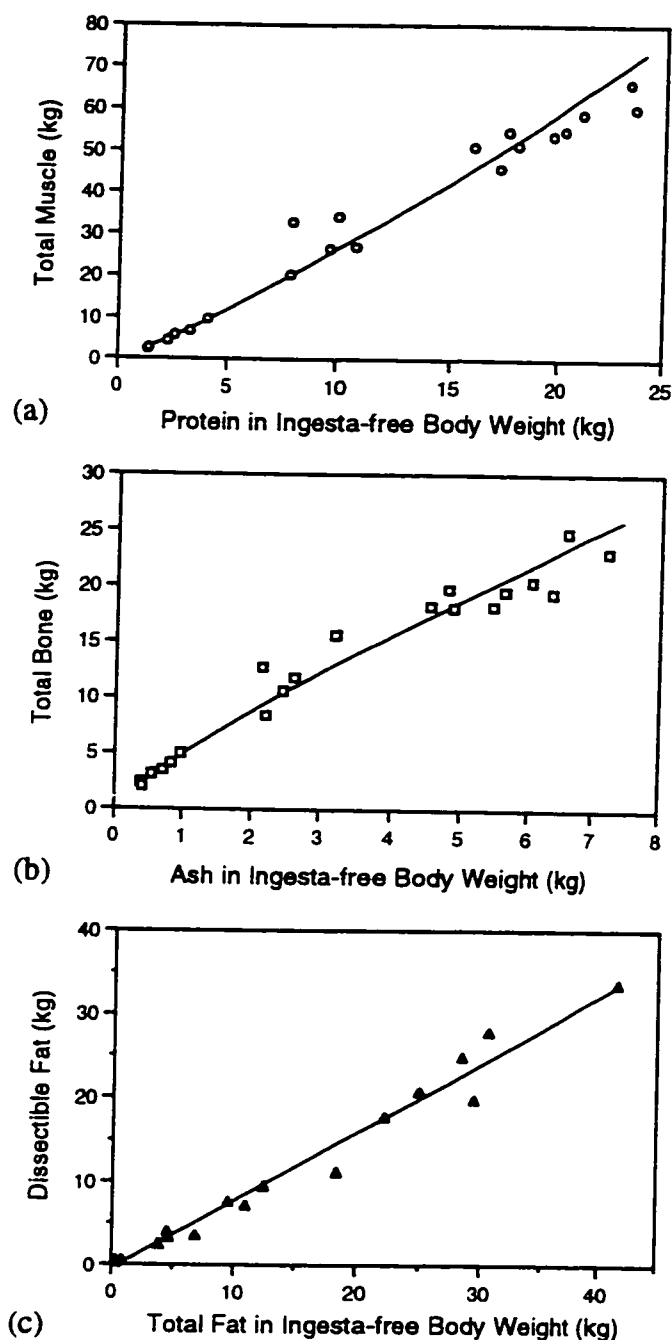


Fig. 4.7 (a) The weight of muscle in relation to the weight of protein in muskoxen. Equation: $\ln(y) = 1.156 \ln(x) + 0.620$, $r^2 = 0.982$, $SEE = 0.151$, $n = 20$, where y is muscle wt. (kg), x is protein wt. (kg).

(b) The weight of bone in relation to the weight of ash in muskoxen. Equation: $\ln(y) = 0.825 \ln(x) - 0.825$, $r^2 = 0.979$, $SEE = 0.120$, $n = 20$, where y is bone wt. (kg), x is ash wt. (kg).

(c) The weight of dissectible fat in relation to the weight of total fat in muskoxen. Equation: $y = 0.817x - 0.425$, $r^2 = 0.976$, $SEE = 1.621$, $n = 20$, where y is dissectible fat wt. (kg), x is total fat wt. (kg).

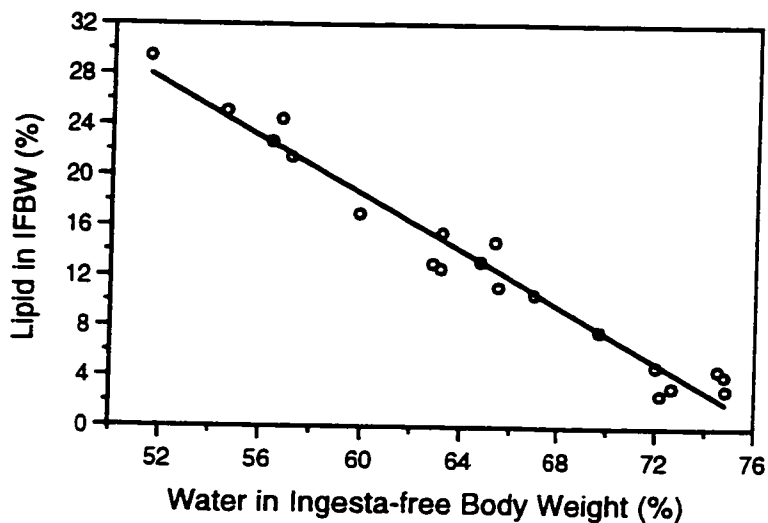


Fig. 4.8. Percent lipid in relation to percent water in the ingesta-free body weight of muskoxen. Equation: $y = -1.114x + 85.36$, $r^2 = 0.962$, $SEE = 1.603$, $n = 20$, where y is % lipid, x is % water. (Note: similar equation for % fat vs. % water: $y = -1.119x + 85.13$, $r^2 = 0.965$, $SEE = 1.535$, $n = 20$, where y is % fat, x is % water).

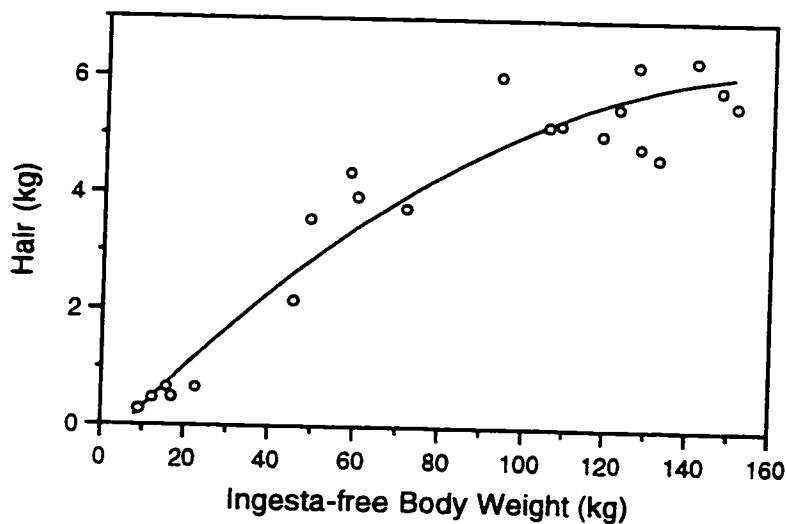


Fig. 4.9. Weight of hair in relation to ingesta-free body weight in muskoxen. Equation: $y = 0.078x - 0.000231x^2 - 0.44$, $r^2 = 0.925$, $SEE = 0.638$, $n = 22$, where x is IFBW (kg), y is pelage weight (kg).

Table 4.1. Fat- and ingesta-free body composition of Victoria Island muskoxen of increasing age.

Values are means (\pm SE).

Age group	<i>n</i>	Ash (%)		Protein (%)		Water (%)	
Near-term fetuses	2	4.75	(0.20)	17.17	(0.20)	78.08	(0.02)
5-15-day-old calves	4	4.89	(0.11)	19.59	(0.59)	75.52	(0.64)
6-month-old calf	1	5.68	-	20.53	-	73.68	-
Yearlings	2	5.21	(0.21)	20.97	(1.38)	73.83	(1.59)
2-3-yr-old cows	5	5.66	(0.20)	20.16	(0.57)	74.17	(0.66)
\geq 4-yr-old cows	6	5.99	(0.20)	20.70	(0.26)	73.31	(0.40)

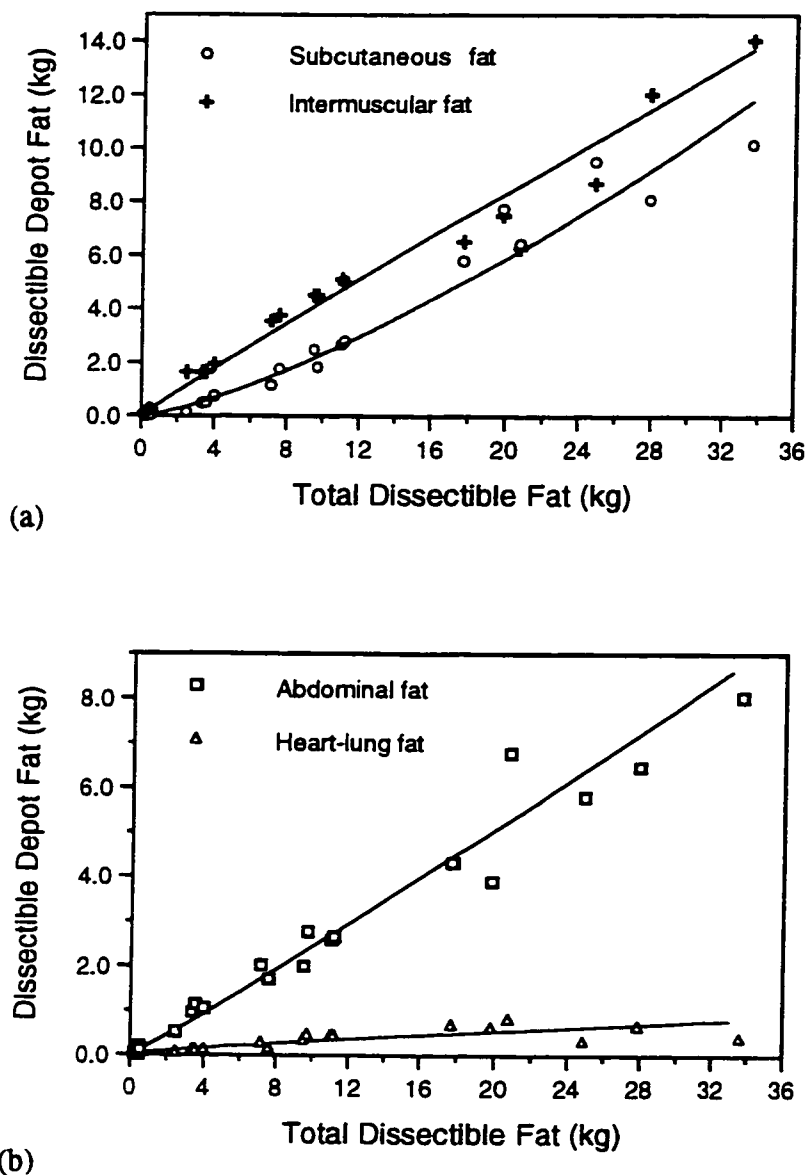


Fig. 4.10 Fat distribution among the major depots in muskoxen.

(a) Intermuscular and subcutaneous. Equations: intermuscular fat: $\ln(y) = 0.952 \ln(x) - 0.731$, $r^2 = 0.988$, $SEE = 0.171$, $n = 22$, where y is intermuscular fat (kg), x is dissectible fat (kg); subcutaneous fat: $\ln(y) = 1.336 \ln(x) - 2.23$, $r^2 = 0.958$, $SEE = 0.454$, $n = 22$, where y is subcutaneous fat (kg), x is dissectible fat (kg).

(b) Abdominal and heart-lung. Equations: abdominal fat: $\ln(y) = 1.055 \ln(x) - 1.535$, $r^2 = 0.966$, $SEE = 0.323$, $n = 22$, where y is abdominal fat (kg), x is dissectible fat (kg); heart-lung fat: $\ln(y) = 0.759 \ln(x) - 2.884$, $r^2 = 0.890$, $SEE = 0.434$, $n = 22$, where y is heart-lung (kg), x is dissectible fat (kg).

much of the 20 % difference between dissectible and total fat weights; we noted widespread marbling in the fatter carcasses. In the seven muskoxen in which muscle was analysed separately from other tissues, fat deposited intramuscularly tended to increase linearly with increasing fatness (Fig. 4.11). In the fattest muskox, fat content of the muscle was 9.2 %, or 5.4 kg of fat compared to 9.0 kg abdominal fat, 10.2 kg subcutaneous fat, and 14.0 kg intermuscular fat⁴.

The extracted lipids of muskoxen at least one year old consisted of 94 to 97 % triglycerides except for one yearling (91.5 %; Appendix 7.1c). The second-largest component was phospholipids and the remaining components were small. The mean total lipid content of the young calves killed in May tended to be lower than in fetuses (3.46 ± 0.48 % vs. 4.43 ± 0.30 %, $P = 0.267$), the triglyceride content of the lipid was lower (68.1 ± 1.6 % vs. 82.1 ± 0.83 %, $P = 0.005$), and the free fatty acid proportion higher (9.10 ± 0.8 % vs. 4.1 ± 0.7 %, $P = 0.02$). Fat dissected from the fetuses was darker in appearance than fat from older animals and calves, and was almost entirely concentrated around the kidneys, heart, and major blood vessels.

4.4.3 Prediction of body composition from condition indices and weight measurements

Muscle weight was accurately estimated from the weights of the five index muscles, with high r^2 's (0.992-0.997) and CV's below 3 % (Fig. 4.12a, Table 4.2), or from a regression that included weights of the carcass, femur and gastrocnemius (R^2 of 0.999 and CV of 1.0 %). Growth coefficients for the individual muscles were all near 1.0: gastrocnemius 0.892, gluteobiceps 1.024, semitendinosus 1.035, semimembranosus 1.028, and extensor carpi radialis 0.900. The coefficients for the first and last of these differed significantly from 1.0 ($P < 0.05$). Neither total body weight, IFBW nor carcass weight predicted muscle weight as well as individual muscle weights (Table 4.2); of the three, carcass weight was best correlated with muscle weight (r^2 of 0.988 and CV of 6.8 %). The coefficients of determination for all these equations were lower when only large females were included, but the SEE's and CV's were relatively small.

Protein weight was most accurately estimated from IFBW (r^2 of 0.992 and CV of 2.5 %), from IFBW and femur weight (r^2 of 0.995 and CV of 1.8 %), or by the hybrid method (CV of 1.7 %). Estimates of protein weight could also be made from carcass weight, total body weight, or the weights of individual muscles (r^2 of 0.976-0.985, and CV of 5.5 to 8.4 %) but when the analysis was limited to large cows, the

⁴ Fat chemically determined is not strictly comparable in weight to fat separated as a tissue, but we make the comparison to provide an approximate scale.

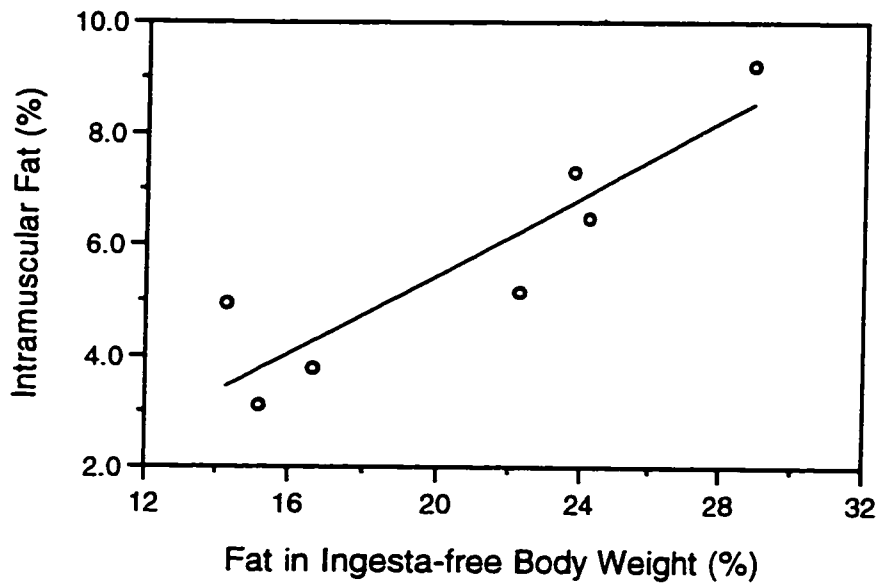


Fig. 4.11. The percentage of fat in muscle in relation to the percentage of total fat in in the ingesta-free body weight of muskoxen. Equation: $y = 0.349 x - 1.521$, $r^2 = 0.774$, $SEE = 1.006$, $n = 7$, where y is % fat in muscle, x is % fat in the IFBW.

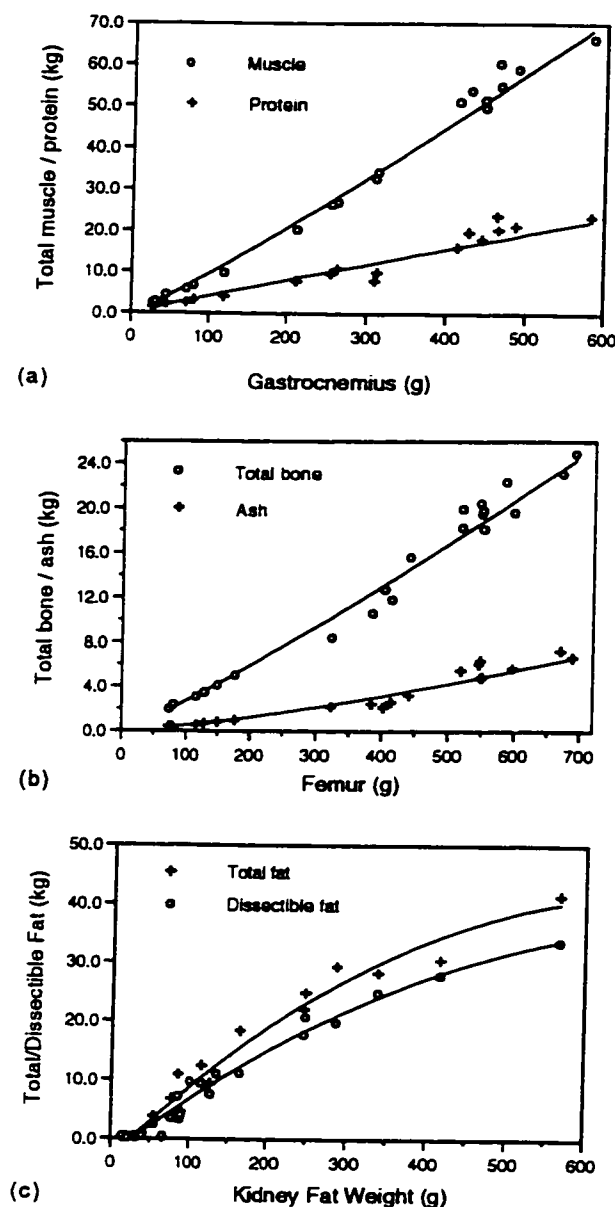


Fig. 4.12 (a) The weight of the gastrocnemius muscle as a predictor of muscle and protein weight in muskoxen. Equations: Muscle: $\ln(y) = 1.114 \ln(x) - 2.864$, $r^2 = 0.994$, $SEE = 0.088$, $n = 20$, where y is muscle wt. (kg), x is gastrocnemius wt. (g); Protein: $\ln(y) = 0.946 \ln(x) - 2.918$, $r^2 = 0.968$, $SEE = 0.176$, $n = 18$, where y is protein wt. (kg), x is gastrocnemius wt. (g).

(b) The weight of the femur as a predictor of bone and ash weight in muskoxen. Equations: Bone: $\ln(y) = 1.141 \ln(x) - 4.266$, $r^2 = 0.988$, $SEE = 0.090$, $n = 21$, where y is bone wt. (kg), x is femur wt. (g); Ash: $\ln(y) = 1.348 \ln(x) - 6.922$, $r^2 = 0.971$, $SEE = 0.175$, $n = 19$, where y is ash wt. (kg), x is femur wt. (g).

(c) The weight of kidney fat as a predictor of dissectible and total fat in muskoxen. Equations: Dissectible fat: $y = 0.102x - 0.0000667x^2 - 2.83$, $r^2 = 0.974$, $SEE = 1.607$, $n = 22$, where y is dissectible fat wt. (kg), x is kidney fat wt. (g); Total fat: $y = 0.129x - 0.0000931x^2 - 3.23$, $r^2 = 0.961$, $SEE = 2.526$, $n = 20$, where y is total fat wt. (kg), x is kidney fat wt. (g).

Table 4.2. Regression equations to predict muscle and protein weight (kg) in the ingesta-free body of muskoxen.

IFBW = ingesta-free body weight; SEE = standard error of estimate; r^2/R^2 = adjusted coefficient of determination; CV = coefficient of variation; * = a non-significant regression ($P > 0.01$);

† = an approximation - see text.

Independent variable(s)	Equation	All muskoxen				Females with IFBW \geq 90 kg			
		n	SEE	r^2/R^2	CV	n	SEE	r^2/R^2	CV
Dependent variable: Muscle weight									
Gastrocnemius (g)	$\ln(y) = 1.114 \ln(x) - 2.864$	20	0.088	0.994	2.8	9	0.051	0.710	1.3
Gluteobiceps (g)	$\ln(y) = 0.974 \ln(x) - 3.148$	20	0.057	0.997	1.9	9	0.035	0.867	0.9
Semimembranosus (g)	$\ln(y) = 0.966 \ln(x) - 2.909$	19	0.095	0.992	2.8	9	0.037	0.845	0.9
Semitendinosus (g)	$\ln(y) = 0.962 \ln(x) - 1.96$	19	0.074	0.995	2.2	9	0.050	0.719	1.2
Extensor carpi radialis (g)	$\ln(y) = 1.106 \ln(x) - 2.032$	20	0.077	0.995	2.5	11	0.069	0.530	1.7
Gastrocnemius (x_1 , g) and Extensor (x_2 , g)	$\ln(y) = 0.573 \ln(x_1) + 0.539 \ln(x_2) - 2.457$	18	0.051	0.998	1.6	9	0.052	0.697	1.3
IFBW (kg)	$y = 0.632(x) - 0.001(x^2) - 3.182$	22	3.270	0.978	9.3	11	0.060	0.643	1.5
Carcass (kg)	$y = 0.981(x) - 0.003(x^2) - 2.507$	22	2.396	0.988	6.8	11	0.054	0.718	1.4
Carcass (x_1 , kg), gastroc. (x_2 , g), femur (x_3 , g)	$\ln(y) = 0.393 \ln(x_1) + 0.407 \ln(x_2) + 0.388 \ln(x_3) - 2.685$	20	0.033	0.999	1.0	9	0.018	0.966	0.4
Total body (kg)	$y = 0.391(x) - 0.0004(x^2) - 0.679$	22	2.781	0.984	7.9	11	0.066	0.575	1.6

Table 4.2 continued

Dependent variable: Protein weight									
Gastrocnemius (g)	$\ln(y) = 0.946 \ln(x) - 2.918$	18	0.176	0.968	8.4	8	0.103	0.448*	3.5
Gluteobiceps (g)	$\ln(y) = 0.827 \ln(x) - 3.161$	18	0.152	0.976	7.0	8	0.066	0.771	2.2
Semimembranosus (g)	$\ln(y) = 0.82 \ln(x) - 2.967$	17	0.165	0.971	7.9	8	0.079	0.670	2.7
Semitendinosus (g)	$\ln(y) = 0.823 \ln(x) - 2.188$	17	0.133	0.981	6.1	8	0.060	0.811	2.0
Extensor carpi radialis (g)	$\ln(y) = 0.947 \ln(x) - 2.235$	18	0.143	0.980	6.5	8	0.063	0.789	2.1
IFBW (kg)	$\ln(y) = 0.955 \ln(x) - 1.64$	20	0.084	0.992	2.5	9	0.069	0.742	2.3
IFBW (x_1 , kg). femur wt (x_2 , g)	$\ln(y) = 0.699 \ln(x_1) + 0.356 \ln(x_2) - 2.679$	18	0.071	0.995	1.8	9	0.041	0.908	1.4
Carcass (kg)	$\ln(y) = 0.866 \ln(x) - 0.878$	20	0.119	0.985	5.5	9	0.108	0.368*	3.7
Total body (kg)	$\ln(y) = 0.856 \ln(x) - 1.467$	20	0.122	0.984	5.7	9	0.099	0.476*	3.4
Hybrid method (see text)		18	0.145†	-	1.7†	8	0.308†	-	1.6†

regressions based on gastrocnemius weight, total body weight and carcass weight were not significant ($P > 0.01$).

