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THE UNIVERSITY OF ALBERTA

BODY COMPOSITION IN RELATION TO SEASONAL  
FORAGE QUALITY IN CARIBOU (Rangifer tarandus groenlandicus) ON  
GOATS ISLAND, NORTHWEST TERRITORIES.

by

JAN Z. ADAMCZEWSKI

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH  
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE  
OF MASTER OF SCIENCE  
in WILDLIFE PRODUCTIVITY AND MANAGEMENT

DEPARTMENT OF ANIMAL SCIENCE

EDMONTON, ALBERTA

SPRING 1987

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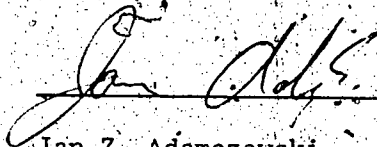
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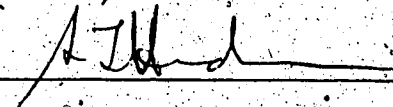
  
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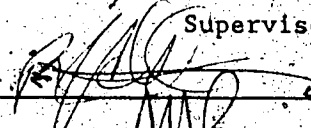
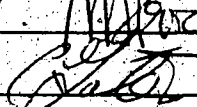
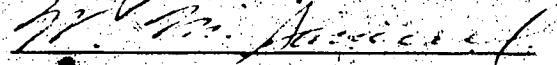
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\_\_\_\_\_  
Supervisor

  
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Date April 21/1987

This study is dedicated to the north,  
to its wild, harsh beauty  
and its humbling vastness.

## ABSTRACT

The isolated, predator-free population of barren-ground caribou (Rangifer tarandus groenlandicus) on Coats Island, Northwest Territories, Canada is ultimately limited by winter food resources. This study was undertaken to examine seasonal cycles of body composition in mature females and calves in relation to available forage, and the relationships between these cycles and population characteristics.

Vegetation available to caribou in summer was low in diversity and density, but provided abundant forage of high quality. Willows (Salix spp.), sedges (Carex spp.), and grasses (Graminae) were the major forage components, and willows were the preferred food throughout summer. Caribou grew and fattened rapidly on this forage, consistently achieving an early winter fatness approaching the extreme fatness in Svalbard reindeer (R. t. platyrhynchus). Mature females had a high rate of pregnancy entering winter. Calves grew rapidly but were unable to fatten to the same extent as adults.

Snow persisted from mid- to late October until June. By March, snow cover was consistently hard and deep, with Canadian hardness generally ranging from 4000 to 9000 g/cm<sup>2</sup> and 50-80 cm of snow on all but exposed wind-blown sites. This snow put most vegetation beyond the reach of caribou and forced them to feed in areas with sparse vegetation of poor quality. Under these conditions body reserves of fat and muscle dwindled; caribou females lost 30-35% of

their carcass muscle mass and nearly all dissectible fat during the two winters of the study, while many calves died, particularly in 1983-84. Unpredictable calf survival, consistently severe depletion of body reserves in females, and frequently poor calf production are suggested as major determinants of population structure and dynamics.