Bone weight could be estimated well from the weights of any of the six individual limb bones (r^2 of 0.974-0.992 and CV of 3.4-5.5) over both weight ranges, with the poorest fit for equations based on the metapodials (Table 4.3; Fig. 4.12b). Growth coefficients for the six bones were all less than 1.0 ($P < 0.05$), and lowest in the most distal bones: femur 0.867, tibia 0.828, metatarsus 0.657, humerus 0.955, radius-ulna 0.846, and metacarpus 0.670. Although all three measures of body weight were strongly correlated with bone weight over the full weight range (r^2 of 0.978-0.984), they were of little value when the analysis was limited to large cows (r^2 of 0.01-0.10). Multiple regressions based on a measure of body weight and femur weight held well over both weight ranges, but their fit was about equal to that based on femur weight alone.

Ash weight was best predicted from IFBW or by the hybrid method (CV of 7.4-8.2 %). Individual bone weights, carcass weight and total body weight could all be used to estimate ash weight, but the CV's were substantial (13-28 %). Despite the poor r^2 values for these equations when limited to large females, the CV's were relatively small because of the limited range in bone weights.

Both dissectible fat weight and total fat weight were less predictable from indices and weight measurements than other components. As a single measurement, kidney fat weight was most strongly related to dissectible and total fat weights (r^2 of 0.961-0.974 and CV of 16.3-20.1) and these relationships held over both weight ranges (Table 4.4; Fig. 4.12c). Although both fat weights were strongly correlated with DBF and the three measures of body weight, the CV's associated with these equations ranged from 20 to 41 %, and the relationships between body weight measures and dissectible fat weight were not significant ($P > 0.01$) when calculated for large females. Multiple regressions which included a measure of body weight, kidney fat weight and up to three other index measurements permitted accurate estimation of dissectible and total fat weight over both size ranges, with CV's of 8-12 %. Most of these equations gave predicted fat weights of just below 0 in young lean calves with < 0.5 kg fat, and tended to over-estimate fat weight of the two fetuses because of their large complement of kidney fat.

As there are no comparable values available for muskoxen, detailed data for each of these animals are listed in Appendix 7.1. For technical reasons, chemical data for two cows (#s 534 and 865) were incomplete.

Table 4.3. Regression equations to predict bone and ash weight (kg) in the ingesta-free body of muskoxen.

IFBW = ingesta-free body weight; SEE = standard error of estimate; r^2/R^2 = adjusted coefficient of determination;CV = coefficient of variation; * = a non-significant regression ($P > 0.01$); † = an approximation (see text).

Independent variable(s)	Equation	All muskoxen				Females with IFBW \geq 90 kg			
		n	SEE	r^2/R^2	CV	n	SEE	r^2/R^2	CV
Dependent variable: Bone weight									
Femur (g)	$\ln(y) = 1.141 \ln(x) - 4.266$	21	0.090	0.988	3.8	10	0.058	0.683	1.9
Tibia (g)	$\ln(y) = 1.195 \ln(x) - 4.214$	20	0.086	0.990	3.8	9	0.055	0.714	1.8
Humerus (g)	$\ln(y) = 1.038 \ln(x) - 3.757$	22	0.076	0.992	3.4	11	0.059	0.669	2.0
Radius-ulna (g)	$\ln(y) = 1.173 \ln(x) - 4.165$	22	0.074	0.992	3.5	11	0.066	0.589	2.2
Metatarsus (g)	$\ln(y) = 1.484 \ln(x) - 4.599$	21	0.134	0.974	5.5	10	0.045	0.801	1.5
Metacarpus (g)	$\ln(y) = 1.463 \ln(x) - 4.628$	22	0.118	0.979	5.3	11	0.048	0.786	1.6
IFBW (kg)	$\ln(y) = 0.834 \ln(x) - 0.985$	22	0.122	0.978	5.1	11	0.097	0.125*	3.2
Femur (x_1 , g) and IFBW(x_2 , kg)	$\ln(y) = 0.782 \ln(x_1) + 0.268 \ln(x_2) - 3.254$	20	0.080	0.991	3.4	10	0.061	0.648	2.0
Carcass (kg)	$\ln(y) = 0.765 \ln(x) - 0.345$	22	0.106	0.983	4.8	11	0.103	0.010*	3.4
Femur (x_1 , g) and Carcass (x_2 , kg)	$\ln(y) = 0.700 \ln(x_1) + 0.299 \ln(x_2) - 2.762$	21	0.079	0.991	2.6	10	0.057	0.690	1.9
Total body (kg)	$\ln(y) = 0.754 \ln(x) - 0.864$	22	0.095	0.987	4.0	11	0.102	0.018*	3.4
Femur (x_1 , g) and Total body (x_2 , kg)	$\ln(y) = 0.635 \ln(x_1) + 0.338 \ln(x_2) - 2.771$	21	0.077	0.992	2.6	10	0.060	0.655	2.0

Table 4.3 continued

Dependent variable: Ash weight									
Femur (g)	$\ln(y) = 1.348 \ln(x) - 6.922$	19	0.175	0.971	21.0	8	0.114	0.364*	6.5
Tibia (g)	$\ln(y) = 1.419 \ln(x) - 6.89$	19	0.184	0.968	21.0	8	0.127	0.217*	7.3
Humerus (g)	$\ln(y) = 1.240 \ln(x) - 6.387$	20	0.140	0.980	16.3	8	0.115	0.465*	6.6
Humerus (x_1 , g), femur (x_2 , g)	$\ln(y) = 3.188 \ln(x_1) - 2.121$ $\ln(x_2) - 5.516$	18	0.128	0.984	15.2	8	0.125	0.240*	7.1
Radius-ulna (g)	$\ln(y) = 1.391 \ln(x) - 6.827$	20	0.157	0.976	18.6	9	0.127	0.343*	7.3
Metatarsus (g)	$\ln(y) = 1.738 \ln(x) - 7.251$	19	0.237	0.946	28.0	8	0.136	0.249*	7.8
Metacarpus (g)	$\ln(y) = 1.714 \ln(x) - 7.285$	20	0.226	0.950	26.8	9	0.118	0.437*	6.7
IFBW	$\ln(y) = 1.001 \ln(x) - 3.111$	20	0.072	0.995	8.2	9	0.093	0.652	5.3
Carcass (kg)	$\ln(y) = 0.907 \ln(x) - 2.307$	20	0.125	0.984	14.6	9	0.125	0.363*	7.1
Total body (kg)	$\ln(y) = 0.898 \ln(x) - 2.930$	20	0.115	0.987	13.4	9	0.126	0.360*	7.2
Hybrid method (see text)		20	0.174†	-	7.4†	8	0.334†	-	5.8†

Table 4.4. Regression equations to predict dissectible and total fat weight (kg) in the ingesta-free body of muskoxen. DBF = depth of back fat; IFBW = ingesta-free body weight; SEE = standard error of estimate; r^2/R^2 = adjusted coefficient of determination; CV = coefficient of variation; * = a non-significant regression ($P > 0.01$); † = an approximation (see text).

Independent variable(s)	Equation	All muskoxen				Females with IFBW \geq 90 kg			
		n	SEE	r^2/R^2	CV	n	SEE	r^2/R^2	CV
Dependent variable: Dissectible fat									
DBF (cm)	$y = 6.379 x + 0.289$	21	3.740	0.861	37.9	11	4.328	0.751	24.6
Kidney fat wt (g)	$y = 0.102 x - 0.0000674 x^2 - 2.83$	22	1.607	0.974	16.3	11	1.236	0.980	7.0
IFBW (kg)	$y = -0.053 x + 0.001 x^2 + 1.194$	20	4.321	0.815	43.8	11	6.417	0.453*	36.5
Carcass (kg)	$y = -0.069 x + 0.003 x^2 + 1.011$	22	3.774	0.859	38.3	11	5.601	0.583*	31.9
Total body (kg)	$y = -0.053 x + 0.001 x^2 + 1.355$	20	3.593	0.830	36.5	11	5.827	0.549*	33.1
Kidney fat (x_1 , g), IFBW (x_2 , kg)	$y = 0.052 x_1 + 0.054 x_2 - 2.466$	20	1.406	0.980	14.3	11	1.739	0.960	9.9
Kidney fat (x_1 , g), IFBW (x_2 , kg), DBF (x_3 , cm)	$y = 0.044 x_1 + 0.047 x_2 + 1.161 x_3 - 2.329$	20	1.251	0.984	12.7	11	1.302	0.977	7.4
Kidney fat (x_1 , g), Carcass (x_2 , kg)	$y = 0.052 x_1 + 0.082 x_2 - 2.372$	20	1.432	0.979	14.5	11	1.733	0.960	9.9
Kidney fat (x_1 , g), Carcass (x_2 , kg), DBF (x_3 , cm)	$y = 0.044 x_1 + 0.072 x_2 + 1.150 x_3 - 2.239$	20	1.287	0.983	13.1	11	1.319	0.977	7.5
Kidney fat (x_1 , g), Carcass (x_2 , kg), DBF (x_3 , cm), Femur lt (x_4 , cm)	$y = 0.034 x_1 + 0.170 x_2 + 1.337 x_3 - 0.417 x_4 + 4.084$	20	1.111	0.988	11.3	11	1.25	0.979	7.1
DBF (x_1 , cm), Carcass (x_2 , kg), Gastroc. (x_3 , g)	$y = 3.17 x_1 + 0.495 x_2 - 0.066 x_3 + 0.228$	20	2.008	0.959	20.4	9	2.594	0.915	14.8

Table 4.4 continued

DBF (x ₁ , cm). Total body (x ₂ , kg)	$y = 4.583 x_1 + 0.046 x_2 - 2.030$	22	3.27	0.894	33.2	11	3.587	0.829	20.4
Kidney fat (x ₁ , g). Total body (x ₂ , kg)	$y = 0.053 x_1 + 0.039 x_2 - 2.439$	20	1.377	0.981	14.0	11	1.723	0.961	9.8
Kidney fat (x ₁ , g). Total body (x ₂ , kg) Femur lt (x ₃ , cm)	$y = 0.045 x_1 + 0.090 x_2 - 0.474 x_3 + 4.673$	20	1.188	0.986	12.0	10	1.564	0.968	8.9
Dependent variable: total fat									
DBF (cm)	$y = 7.626 x + 1.042$	20	5.19	0.835	41.5	9	6.189	0.583	25.5
Kidney fat wt (g)	$y = 0.129 x - 0.0000931 x^2 - 3.323$	20	2.53	0.961	20.2	9	2.2	0.947	9.1
IFBW (kg)	$\ln(y) = 1.787 \ln(x) - 5.535$	20	0.318	0.969	20.6	9	0.239	0.698	7.5
Carcass (kg)	$y = -0.002 x + 0.003 x^2 + 0.433$	20	3.626	0.919	29.9	9	5.858	0.626*	24.1
Total body (kg)	$y = -0.053 x + 0.001 x^2 + 1.355$	20	3.593	0.921	28.7	9	5.341	0.689*	22.0
Kidney fat (x ₁ , g). IFBW (x ₂ , kg)	$y = 0.051 x_1 + 0.107 x_2 - 3.418$	18	1.553	0.986	12.4	9	2.011	0.956	8.3
Kidney fat (x ₁ , g). IFBW (x ₂ , kg). Femur wt (x ₃ , g)	$y = 0.040 x_1 + 0.205 x_2 - 0.019 x_3 - 1.615$	18	1.337	0.989	10.7	8	2.329	0.934	9.6
Kidney fat (x ₁ , g). IFBW (x ₂ , kg). Femur wt (x ₃ , g). Gastroc. (x ₄ , g)	$y = 0.036 x_1 + 0.187 x_2 - 0.043 x_3 + 0.035 x_4 - 0.498$	18	1.003	0.994	8.0	7	0.126	0.999	0.5
Kidney fat (x ₁ , g). Carcass (x ₂ , kg)	$y = 0.052 x_1 + 0.155 x_2 - 3.182$	18	1.685	0.983	13.5	9	1.994	0.957	8.2
Kidney fat (x ₁ , g). Carcass (x ₂ , kg). Femur lt (x ₃ , cm)	$y = 0.041 x_1 + 0.288 x_2 - 0.548 x_3 + 5.094$	18	1.428	0.988	11.4	8	2.410	0.930	9.9
Kidney fat (x ₁ , g). Carcass (x ₂ , kg). Femur lt (x ₃ , cm). DBF (x ₄ , cm)	$y = 0.030 x_1 + 0.298 x_2 - 0.637 x_3 + 1.289 x_4 + 6.577$	18	1.216	0.991	9.7	8	2.739	0.909*	11.3

Table 4.4 continued

Kidney fat (x_1 , g), Carcass (x_2 , kg), Femur lt (x_3 , cm), DBF (x_4 , cm), Gastroc. (x_5 , g)	$y = 0.034 x_1 + 0.179 x_2$ $- 1.043 x_3 + 1.142 x_4$ $+ 0.035 x_5 + 11.398$	18	1.031	0.994	8.2	7	1.212	0.985*	5.0
DBF (x_1 , cm), Carcass (x_2 , kg), Femur wt (x_3 , g)	$y = 2.257 x_1 + 0.540 x_2$ $- 0.048 x_3 + 1.849$	18	1.931	0.978	15.4	8	4.974	0.700*	20.5
Kidney fat (x_1 , g), total body (x_2 , kg)	$y = 0.053 x_1 + 0.074 x_2$ $- 3.284$	18	1.627	0.984	13.0	9	1.440	0.977	5.9
Kidney fat (x_1 , g), Total body (x_2 , kg), Femur lt (x_3 , cm)	$y = 0.039 x_1 + 0.161 x_2$ $- 0.757 x_3 + 8.033$	18	1.100	0.993	8.8	8	1.328	0.979	5.5

4.5 Discussion

4.5.1 Body composition in muskoxen compared with other mammals

In general, the body composition of muskoxen was comparable to that reported in other mammals (Reid *et al.* 1968; Clawson *et al.* 1991) with respect to changes in fat, protein, water and ash during growth, and was particularly similar to the patterns noted in cattle (Berg and Butterfield 1976) and sheep (Russel *et al.* 1971; Agricultural Research Council 1980). However, muskoxen had a relatively high weight of ingesta, a large proportion of protein in the pelage, and a large proportion of bone in the head.

The large weight of ingesta in older muskoxen is consistent with their designation as "grazers" (Hofmann 1989); ingesta may account for more than 30 % of the body weight of grazers accustomed to low-quality forages (Mould *et al.* 1982; Weyreter *et al.* 1987). Staal and Thing (1991) reported a mean ingesta weight of 19.9 % in 8 muskoxen from Greenland in winter, somewhat lower than the 26.3 % we found in 16 muskoxen. This large and variable gut fill makes body weight a relatively poor estimator of body composition, particularly fatness, in muskoxen.

The highly insulative coat of muskoxen represents a considerable investment of protein, as in sheep (Agricultural Research Council 1980). On average, hair was 4.5 % of IFBW in adult female muskoxen, or 4.0 % if the coat, normally quite dry, contained 10 % moisture. A comparable value for the winter coat of white-tailed deer, calculated from Robbins *et al.* (1974), was 1.4 % of IFBW, about one-third the value in muskoxen. White *et al.* (1991) estimated that adult female muskoxen grow and shed on average 2.61 kg of qiviut, or wool, annually. If the same was true for the muskox cows in this study, then the coarse outer guard hairs and undercoat have approximately equal weight.

The mean ash content of muskox IFBW among adults (4.7 ± 0.13 %) was comparable to that of cattle (3.0-6.1 %) and sheep (1.7-5.8 %; Reid *et al.* 1968). Using only muscle and bone weight from the carcass, muscle:bone ratio was $3.75:1 \pm 0.15$ among six large muskox cows, compared with ratios of 4.1 to 5.1:1 in mature cattle (Berg and Butterfield 1976) and 3.6 to 5.4:1 in various breeds of sheep (Butterfield 1988). Our impression that adult muskox heads are particularly heavy was consistent with the proportion of the total bone found there (21 % compared with 17.6 % in sheep; Wallace 1948). Muskoxen of both sexes use their heavy heads in agonistic interactions with conspecifics and predators (Gray 1987).

The strong linear or near-linear relationships between anatomical and chemical components of the body in muskoxen are consistent with the findings of Murray *et al.* (1975) in cattle and Russel *et al.* (1968) in sheep. Berg and Butterfield (1976) noted that approximately 50% of the protein of the IFBW of cattle was in the skeletal

musculature, very similar to the proportion we found in muskoxen. In Svalbard reindeer, the comparable figure is 65 % (calculated from Reimers *et al.* 1982), suggesting that a greater proportion of the protein in the IFBW is contained in the viscera of bovid ruminants than in cervids.

4.5.2 Fat content and distribution in muskoxen compared with other ruminants

Both the degree of fattening and the distribution of fat in muskoxen, from fetus to full-grown female, were similar to those reported in domestic sheep and cattle. The fattening we found in female muskoxen exceeded that in any wild ruminant except for high-arctic Svalbard reindeer (Reimers *et al.* 1982; Tyler 1987) although it fell short of the extremes noted in domestic livestock (Reid *et al.* 1968), hibernating mammals, carnivores, or some marine mammals (Pond and Mattacks 1985).

The mean dissectible fat content of the three fattest muskoxen in this study (15.3 % of whole body weight) was similar to that of 13 mature Svalbard reindeer females in the fall (16.8 % of whole body weight; Tyler 1987) although even fatter Svalbard reindeer (28.6 % fat) have been reported (Reimers *et al.* 1982). However, muskoxen may be able to fatten more than reported here. The mean DBF and kidney fat weight of five non-lactating muskox cows examined in September and November 1990 was 4.8 ± 0.1 cm and 577 ± 19 g, respectively (J. Z. Adamczewski, unpubl. data), compared with 4.3 ± 0.2 cm and 441 ± 67 g for the three fattest females in this study. Captive muskox cows have exceeded 250 kg in body weight in Alaska (White *et al.* 1991) and 270 kg in Saskatchewan (Adamczewski *et al.* 1994a) and may be fatter than any free-ranging muskoxen.

In muskoxen, the intermuscular fat depot was the largest with the subcutaneous slightly smaller and the abdominal fat also substantial. This is consistent with the pattern in cattle (Johnson *et al.* 1972), although there are some differences in fat distribution among breeds (Berg and Butterfield 1976). Fattening in sheep follows a similar pattern to muskoxen except that the subcutaneous depot tends to outweigh the intermuscular at an early stage of fattening (Russel *et al.* 1971; Kempster 1980). The allometric growth coefficients for fat depots in muskoxen were consistent with those of cattle: highest for late-maturing subcutaneous fat, intermediate for internally deposited fat, and lowest for intermuscular fat (Jones *et al.* 1980; Kempster 1980).

Intramuscular fat deposition in muskoxen increased with fatness in the seven animals examined, a pattern consistent with marbling and intramuscular fattening in cattle (Johnson *et al.* 1973) and sheep (Lohse *et al.* 1973). This fat accounted for the majority of the 20 % difference between weights of dissectible fat and total fat in the

muskoxen, while the remainder of the difference was likely fat within the marrow (5-8 % of total fat in sheep, Russel *et al.* 1971). Dissectible fat is strongly correlated with total fat in cattle (Berg and Butterfield 1976) and in Svalbard reindeer (Reimers and Ringberg 1983), although the relationship in the latter tended to be curvilinear, with dissectible fat weight and total fat weight converging in very fat reindeer. The lack of this convergence in muskoxen may reflect the increase in intramuscular fat deposition with advanced fatness, which is not typical of Svalbard reindeer (Reimers *et al.* 1982) or caribou (Adamczewski *et al.* 1987b).

The fat content of the two muskox fetuses (4.2 and 4.6 % of IFBW) was similar to that of newborn cattle (4.0-4.6 % of IFBW; Agricultural Research Council 1980), slightly higher than that of newborn sheep (3.0-3.5 % of IFBW; Agricultural Research Council 1980), and about twice the fat content of newborn red deer (*Cervus elaphus*, Adam *et al.* 1988) and white-tailed deer (Robbins and Moen 1975). As these two muskox fetuses were still an estimated three weeks before term, the fat content of newborn muskox calves may be slightly higher. The appearance and distribution of the fetal fat was consistent with the abundant brown fat described by Blix *et al.* (1984) in newborn muskoxen. Muskox calves apparently catabolize much of this fat in their first postnatal days, as the fat content of the four very young calves tended to be lower than that of the fetuses, and the lipids from the young calves contained less triglyceride and more free fatty acids than the fetal lipids. Johnson *et al.* (1972) noted a similar pattern in fat content of cattle fetuses and young calves.

The large fat reserves of female muskoxen provide a buffer against nutritional shortfalls during winter, but their primary purpose may be to support late-winter lactation. Given the slow metabolism of muskoxen (Nilssen *et al.* 1994), fat reserves might supply a greater proportion of over-winter energy needs than in Svalbard reindeer (up to 25 %; Tyler 1987). However, pregnant muskox cows lose fat relatively slowly during the initial 6-7 months of winter, but at a much increased rate after parturition (White *et al.* 1989; Adamczewski *et al.* 1992). Tyler (1987) suggested that the primary role of large fat reserves in Svalbard reindeer females, as in many mammals (Pond 1984), was to support reproductive costs. Unlike reindeer, which usually calve just as new plant growth begins, muskoxen calve earlier and must support 6-8 weeks of lactation without access to nutritious spring forage (Thing *et al.* 1987; Adamczewski *et al.* 1992). Adequate maternal fat reserves in this late winter period may be essential for early calf growth and help enable muskox calves to digest spring and summer forage as fully functional ruminants.

Although solvent-extracted lipids are often regarded as the equivalent of triglycerides or fat available as energy reserves, our results suggest that in muskoxen in good condition, equating solvent-extracted fat with triglyceride involves a 2-4 % over-estimation. In lean animals, however, the proportion of non-glycerides may exceed 25 % and a greater proportional error may arise.

4.5.3 Prediction of body composition in muskoxen

Many methods of estimating body composition, particularly fat content, have been proposed for ungulates (e.g. see Franzmann 1985; Price and White 1985; Huot 1988). Robbins (1983) noted that a useful measure of condition should have a strong linear or near-linear relationship to the component it estimates, over its full range. Our results indicate that body composition of muskoxen can be estimated accurately in the field, but that the variance attached to these estimates remains too large to distinguish between individuals of similar condition and that these methods are best applied to comparisons of groups. Ingesta-free body weight was particularly useful in estimating body composition but this measurement is tedious and labour-intensive. Carcass weight, kidney fat weight, DBF, the weight of an indicator muscle, and the weight and length of one of the limb bones are measurements which can be collected relatively easily in the field and will provide good estimates of body composition in muskoxen.

The strong relationships between body component weights and body weight in growing muskoxen have been demonstrated in other species (Butterfield 1966; Reid *et al.* 1968; Robbins *et al.* 1974; Berg and Butterfield 1976) but some of these relationships were much weaker in sub-adult or adult females. Fat weight was particularly difficult to estimate from any measure of body weight in muskoxen, and bone weight was poorly related to all measures of body weight in 3+ females. These findings echo the observations of Reid *et al.* (1968) who noted that prolonged submaintenance feeding followed by refeeding "deranged" the nearly fixed relationship between body weight and chemical component weights in mammals. The older muskoxen we studied likely had repeated, individually variable histories of weight loss and gain and this variability affected the predictability of all components from weight.

Ingesta-free body weight was much better related than whole body weight to body composition in muskoxen, as has been generally recognized in ruminants (O'Donovan 1984). Although whole body weight was about as well related to composition as carcass weight in the 22 animals studied, we suggest carcass weight as preferable because it was unaffected by the substantial variation in gut fill associated

with season and reproductive status that is apparent in the larger data set from Victoria Island muskoxen (see Chapter 5).

Weights of dissectible fat and total fat proved more difficult to estimate accurately than other components in muskoxen, as in other ruminants (Berg and Butterfield 1976; Price and White 1985; Huot 1988) and this was particularly true of adults. Fat weight was best predicted from multiple regressions which were based on measures of body weight, internal fat (kidney fat) and carcass fat (DBF), and one or two indices of lean body weight (femur weight or length, and gastrocnemius weight) - in effect, estimating fatness from fat measurements, while taking into account the animal's size and lean body weight. A multiple regression based on kidney fat weight and DBF was a good predictor of fatness in caribou (Adamczewski *et al.* 1987b). The equations for muskoxen were least accurate at the lower end of their range, in very lean newborn calves and in fetuses, both of which have minimal fat reserves. We suspect that body fat could be estimated accurately from weight in these animals, but we had relatively few data from calves on which to base such equations.

Kidney fat weight was better correlated with fat weight in muskoxen than any other measurement, and has been used as a condition index in many species (Huot 1988), although sometimes with considerable variance around the regression line (Finger *et al.* 1981). We suspect that the strength of the relationship between kidney fat weight and fat weight in this study stemmed in part from the consistent manner in which one of us (JZA) identified the kidney fat in the study animals. We obtained the most consistent results when the kidneys and kidney fat were removed from the carcass after the fat had cooled and hardened, and the kidneys with fat were pulled gently away from surrounding fat. Although DBF was a poorer measure of fatness than kidney fat weight, it was linearly correlated with fat weight and has been widely used in domestic animals (Price and White 1985) and Svalbard reindeer (Tyler 1987).

Protein and ash weight were best estimated from IFBW or by the hybrid method. The latter is analagous to the estimation of body composition by body water dilution (Sheng and Huggins 1979), as both assume a constant fat-free composition of protein, ash and water. The equation predicting fatness from % water in muskoxen was very similar to the one given by Reid *et al.* (1968) for cattle, but estimation of fatness by water dilution in muskoxen may be subject to considerable error due to large and variable gut fill. If IFBW cannot be measured, estimates of protein and ash weight can be made from carcass weight or from the weights of indicator muscles and bones, but the variance attached to these estimates does not permit distinction between individual muskoxen of similar size and condition.

Although protein and ash weight were best predicted from IFBW, weights of dissectible bone and muscle were better estimated from individual bones and muscles, respectively, as has been shown in domestic species (Butterfield and May 1966; Berg and Butterfield 1976; Price and Berg 1976, 1977). The allometric growth coefficients for individual muscles and bones of muskoxen were consistent with those in cattle (Berg and Butterfield 1976). All five individual muscles served well as estimators of muscle weight and had near-linear relationships with muscle weight throughout their range. Similarly, the individual bones were good estimators of bone weight and the slightly poorer predictors were the more distal bones, which mature earlier and thus have the most curvilinear relationships with total bone weight, of the limb bones (Wallace 1948). The individual muscles did not predict protein weight as accurately as they did muscle weight, perhaps because about half the protein was in non-muscle tissues such as the viscera, which may respond differently to nutritional changes. Similarly, all tissues contain some ash, and this component does not depend entirely on bone weight; this may account for the lack of better agreement between the weights of individual bones and ash weight of the entire body.

Because we were interested in quantifying seasonal changes in body composition of muskoxen, accurate estimates of component weights were important. However, in many situations, comparisons are made among populations of ungulates or between years (Huot 1988) and there is less need for exact measures of body composition. For such applications, we suggest that carcass weight, kidney fat weight, DBF, and the weight of an indicator muscle and bone are satisfactory measurements of condition and size in muskoxen.

4.6 Conclusion

The patterns in anatomical and chemical body composition of muskoxen from Victoria Island were generally consistent with those of other ruminants, and were particularly similar to those of domestic sheep and cattle. Muskoxen differed from most ruminants in having a relatively high weight of ingesta, a substantial proportion of IFBW as hair, and a relatively large weight of bone in the head. Fat distribution and the extent of fattening in muskox fetuses, calves and cows were most comparable to those described in cattle. The substantial fat reserves accumulated by muskox cows in autumn may be essential for successful late-winter lactation, and may provide a substantial portion of over-winter energy requirements. Weights of protein and ash in muskoxen could be estimated readily from IFBW or as a proportion of IFBW following subtraction of estimated fat weight, although weights of muscle and bone were best

predicted from individual muscles or bones, respectively. As in other ruminants, weights of dissectible and total fat were less predictable in muskoxen, and could best be estimated from multiple regression equations which included kidney fat weight and/or DBF, a measure of body weight, and weights of indicator bones and muscles as independent variables.

CHAPTER 5. SEASONAL PATTERNS IN BODY COMPOSITION AND REPRODUCTION OF FEMALE MUSKOXEN FROM VICTORIA ISLAND, NORTHWEST TERRITORIES¹

5.1 Abstract

We analysed the body composition and reproductive status of 202 muskox cows (*Ovibos moschatus*) from Victoria Island, Northwest Territories, Canada, during 16 collections carried out by Inuit hunters in April, May, July, August, September and November from 1989 to 1993. During this time, the density of muskoxen on this arctic island increased slowly and they numbered about 45,000 in 1993. Hunting was limited and predation by wolves (*Canis lupus*) appeared low, and there was no evidence of winter mortality. Because between-year variation in body composition was small, we relied primarily on seasonal comparisons of 4-year-old or older (adult) females from all collections, using analysis of covariance (ANCOVA) where the main effects were month and reproductive status, and femur weight was the covariate used to correct for variation in body size.

Adult muskox cows were lightest and leanest in May, when the ingesta-free body weight (IFBW) and estimated fat weight of newly-lactating adult cows were 116 ± 2 kg (adjusted mean \pm SE) and 13.7 ± 0.8 kg, respectively, and those of nonlactating cows were a similar 112 ± 3 and 12.2 ± 1.6 kg. Thereafter, the IFBW and fat weight of lactating cows were virtually unchanged until July, increased rapidly during August, peaked in September at 166 ± 4 kg and 37.8 ± 1.8 kg, then decreased to 148 ± 2 and 31.2 ± 1.2 in November. In contrast, the IFBW and fat weight of nonlactating cows increased throughout summer, reached a higher peak in September (176 ± 7 and 45.1 ± 3.4 kg; $P < 0.01$) and changed little by November (164 ± 2.1 and 44.5 ± 1.1 kg). Seasonal changes in weight of protein, muscle, ash, and the dressed carcass paralleled changes in IFBW, although changes in fat were the largest and most affected by lactation. The weights of the liver, kidneys and ruminoreticulum tissue varied strongly with season, but the peak values in July or August coincided with the highest food quality, not the greatest body weight. The weight of ingesta, primarily rumen contents, increased during the year from April (20.9 % of body weight) to November (27.8 %). Seasonal patterns in 2- and 3-year-old females were generally similar to those in older cows, although the younger cows were lighter and leaner.

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Pregnancy rates in this population increased from 0 in females 1.5 years old in the autumn to 25 % in 2.5 year-olds and 62.5 % in cows at least 3.5 years old. Mammary gland weight in lactating females peaked in July and August, suggesting that peak milk production did not occur until 2-3 months after calving, and lactation was sometimes extended to a year or more. Lactation in November did not preclude pregnancy, but females which were pregnant at this time were fatter and heavier than nonpregnant cows.

The seasonal patterns in body composition of muskoxen were generally comparable to those of temperate and arctic cervids, although the relative weights of rumen contents were exceptionally large. The ability of muskoxen to maintain condition through the long arctic winter is unique and the extent of fattening is similar to that of Svalbard reindeer (*Rangifer tarandus platyrhynchus*). Results from this study and others suggest substantial flexibility in reproductive patterns of muskoxen, and a considerable sensitivity of pregnancy rates to nutritional influences.

5.2 Introduction

Muskoxen (*Ovibos moschatus*) are relatively large grazers (Staal and Thing 1991) living in an arctic environment characterized by short cool summers and cold winters which may last 9-10 months (Gunn 1982). Most tundra ranges are sparsely vegetated and during winter access to forage is often markedly restricted by snow and ice (Jingfors 1981; Gray 1987; Schaefer and Messier 1995). During severe winters, muskox numbers can be reduced by malnutrition (Miller *et al.* 1977; Gunn 1982) and muskox densities have fluctuated widely (Gunn 1990; Barr 1991; Forchhammer and Boertmann 1993). Like other arctic and temperate ruminants (Tyler and Blix 1990), muskoxen curtail their energy needs during winter by reducing their activity (Jingfors 1981) and requirements for forage and energy (White *et al.* 1984; Adamczewski *et al.* 1994a). Female muskoxen also gain large quantities of body protein and fat during summer and fall (Thing *et al.* 1987) and these stores may provide insurance both against dietary shortfalls and the energy costs of early lactation during late winter. As in other mammals, the size of these reserves may also influence fertility in female muskoxen.

Although fat can enable some mammals to fast for extended periods, wild cervids tend to have low levels of fat deposition (Pond and Mattacks 1985; Tyler and Blix 1990), their fasting metabolic rates are relatively high (Tyler and Blix 1994) and they remain active throughout winter. As a result, fat and protein catabolism supply at most 25 % of over-winter energy requirements even in exceptionally fat Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Tyler 1987) and usually much less.

However, fat content can reach at least 29 % of ingesta-free body weight (IFBW) in female muskoxen entering winter (Adamczewski *et al.* 1995) while the maintenance energy requirements of muskoxen on low planes of nutrition during winter are exceptionally low (White *et al.* 1991; Adamczewski *et al.* 1994a). Substantial fat stores might provide a larger proportion of over-winter energy requirements in muskoxen than in cervids.

Fat stored by female muskoxen during autumn may also be essential for successful late-winter lactation. The timing and extent of fat deposition differ profoundly among groups of mammals, but fat is commonly stored in advance of a major reproductive cost (Pond 1984). Muskoxen are unique in calving up to eight weeks before snowmelt (Gray 1987) and lactating females sustain these energetically costly weeks without access to nutritious spring forage (Thing *et al.* 1987). Adequate maternal fat stores may be critical during this period.

Among eutherian mammals, species with relatively low metabolic rates tend to have relatively low fecundity, low rates of population increase and dampened population fluctuations (McNab 1986 1987). Muskoxen, which have exceptionally low metabolic rates (Nilssen *et al.* 1994) and maintenance requirements relative to their size (White *et al.* 1984, Adamczewski *et al.* 1994a), might be expected to have relatively low pregnancy rates. It has also been shown that the nutrient demands of lactation may impair recovery of body reserves and fertility in sheep (Doney *et al.* 1981), red deer (*Cervus elaphus*; Albon *et al.* 1986) and other mammals (Frisch 1984). Failure to adequately restore body fat and protein depleted by lactation may in part explain the highly variable calf productivity observed in muskoxen. Although pregnancy rates among mature female muskoxen can exceed 90 % in populations growing exponentially (Latour 1987; Rowell 1989) and in well-fed captive animals (Rowell 1991), observations of low or non-existent calf productivity in free-ranging muskoxen are common (Tener 1965; Gunn 1982; Gray 1987; Reynolds 1989).

The profound physiological changes associated with season, lactation and altered nutrition in ruminants also affect the weights of organs such as the liver, kidneys and portions of the gastrointestinal tract (Mitchell *et al.* 1976; O'Donovan 1984; Adamczewski *et al.* 1987). Ruminants may have a highly variable quantity of ingesta depending on their condition, nutrient demands and diet quality (Agricultural Research Council 1980; O'Donovan 1984). Changes in these organs and tissues may provide insights into the adaptation of muskoxen to nutrient demands and diet quality throughout the year.

To evaluate the extent and reproductive significance of seasonal changes in body composition of female muskoxen, we carried out a field study from 1989 to 1993 on Victoria Island, Northwest Territories (NWT), Canada, in cooperation with Inuit hunters from Cambridge Bay, NWT. The results are evaluated in relation to the seasonal ecology and reproduction of this arctic species, and compared with patterns in other wild ruminants, particularly the caribou which often share range with muskoxen. A part of this material has been published in brief (Adamczewski *et al.* 1992).

5.3 Materials and methods

5.3.1 Study area and population

The numbers of muskoxen on Victoria Island, as in much of the Canadian arctic, have fluctuated widely in the past but increased from 1970 to 1989 (Gunn 1990). In 1993 the population had grown to an estimated 45,000 muskoxen (A. Gunn, unpubl.; Fig. 5.1). There were no reports of winter mortality among muskoxen on southern Victoria Island between 1989 and 1993, although the area was much used by Inuit hunters from Cambridge Bay (A. Wamikon and D. Kaomayok, pers. comm.). Predation by wolves (*Canis lupus*) was infrequent during the study period because they were intensively hunted and habitat suitable for denning is considered rare (D. Smith and D. Kaomayok, pers. comm.).

The tundra on southern Victoria Island is flat or rolling terrain, with large relatively barren rocky areas and eskers interspersed with wet or mesic meadows and myriad lakes and ponds. The vegetation of this area has been described in detail by Schaefer and Messier (1994). We did not encounter any of the relatively lush vegetation found on northern Banks Island or in other "muskox refugia" (Thomas *et al.* 1981), where anomalies of climate and topography permit relatively high forage and muskox densities. Most of the snow in the study region melted during June, plants flowered in July, and the first snow that remained all winter usually fell at the end of September. Mosquitoes (*Aedes* sp.) were abundant during July but had nearly disappeared by early August.

Muskoxen in the NWT are hunted under a conservative community-based quota system for subsistence, commercial meat production, and sport (Gunn *et al.* 1991). After investigation, the carcasses of study animals were taken to a small meat plant in Cambridge Bay as part of this community's commercial quota.

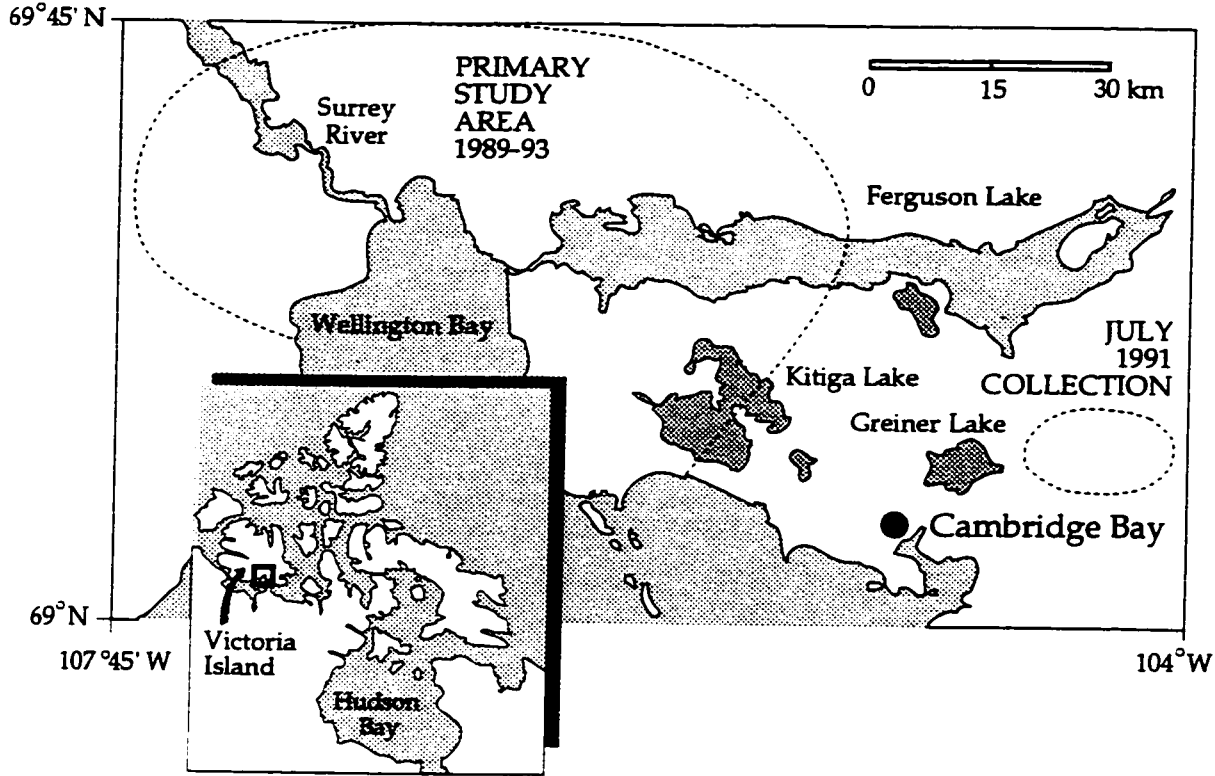


Fig. 5.1. The study area on southern Victoria Island, Northwest Territories, Canada.

5.3.2 Field collections and measurements

Muskoxen were hunted during 15 collections in April, May, July, August, September, and November from 1989 to 1993 (Table 5.1). In addition, we include data from a 16th hunt conducted in November 1992 for an associated study of digestive tract morphology. During winter (April, May, and November) hunters ranged widely by snowmobile and sled and brought shot muskoxen back to a field camp, but in summer and autumn (July, August and September) all field equipment was brought by all-terrain four-wheeled vehicle or boat to the site of hunts. The single July hunt was carried out at a site closer to Cambridge Bay to facilitate the rapid return of meat to the community (Fig. 5.1).

Approximately 20 muskoxen were shot during each hunt, with adult females (four years old or older) forming the primary group of interest; calves accompanying these females were also shot. Hunters searched for muskox herds using local knowledge and concentrated on smaller herds in May to avoid confusion among cow-calf pairs. To minimize orphaning, lactating females and their calves were usually shot first (from any one herd) between May and September. Because we could not pursue the remaining muskoxen as rapidly in summer as in winter, lactating cows are over-represented in these collections. Although the animals shot were not a random sample, the hunters consistently shot cows from the first herd that contained suitable animals, with the exceptions noted. On average 12-13 cows were taken from five herds (Table 5.1) during each collection and we believe these animals were representative of the population on southern Victoria Island.

Measures of weight, condition and reproductive status made during the 16 collections are listed in Table 5.2. For brevity, we use the term "rumen" in place of "ruminoreticulum" throughout this paper. Weights greater than 1 kg were measured to $\pm < 1\%$ using calibrated spring scales with capacities of 225 kg, 100 kg, and 15 kg. Smaller items were weighed to ± 1 g on a triple-beam balance. Fetal linear measurements and femur lengths were recorded using calipers or a steel tape measure, and back fat thickness (DBF) was measured near the base of the tail to ± 1 mm using a ruler. Muskoxen were aged up to 5 years or older using tooth wear and eruption patterns (Henrichsen and Grue 1980). All animals were also examined for the presence of lungworms, abomasal nematodes and gross lesions. These results will be reported elsewhere, but the muskoxen were largely devoid of parasites and in excellent health.

To provide an index of seasonal diet quality, we froze samples of rumen contents from 6 cows shot during each hunt in 1989 and 1990. These samples were freeze-dried and analysed for nitrogen by the Kjeldahl method and for acid-detergent

Table 5.1. Numbers of female muskoxen of different age classes shot during collections on Victoria Island, 1989-1993. Females of age class 2 were 1.9 - 2.7 years old (April-November), females of age class 3 were 2.9-3.7 years old, etc.

Dates	Age Class				No. herds sampled	Dates	Age Class				No. herds sampled
	2	3	4	5+			2	3	4	5+	
1989						1991					
April 4-8	2	3	4	4	5	April 5-8	2	1	6	11	10
May 19-22	-	3	-	8	5	May 17-20	1	1	1	10	7
Aug. 10-15	-	3	1	4	4	Aug. 12-15	1	1	2	4	3
Nov. 18-22	-	2	-	5	4	Nov. 7-11	2	3	6	9	6
1990						1992					
April 9-10	-	1	4	6	4	April 9-12	1	1	4	11	4
May 16-18	-	2	4	8	5	Nov. 6-9	-	-	3	7	4
July 10-15	-	1	5	3	6	1993					
Sept. 2-7	-	-	3	6	4	May 18-21	-	2	3	10	5
Nov. 9-12	2	7	4	4	4	Totals	11	31	50	110	80

Table 5.2. Measurements of weight, condition and reproductive status of muskoxen shot on Victoria Island, 1989-1993.