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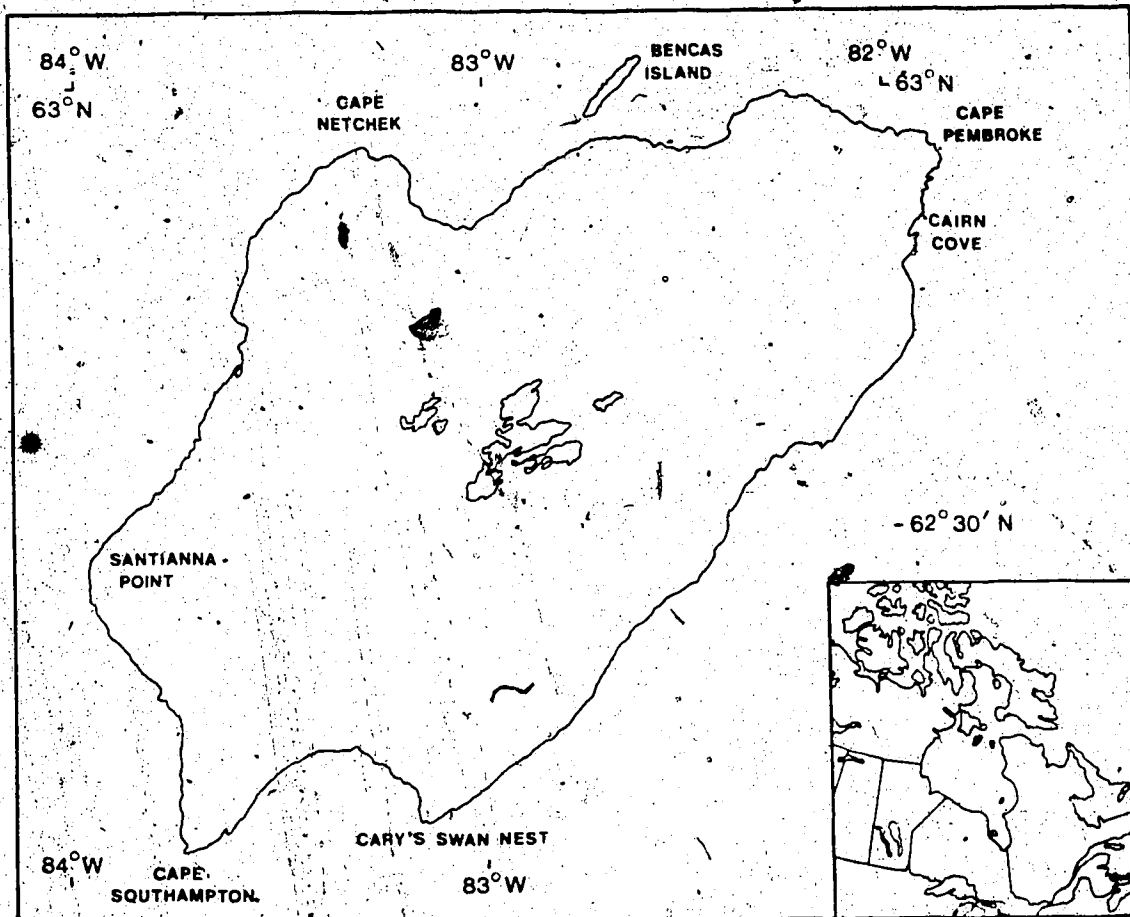
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## Chapter 1. Introduction.

Coats Island in northern Hudson Bay (Fig. 1.1) harbors an isolated population of barren ground caribou (Rangifer tarandus groenlandicus). The origin of the population is unknown, but caribou have existed on Coats Island since at least 1919 (Polunin 1948). Southampton Island, to the north, is the nearest and likeliest historic source of these caribou, although wolves, also native to Southampton Island, have not been recorded on Coats Island. Caribou on Coats Island have been known to attain exceptional weight and fatness during summer (Parker 1975) but extensive winter mortality, poor calf production, and poor calf survival have often occurred (Gates et al. 1986). Given a virtual lack of predation and limited hunting, it seemed probable that long winters, hard snow, and sparse vegetation controlled the dynamics and ecology of this population. This study was initiated to examine seasonal cycles of body composition in mature females and calves in relation to available forage, and the relationships between these parameters and population characteristics.