Measurement	Reference or Notes	Measurement	Reference or Notes
Body weight		Measures of condition or size	
Body weight	Whole body except blood lost at death	Depth of back fat (DBF)	Riney 1955; maximum depth invariably occurred at base of tail
Carcass weight	The skinned, eviscerated carcass; limbs disarticulated at carpal and tarsal joints and head removed just before the atlas vertebra	Kidney fat weight	Riney 1955; kidneys removed with fat from body after fat had hardened; fat extending beyond long axes of kidneys not included
Ingesta-free body weight (IFBW) ¹	Weight of the entire body minus weight of ingesta and of gravid uterus in pregnant females	Femur marrow fat content ⁴	Estimated as proportion (%) of marrow weight left after freeze-drying
Organ and Ingesta Weight		Gastrocnemius weight	Adamczewski <i>et al.</i> 1995; trimmed of fat & tendon
Liver	-	Femur weight	Weight of bone, trimmed of all fat, tendon and muscle
Kidneys (without fat)	-	Femur length	Maximal length
Heart ²	Weighed after removing pericardium and cutting great vessels just distal to atria	Reproductive data	
Spleen ²	-	Pregnancy and lactation status	Yes/No
Rumen ³	Weighed full and empty	Full uterus weight	Weighed after cutting just distal to cervix
Omasum ²	Weighed full and empty	Fetal weight	Weighed after being stripped of amniotic fluids (April only)
Abomasum ²	Weighed full and empty	Fetal sex	Male/Female
Small intestine ²	Weighed full and empty	Fetal crown-rump length	Pharr <i>et al.</i> 1994
Caecum ²	Weighed full and empty	Fetal transcranial diameter	Pharr <i>et al.</i> 1994
Large intestine ²	Weighed full and empty	Mammary gland weight	Weighed after rough trimming of extraneous fat

Table 5.2 continued

Measurement	Reference or Notes	Measurement	Reference or Notes
Estimated weight of body components ⁵			
Total fat	Adamczewski <i>et al.</i> 1995; chemically extracted fat, excluding phospholipid & cholesterol	Dissectible fat	Adamczewski <i>et al.</i> 1995; fat weighed after dissection of all body parts, not including marrow
Protein	Adamczewski <i>et al.</i> 1995; excludes hair, hooves & horns	Muscle	Adamczewski <i>et al.</i> 1995; all skeletal muscle of carcass & head
Ash	Adamczewski <i>et al.</i> 1995; measured in muffle furnace	Bone	Adamczewski <i>et al.</i> 1995; bones from carcass, head & lower limbs

¹ Measured in 1989; estimated in following years from carcass weight and liver/kidney weight (see text).

² Measured in 1989 only.

³ Measured in 1989 and 1990; rumen content weight estimated in following years by weighing full rumen, and subtracting empty rumen weight of similar-sized females at same time of year from 1989 and 1990.

⁴ Not measured in 1993

⁵ See text for details

fibre (ADF) by Van Soest's (1982) method. Corresponding values for April, May and November for the two years were very similar and were combined in an overall seasonal comparison.

5.3.3 Estimated body component weights

Ingesta-free body weight (IFBW) was measured only during 1989. Thereafter we calculated IFBW from carcass and kidney weight or from carcass and liver weight (if kidney weight was missing), using one of the following regression equations developed by stepwise regression where the partial F-to-enter was significant at $P < 0.05$ for all independent variables:

(1) $\ln(y) = 0.279 + 0.913 \ln(x_1) + 0.106 \ln(x_2)$, $r^2 = 0.994$, $s.e.(est.) = 0.050$, $n = 63$, where y is IFBW in kg, x_1 is carcass weight in kg, and x_2 is weight of both kidneys in g.

(2) $\ln(y) = 0.787 + 0.917 \ln(x_1) + 0.074 \ln(x_2)$, $r^2 = 0.994$, $s.e.(est.) = 0.052$, $n = 65$, where y is IFBW in kg, x_1 is carcass weight in kg, and x_2 is liver weight in kg.

Weights of chemical and dissectible body components were estimated from regression equations established from 22 representative muskoxen in which anatomical and chemical body composition were determined in addition to weight and condition index measurements (Adamczewski *et al.* 1995). Dissectible and total fat weights were estimated from DBF, kidney fat weight, carcass weight, gastrocnemius weight and the weight or length of the femur; muscle weight was estimated from the weight of the gastrocnemius and bone weight from the weight of the femur; protein weight (not including hair, horns, or hooves) and ash weight were estimated from IFBW.

5.3.4 Measures of reproductive status

Muskoxen were classed as lactating if milk could be expressed from the teats. Pregnancy was obvious in November or April but we were not equipped to identify early embryos in September due to their microscopic size. Measurements of the pregnant uterus are listed in Table 5.2. Crown-rump lengths of November embryos were used to estimate conception dates using the regression equation of Pharr *et al.* (1994). We were unable to use the fetal data from April in this manner because they were well outside the range of this regression. These conception dates were then used to project calving dates assuming that the duration of gestation was 235 days (Rowell *et al.* 1993). The ovaries of females shot during the breeding season (August and September) were fixed in 10 % neutral-buffered formalin and examined later at the

University of Saskatchewan by ultrasonography and sectioning. The presence and size of corpora lutea and follicles ≥ 4 mm in diameter were recorded.

5.3.5 Statistical analyses

Initial inspection and analyses of variance (ANOVA) indicated that between-year variation in weight and condition of 4-year-old and older (adult) muskox females, although often significant ($P < 0.01$), was relatively small compared with the effects of reproductive status and season. We also found that seasonal patterns in weight, pregnancy rate and condition of 4-year-old females were very similar to those of 5-year-old or older (5+) females, although 4-year-olds tended to be slightly smaller, lighter and leaner. Therefore, to assess the effects of season and reproductive status on muskox body composition, we combined data from all adult females from the 16 collections and used analysis of covariance (ANCOVA) in which femur weight was the covariate and the main effects were month and reproductive status (lactating vs. non-lactating or pregnant vs. non-pregnant). Femur weight was chosen as the covariate to correct for size differences because this bone has a near-linear relationship with total bone weight (Adamczewski *et al.* 1995). A unit of weight also seemed appropriate as a covariate for other measures of weight, and femur weight, but not femur length, differed statistically between 4-year-old and 5+ females. With the inclusion of the covariate for body size, no differences between 4-year-old and 5+ females were significant ($P > 0.10$). We present adjusted means for overall seasonal comparisons, except for organ and ingesta weights measured only in 1989, because the covariates were not significant in these cases. Individual pairs of adjusted means were compared using Bonferroni-adjusted *t*-tests. Estimated bone weight and the femur:length ratio of adult females were compared among months and between lactating and nonlactating females using 2-way ANOVA because bone weight estimates were based on femur weight, the covariate. Because breeding females could have one of four reproductive conditions in November and April: (1) L/P, (2) L/NP, (3) NL/P or (4) NL/NP (where L = Lactating, P = Pregnant and N is negative), we carried out separate analyses of weight and condition in adult females for these two months, using ANCOVA with main effects being pregnancy and lactation status.

Seasonal changes in weight and condition of 2- and 3-year-old females were compared using ANOVA and we presented unadjusted means for these groups because adjusted means (from ANCOVA) obscured the substantial growth occurring in these animals. The data for these younger females were fragmentary and did not permit detailed analysis.

Between-year differences in weight and condition of adult females were evaluated by analysing separately the four April collections, the four May collections, and the four November collections, using ANCOVA with reproductive status and year as main effects and femur weight as the covariate. We obtained monthly summaries of temperature and snow accumulation for 1989 to 1993, measured at the Cambridge Bay airport by the Canadian Atmospheric Environment Service, to compare with patterns in condition and pregnancy rate.

We evaluated relationships between maternal condition and fetal weight and length in pregnant cows in April using simple regression analysis, and compared the characteristics of fetuses from cows of different age-classes, and of male and female fetuses, using one-way ANOVA. Pregnancy rates from the eight individual collections in November and April were compared using Chi-square analysis; thereafter, the pregnancy rates recorded in November 1990 and April 1991 were compared using Bonferroni-adjusted Chi-square analysis. The summed pregnancy rates for November and April were compared using Fisher's exact test. Seasonal changes in rumen content ADF and nitrogen were analysed using one-way ANOVA followed by Scheffé's multiple-range comparison. Analyses were carried out using the paired programs Statview SE+ Graphics and Superanova (Abacus Concepts 1991, Calabasas, California.).

Owing to the scarcity of published data on muskox weight and condition, unadjusted seasonal means for weight and condition of 4-year-old and 5+ females are listed in Appendix 7.2.

5.3.6 Seasonal comparisons of lactating and nonlactating muskoxen

Most comparisons of seasonal patterns in adult females were made after separating the data into lactating and nonlactating groups because it was apparent that they differed consistently in weight and condition. In the absence of significant selective mortality from malnutrition, predation or hunting, we assumed that pregnant females in April and lactating females in May, July, August, September and November could be compared over time. The reproductive history of nonlactating females throughout the year is less clear: females which were not lactating in November or during the summer could have lost their calves, might not have been pregnant the previous winter, or could have aborted. Because a third or more of the adult cows were not pregnant in April, it seems likely that most of the nonlactating females shot between May and November had not calved that year.

The reproductive history of nonlactating females in April is also somewhat unclear because weaning times vary in muskoxen. Supplementally-fed captive females in Fairbanks, Alaska weaned their young between late December and February (White *et al.* 1989) while poorly fed females sometimes extended lactation to more than a year (R. G. White, pers. comm.). Females still lactating in early April on Victoria Island must have been lactating for nearly a year. However, females which were not lactating in April could have weaned their young earlier, lost their calves, or not been pregnant the previous season. Values from nonlactating cows in April are thus not directly comparable to data from cows which were nonlactating during the previous summer and autumn.

5.4 Results

5.4.1 Changes in body weight and condition of adult cows

From May to September, the mean body weight, IFBW and carcass weight of lactating cows increased ($P < 0.01$) by 29, 43 and 43 %, respectively, while the comparable increases among nonlactating cows were 31, 57, and 59 % ($P < 0.01$; Fig. 5.2). Overall, nonlactating females had greater IFBW and carcass weight ($P = 0.02$ and $P < 0.01$, respectively) than lactating females, although whole body weight was similar in the two groups. Lactating females gained no weight from May until July, but gained it rapidly from July until August and lost IFBW ($P < 0.01$) and carcass weight ($P = 0.02$) from September to November. In contrast, nonlactating cows gained weight earlier², reached greater weight in September, and had similar IFBW in September and November.

The major dissectible and chemical body components all fluctuated with season ($P < 0.05$; Fig. 5.2), but total and dissectible fat weights changed most and accounted for much of the overall weight change. The fat weight of lactating and nonlactating females was similar at the seasonal minimum in May (13.7 ± 0.8 kg and 12.2 ± 1.6 kg, respectively; adjusted mean \pm SE) but thereafter nonlactating females deposited fat sooner than lactating cows, which deposited little fat until August and did not catch up to nonlactating cows. Nonlactating females also maintained peak fatness from September, (45.1 ± 3.4 kg) to November, but the fat weight of lactating females declined ($P = 0.01$) over this period (37.8 ± 1.8 to 31.2 ± 1.2 kg) and was then lower ($P < 0.01$) than in nonlactating cows. The mean rate of fat loss in cows pregnant in April

² Of the two nonlactating females shot in August, one was fatter and heavier than all the lactating cows. The other was exceptionally lean, and we suspect she might have recently weaned a yearling. The mean values for nonlactating cows in August are likely inappropriately low due to the small sample size.

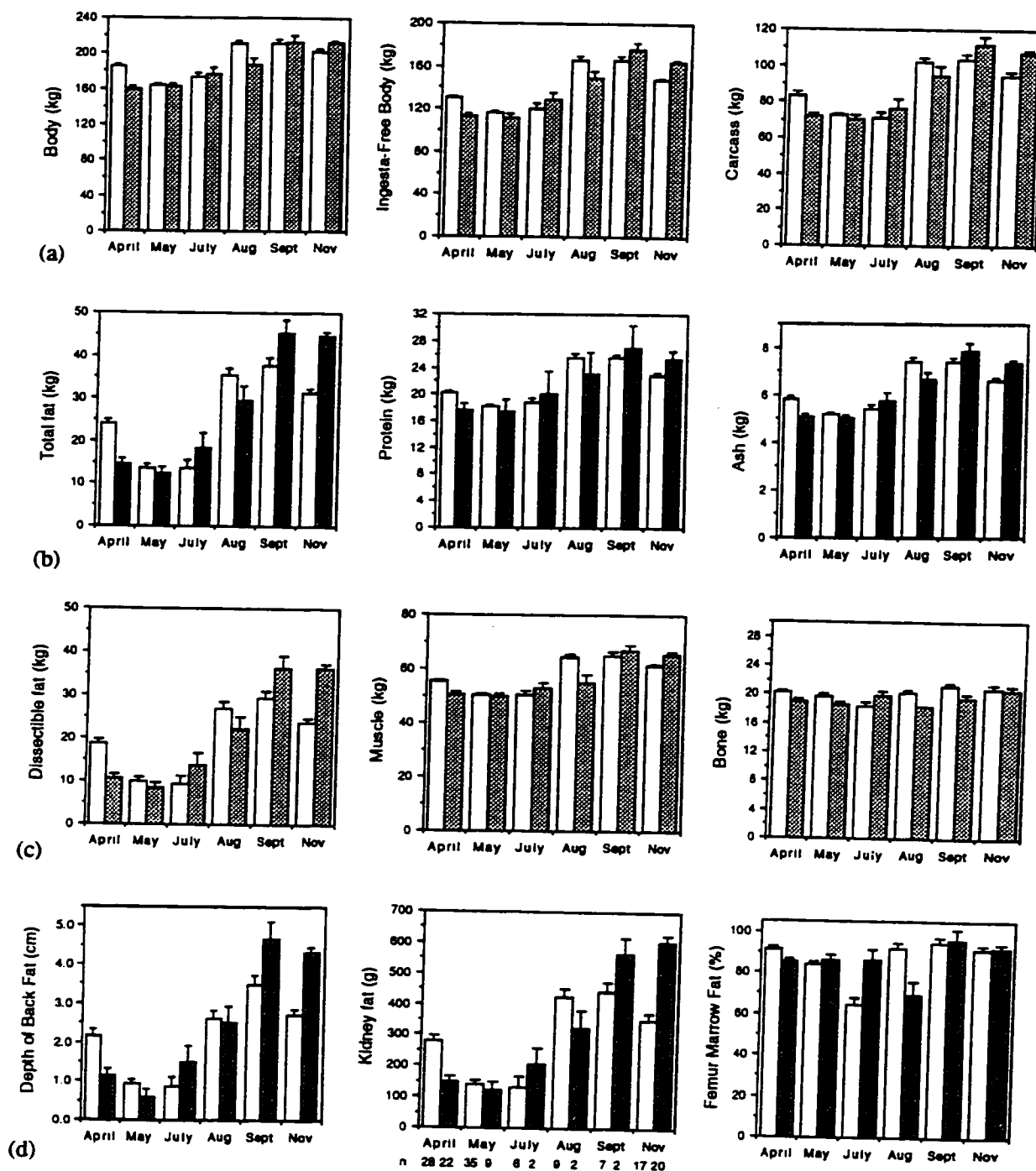


Fig. 5.2. Seasonal changes in weight and composition of adult muskox cows on Victoria Island, 1989-1993. Adjusted means \pm 1 S.E., except for bone weight, means \pm 1 S.E. Open bars - cows either pregnant in April or lactating May - Nov.; shaded bars - cows either not pregnant in April or nonlactating May - November. Sample numbers shown for kidney fat weight apply to all graphs. (a) Measures of body weight. (b) Body composition. (c) Major dissectible tissues. (d) Indices of fatness.

and lactating in May was 242 g/day over a 40-day period, approximately double the rate of fat loss among pregnant females (125 g/day) during the previous five months.

Seasonal patterns in kidney fat weight and DBF, included here for comparison with data from other field studies, paralleled those in total and dissectible fat weight (Fig. 5.2). There was a small but significant seasonal change in femur marrow fat ($P < 0.01$), with peak values in September coinciding with peak fatness. Lactation had little effect on marrow fat but this index decreased ($P < 0.01$) from $83.9 \% \pm 1.3$ in May to $64.5 \% \pm 2.8$ in July in lactating cows, even though their overall fatness and weight were unchanged³.

As with fat, lactating and nonlactating cows were nearly equal in protein and muscle weight at the seasonal minimum in May. Thereafter, protein and muscle weight in nonlactating females increased more rapidly than in lactating cows ($P < 0.01$), but the September peak values of 27.0 ± 1.0 kg protein and 67.0 ± 2.1 kg muscle in nonlactating cows and 25.5 ± 0.5 kg protein and 65.2 ± 1.2 kg muscle in lactating cows were similar. The most rapid losses in protein (55.5 g/day) and muscle (132.5 g/day) occurred in females which were pregnant in April and lactating in May, compared to 33.1 g/day and 71.9 g/day, respectively, in pregnant females during the previous five months of winter.

The seasonal pattern in ash weight of adult females closely followed seasonal changes in IFBW. There was a small but significant seasonal change ($P < 0.01$) in bone weight and the femur weight:length ratio, with the greatest values in September and November, when body weight was greatest. Bone weight and the femur weight:length ratio were not affected by lactation status ($P = 0.44$ and 0.58 , respectively), although there was a significant month-by-lactation interaction ($P = 0.02$ and $P < 0.01$) for both measurements.

5.4.2 Changes in ingesta weight, organ weight, and diet quality of adult cows

The weight of ingesta of female muskoxen increased ($P < 0.01$) from April to November, as did the weight of rumen contents, the largest portion of the ingesta (Fig. 5.3). Ingesta as a proportion of body weight were largest in November (27.8 %) and smallest in April (20.9 %) and August (21.4 %). Rumen contents accounted for a maximum of 77.1 % of ingesta weight in November and a minimum of 67.6 % in August. Lactating females had more rumen contents than non-lactating females ($P =$

³ The lower mean marrow fat value for nonlactating cows in August is exceptionally low due to the one small lean female, which we believe was not representative of most nonlactating cows.

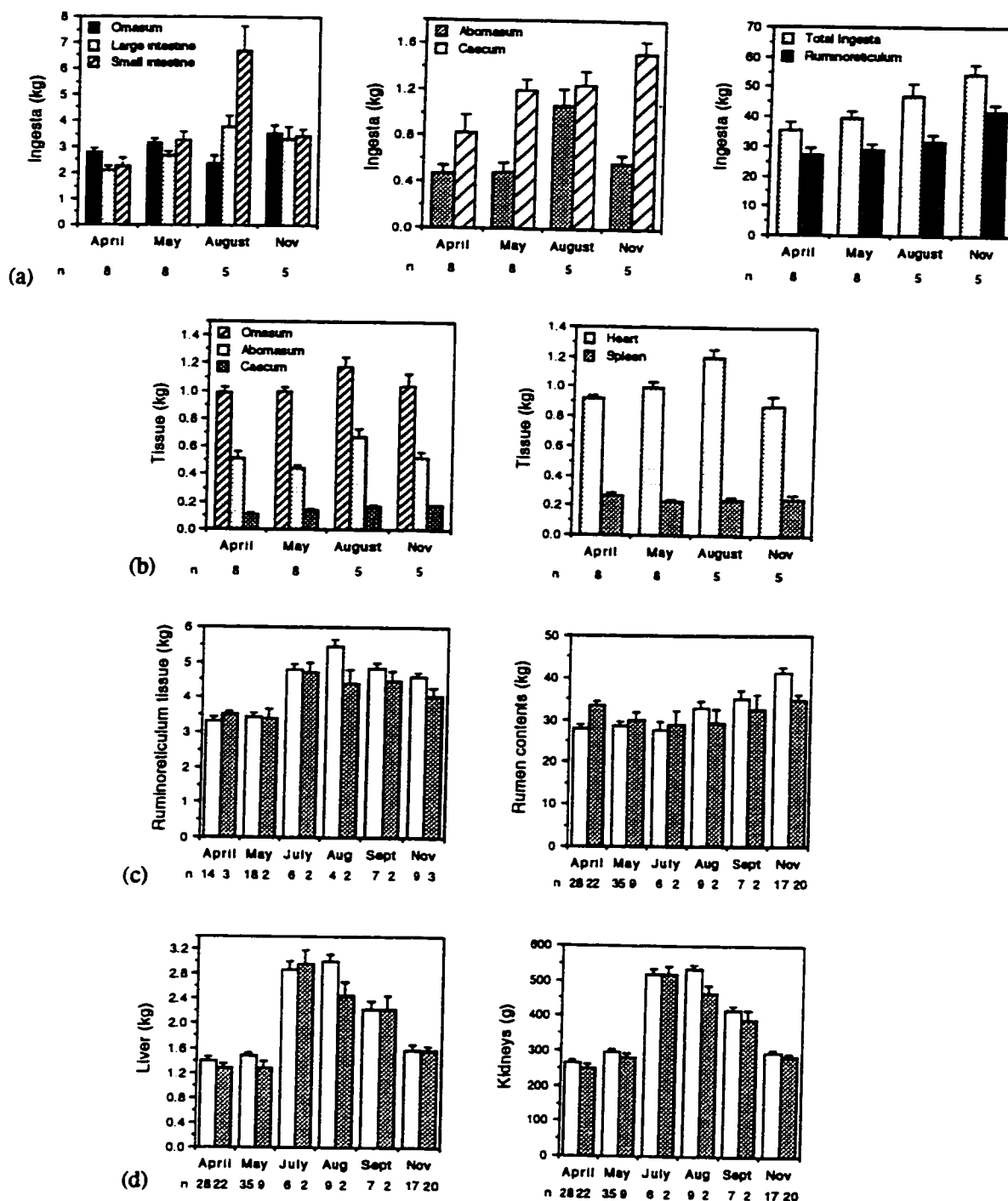


Fig. 5.3. Seasonal changes in weight of ingesta and viscera of adult muskox cows on Victoria Island, 1989-1993. (a) Ingesta weights measured in 1989; means \pm 1 S.E. (b) Weights of gut tissues and organs measured in 1989; means \pm 1 S.E. (c) Weight of the rumen full and empty; adjusted means \pm 1 S.E. Open bars - cows either pregnant in April or lactating May - Nov.; shaded bars - cows either not pregnant in April or nonlactating May - Nov. (d) Liver and kidney weights; adjusted means \pm 1 S.E. Open bars - cows either pregnant in April or lactating May - Nov.; shaded bars - cows either not pregnant in April or nonlactating May - Nov.

0.03) with the most pronounced difference in November when lactating cows had 6.7 kg more than nonlactating cows.

The weights of ingesta within the more distal parts of the gastrointestinal tract all changed with season ($P < 0.01$) but the patterns differed. Abomasal content doubled in August (2.3 % of ingesta) and otherwise varied little with season (1.1-1.3 %), while omasal content was greatest in November (6.5 %) and least in August (5.1 %). Content of the small intestine likewise increased sharply in August (14.2 %) but otherwise remained relatively constant (6.3-8.2 %), while content of the large intestine was relatively constant (6.0-6.8 %) but greatest in August (8.1 %). Caecal contents remained relatively constant (2.3-3.0 %) throughout the year while increasing in absolute terms between April and November.

Rumen tissue weight showed a pronounced seasonal fluctuation ($P < 0.01$) with a peak in July and August, and was slightly greater in lactating females than nonlactating ones throughout the year ($P = 0.01$; Fig. 5.3). Caecal tissue weight increased ($P = 0.02$) during the year in proportion to caecal content, while omasal tissue weight varied little but was greatest in August. Abomasal tissue weight also varied with season ($P = 0.05$) and peaked in August.

Weights of the liver and kidneys fluctuated widely with season ($P < 0.01$) in adult females, with peak values in July and August that were about double the weight during April and May (Fig. 5.3). Weights of these two organs also tended to be greater in lactating cows than in nonlactating cows; the difference was significant for the kidneys ($P = 0.05$) but not the liver ($P = 0.24$). Weight of the heart was also strongly affected by season ($P < 0.01$) with a peak in August and a pattern paralleling muscle weight. The weight of the spleen was unaffected by season.

Nitrogen and ADF in muskox rumen contents followed strong seasonal patterns ($P < 0.01$) with nearly opposite trends (Fig. 5.4). Nitrogen was highest in July, then declined through August, September and November, with each step being significant ($P < 0.05$), while winter values (November to May) varied little.

5.4.3 November and April: the effects of pregnancy and lactation on body composition of adult cows

Of the adult muskoxen examined in November, pregnant nonlactating cows were substantially heavier ($P = 0.05$) and fatter ($P < 0.01$; 44.9 ± 1.0 kg fat) than pregnant lactating cows (36.5 ± 1.5 kg fat), which were in turn heavier ($P = 0.2$) and fatter ($P < 0.01$), by about the same proportion, than nonpregnant lactating cows ($28.1 \pm$

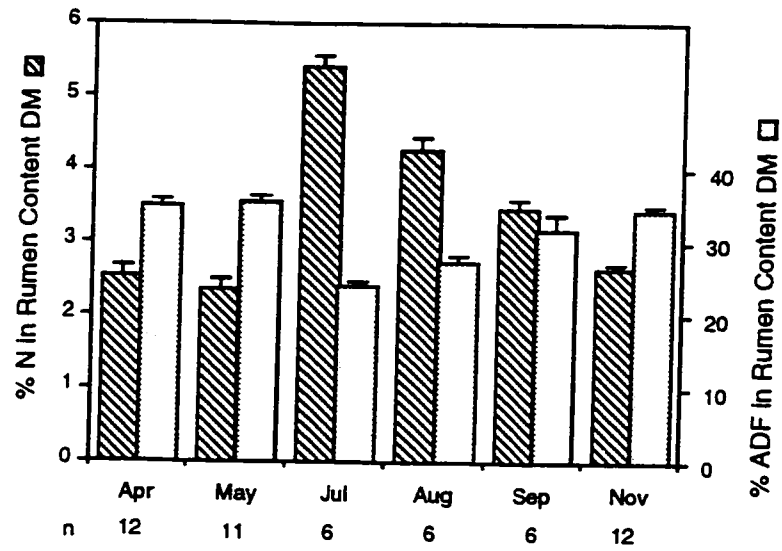


Fig. 5.4. Seasonal changes in acid-detergent fibre (ADF) and nitrogen (N) in freeze-dried rumen contents from muskox cows from Victoria Island, 1989-1990. Means \pm 1 S. E.

1.4 kg fat; Table 5.3). Lactation, but not pregnancy, was associated with an increased weight of rumen contents in November.

In April, pregnant nonlactating adult cows were again the heaviest, fattest group (23.9 ± 1.0 kg fat; $P < 0.01$) followed by nonpregnant nonlactating cows (18.3 ± 1.9 kg fat) and nonpregnant, lactating cows (12.6 ± 1.4 kg fat; Table 5.3). As in November, lactation rather than pregnancy was associated with increased rumen contents.

5.4.4 Changes in body composition of 2 and 3-year-old cows

The seasonal patterns in body composition of 3-year-old females generally matched those of older cows, although 3-year-olds were consistently lighter and leaner, their organs smaller, and their ingesta weight less than those of older cows (Table 5.4). Three-year-old females were exceptionally lean if they were lactating during May, with 4.9 ± 0.3 kg fat and femur marrow fat of 61.6 ± 10.7 %. The body weight of 3-year-olds approached that of older females by November, when the unadjusted IFBW of pregnant nonlactating 3-year-olds was 146.1 ± 4.2 kg, compared to 151.6 ± 1.4 kg in 4-year-olds and 173.4 ± 3.7 kg in 5+ females. These younger cows were leaner at this time of year than older cows (19.6 fat % in the IFBW, compared to 27.9 % in 4-year-olds and 26.8 % in 5+ females) although much of their lean body growth had been completed.

Two-year-old muskox cows were lighter and leaner than 3-year-olds, although their lean growth during the year was proportionately greater (Table 5.5). In November the four 2-year-olds had a mean IFBW of 104.8 ± 11.5 kg, 41.3 kg less than the seven pregnant 3-year-olds. At this time, the 2-year-olds had accumulated less fat in absolute terms than pregnant 3-year-olds but had a similar proportion of fat (23.8 % fat vs. 19.6 % in 3-year-olds). The seasonal patterns in weight of rumen contents, rumen tissue, liver and kidneys of 2-year-old cows resembled those of older cows.

5.4.5 Patterns in reproduction

In August, all muskox females at least 2.5 years old had numerous small follicles and at least one ≥ 7 mm in diameter, and there were no apparent differences between nonlactating and lactating cows (Table 5.6). In September, all but one female had a large corpus luteum and this individual had a 17 mm follicle. Three of the lactating females had cystic corpora lutea.

The estimated dates of conception of cows ranged from August 18 to Oct. 2, with a large cluster centred on a median of August 28 (24 of 31) and a second smaller cluster centred on a median of Sept. 21 (Fig. 5.5). This biphasic distribution was not

Table 5.3. Weight and condition of adult muskox cows collected in November and April, 1989-92, from Victoria Island. Adjusted means are presented ± 1 S.E. except for bone weights, which are (unadjusted) means ± 1 S.E. Values are in kg except where noted. The non-pregnant, non-lactating cow in November was an older female; two non-lactating, non-pregnant cows were excluded due to pyometra. P = pregnant, L = Lactating; N = Not.

Measurement	November				April			
	P, L	P, NL	NP, L	NP, NL	P, NL	NP, L	NP, NL	NP, NL
Sample number	8	17	9	1	24	14	7	7
Total body	211.8 \pm 4.0	216.3 \pm 2.6	203.4 \pm 3.7	228.8	186.5 \pm 2.0	156.1 \pm 2.6	167.7 \pm 3.6	
Ingesta-free body	156.5 \pm 3.0	166.4 \pm 1.9	147.5 \pm 2.7	181.6	130.8 \pm 1.9	107.8 \pm 2.7	123.3 \pm 3.5	
Carcass	100.7 \pm 2.2	108.2 \pm 1.4	94.3 \pm 2.0	119.3	84.0 \pm 1.5	69.2 \pm 2.0	77.7 \pm 2.6	
Total fat	36.5 \pm 1.5	44.9 \pm 1.0	28.1 \pm 1.4	46.9	23.9 \pm 1.0	12.6 \pm 1.4	18.3 \pm 1.9	
Dissectible fat	27.8 \pm 1.2	36.7 \pm 0.8	21.0 \pm 1.1	38.2	18.5 \pm 0.9	8.8 \pm 1.2	13.4 \pm 1.6	
Protein	24.2 \pm 0.4	25.6 \pm 0.3	22.8 \pm 0.4	27.8	20.4 \pm 0.3	16.9 \pm 0.4	19.2 \pm 0.5	
Muscle	64.5 \pm 1.1	67.1 \pm 0.7	62.0 \pm 1.1	69.4	55.8 \pm 0.7	49.6 \pm 0.9	53.3 \pm 1.2	
Ash	7.01 \pm 0.13	7.45 \pm 0.09	6.61 \pm 0.12	8.13	5.86 \pm 0.09	4.83 \pm 0.12	5.52 \pm 0.12	
Bone	21.8 \pm 0.6	20.4 \pm 0.4	19.9 \pm 0.5	23.9	20.4 \pm 0.4	19.0 \pm 0.3	19.7 \pm 0.7	
Depth of back fat (cm)	3.0 \pm 0.2	4.2 \pm 0.1	2.4 \pm 0.2	3.8	2.1 \pm 0.1	0.9 \pm 0.2	1.5 \pm 0.3	
Kidney fat (g)	424 \pm 28	614 \pm 19	299 \pm 26	609	278 \pm 17	119 \pm 22	191 \pm 30	
Femur marrow fat (%)	92.1 \pm 1.1	92.0 \pm 0.9	90.4 \pm 1.3	92.3	90.9 \pm 1.3	86.9 \pm 1.9	82.6 \pm 2.4	
Rumen contents	42.5 \pm 1.6	35.6 \pm 1.2	41.8 \pm 1.5	37.5	28.1 \pm 0.9	34.4 \pm 1.2	33.0 \pm 1.7	
Rumen tissue	4.56 \pm 0.10	4.23 \pm 0.07	4.44 \pm 0.09	4.02	3.36 \pm 0.08	3.43 \pm 0.11	3.60 \pm 0.15	
Kidneys (g)	307 \pm 9	297 \pm 6	308 \pm 9	293	268 \pm 9	247 \pm 12	263 \pm 16	
Liver	1.62 \pm 0.05	1.61 \pm 0.03	1.61 \pm 0.04	1.63	1.40 \pm 0.05	1.24 \pm 0.07	1.40 \pm 1.0	

Table 5.4. Seasonal changes in weight and condition of 3-year-old muskox cows from Victoria Island, 1989-1993. Means are presented \pm 1 S.E. and are in kg except where noted. L = lactating; P = pregnant; N = not.

Measurement	April		May		July		August		November	
	P, NL	NP, NL	NP, L	NP, NL	L	L	L	NL	P, NL	NL, NP
Sample number	2	2	3	4	1	3	1	1	7	2
Body	158.7 \pm 1.3	157.5 \pm 15.5	126.7 \pm 4.9	126.5 \pm 5.8	151.0	187.6 \pm 3.4	168.0	192.4 \pm 4.2	177.0 \pm 4.5	
Ingesta-free body	114.2 \pm 0.7	113.5 \pm 7.7	87.8 \pm 3.9	96.5 \pm 6.6	102.1	141.2 \pm 4.6	137.8	146.1 \pm 4.2	131.1 \pm 7.2	
Carcass	72.3 \pm 1.8	72.5 \pm 4.0	54.3 \pm 1.7	61.1 \pm 5.0	60.0	88.2 \pm 2.5	86.0	95.3 \pm 2.0	84.3 \pm 3.3	
Total fat	19.3 \pm 0.9	17.1 \pm 0.7	4.9 \pm 0.3	10.6 \pm 3.1	9.7	30.1 \pm 0.7	30.7	36.5 \pm 2.6	28.9 \pm 0.3	
Dissectible fat	15.4 \pm 0.8	11.9 \pm 0.9	3.1 \pm 0.2	7.9 \pm 1.7	7.3	22.8 \pm 0.7	23.8	28.7 \pm 1.5	23.2 \pm 0.1	
Protein	17.9 \pm 0.1	17.8 \pm 1.2	13.9 \pm 0.6	15.2 \pm 1.0	16.1	21.9 \pm 0.7	21.4	22.6 \pm 0.6	20.4 \pm 1.1	
Muscle	50.3 \pm 1.1	50.5 \pm 4.5	40.7 \pm 0.9	41.0 \pm 2.7	43.9	58.7 \pm 1.6	53.4	61.2 \pm 2.0	54.9 \pm 0.6	
Ash	5.11 \pm 0.03	5.08 \pm 0.34	3.93 \pm 0.18	4.32 \pm 0.30	4.57	6.32 \pm 0.22	6.17	6.54 \pm 0.19	5.87 \pm 0.33	
Bone	18.7 \pm 0.5	17.9 \pm 1.3	18.0 \pm 0.1	15.8 \pm 0.7	18.8	19.1 \pm 0.8	16.6	20.0 \pm 0.5	18.7 \pm 0.3	
Depth of back fat (cm)	2.90 \pm 0	2.10 \pm 0.70	0.20 \pm 0.06	1.00 \pm 0.3	1.00	2.73 \pm 0.15	3.20	4.08 \pm 0.29	4.00 \pm 0.30	
Kidney fat (g)	201 \pm 28	144 \pm 11	48 \pm 6	108 \pm 23	114	362 \pm 9	361	434 \pm 21	337 \pm 2	
Femur marrow fat (%)	89.6 \pm 2.7	90.6 \pm 0.8	61.6 \pm 10.7	89.6 \pm 2.9	52.4	93.4 \pm 0.3	89.3	92.7 \pm 1.5	92.8 \pm 3.9	
Rumen contents	21.9 \pm 1.0	31.3 \pm 3.7	26.6 \pm 2.7	25.0 \pm 1.9	21.4	31.9 \pm 1.2	24.3	37.3 \pm 2.0	36.5 \pm 0.2	
Rumen tissue	2.39 \pm 0.23	3.45 \pm 0.55	2.87 \pm 0.27	2.38 \pm 0.24	4.60	4.93 \pm 0.09	4.70	3.90 \pm 0.12	3.46 \pm 0.18	
Kidneys (g)	220 \pm 2	239 \pm 53	228 \pm 10	220 \pm 4	458	478 \pm 18	362	262 \pm 14	243 \pm 23	
Liver	1.24 \pm 0.08	1.21 \pm 0.17	0.97 \pm 0.03	1.32 \pm 0.20	2.60	2.81 \pm 0.02	2.26	1.49 \pm 0.05	1.36 \pm 0.02	

Table 5.5. Seasonal changes in weight and condition of 2-year-old muskox cows from Victoria Island, 1989-1993. Means are presented \pm 1 S.E. and are in kg except where noted. There were no lactating or pregnant cows.

Measurement	April	May	August	November
Sample number	4	1	1	4
Body	101.5 \pm 7.4	100.0	160.0	137.6 \pm 13.4
Ingesta-free body	77.5 \pm 6.7	71.0	130.8	104.8 \pm 11.5
Carcass	49.4 \pm 4.6	45.0	80.0	66.3 \pm 7.6
Total fat	9.3 \pm 1.2	2.8	28.2	24.5 \pm 5.2
Dissectible fat	6.5 \pm 1.1	2.5	22.3	19.3 \pm 4.2
Protein	12.4 \pm 1.0	11.4	20.4	16.5 \pm 1.7
Muscle	35.6 \pm 2.9	31.8	53.5	45.4 \pm 4.4
Ash	3.47 \pm 0.30	3.18	5.86	4.69 \pm 0.50
Bone	14.1 \pm 0.9	14.2	18.7	15.9 \pm 0.8
Depth of back fat (cm)	1.10 \pm 0.28	0.30	3.50	2.95 \pm 0.53
Kidney fat (g)	107 \pm 8	56	342	334 \pm 75
Femur marrow fat (%)	87.5 \pm 0.9	78.3	90.0	90.4 \pm 2.8
Rumen contents	17.6 \pm 1.9	20.8	25.2	28.0 \pm 1.5
Rumen tissue	2.28 \pm 0.02	2.20	3.80	2.99 \pm 0.20
Kidneys (g)	176 \pm 14	174	410	257 \pm 31
Liver	0.98 \pm 0.09	0.90	2.24	1.23 \pm 0.05

Table 5.6. Largest dimension (mm) of follicles (F) \geq 4 mm in diameter and corpora lutea (CL) in ovaries from muskox cows at least 2.3 years old, shot in August and September on Victoria Island. Small follicles (\leq 4 mm in diameter) were common in all ovaries. L = lactating; NL = not lactating.

August 10-15, 1989			September 2-7, 1990			August 12-15, 1991		
Age	L/NL	F/CL size	Age	L/NL	F/CL size	Age	L/NL	F/CL size
3.3	L	F 8, F 12	4.4	L	CL 13	2.3	NL	F 10
3.3	L	F 9, F 9	4.4	L	cystic CL 18	3.3	NL	F 9, F 9
3.3	L	F 7, F 12	4.4	NL	F 6, CL 15	4.3	L	F 9, F 9
4.3	NL	F 14, F 12	4.4	NL	CL 13	4.3	NL	F 7
5+	L	F 7, F 16	5+	L	F 16, CL 10	5+	L	F 5, F 7, F 7
5+	L	F 13, F 12	5+	L	F 17	5+	L	F 8, F 8
5+	L	F 6, F 9, F 11	5+	L	F 9, CL 14	5+	L	F 7, F 5
5+	L	F 14, F 11	5+	L	cystic CL 19			
			5+	L	cystic CL 19			
			5+	L	CL 18			

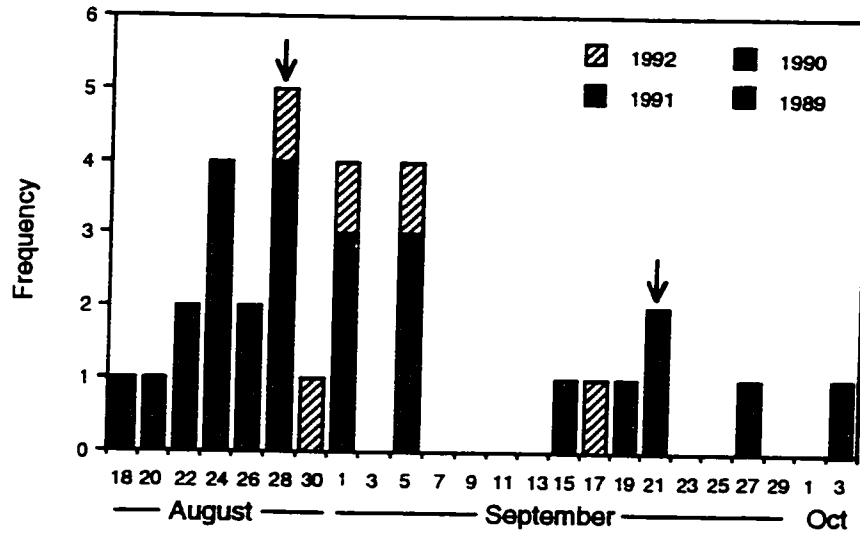


Fig. 5.5. Estimated conception dates of muskox cows from Victoria Island based on November collections, 1989-1993. Arrows indicate median dates for the two clusters.

affected by reproductive status (lactating or not) or age (3, 4, or 5+) of the cows, and did not appear to differ from year to year. Based on these conception dates, the peak of calving would have occurred in the last week of April, with the earliest calves born in mid-April and the latest at the end of May. Our field observations and those of J. A. Schaefer (pers. comm.) indicate that the earliest calf was seen on April 23 and that most calves were born in the first week of May. Of 44 adult cows shot in May, one was still pregnant on May 16, 1989, and a second was still pregnant on May 19, 1993.

Overall pregnancy rates among the muskoxen increased with age, from 0 among yearlings to 25 % among females 2.5 years old during the breeding season and 62.5 % among females at least 3.5 years old (Table 5.7). The pregnancy rates of 3.5-year-old, 4.5-year-old and 5+ females were similar and averaged 69.6 % in November and 56.0 % in April, although this apparent decrease was not significant ($P = 0.20$). There was significant variation in pregnancy rate among the eight collections ($P = 0.03$), most likely due to the exceptionally low pregnancy rate in April 1991, but the apparent decrease from 83 % (10 of 12) in November 1990 to 35 % (6 of 17) in April 1991 was not significant ($P = 0.16$). The sex ratio of fetuses in which sex was identified was 24 females: 24 males and there were 12 females and 13 males among newborn calves shot in May.

Lactation in November did not preclude pregnancy among adult cows in this population. Eight cows were pregnant and lactating, nine were not pregnant and lactating, 17 were pregnant and not lactating, and an additional three (two with pyometra) were neither pregnant nor lactating (Table 5.3). By April, in contrast, there were no longer any pregnant lactating muskoxen, but 24 were pregnant and not lactating, 14 were still lactating but not pregnant, and seven (one with pyometra) were neither pregnant nor lactating (Table 5.3). Some muskox cows may extend lactation for well over a year on Victoria Island: one female shot on September 2, 1990 was accompanied by a small female yearling and was lactating. Her mammary gland weight was about half that of females that were suckling calves of the year. Mammary weight of lactating cows changed strongly with season ($P < 0.01$), with peak weight in July and August and the smallest weights in cows still lactating in April (Fig. 5.6).

In April, the gravid uterus and fetus of pregnant females weighed on average 18.8 ± 0.7 kg and 10.0 ± 0.5 kg, respectively, and sex did not affect fetal size or weight (Table 5.8). Fetal size and weight were similar among females bred at 3.5 years or older, although the two fetuses of females bred at 2.5 years were shorter and lighter ($P < 0.05$) than those of older cows. The two years during which fetal weight was greatest (1990 and 1992) were also the years during which the collection was conducted on the

Table 5.7. Muskox pregnancy rates on Victoria Island, 1989-1992; 4.5-yr-old cows could not be distinguished from older cows in April. There were no twins.

A. Pregnancy rates by age.				B. Pregnancy rates by collection, in cows at least 3 years old during the breeding season.							
Age (yrs) at time of breeding season	No. preg.	No. not preg.	% preg.	April			November				
				Year	No. preg.	No. not preg.	% preg.	Year	No. preg.	No. not preg.	% preg.
1.5	0	7	0	1989	6	4	60.0	1989	2	5	28.6
2.5	2	6	25.0	1990	6	4	60.0	1990	10	2	83.3
3.5	17	10	63.0	1991	6	11	35.3	1991	14	3	82.4
4.5+	43	26	62.3	1992	10	3	76.9	1992	6	4	60.0

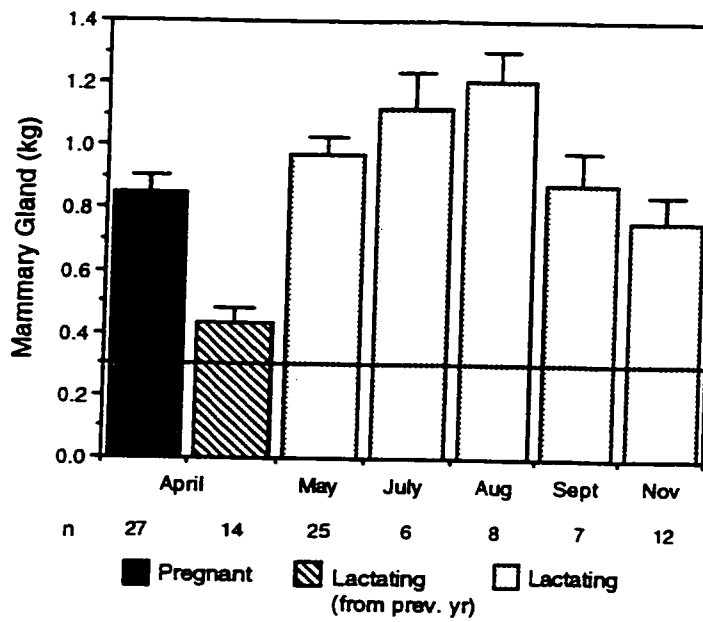


Fig. 5.6. Untrimmed mammary gland weight of pregnant or lactating adult muskox cows from Victoria Island, 1989-1993. Means \pm 1 S.E. Horizontal line - mean mammary gland weight from 6 non-pregnant, non-lactating cows in April.

Table 5.8. Weight and size of muskox uteri and fetuses in April, 1989-1992, on Victoria Island. Means are presented ± 1 S.E. and are in kg except where noted.