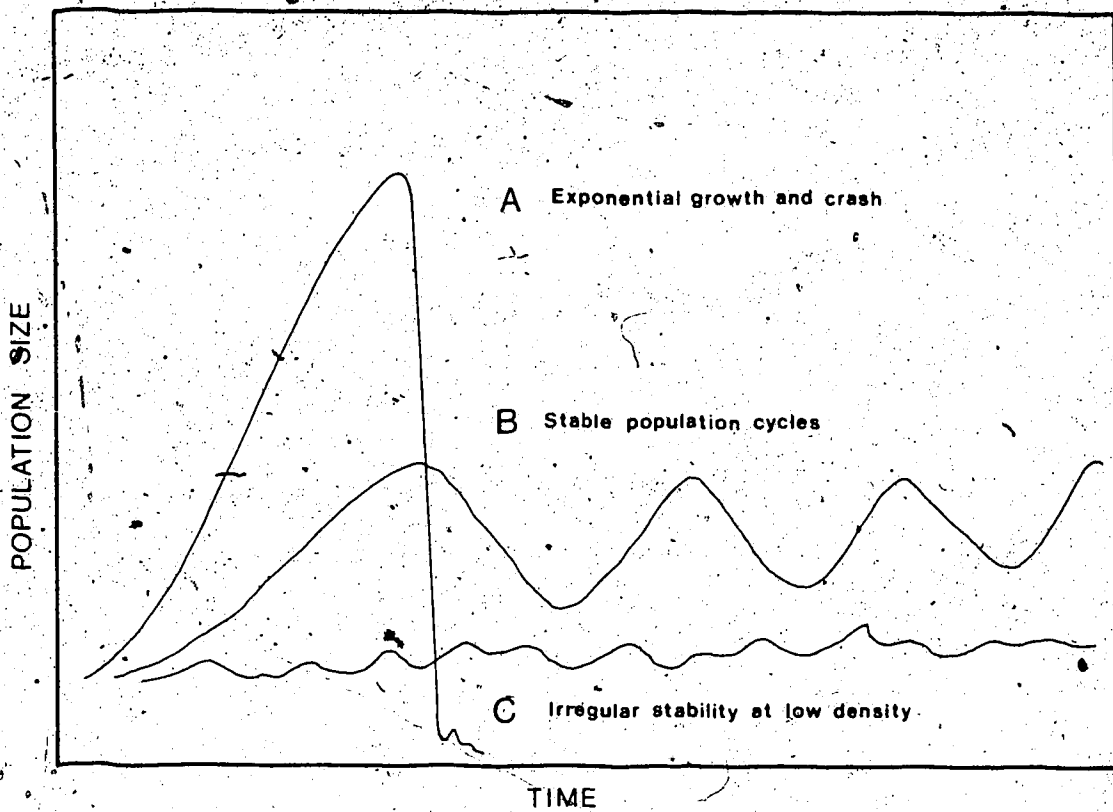
Populations of reindeer and caribou confined to an island or other bounded range may follow a number of patterns (Fig. 1.2, based on Caughley 1970). The pattern of variability in environmental severity, and the density, diversity, and resiliency of the vegetation used as forage are keys to the stability of such insular

Fig. 1.1. Coats Island, Northwest Territories, Canada.



COATS ISLAND, NORTHWEST TERRITORIES

Fig. 1.2. Possible outcomes of an ungulate expansion to new range  
(based on Caughley 1970).



populations. The most unstable (type A, Fig. 1.2), has occurred where reindeer were introduced to islands with vegetation dominated by rich but fragile lichen resources (St. Paul Island - Scheffer 1951, St. Matthew Island - Klein 1968) and where winters varied considerably in severity. Stable population cycles (type B, Fig. 1.2) are rare in insular reindeer and caribou because arctic weather is generally unpredictable and frequently severe. Reindeer introduced to St. George Island (Scheffer 1951) are probably an example of a type C population, remaining at a low density because of consistently severe winters. Most insular populations of reindeer follow a pattern intermediate between types B and C; well established, but subject to winters of variable severity. Svalbard reindeer (*R. t. platyrhynchus*) historically depleted their lichen resources and now depend on resilient graminoids and mosses (Reimers 1977). Reindeer introduced to South Georgia (*R. t. tarandus*) also depend on grazing-resistant graminoids (Leader-Williams *et al.* 1981). In both cases, populations gain stability from a consistent annual reduction of forage availability by ice or deep snow, which act to prevent over-use of forage (*op. cit.*). Peary caribou (*R. t. pearyi*) also suffer from drastic reductions in forage availability due to deep, hard snow (Miller *et al.* 1982, Thomas and Edmonds 1983) and these have recently been severe (Gunn *et al.* 1981). Skoog (1968) and Formozov (1946) have documented examples of populations altogether extirpated by severe icing.