A. Male and female fetuses.			B. Age-specific fetal measurements.			
Measurement	Females	Males	Measurement	Age at time of breeding (years)		
Sample #	16	14		2.5	3.5	4.5+
Unopened gravid uterus	18.5 \pm 0.7	19.1 \pm 0.9	Sample #	2	10	18
Fetus	10.2 \pm 0.5	9.8 \pm 0.6	Fetus	6.0 \pm 1.0	10.5 \pm 0.4	10.2 \pm 0.5
Crown-rump length (cm)	56.6 \pm 1.1	57.2 \pm 1.2	Crown-rump length (cm)	48.0 \pm 1.0	57.9 \pm 0.9	57.3 \pm 1.0
Transcranial diameter (cm)	7.94 \pm 0.18	7.94 \pm 0.21				

C. Between-year variation in fetal weight and length.				
Measurement	Year			
	1989	1990	1991	1992
Sample number	7	6	6	11
Fetus	8.2 \pm 0.8	10.8 \pm 0.6	10.1 \pm 0.3	10.7 \pm 0.7
Crown-rump length (cm)	54.4 \pm 2.1	56.9 \pm 1.2	59.0 \pm 0.9	57.3 \pm 1.3

latest dates in April, but fetal size and weight were not significantly affected by the year ($P = 0.07$). There were no significant relationships between any maternal characteristics (IFBW, fat, protein or bone weight) and fetal characteristics (weight, length, and weight/length ratio; $P > 0.1$, $r^2 < 0.1$).

5.4.6 Between-year differences in muskox condition and weather patterns

Between-year differences in weight of the ingesta-free body, fat and liver of adult females were small compared with seasonal changes in these measurements (Fig. 5.7). There were trends toward a decline in IFBW, fat weight and liver weight from 1989 to 1993 during April and May, but not in November. Statistically, the year influenced IFBW in April and May ($P < 0.01$) but not in November ($P = 0.49$), while fat weight differed among years in April and November ($P < 0.01$) but not in May ($P = 0.09$). Liver weight varied among years in April ($P < 0.01$), but not in May ($P = 0.84$) or November ($P = 0.38$).

Monthly temperatures in Cambridge Bay peaked in July and August, were lowest in February, did not rise above -7 °C between November and April, and varied little among years (Fig. 5.8). Snow accumulated from late September onward and reached its greatest depth in April or May before melting rapidly in June. Snow accumulated earliest and became deepest in 1992-93, while the winter of 1990-91 was unique in that little snow fell early but snow depth increased rapidly in February and March (Fig. 5.8). We did not encounter ground-fast ice or ice layers during the study winters.

5.5 Discussion

5.5.1 Body composition of muskoxen and other ruminants

The body composition of Victoria Island muskox cows confirms the classification of muskoxen as grazers adapted to poor-quality sedges and grasses, and indirectly confirms the conservative energetics of this species. Compared with other muskox populations and other temperate and arctic ruminants, muskoxen on Victoria Island were clearly affected by winter-imposed restrictions during the study years, but were not heavily stressed by them.

Muskoxen have the relatively large rumen, large omasum and small caecum (Staaland and Thing 1991) typical of grazers (Hofmann 1989), and their winter diets are usually dominated by sedges and grasses on Victoria Island (Schaefer and Messier 1995) as elsewhere (Thing *et al.* 1987, Raillard 1992). The relative weight of ingesta in November was large even for pronounced grazers (cf. Hofmann 1989), and similar to

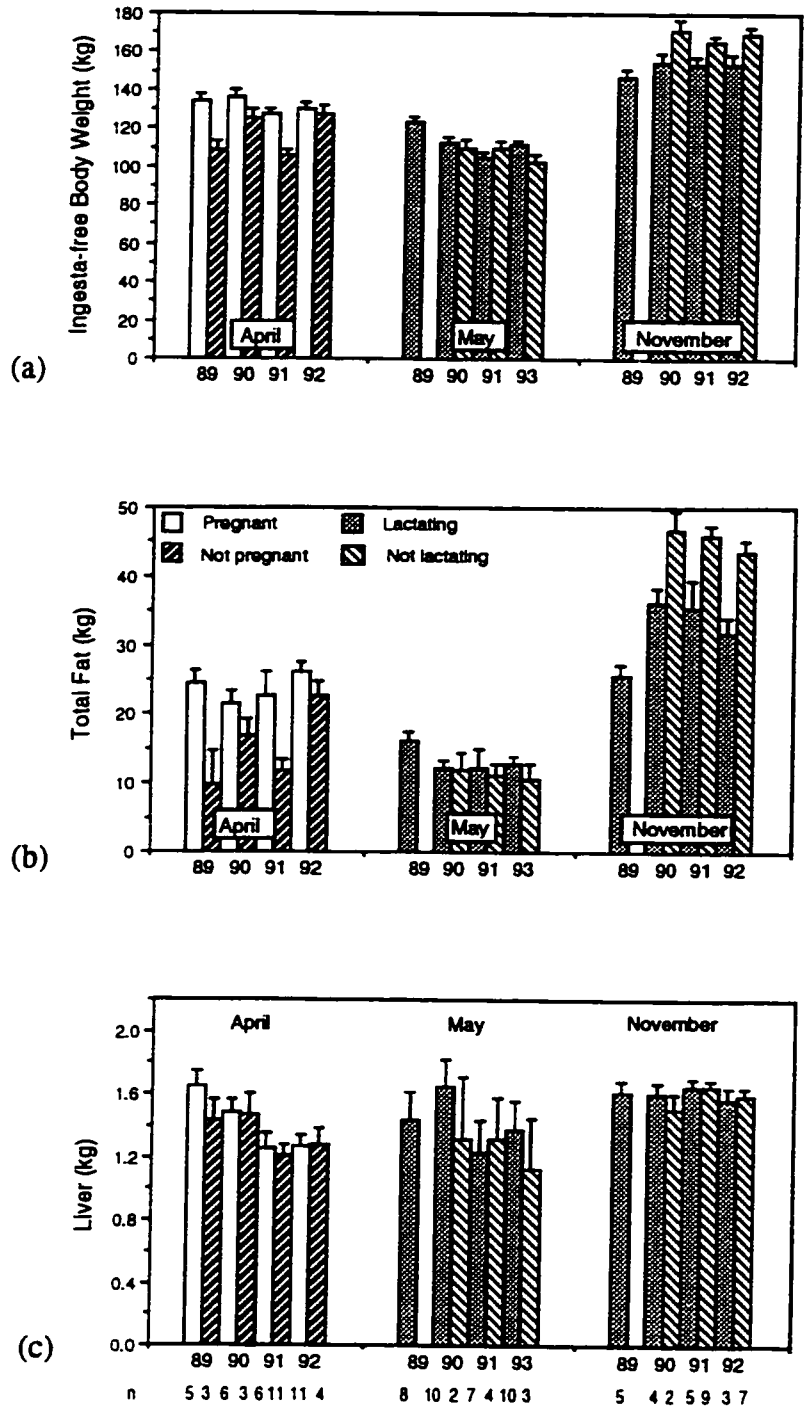


Fig. 5.7. Year-to-year variation in weight of the ingesta-free body, fat, and liver of adult muskox cows on Victoria Island, 1989-1993. Adjusted means \pm 1 S.E. Legend for total fat applies for all three figures.

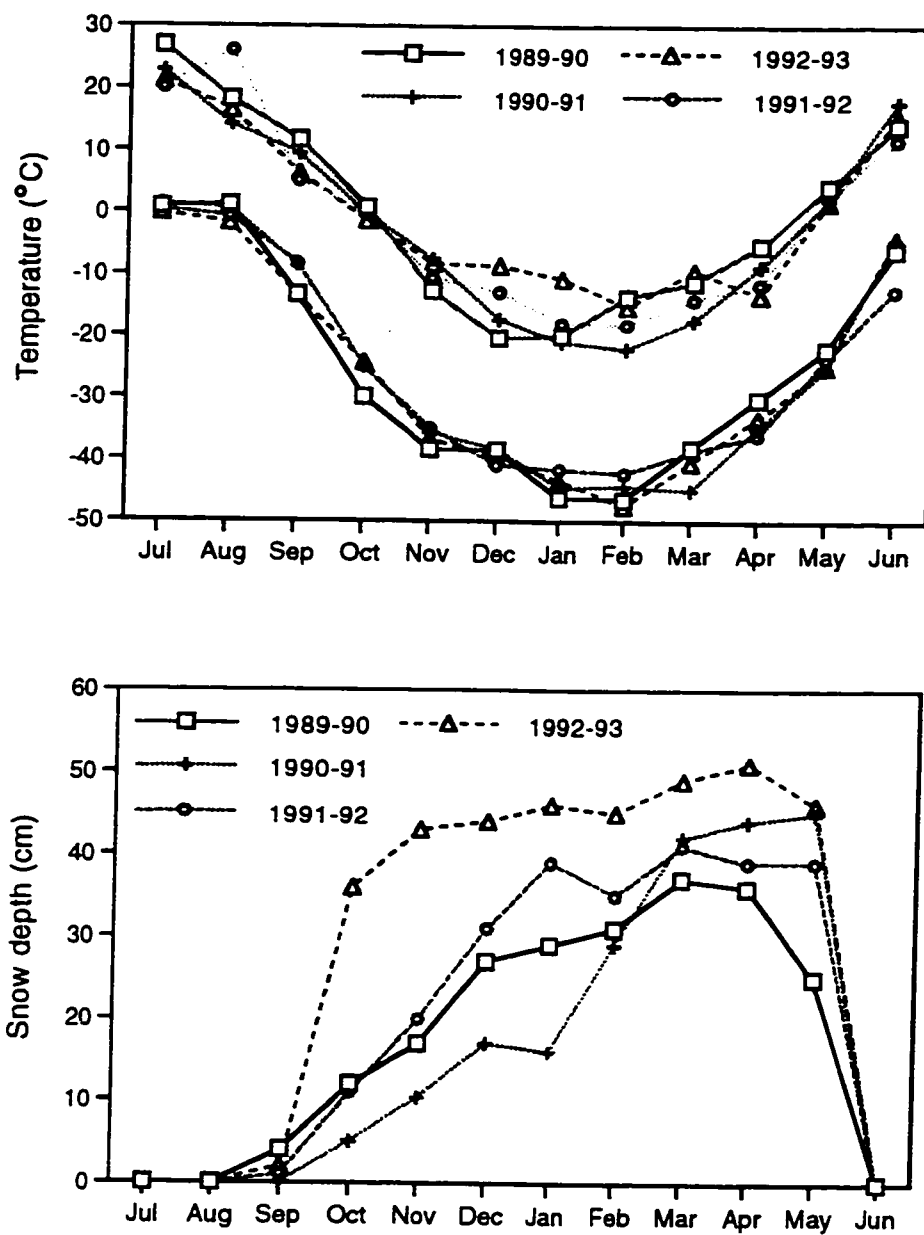


Fig. 5.8. (a) Monthly maximum and minimum temperatures in Cambridge Bay, Victoria Island, 1989-1993.
 (b). Monthly snow depths in Cambridge Bay during the study years.

that of Heidschnucken sheep (Weyreter *et al.* 1987) and Bangali cattle (Mould *et al.* 1982) adapted to high-straw diets. The omasal weight of muskoxen was particularly large; expressed as a proportion of carcass weight, omasal tissue was greater in muskoxen (1.24 %) than in cattle, sheep or goats, and comparable to that of water buffalo (*Bubalus bubalis*; 1.23 %) (cf. McSweeney 1988). The slow rates of passage (Adamczewski *et al.* 1994b), high digestibility of grass hay and other high-roughage diets (White *et al.* 1984; Adamczewski *et al.* 1994a,b) and their ability to maintain condition through the long arctic winter (Thing *et al.* 1987; this study) confirm the excellent adaptation of muskoxen to low-quality graminoid diets.

The ability of muskoxen to make good use of high-quality forage during summer is indicated by the sometimes large proportion of browse in their summer diets (Thing *et al.* 1987, Oakes *et al.* 1992) and by the sharply increased weights of abomasal and small intestine contents we measured in August. These weights lead us to speculate that the ventricular groove is functional when food quality is high, and permits muskoxen to maximize use of plant cell contents by by-passing the rumen and digesting this material directly. Such use of the ventricular groove has been postulated by Hofmann (1989) in adult ruminants and in muskoxen by R. G. White (pers. comm.).

The visceral weights of muskoxen confirm the low metabolic rates (Nilssen *et al.* 1994) and low energy requirements (White *et al.* 1991; Adamczewski *et al.* 1994a) of this species in winter, particularly when compared with those of cervids. Expressed as a proportion of whole body weight, the liver, heart and kidneys of muskox cows in November were 0.79, 0.43, and 0.14 % of body weight. The comparable values for caribou cows on Coats Island, NWT, at the same time of year were 1.29, 1.06, and 0.21 %, respectively (Adamczewski *et al.* 1987), while those of nonpregnant nonlactating Jersey cows were 1.30, 0.35, and 0.26 % (Smith and Baldwin 1974). Because the liver, heart, kidneys and gut are metabolically highly active tissues which can account for more than 50 % of whole-body energy consumption (Smith and Baldwin 1974; Burrin *et al.* 1990), the low values for muskoxen are consistent with a highly conservative energy metabolism. Furthermore, the seasonally much reduced weights of the liver, kidneys and rumen tissue imply reduced energy requirements in winter. While comparable seasonal cycles in visceral weight occur in red deer (Mitchell *et al.* 1976) and caribou (Adamczewski *et al.* 1987), the weights of these "costly" organs, and accordingly the animals' metabolic rates and energy needs, remain proportionately greater in cervids than in muskoxen.

The winter conditions experienced by muskoxen in this study and in Greenland (Thing *et al.* 1987) allowed them to maintain good condition throughout the year, and

were not severe enough to affect fetal growth rates. More severe winters can result in extensive mortality in muskoxen (Miller *et al.* 1977; Gray 1987; Forchhammer and Boertmann 1993) and were likely responsible in part for the low muskox densities on Victoria Island during the 1950's and 1960's (Gunn 1990). The minimal between-year variation in muskox condition during this study, despite substantial variation in snow accumulation, indicates that the muskoxen were able to adapt to winter conditions by altering feeding behaviour or habitat selection. We recognize, however, that the effects of snow on feeding patterns of muskoxen are complex (Raillard 1992; Schaefer and Messier 1995) and not necessarily apparent from simple measurements of snow depth.

The overall seasonal cycle in body weight and composition of muskoxen is comparable in amplitude to that of Svalbard reindeer (Reimers *et al.* 1982; Reimers and Ringberg 1983; Tyler 1987) and insular reindeer and caribou (Leader-Williams and Ricketts 1982; Adamczewski *et al.* 1987), which share the extreme seasonality of forage quality and availability experienced by muskoxen. Both species breed when they are near peak condition, but muskoxen breed and calve several weeks earlier than caribou. The late-winter parturition with rapid weight loss of early lactation and prolonged lactation through the long arctic winter are unique features of muskoxen.

5.5.2 Factors contributing to large seasonal changes in muskox body composition

The marked seasonal patterns in weight, condition and organ size of muskox cows on Victoria Island in part reflect a balance of nutrient income and use forced by the quality of available forage. However, there was circumstantial evidence that wild muskoxen, like captive ones, were predisposed to weight gain in late summer and weight loss in late winter. The observed seasonal patterns were further modified by the pervasive effects of lactation.

The substantial seasonal changes in fat indices and body weight of muskox females in Jameson Land, northeast Greenland (Thing *et al.* 1987) were similar to those reported here, but carcass weight was higher throughout the year in Greenland. Patterns in body weight (White *et al.* 1989; Adamczewski *et al.* 1994a) and body composition (White *et al.* 1989) of lactating captive muskoxen were also similar to those estimated here, particularly with respect to the use of fat during early lactation and the rapid recovery of body reserves in late summer. However, the large seasonal changes in protein and muscle weight we estimated were unlike the minimal seasonal changes in protein estimated in captive Alaskan muskoxen (White *et al.* 1989). This difference may stem in part from the different methods of estimating body composition - from index and weight measurements in our study and from body-water space in the Alaskan

study. It is also likely that the greater seasonal changes in free-ranging animals reflect the very poor diet quality (Thing *et al.* 1987; Staal and Olesen 1992) and restricted forage availability (Raillard 1992; Schaefer and Messier 1995) encountered by wild muskoxen in winter. The ratio of fat:protein in weight loss (3.8-4.4:1) of pregnant and lactating muskox cows was similar to that shown in cattle (Agricultural Research Council 1980).

Body components other than fat and protein were also strongly affected by seasonally altered metabolism in muskoxen, as in other ruminants (O'Donovan 1984). The marked summer to winter weight reductions of the liver, kidneys, and rumen tissue provided evidence of reduced nutrient availability in winter, although they were not synchronized with patterns in body weight. The pliancy of these organs to recent nutrition has been experimentally shown in domestic ruminants (O'Donovan 1984; Burrin *et al.* 1989) and seasonal variation in weight of these organs in parallel with changing forage quality has been demonstrated in cervids (Mitchell *et al.* 1976; Adamczewski *et al.* 1987). The small but significant seasonal changes in estimated bone weight and in the weight:length ratio of the femur indicated that muskox bones, like those of other species (Currey 1984), were responsive to the altered loads imposed by fluctuating body weight. Large summer-winter fluctuations in mineral metabolism are also known to occur in wild muskoxen (Staal and Thing 1991).

The rapid protein and fat gain by muskoxen in August, out of step with plant phenology and diet quality, may be evidence of a predisposition to gain weight at this time of year, as the same pattern has been observed in captive muskoxen in Alaska (White *et al.* 1989; Groves 1992) and Saskatoon (Adamczewski *et al.* 1994b), even when diet quality was constant. This tendency may be under the control of hormones such as insulin and insulin-like growth factor-one (IGF-1); the latter is elevated in autumn in female muskoxen (Adamczewski *et al.* 1992). This hormone is highly correlated with lean growth rate in cattle (Kerr *et al.* 1991) and is apparently influenced by photoperiod in reindeer (Suttie *et al.* 1991) and by melatonin in red deer (*Cervus elaphus*; Suttie *et al.* 1992). White-tailed deer (*Odocoileus virginianus*) likewise appear predisposed to fattening in autumn (Abbott *et al.* 1984; Verme 1988).

Additional support for a predisposition to weight gain in late summer is provided by the weights of the liver, kidneys and empty rumen, which did not decline from July to August even though diet quality, based on analyses of rumen contents, had peaked in July and begun to decline by mid-August. We speculate that by selective foraging, more intensive feeding, and perhaps by increasing the mass of rumen contents in August, muskoxen "stretched out" the summer intake of highly digestible nutrients

past the peak in forage quality. High nutrient intake during the late summer period is clearly essential for lactating muskoxen, which concentrate nearly all their fat and protein gain into a few weeks (Thing *et al.* 1987; White *et al.* 1989; this study).

A portion of the late-winter weight loss of muskoxen on Victoria Island may similarly reflect an endocrine-mediated predisposition to reduce weight, as well-fed nonbreeding captive muskoxen also consistently lose weight at this time of year (White *et al.* 1989; Groves 1992; Adamczewski *et al.* 1994b). Such a predisposition might account for the lower weight of rumen contents maintained by all muskox cows in April and May than in November, despite comparable diet quality. Gut fill is influenced by daylength in sheep (Forbes *et al.* 1979) and by melatonin in red deer (Domingue *et al.* 1992). Conversely, the maximal ingesta and rumen content weights measured in all cows in November may partly indicate a need to maintain high nutrient intake at a time when continued lactation and the maintenance of pregnancy (see further discussion) may depend on good nutritional status and condition.

The heavy nutrient demands of lactation (Oftedal 1985) were evident in muskoxen throughout the year, and particularly in May and November. The higher weight of rumen contents of lactating muskoxen, indicating compensatory efforts, is similar to that of lactating red deer (Mitchell *et al.* 1976) and domestic ruminants (Smith and Baldwin 1974; Agricultural Research Council 1980). The greater weights of the liver, kidneys, and rumen tissue are also comparable to those in other ruminants (Smith and Baldwin 1974; Mitchell *et al.* 1976) and imply a greater maintenance energy cost (Smith and Baldwin 1974) in addition to the cost of milk production. Although milk production after September was likely much lower than in summer, the quality of forage available was also much reduced. As a result, the cost of lactation relative to available nutrients was probably substantial in winter, as shown by the reduced fat reserves of lactating cows in November and the leanness of cows still lactating in April. The apparent preferential use of marrow fat during early lactation, out of step with the overall pattern in fatness, echoes results of studies showing variable responsiveness of different fat depots to physiological stimuli (Pond *et al.* 1986; Flint and Gardner 1993). Although we were unable to demonstrate a strong effect of lactation on bone weight of muskoxen, the significant lactation-by-month interaction in bone weight suggests that such an effect occurred but was obscured by small sample numbers and confounding variation in body size. Depletion of bone stores of calcium and phosphorus during early lactation is common in domestic ruminants (Reid 1961). Thus the patterns in body composition of muskox cows on Victoria Island are not just a simple balance of nutrient

intake and use, but also intimate the physiological effects of season and reproductive condition.

5.5.3 Muskox breeding and calving dates on Victoria Island

The breeding and calving dates of muskoxen on Victoria Island agree with Tener's descriptions (1965) and appeared to peak 1-2 weeks later than on Banks Island (Rowell 1991). Based on the estimated peak in conceptions at the end of August and field observations of newborn calves, gestation length on Victoria averaged about a week more than 235 days, the mean gestation length measured by Rowell *et al.* (1993) in captive muskoxen. Without severe nutritional stress and with consistent year-to-year condition of muskox cows, reproductive activity was likely cued by photoperiod, as has been shown in many mammals living in seasonal environments (Bronson and Heideman 1994) and postulated in muskoxen (Tener 1965; Tedesco *et al.* 1992). The biphasic pattern in conception dates, with medians separated by about the duration of an estrous cycle (Rowell and Flood 1988), implies that most conceptions occurred during the first overt estrous cycle and the rest during the second. This pattern in conceptions may in part account for the substantial variation in calving dates of muskoxen (Tener 1965; Thing *et al.* 1987; White *et al.* 1989).

5.5.4 Flexibility in lactation patterns of muskoxen

Both the shape of the lactation curve and the duration of milk production appear to be flexible in muskoxen, based on the mammary weights reported here and the results of White *et al.* (1989) in captive muskoxen. Mammary weight or volume is correlated with milk production in goats (Linzell 1966; Knight and Peaker 1984) and other species (Linzell 1972) although milk production depends on the relative secretory activity of mammary cells as well as their numbers (Knight and Peaker 1984). In addition, the mammary weights we recorded in August and later may have been marginally inflated by fat accretion. These considerations notwithstanding, we infer that muskoxen on Victoria Island did not achieve peak lactation until July, more than two months after calving, and that milk production was maintained at a high level into August before decreasing markedly. Milk production in captive muskoxen in Alaska peaked on average about three weeks after calving, but there were substantial between-year and individual differences in lactation curves (White *et al.* 1989). Most strikingly, milk production did not peak until at least 60 days post-calving in 1984, the year of a particularly poor hay crop (White *et al.* 1989). Taken together, these results imply that the level of milk production in muskoxen is sensitive to nutrient availability, as in other

ruminants (Peart 1970; Wood 1976; Loudon, Darroch and Milne 1984). Moreover, free-ranging muskoxen, while they deplete fat reserves rapidly during the early weeks of lactation without access to green forage, depend on highly nutritious spring forage for peak milk production, as do temperate and arctic cervids (Ofstedahl 1985). The shape of the postulated lactation curve resembles that of beef cattle (Walker and Pos 1963), with a peak two to three months after calving, and the suckling of yearlings is comparable to that observed in bison (Van Vuren and Bray 1986) and has been noted previously in muskoxen (Tener 1965; Gray 1987). A summer peak in lactation would also be consistent with the lack of repletion of body stores in lactating muskoxen between May and July. Weaning times in muskoxen vary from December to February in supplementally-fed captive cows (White *et al.* 1989) to over a year in poorly-fed nonpregnant captive cows (R. G. White, pers. comm.), or nonpregnant wild muskoxen (Jingfors 1984; Gray 1987; this study). Such plasticity in lactation patterns underscores the sensitivity of reproduction to nutrient balance in muskoxen.

5.5.5 Nutrition, body condition and reproductive rate in muskoxen

How do nutrition and body condition affect conception and pregnancy rates in female muskoxen? Although muskox cows can calve in consecutive years, poor maternal condition or nutritional status may interfere with ovulation or conception during the breeding season and with early pregnancy, based on evidence from Victoria Island, other wild muskox populations, and captive muskoxen. Together with the apparent variation in the magnitude and duration of milk production, these observations characterize reproduction in muskoxen as flexible and finely tuned to nutrient supply.

White *et al.* (1989) suggested that poor condition or nutrition in lactating muskoxen might interfere with ovulation or conception, as has been shown in lactating bison (Kirkpatrick *et al.* 1993). Muskox herds have been observed in which there were no calves (Tener 1965), and Gray (1987) recorded three consecutive years (1968-70) on Bathurst Island during which there were no calves born, rutting behaviour was much reduced, and several animals died of malnutrition. Under such circumstances, nutritional anestrus and low ovulation rates might be expected.

While nutrition and body condition likely influence ovulation rate in Victoria Island muskoxen and in other populations, our results suggest that these factors can also affect reproductive rate after ovulation, and that post-ovulation effects were likely the major ones on Victoria Island during the study years. The substantial fat reserves, the appearance of large ovarian follicles in August, and particularly the large corpora lutea

noted in lactating cows in early September⁴ near the peak in estimated conception dates, all point to a high ovulation rate in this population. These data do not allow us to determine whether the 70 % pregnancy rate in November resulted from fertilization failures or embryo mortality, but limited evidence favours the latter. Pregnancy rates exceeding 90 % have been documented in wild muskox populations (Jingfors and Klein 1982; Latour 1987; Rowell 1989). In cattle, pregnancy losses to embryonic mortality following one service are typically three to four times greater than losses to fertilization failure (Sreenan and Diskin 1986) and a large portion of embryo mortality can be ascribed to nutrition in cattle and sheep (Robinson 1986). The greater fatness of pregnant lactating cows compared to nonpregnant lactating cows in November indicates that the probability of being pregnant at this time of year is much enhanced by good condition, as has been shown in many species (White 1983).

Lactating females that lose condition in early winter might be particularly susceptible to pregnancy loss. We propose here one mechanism for such losses, although we recognize that the nutritional regulation of reproduction is not simple (I'Anson *et al.* 1991). Lactation tends to depress circulating levels of IGF-1 in cattle (Kerr *et al.* 1991) and muskoxen (Adamczewski *et al.* 1992), and IGF-1 levels are very sensitive to nutritional disturbance (Clemmons and Underwood 1991; Maguire *et al.* 1992). Serum levels of IGF-1 in muskoxen were at very low levels in November (Adamczewski *et al.* 1992). Circulating levels of IGF-1 in cattle are correlated with ovarian IGF-1 concentrations (Spicer and Geisert 1992), which are in turn positively correlated with luteal progesterone secretion (McArdle and Holtorf 1989; Sauerwein *et al.* 1992), the prerequisite for the maintenance of early pregnancy. The formation of a corpus luteum with inadequate progesterone output has been suggested as a cause of lower pregnancy rates in poorly-fed cattle (Spicer, Tucker and Adams 1990; Schrick *et al.* 1992) and supplemental progesterone can reduce embryonic mortality in cattle (Diskin and Sreenan 1986). These relationships would provide one means for the nutritional regulation of pregnancy rate in muskoxen during early winter. It is tempting to speculate that some of the apparent pregnancy loss in muskoxen is associated with the disappearance of the corpus luteum at 14-16 weeks of pregnancy and a probable switch to progesterone of placental origin (Rowell *et al.* 1993). Rowell (1991) suggested that this highly unusual pattern in the physiology of pregnancy in muskoxen might allow a window for the termination of pregnancy. Since diet quality decreased

⁴ The cystic corpora lutea we observed in September 1990 would likely have functioned like normal corpora lutea; this condition is common in cycling cattle, where the incidence may be up to 40 % (Roberts 1986).

from September to November, the muskox cows which conceived in the second smaller cluster of conceptions in late September and early October might be particularly susceptible to pregnancy failure.

The November-April decrease in pregnancy rate of muskoxen was not statistically significant and neither was the apparent decrease from 83 % in November 1990 to 35 % in April 1991. Was the exceptionally low pregnancy rate in April 1991 simply an artifact of small sample numbers, or was there a real change during this winter? The 70 % pregnancy rate in November is not unusually low for large bovids such as wild bison (*Bison bison*; Gates and Larter 1990; Kirkpatrick *et al.* 1993) or cattle (Sreenan and Diskin 1986). However, abortions, or pregnancy losses after the end of the embryonic phase (ca. 45 days in cattle; Ayalon 1978) are typically rare in ruminants (Sreenan and Diskin 1986). Because the cows shot in April 1991 were hunted using procedures identical to those in other winter collections and this was the largest single hunt during the study, with animals sampled from 10 different herds, the probability of a biased sample appears low. The snow data from Cambridge Bay provided no obvious reason for the apparent decline in pregnancy rate in 1990-91, except that this winter was exceptional in having little snow early but greatly increased snow depth in mid-winter. If foraging opportunities decreased sharply, the animals' nutritional status, but not necessarily their body condition, might also have decreased. A 48-hour fast during late pregnancy has been associated with premature delivery in sheep (Fowden and Silver 1985) and in horses (Silver and Fowden 1982; 30-hour fast) and the sensitivity of gonadotropin and steroid secretion to rapid changes in animals' nutritional status is well documented (Bronson and Manning 1991). The progesterone profile of late-pregnant muskox cows is again unusual among ruminants, with an apparently precipitous decline at 20-22 weeks of pregnancy (Rowell *et al.* 1993). These patterns are at best suggestive, but we raise the possibility that a third annual period exists during which muskox reproductive rates are sensitive to nutritional influences, in addition to the breeding season and the autumn-early winter period.

The overall pregnancy rate in cows at least 3.5 years old on Victoria Island was 56 % in April, if all four years are included, or 67 % if the 1991 data are excluded. These values indicate that some cows calved in alternate years, as has been suggested elsewhere (Tener 1965; Thing *et al.* 1987) but others calved in consecutive years. The reproductive histories of individual muskox cows can differ substantially (Reynolds 1989). Our results also suggest that the pregnancy rate of muskoxen is a more sensitive indicator of winter conditions than maternal body condition.

5.6 Conclusion

Seasonal patterns in body composition and reproduction of muskoxen agree with overall trends in energetics, food habits and reproduction in eutherian mammals (McNab 1986, 1987): as relatively large herbivores with a slow metabolism and a conservative lifestyle, muskoxen are slow-growing, lactation is a major nutrient expenditure, and their primary forages are of low quality. With the exception of populations growing exponentially on good range (Jingfors and Klein 1982; Rowell 1991), muskoxen exhibit slow maturation and low or moderate calf productivity. Gunn (1992) has argued that the population dynamics of muskoxen are more closely linked to their forage base than the dynamics of caribou. Our results lend support to this hypothesis. Pregnancy rates of caribou, although affected by condition during the breeding season (Dauphiné 1976; Thomas 1982; Cameron *et al.* 1993), often remain high despite harsh winters and severe loss of condition (Bergerud 1980; Gunn, Miller and Thomas 1981; Adamczewski *et al.* 1987), their recovery of condition can be very rapid (Leader-Williams and Ricketts 1982; Tyler 1987; Adamczewski *et al.* 1987), and females typically reach reproductive maturity a year earlier than muskoxen (Sjenneberg and Slagsvold 1968; Dauphiné 1976). In contrast, our results indicate that the pregnancy rates of muskoxen are commonly low or moderate and are subject to nutritional influences during at least two periods of the year, in spite of good maternal condition. The absence of calves and reduced rutting behaviour observed for three consecutive years in muskoxen on Bathurst Island (Gray 1987) further intimates that they may sometimes be unable to recover sufficient body reserves in one summer to breed. The organ and ingesta weights we measured, along with the relatively slow decline in condition during winter, provide evidence of the minimal energy needs and excellent adaptation of muskoxen to low-quality graminoid forages. These characteristics make possible the unique late-winter parturition of muskox cows and the ability of muskox calves to utilize summer forages as full ruminants.

CHAPTER 6. THE ECOLOGICAL IMPLICATIONS OF A SLOW METABOLISM AND A CONSERVATIVE LIFESTYLE IN MUSKOXEN

Muskoxen are well adapted to digestion of low-quality forage at remarkably low intake, can deposit substantial fat and conserve it during winter, and show a considerable sensitivity of reproduction to nutrition. These patterns can be drawn from the research presented here, together with related studies of metabolism (Nilssen *et al.* 1994), nutrition (White *et al.* 1984, Staal and Thing 1991, Staal and Olesen 1992), body composition (Thing *et al.* 1987, White *et al.* 1989) and reproduction (Rowell 1991). The benefits of this suite of features, centred on a slow metabolism and clearly those of a K-selected species, are substantial. Are there also less advantageous aspects? In this final section, the ecological implications of these related characteristics of muskoxen are considered briefly.

The advantages of a slow metabolism and substantial fat stores in muskoxen can be summarized as follows. Caribou, as the other large arctic herbivore, serve as a useful species for comparison¹.

(1) Unlike large bovine grazers, muskoxen require relatively little forage in winter. The absolute feed requirements of muskoxen in winter are similar to those of caribou weighing less than half as much (cf. Fancy 1986, Crête *et al.* 1993). On thinly vegetated tundra covered with hard snow, there is great advantage in needing little food.

(2) Muskoxen need not forage widely in search of high-quality food. The sedentary activity patterns of muskoxen in winter have been documented (Jingfors 1981, Raillard 1992). In much of the arctic, grasses and sedges are among the most common plants (Wielgolaski *et al.* 1982). Raillard (1992) estimated that muskoxen grazed 3.9 ± 1.4 % of the available shoots in wet sedge meadows on Ellesmere Island during the 2-month growing season, but 43.7 ± 5.1 % of them during the other 10 months. Their diet in winter included large proportions of the dead plant material in these meadows. Caribou, by comparison, are nomadic herbivores that often forage widely in search of suitable food (Russell *et al.* 1993). Reindeer offered diets of 100 % grass hay either refused to eat it or lost weight on this diet (Syrjälä-Qvist 1985). Of the subspecies of caribou and reindeer, the most grazer-like, and the most muskox-like, is the Svalbard reindeer, which has the slowest metabolism (Nilssen *et al.* 1984), greatest

¹ The comparison between caribou and muskoxen is partly confounded by differences in body size and evolutionary background. Muskoxen can also be viewed as a more specialized species and caribou as a more generalized one. Because these species are often sympatric and no other large herbivores currently exist on the tundra, the comparisons are made despite these caveats.

fat reserves (Reimers *et al.* 1982, Tyler 1987), most sedentary activity (Tyler and Øritsland 1989) and most pronounced adaptation of the alimentary tract to a grazer's diet (Staal and White 1991).

(3) The ability of muskoxen to maintain weight on relatively small quantities of low-quality forage permits them to conserve body reserves for unfavourable conditions during winter. Arctic weather and snowfalls are unpredictable and variable. On Victoria Island, mid-winter thaws and rains occurred in the 1950's (D. Kaomayok, pers. comm.). Elsewhere such conditions have proved catastrophic for caribou (Skoog 1968) and muskoxen (Vibe 1954, in Tener 1965). Muskoxen and caribou were both rare on Victoria Island during the 1950's and 1960's (Gunn 1990). Under these circumstances, substantial reserves, particularly fat, could mean the difference between survival and death. The contribution of body reserves to over-winter energy requirements has been estimated at 15-25 % in female Svalbard reindeer (Tyler 1987) and 14-19 % in female caribou on Coats Island, NWT (Adamczewski *et al.* 1993). Because female muskoxen can deposit about as much fat as Svalbard reindeer and have a slower metabolism, body reserves could well contribute more to the winter needs of muskoxen than to those of caribou, and thus serve as stronger insurance in severe winters.

(4) The late-winter parturition of muskoxen, several weeks before that of caribou, would be unlikely without the low maintenance costs, digestive adaptations and ability of muskoxen to conserve fat in winter. Although peak lactation may not occur in wild muskoxen until summer (Chapter 5), the rapid depletion of fat in parturient muskox females from April to May (Chapter 5) is comparable to that in newly-lactating cattle, goats and sheep (Vernon and Flint 1984). Estimates of the contribution of body fat to milk production in the initial weeks of lactation in these species range up to 50 % or more, depending on plane of nutrition and maternal condition (Vernon and Flint 1984). This reproductive schedule gives muskox calves a "jump-start" on summer growth and allows them to make use of forage throughout the growing season as full ruminants, while gaining additional nutrients from milk. On Victoria Island, muskox calves weighed 70-90 kg by 6 months of age, more than adult female caribou, and had deposited substantial fat (1.5-2.5 cm back fat). This extended calf growth was largely made possible by maternal energetic and digestive traits.

The less advantageous aspects of the conservative energetics and lifestyle of muskoxen are not as intuitively apparent, but they are considerable. Were a slow metabolism entirely advantageous in the arctic, then a slow metabolism should be expected in caribou and other northern herbivores. This is not the case. Caribou have a

relatively rapid metabolism (Tyler and Blix 1990) but are a far more successful species than muskoxen in terms of diversity, numbers, range, and niche breadth. A discussion of the disadvantageous implications of a slow metabolism and sedentary lifestyle in muskoxen follows.

(1) A slow metabolism is generally associated with low productivity. In eutherian mammals, high weight-scaled basal metabolic rates are positively albeit loosely correlated with rapid growth, early weaning, high fecundity, and a high intrinsic rate of population increase, r_m (McNab 1980, 1987, Hennemann 1983, Kurta and Ferkin 1991). These relationships are not universally accepted (Harvey *et al.* 1991), vary among taxa (Hayssen and Lacy 1985), and are also affected by life-history traits such as food habits (McNab 1986). Muskoxen follow McNab's patterns well: their primary foods are of low quality, their growth is relatively slow (Parker *et al.* 1990), they mature late (Tener 1965, Chapter 5), and their reproductive rates are usually low (Tener 1965, Gray 1987, Thing *et al.* 1987, Chapter 5). While muskoxen are capable of a high r under exceptional circumstances (Gunn *et al.* 1991), the realized r of most muskox populations is likely to remain low.

Intrinsically low population productivity would be a severe handicap under heavy mortality, and would slow recovery during favourable periods. Severe hunting extirpated muskoxen in Alaska in the 1860's and nearly eliminated them from the Canadian mainland in the late 19th century (Barr 1991). The recovery from these ebb densities took many decades, much of it under full protection from hunting. There is little information on rates of wolf predation on muskoxen, but Tener (1965) and Gray (1987) noted that wolves kill muskox bulls, cows, and immature animals, while calves are easy prey if separated from the herd. In muskox herds where calf productivity is low, the loss of even a few calves to wolves would have a serious impact on herd numbers (Tener 1965). Caribou, in contrast, have rarely been documented with pregnancy rates below 80-85 % in animals at least 3 years old (Bergerud 1980, Thomas and Barry 1990), mature at least a year earlier than muskoxen (cf. Dauphiné 1976, Sjenneberg and Slagsvold 1968), and recover from the costs of lactation more quickly than muskoxen (Parker *et al.* 1990). In wild wapiti (*Cervus elaphus*) cows with a mature weight of ca. 250 kg, greater than that of muskoxen, pregnancy rates averaged 24 % in 1-year-olds and 93 % in females ≥ 2 years old (Flook 1970). While more Peary caribou than muskoxen died during severe winters on the western Queen Elizabeth Islands in the 1970's (Miller *et al.* 1977), they were likely also able to recover numbers more quickly under favourable conditions. Gray's (1987) observations of three

consecutive years of non-existent calf productivity in Bathurst Island muskoxen has no parallel in caribou or other cervids.

(2) Muskoxen live in a strongly variable environment, but are not well-suited to long-range movements. Historically large fluctuations in density of muskoxen (Vibe 1967, Gunn 1982, 1990, Barr 1991, Forchhammer and Boertmann 1993) indicate that muskox range conditions have also varied greatly. The ability of caribou to move long distances has long been recognized (Kelsall 1968) and includes long-range seasonal movements between islands of the arctic archipelago (Miller and Gunn 1980), with high energetic efficiency (Fancy 1986). Caribou are also strong swimmers (Kelsall 1968). No such between-island movements occur in muskoxen, they swim poorly, if at all (Gray 1987) and avoid walking over ice unless it is covered by hard snow (Gray 1987). Muskoxen are heavy-bodied and stout-limbed. Their efficiency of locomotion has not been measured but is likely low. A winter foraging strategy based on minimal movement and heavy use of local forage (cf. Raillard 1992) would be a handicap if snow and ice, or heavy grazing, reduced forage availability to near-zero and required movement to distant terrain. The relatively small heart of muskoxen may well contribute to lower maintenance requirements, but would be a handicap should a more cursorial mode of existence be required. The factors which limit the southerly range of muskoxen are not well defined, but increased susceptibility to a diversity of predators and a poor ability to cope with deep, soft snow may well be important. In both cases the limited "athleticism" and heavy-bodied, short-legged conformation of muskoxen are disadvantageous.

The persistence of muskoxen and caribou through several ice ages, and their continued sympatric existence on many arctic islands, shows that the challenge of being a large herbivore on the arctic tundra can be "solved" by different strategies, each with its advantages and disadvantages. As the only large tundra grazer, muskoxen are a marvelous example of adaptive radiation in mammals.

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Appendix 7.1 Anatomical and chemical body composition of 20 muskoxen and 2 muskox fetuses from Victoria Island, Northwest Territories.

7.1a. Anatomical data. Values are weights in kg except where noted otherwise.

Animal #	Sex	Age (yrs)	Whole body	Ingesta	IFBW ^b	Total muscle	Gastroc nemius (g)	Total Bone	Total Dissectible fat	Depth of back fat (cm)	Kidney fat ^c (g)	Hair	Carcass e	Carcass Muscle	Carcass Bone	Carcass Fat	Carcass Other Tissue
574	F	4	203.0	39.4	147.1	66.27	582	24.89	20.09	2.9	286	5.840	99.4	64.21	17.22	14.48	2.41
568	F	3	135.0	41.4	93.6	51.09	414	19.81	7.14	0.9	85	6.024	68.5	49.25	13.17	4.46	1.31
569	M	1	79.5	19.5	60.0	26.95	263	11.82	3.54	1.7	77	3.943	35.9	26.34	8.49	2.40	0.41
616	M	0.1	25.0	2.4	22.6	9.70	119	5.01	0.51	0.2	40	0.666	14.0	9.41	3.55	0.21	0.25
624	F	5+ ^a	175.0	33.9	141.1	60.28	463	23.11	17.70	1.2	247	6.332	89.0	58.20	15.54	12.41	1.11
625	M	0.1	19.0	2.1	16.9	6.89	81	4.13	0.46	0	14	0.500	10.5	6.52	3.06	0.39	0.20
626	M	0.1	17.5	1.8	15.7	5.87	69	3.49	0.21	0.1	21	0.664	8.1	5.66	2.43	0.09	0.16
633	M	0.1	13.0	0.7	12.3	4.45	44	3.12	0.38	0.1	32	0.476	7.5	4.32	2.11	0.16	0.26
707	F	5+	169.0	50.4	118.6	51.47	445	18.27	20.73	3.3	248	5.060	75.6	50.43	12.34	13.43	1.31
709	M	0.5	61.0	15.5	45.5	20.30	213	8.41	3.35	0.7	87	2.162	27.3	19.65	6.11	2.11	0.45
711	F	5+	173.0	45.1	127.9	54.96	465	19.59	11.19	1.6	165	4.844	80.0	54.36	13.40	7.46	1.31
825	M	1	78.0	19.8	58.2	26.49	255	10.62	2.48	0.2	54	4.364	33.5	25.61	7.21	1.72	0.63
832	F	4	150.0	44.7	105.3	45.88	-	18.27	9.49	1.9	116	5.189	62.5	43.96	12.78	6.50	1.31
834	F	3	154.0	45.7	108.3	49.78	447	19.95	9.70	1.8	101	5.220	70.0	47.68	13.78	5.91	1.41
865	F	5+	166.0	43.4	122.6	51.64	446	22.33	11.03	1.1	135	5.522	72.5	50.59	15.62	7.46	1.35
947	F	3.5	181.0	47.6	132.4	53.76	428	20.47	27.87	4.6	417	4.665	88.0	51.23	15.93	21.43	1.60

Appendix 7.1a cont'd

Animal #	Sex	Age (yrs)	Whole body	Ingesta	IFBW ^b	Total muscle	Gastroc nemius (g)	Total Bone	Total Dissectible fat	Depth of back fat (cm)	Kidney fat ^c (g)	Hair	Carcass	Carcass Muscle	Carcass Bone	Carcass Fat	Carcass Other Tissue
949	F	3.5	186.0	58.0	127.0	55.23	-	18.14	24.86	4.3	338	6.241	98.0	54.21	13.27	19.02	2.13
953	F	2.5	108.0	36.6	71.4	34.16	314	15.64	7.58	1.8	127	3.749	48.0	31.56	11.31	5.33	0.75
955	F	5+	197.0	45.1	150.9	58.91	488	19.45	33.62	4.0	568	5.570	99.0	57.86	13.19	25.80	1.82
1021	F	2	84.0	17.5	66.5	32.77	310	12.77	4.00	0.4	89	3.551	41.0	31.60	8.49	2.76	0.81
5740	F ^d	0	9.26	0.24	9.02	2.37	26.5	2.00	0.43	0.1	30	0.284	4.15	2.17	1.37	0.28	0.15
5840	M ^d	0	9.52	0.36	9.16	2.76	29.7	2.35	0.53	0.1	66	0.278	4.35	2.58	1.62	0.33	0.12

^a Muskoxen classified as 5+ were at least 5 yrs old.

^b IFBW is ingesta-free body weight, or weight of the whole body minus ingesta and minus the gravid uterus. Animals 947, 949 and 955 were in early pregnancy with a gravid uterus less than 1 kg; # 574 had a gravid uterus weighing 16.5 kg.

^c Kidney fat was trimmed according to Riney (1955).

^d Fetuses from cows ca. 3 wks before parturition.

^e Total weights of carcass tissues do not exactly match carcass weight because only one side was dissected and the side tissue weights were doubled.

Appendix 7.1b. Bone weights (wt) and lengths (lt).