Coats Island caribou also exhibit a population pattern



intermediate between types B and C. Population surveys from 1974 to 1984 have evinced rapid increases, crashes due to severe winters, and generally unpredictable patterns (Table 1.1). Numbers have ranged from an estimated high of 6200 prior to the severe die-off of 1975, to 1800 after it, and more recently (1980-1984) about 2000. Limited composition data indicate a very high proportion of mature females in the population (Table 1.2), with a correspondingly large capacity for calf production. However, calf production has been poor or a virtual failure during some years. Calves also appear to be very susceptible to winter undernutrition; an excellent calf crop in 1983 was decimated during the following winter. Differential mortality between males and females begins early: female calves tend to survive winter better. Seventy-one per cent of 62 calves classified in May, 1983 were females, and 62 % of 58 calves in May 1984 were females. Caribou generally have a near 50:50 male:female ratio among calves at birth (Bergerud 1980). Inuit harvests have tended to exacerbate the dearth of males by concentrating harvests in northern areas where there are relatively high proportions of males. However, the mean annual harvest of 139 (s.e. 20) for the years 1968 to 1983 has not affected population trends nearly as much as natural mortality.

Studies of body composition have proved a valuable measure in analysing population dynamics of reindeer and caribou. Calf production depends on the female gaining and conserving adequate body reserves throughout conception, pregnancy and lactation. Females in poor condition in the fall are unlikely to breed (Dauphine 1976) and

TABLE 1.1. Population estimates for Coats Island caribou, 1975-1984.

Date	Estimated number of caribou	Notes
June 1975	1814 (320) live 4415 (735) dead	78 additional dead caribou on Bencas Island.
April 1976	868 (335) live	poor visibility during census.
Nov. 1978	4236 (376) live	
April 1980	1191 (223) live	poor visibility during census.
June 1980	1672 (224) live 170 (40) dead	estimate excludes newborn calves.
June 1984	2130 (228) live	only 3 carcasses seen on survey but 23 dead calves and 1 dead bull found within 6 km of Cary's Swan Nest, March-April 1984.

adapted from Gates *et al.* (1986). Based on strip-transect surveys from low-flying fixed-wing aircraft. (standard error of estimate in parentheses).

TABLE 1.2. Composition of the caribou population on Coats Island. (% in parentheses).

Date	Total >1 yr	Mature males	Juvenile males	Cows	Calves	Calves: 100 cows
June 1975 <sup>a</sup>	311				12	
Nov. 1978 <sup>a</sup>	880				113	
June 1980 <sup>a</sup>	342				32	
Nov. 1981 <sup>a</sup>	562	60(10.7)			356	76.1 <sup>d</sup>
Nov. 1982 <sup>b</sup>	67	7(10.4)	2(3.0)	58(86.6)	33	56.9
May 1983 <sup>c</sup>	311	31(9.8)	22(7.0)	262(83.2)	78	29.8
Oct. 1983 <sup>b</sup>	94			94	86	102.1
May 1984 <sup>c</sup>	506	26(5.1)	63(12.5)	417(82.4)	58	13.9
June 1984 <sup>a</sup>	407				161	47.5 <sup>d</sup>

adapted from Gates *et al.* (1986).

a - estimated during aerial survey.

b - estimated for intensive study area; ground-based.

c - estimated from island-wide ground-based survey.

d - cows assumed to be 83.2% of adults.

females in poor condition in late winter are unlikely to be pregnant (Thomas 1982). Recruitment in winter-stressed reindeer and caribou populations depends on calves conserving enough fat and protein to survive until spring. This, in turn, requires sufficient nutrition in summer for growth and fattening. Calves typically have poorer body reserves than adults and are more susceptible to undernutrition during severe winters (Reimers *et al.* 1982, Reimers and Ringberg 1983). Poor calf survival, variable calf production and winter-caused death are prominent features of the Coats Island population. Since these caribou appeared generally healthy (Table 1.3), an intensive study of body composition in females and calves, seasonal nutrition, and forage resources seemed crucial to understanding the dynamics of Coats Island caribou.

There were two objectives in this study:

1. To assess the adequacy of forage available to caribou on Coats Island during all seasons.
2. To evaluate seasonal changes in body composition of mature female caribou and calves in relation to diet, and to relate these changes to reproduction, calf survival, and other population parameters.

To meet these objectives, the following questions were considered:

TABLE 1.3. Analyses of samples from Coats Island caribou for brucellosis and parasites.