Anim- al #	Femur wt (g)	Femur lt (cm)	Tibia wt (g)	Tibia lt (cm)	Metatarsus wt (g)	Metatarsus lt (cm)	Humerus wt (g)	Humerus lt (cm)	Radius- ulna wt (g)	Radius- ulna lt (cm)	Metacar- pus wt (g)	Metacar- pus lt (cm)
574	689	31.3	504	30.8	-	-	762	29.4	520	35.4	-	-
568	549	29.4	390	28.8	158	16.0	627	28.0	428	33.5	172	15.3
569	413	25.0	292	24.6	130	14.8	448	23.7	313	27.8	140	13.9
616	176	17.3	142	17.2	66	11.7	183	16.6	140	19.9	70	11.0
624	670	30.3	456	29.3	183	16.8	772	27.5	513	33.8	201	15.7
625	149	16.6	114	16.7	52	11.2	150	16.0	121	19.0	60	10.3
626	129	15.6	98	15.7	52	10.2	128	15.3	102	18.0	54	9.9
633	117	14.6	85	14.8	45	10.3	113	14.2	94	17.2	50	9.9
707	519	27.9	367	27.9	150	15.5	622	26.7	419	32.8	165	15.0
709	323	21.5	221	20.9	107	13.1	330	20.2	233	23.9	114	12.5
711	597	30.2	425	29.7	163	16.0	698	28.1	472	34.3	187	15.5
825	384	24.3	281	24.5	130	15.2	404	23.1	294	27.3	151	14.3
832	-	-	-	-	146	15.6	590	26.4	397	32.6	163	14.9
834	519	29.3	381	28.8	149	16.4	663	28.2	427	33.9	165	15.6
865	584	29.9	-	29.2	170	16.5	705	27.8	460	33.9	185	15.5
947	546	28.3	384	28.0	150	15.7	620	26.4	417	32.1	175	15.0

Appendix 7.1b cont'd

Anim- al #	Femur wt (g)	Femur lt (cm)	Tibia wt (g)	Tibia lt (cm)	Metatar- sus wt (g)	Metatar- sus lt (cm)	Humerus wt (g)	Humerus lt (cm)	Radius- ulna wt (g)	Radius- ulna lt(cm)	Metacar- pus wt (g)	Metacar- pus lt (cm)
949	551	29.6	401	28.5	-	-	654	26.7	451	32.5	168	14.8
953	441	26.3	316	25.9	139	15.5	472	23.9	332	29.3	158	14.7
955	548	28.3	388	27.5	152	15.3	635	26.2	421	32.5	168	14.6
1021	402	26.2	300	26.2	136	15.5	394	24.3	303	28.9	151	14.9
5740	74	13.4	61	14.0	38	9.6	69	12.9	61	15.5	38	9.0
5840	80	13.7	62	13.8	40	9.6	78	13.1	67	15.4	43	9.1

Appendix 7.1c. Chemical composition and lipid proportions.

Anim- al #	Chemical Composition of Adjusted IFBW ^a							Composition of Lipid Extracts					
	Adjusted IFBW (kg)	% Water	% Protein	% Ash	% Lipid	% Chol- esterol esters	% Trigly- cerides	% Free Fatty Acids	% Digly- cerides	% Chol- esterol	% Mono- glycerides	% Phos- pholipids	
574	139.49	57.13	16.72	4.72	21.43	0	97.19	0.94	0.19	0.58	0	0.99	
568	85.94	62.80	18.60	5.57	13.02	0	96.33	1.28	0	0.45	0	1.75	
569	55.42	63.13	19.52	4.73	12.62	0	95.88	1.10	0	0.35	0	2.40	
616	21.80	71.98	18.72	4.43	4.88	1.18	70.02	10.55	0.65	5.15	0.79	10.49	
624	132.79	59.84	17.74	5.42	16.99	0.02	96.19	1.54	0.05	0.38	0.01	1.63	
625	16.33	72.17	20.12	5.06	2.64	0.36	70.08	6.70	0	5.90	0	15.26	
626	14.99	74.82	17.39	4.72	3.07	1.31	63.43	9.19	0.36	6.54	0	17.25	
633	11.78	72.62	19.43	4.69	3.26	1.63	69.32	9.97	0.30	5.16	0.23	12.05	
707	111.89	56.36	16.09	4.88	22.67	0.02	96.99	0.96	0.18	0.42	0	1.29	
709	43.10	65.46	18.24	5.14	11.16	0	93.95	2.64	0.24	1.12	0	1.84	
711	121.31	63.18	16.71	4.64	15.47	0.02	96.69	1.42	0.19	0.67	0	0.91	
825	53.36	69.65	18.10	4.61	7.65	0.41	91.48	2.30	0.30	1.61	0	3.51	
832	98.32	64.73	17.50	4.62	13.16	0	95.88	0.16	0.27	1.61	0	1.86	
947	126.09	54.54	15.60	4.78	25.08	0.04	94.77	1.61	0.48	1.52	0	1.42	

Appendix 7.1c cont'd

Anim- al #	Chemical Composition of Adjusted IFBW ^a					Composition of Lipid Extracts						
	Adjusted IFBW (kg)	% Water	% Protein	% Ash	% Lipid	% Chol- esterol esters	% Trigly- cerides	% Free Fatty Acids	% Digly- cerides	% Chol- esterol	% Mono- glycerides	% Phos- pholipids
949	119.19	56.72	14.74	4.09	24.46	0.01	94.79	2.12	0.23	0.75	0.15	1.75
953	66.39	65.29	15.08	4.84	14.78	0.02	94.18	2.14	0.34	0.91	0	2.16
955	143.80	51.46	14.69	4.42	29.43	0.03	95.91	2.07	0.22	0.86	0.09	0.74
1021	62.37	66.95	17.68	4.79	10.58	0	93.57	1.96	0.23	1.19	0	2.75
5740	8.66	74.48	16.15	4.72	4.64	0.38	82.96	3.33	0.19	2.99	0	9.14
5840	8.74	74.76	16.66	4.36	4.21	0.54	81.33	4.79	0.13	2.80	0	9.38

^a Adjusted IFBW is IFBW minus weight of the hair, hooves and horns.

Appendix 7.2a Seasonal changes in weight and condition of 4-year-old muskox cows on Victoria Island, 1989-1993. Means are presented \pm 1 S.E. and are in kg except where noted. L = lactating; P = pregnant; N = not.

Measurement	April			May			July		
	P, NL	NP, L	NP, NL	P, NL	NP, L	NP, NL	L	NL	NL
Sample number	10	4	4	2	3	3	4	4	1
Body	178.0 \pm 3.7	144.0 \pm 3.8	168.1 \pm 12.0	152.5 \pm 6.5	150.0 \pm 6.7	138.5 \pm 5.3	157.3 \pm 2.6	162.5	162.5
Ingesta-free body	127.7 \pm 3.4	104.9 \pm 5.8	121.4 \pm 13.0	98.2 \pm 3.3	107.2 \pm 7.3	96.1 \pm 6.0	108.3 \pm 3.3	120.9	120.9
Carcass	82.7 \pm 2.3	67.0 \pm 4.3	77.2 \pm 8.7	62.0 \pm 2.0	67.7 \pm 4.5	61.1 \pm 4.1	63.7 \pm 2.2	72.0	72.0
Total fat	23.7 \pm 1.4	11.9 \pm 2.3	17.9 \pm 5.3	11.0 \pm 1.5	10.8 \pm 2.5	9.0 \pm 2.0	11.0 \pm 1.3	15.8	15.8
Dissectible fat	18.7 \pm 1.2	8.9 \pm 1.9	12.9 \pm 3.9	8.9 \pm 1.2	8.0 \pm 1.5	6.3 \pm 1.7	7.7 \pm 0.8	11.6	11.6
Protein	19.9 \pm 0.5	16.5 \pm 0.9	18.9 \pm 1.9	15.5 \pm 0.5	16.8 \pm 1.1	15.2 \pm 0.9	17.0 \pm 0.5	18.9	18.9
Muscle	54.7 \pm 1.7	46.2 \pm 1.5	54.4 \pm 4.6	42.8 \pm 0.5	46.7 \pm 2.6	43.9 \pm 1.7	45.6 \pm 1.9	50.1	50.1
Ash	5.72 \pm 0.15	4.70 \pm 0.26	5.43 \pm 0.58	4.40 \pm 0.15	4.80 \pm 0.33	4.30 \pm 0.27	4.84 \pm 0.15	5.41	5.41
Bone	19.6 \pm 0.5	18.2 \pm 0.6	19.9 \pm 0.9	17.5 \pm 0.6	18.9 \pm 0.0	17.8 \pm 0.5	18.4 \pm 0.5	19.3	19.3
Depth of back fat (cm)	2.36 \pm 0.13	1.00 \pm 0.26	1.13 \pm 0.53	0.85 \pm 0.25	0.90 \pm 0.12	0.77 \pm 0.38	0.83 \pm 0.17	1.40	1.40
Kidney fat (g)	284 \pm 28	127 \pm 24	174 \pm 61	157 \pm 35	102 \pm 21	89 \pm 16	113 \pm 15	163	163
Femur marrow fat (%)	90.5 \pm 0.6	85.5 \pm 3.4	80.3 \pm 12.6	86.7 \pm 0	79.2 \pm 3.1	86.9 \pm 2.2	62.0 \pm 7.2	87.2	87.2
Rumen contents	25.3 \pm 1.8	32.4 \pm 2.2	33.0 \pm 2.2	30.0 \pm 0	25.2 \pm 0.6	26.0 \pm 2.7	24.6 \pm 0.7	24.5	24.5
Rumen tissue	3.10 \pm 0.13	3.08 \pm 0.03	3.48 \pm 0.34	2.96 \pm 0	3.11 \pm 0.10	3.13 \pm 0.03	4.53 \pm 0.17	4.50	4.50
Kidneys (g)	237 \pm 15	237 \pm 8	275 \pm 23	241 \pm 11	260 \pm 20	220 \pm 13	478 \pm 10	480	480
Liver	1.27 \pm 0.04	1.19 \pm 0.08	1.46 \pm 0.13	-	1.24 \pm 0.12	1.13 \pm 0.04	2.62 \pm 0.08	2.58	2.58

Appendix 7.2a continued

Measurement	August		September		November		
	L	NL	L	NL	P, L	P, NL	NP, L
Sample number	1	2	1	2	1	7	2
Body	195.0	180.0 ± 20	227.0	209.3 ± 2.2	210.0	197 ± 3.2	183.5 ± 17.5
Ingesta-free body	164.0	142.9 ± 22	171.6	172.8 ± 7.2	165.0	151.6 ± 1.4	136.3 ± 7.8
Carcass	102.0	91.0 ± 19	107.0	109.8 ± 4.8	107.0	98.8 ± 0.9	87.0 ± 6.0
Total fat	37.6	28.3 ± 14.4	39.4	44.5 ± 0.9	39.9	42.3 ± 0.9	30.8 ± 0.7
Dissectible fat	28.7	22.2 ± 3.3	26.4	26.6 ± 1.1	25.5	23.5 ± 0.2	21.2 ± 1.2
Protein	25.3	22.2 ± 3.3	26.4	26.6 ± 1.1	25.5	23.5 ± 0.2	21.2 ± 1.2
Muscle	64.3	-	71.3	65.5 ± 1.0	71.0	61.4 ± 0.6	58.0 ± 3.3
Ash	7.35	6.40 ± 1.00	7.69	7.74 ± 0.32	7.40	6.79 ± 0.06	6.10 ± 0.35
Bone	18.9	-	22.7	19.5 ± 0.5	21.5	19.1 ± 0.3	18.6 ± 0.6
Depth of back fat (cm)	3.70	2.55 ± 1.25	2.90	4.70 ± 0	2.60	4.71 ± 0.15	2.90 ± 0
Kidney fat (g)	431	316 ± 24	465	559 ± 19	458	591 ± 25	372 ± 24
Femur marrow fat (%)	86.1	-	97.0	96.0 ± 1.0	90.0	93.6 ± 0.7	92.6 ± 0
Rumen contents	29.5	28.3 ± 3.2	43.8	32.1 ± 2.4	39.3	33.6 ± 1.3	35.2 ± 7.6
Rumen tissue	4.50	4.42 ± 0.08	5.16	4.40 ± 0.10	4.66	4.16 ± 0.10	4.25 ± 0.05
Kidneys (g)	442	448 ± 24	447	384 ± 10	315	262 ± 5	293 ± 19
Liver	2.76	2.38 ± 0.08	2.25	2.19 ± 0.01	1.60	1.53 ± 0.04	1.44 ± 0.01

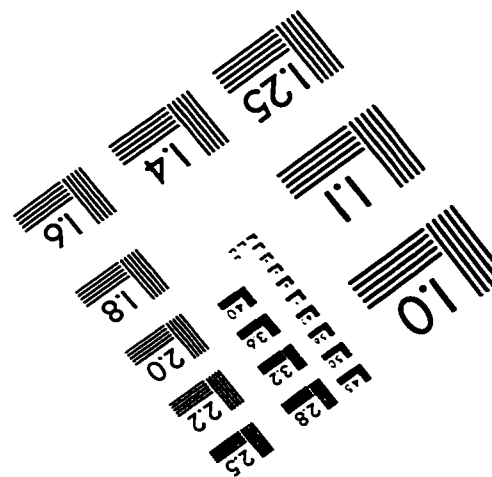
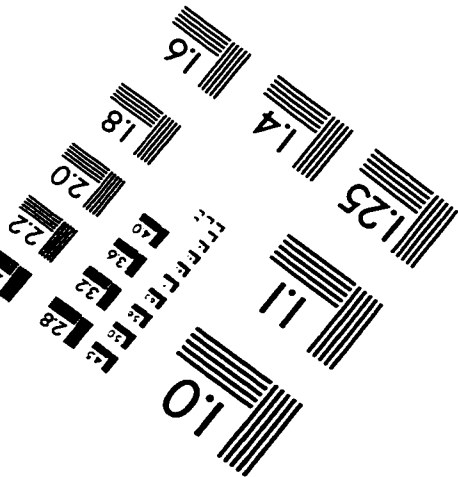
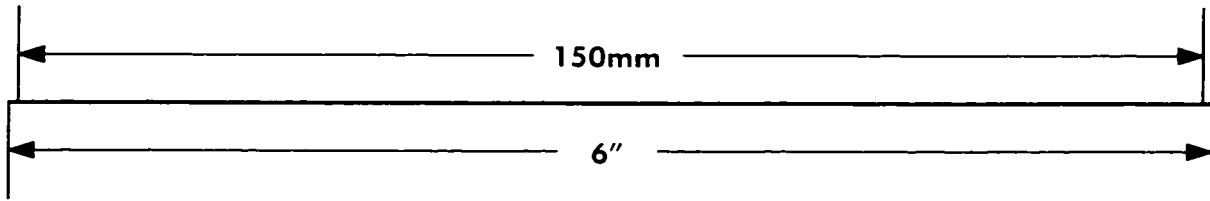
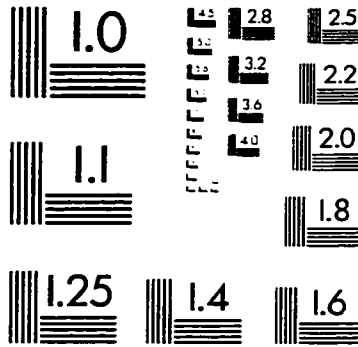
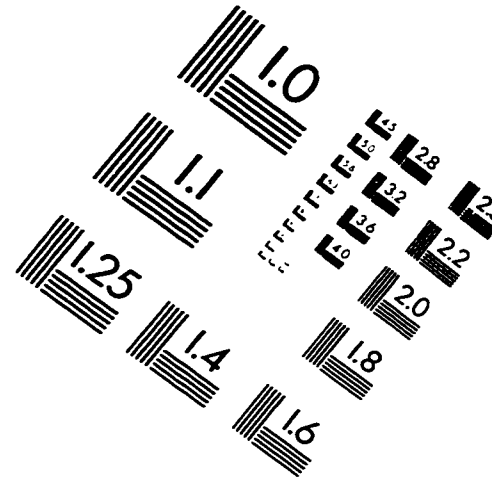
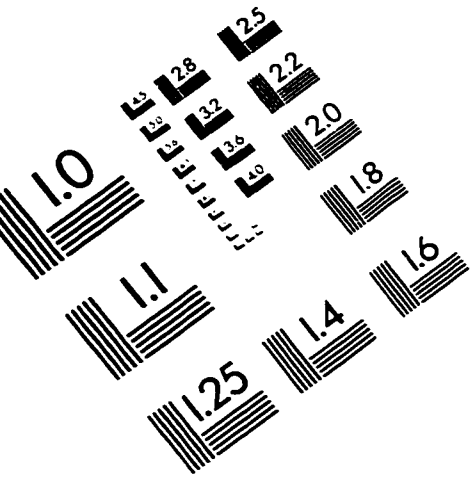
Appendix 7.2b Seasonal changes in weight and condition of 5+ muskox cows on Victoria Island, 1989-1993. Means are presented \pm 1 S.E.; values are in kg except where noted. L = lactating; P = pregnant; N = not.

Measurement	April		May		July		August		September	
	P, NL	NP, L	NP, NL	P, NL	L	L	NL	L	L	L
Sample number	18	10	4	32	4	2	1	7	7	6
Body	196.4 \pm 3.4	152.2 \pm 2.7	165.3 \pm 7.8	162.5 \pm 2.0	160.8 \pm 4.8	170.5 \pm 10.5	189.0	221.3 \pm 3.4	218.8 \pm 3.1	
Ingesta-free body	135.6 \pm 2.9	102.9 \pm 2.2	120.7 \pm 5.9	115.1 \pm 2.2	110.2 \pm 3.9	116.8 \pm 12.2	135.8	172.7 \pm 0.8	172.8 \pm 5.0	
Carcass	87.4 \pm 1.9	66.6 \pm 1.4	75.4 \pm 4.9	72.1 \pm 1.4	68.8 \pm 2.3	68.5 \pm 7.5	80.5	106.2 \pm 1.2	108.3 \pm 3.6	
Total fat	24.4 \pm 1.1	11.9 \pm 0.9	17.6 \pm 3.8	13.8 \pm 0.7	11.3 \pm 0.4	13.2 \pm 4.2	21.0	38.4 \pm 1.7	39.1 \pm 2.3	
Dissectible fat	18.4 \pm 1.0	8.4 \pm 0.7	13.3 \pm 2.9	10.2 \pm 0.6	7.5 \pm 0.2	9.7 \pm 2.3	15.8	29.0 \pm 1.2	30.2 \pm 2.1	
Protein	21.1 \pm 0.4	16.2 \pm 0.3	18.9 \pm 0.9	18.0 \pm 0.3	17.3 \pm 0.6	18.3 \pm 1.8	21.1	26.6 \pm 0.1	26.6 \pm 0.7	
Muscle	58.0 \pm 1.3	47.7 \pm 0.9	51.7 \pm 3.3	50.1 \pm 0.8	48.9 \pm 1.7	46.9 \pm 5.9	50.1	68.2 \pm 1.1	67.9 \pm 1.3	
Ash	6.07 \pm 0.13	4.61 \pm 0.10	5.40 \pm 0.27	5.15 \pm 0.10	4.93 \pm 0.18	5.23 \pm 0.55	6.08	7.73 \pm 0.04	7.74 \pm 0.22	
Bone	20.6 \pm 0.4	19.3 \pm 0.2	19.5 \pm 1.1	19.8 \pm 0.3	19.5 \pm 0.7	18.3 \pm 1.6	20.4	20.9 \pm 0.1	20.9 \pm 0.3	
Depth of back fat (cm)	2.03 \pm 0.17	0.96 \pm 0.17	1.73 \pm 0.59	1.00 \pm 0.09	0.53 \pm 0.16	1.20 \pm 0	1.60	2.63 \pm 0.20	3.48 \pm 0.36	
Kidney fat (g)	272 \pm 20	118 \pm 13	189 \pm 49	143 \pm 11	97 \pm 2	129 \pm 32	243	465 \pm 25	451 \pm 42	
Femur marrow fat (%)	90.9 \pm 0.6	87.9 \pm 1.1	84.3 \pm 5.7	84.3 \pm 1.9	85.0 \pm 1.2	69.5 \pm 11.7	85.3	93.1 \pm 1.1	94.3 \pm 0.7	
Rumen contents	30.5 \pm 1.1	32.9 \pm 1.2	33.7 \pm 3.5	28.7 \pm 0.9	30.2 \pm 2.4	28.4 \pm 1.7	33.1	33.9 \pm 1.5	35.2 \pm 1.4	
Rumen tissue	3.55 \pm 0.11	3.46 \pm 0.05	3.66 \pm 0.15	3.42 \pm 0.03	3.40 \pm 0.02	4.64 \pm 0.24	4.86	5.29 \pm 0.23	4.96 \pm 0.06	
Kidneys (g)	295 \pm 12	233 \pm 11	250 \pm 19	297 \pm 6	295 \pm 16	530 \pm 29	554	561 \pm 16	432 \pm 11	
Liver	1.50 \pm 0.10	1.18 \pm 0.03	1.31 \pm 0.08	1.48 \pm 0.11	1.43 \pm 0.07	3.05 \pm 0.13	3.30	3.07 \pm 0.06	2.32 \pm 0.02	

Appendix 7.2b continued

Measurement	November			
	P, L	P, NL	NP, L	NP, NL
Sample number	7	10	7	1
Body	223.2 ± 3.5	225.3 ± 4.3	200.1 ± 7.9	257.0
Ingesta-free body	164.0 ± 4.8	173.3 ± 3.7	143.7 ± 5.6	203.7
Carcass	105.2 ± 3.2	112.7 ± 2.5	92.0 ± 3.7	133.0
Total fat	36.9 ± 1.8	46.4 ± 0.8	26.6 ± 2.1	49.2
Dissectible fat	28.2 ± 0.9	37.5 ± 1.0	19.9 ± 1.7	39.5
Protein	25.3 ± 0.7	26.7 ± 0.5	22.3 ± 0.8	31.1
Muscle	67.3 ± 2.5	69.7 ± 1.1	60.2 ± 2.3	78.8
Ash	7.34 ± 0.21	7.76 ± 0.17	6.43 ± 0.25	9.12
Bone	21.8 ± 0.7	21.3 ± 0.5	20.2 ± 0.6	23.9
Depth of back fat (cm)	2.81 ± 0.18	4.00 ± 0.19	2.47 ± 0.21	3.10
Kidney fat (g)	427 ± 19	627 ± 26	273 ± 35	628
Femur marrow fat (%)	91.5 ± 1.4	91.1 ± 0.6	90.7 ± 2.1	.
Rumen contents	44.7 ± 1.4	36.4 ± 1.3	42.3 ± 2.1	41.8
Rumen tissue	4.65 ± 0.20	4.24 ± 0.02	4.40 ± 0.12	4.30
Kidneys (g)	329 ± 15	312 ± 12	293 ± 17	353
Liver	1.70 ± 0.06	1.63 ± 0.06	1.59 ± 0.07	1.84

IMAGE EVALUATION TEST TARGET (QA-3)



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