Problem	Sample number	Test method	Result	Notes
Brucellosis	26	standard serum test	all negative	- tests done at Animal Pathology Lab, University of Saskatchewan - samples from females and calves, various seasons
Lungworm <u>Elaphostrongylus cervi</u>	26	Baermann Technique for nematode larvae	all negative	- tests done at Dep't of Biology, Lakehead University, by Dr. M. Lankester - winter samples from females and calves
Small cysts in skeletal muscles	2	Microscopic examination	Probably cysticerci larvae of <u>Taenia krabbei</u>	- no exact records taken, but probably present in 20-40% of caribou studied, in various numbers; identified by Dr. Lankester - mature tapeworm found in canids; little effect on caribou
Gastro-intestinal parasites	25	Baermann Technique for nematode larvae	all negative	- summer samples from males and females shot in 1981 - done by J. B. Gray, Dep't of Zoology, University of Alberta
		Flotation Technique for parasite eggs (10 by Sheather's Sugar, 15 by zinc sulphate)	2 cases positive for <u>Monezia</u> sp. 2 cases positive for Osterategid-type eggs 4 cases positive for Nematodirid-type eggs	- # of eggs 2 and 49 - # of eggs 1 and 3 - # of eggs 1, 2, 2, and 2 - results indicate low prevalence and low intensity

Information on warbles (Oedomegna tarandi) is presented in Chapter 4

1. a. Is vegetation available in summer sufficient to sustain rapid growth and fattening and the recovery of body reserves?

b. How does snow cover limit the quantity and quality of forage available during winter?

c. What seasonal changes in diet composition, diet quality, and habitat use are forced by environmental limitations?

2. a. Can winter-stressed caribou females recover body reserves sufficiently over summer to achieve high pregnancy rates?

b. How severely are the body reserves of females stressed during winter, and what effect does this stress have on fetal growth and pregnancy?

c. Can calves grow and fatten rapidly enough over summer to survive severe winters?

The study is presented in three papers. The first paper is intended to meet the first objective - an environmental assessment of forage, snow, limitations, and seasonal diets. The second paper presents an evaluation of techniques used to measure body reserves of caribou, and the third paper is intended to meet the second objective - an analysis of seasonal changes in body composition and their relationship to reproductive parameters.

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## Chapter 2. The limiting effects of snow on seasonal habitat use and diets of caribou.

### 2.1 Introduction

Insular populations of caribou and reindeer are rarely limited by the quality of summer nutrition; the short but productive arctic summer typically produces vascular plants with concentrated nutrients (Bliss et al. 1973, Maessen et al. 1983). In most populations, such forage permits rapid growth and maturation of young animals, and the recovery of body reserves and reproductive capacity after winter (Klein 1970, Reimers 1980, Reimers et al. 1982). However, forage available in winter and a restrictive snow cover lasting 7-10 months typically limit the dynamics of island populations. Reindeer may depend on highly digestible lichens (Kelsall 1968, Gaare and Skogland 1975, Thompson and McCourt 1981), but lichens are easily over-grazed (Pegau 1970), often with disastrous results on islands (Scheffer 1951, Klein 1968). Reindeer on Svalbard (R. t. platyrhynchus) and South Georgia (R. t. tarandus) depend on more resilient graminoids, and these populations are more stable (Staal and Punsvik 1980, Punsvik et al. 1980, Leader-Williams et al. 1981). Reindeer on these islands annually find part of their range unavailable under ice or deep, hard snow (Reimers 1977, Leader-Williams et al. 1981). Severe forage restrictions decimated Peary caribou (R. t. pearyi) during the 1970's (Gunn et al. 1981) and populations may be extirpated under

conditions of severe icing (Vibe 1967, Skoog 1968).

Coats Island, Northwest Territories, Canada supports an isolated population of some 2,000 barren-ground caribou (Rangifer tarandus groenlandicus) primarily limited by unpredictable winter undernutrition (Gates et al. 1986). Caribou attain exceptional fatness in summer (Parker 1975, Chapter 4) despite sparse vegetation of low diversity (Gillett 1976). There is no record of icing on Coats Island but winters in this region are long and harsh and snow is consistently hard. Caribou dying of undernutrition on Coats Island have typically had full rumens (Gates et al. 1986), suggesting that food quality, as well as quantity, is a limiting factor in winter.

The unique conditions found on Coats Island prompted a detailed study of seasonal nutrition. There were two objectives: (1) to assess the adequacy of forage on range used in summer, and (2) to determine the qualitative and approximate quantitative effects of snow on forage availability and resulting nutrition in winter. The study comprises an analysis of vegetation of five broad range types, snow measurements during two consecutive winters, and resulting caribou habitat use, diet composition, and diet quality during two seasonal cycles.

## 2.2 Materials and Methods

The study area was described by Gates *et al.* (1986). All measurements, with the exception of composition surveys in May 1983 and May 1984 and the 1979 vegetation study, were collected within 10-15 km of Cary's Swan Nest (62° 5' N, 83° 11' W), at the southern end of Coats Island. Except for an area of Precambrian upland at the northeast end of the island, this study area has vegetation and topography typical of much of coastal Coats Island: large areas of wetland interspersed with irregular strand lines and raised beaches of shattered limestone.

### 2.2.1 Vegetation studies

Five range types used by caribou in distinguishable seasonal patterns were selected in September 1982 for both the snow and vegetation studies. The range types tended to occur in series in the study area (Fig. 2.1). Range types defined were:

(1) Ridge crests (Dryas barrens) - barren tops of strand lines and raised beaches, with less than 25% vegetative cover and with vegetation dominated by mat plants.

(2) Dryas-lichen slopes - dry slopes of strand lines below the crests, and in a few cases dry upland heath-like areas; more than 75% vegetative cover, and dominated by cushion plants and lichens. Transitions between crests and slopes were typically abrupt.

(3) Mesic meadows - usually hummocky lowland, with sedges (Carex

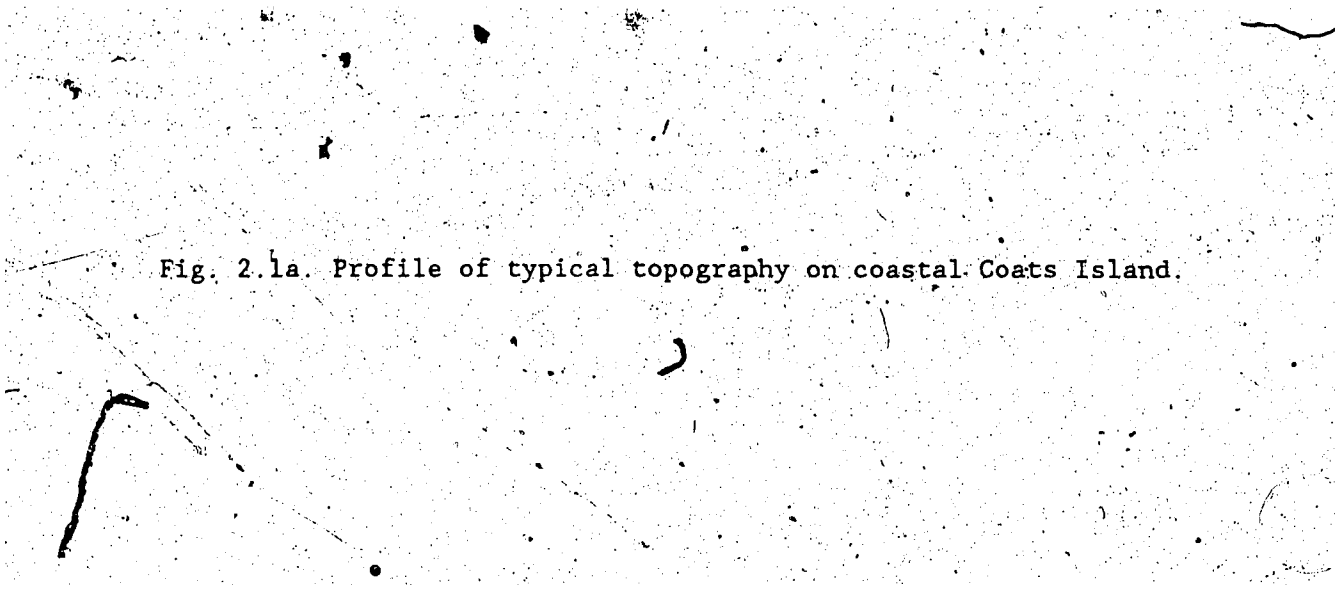
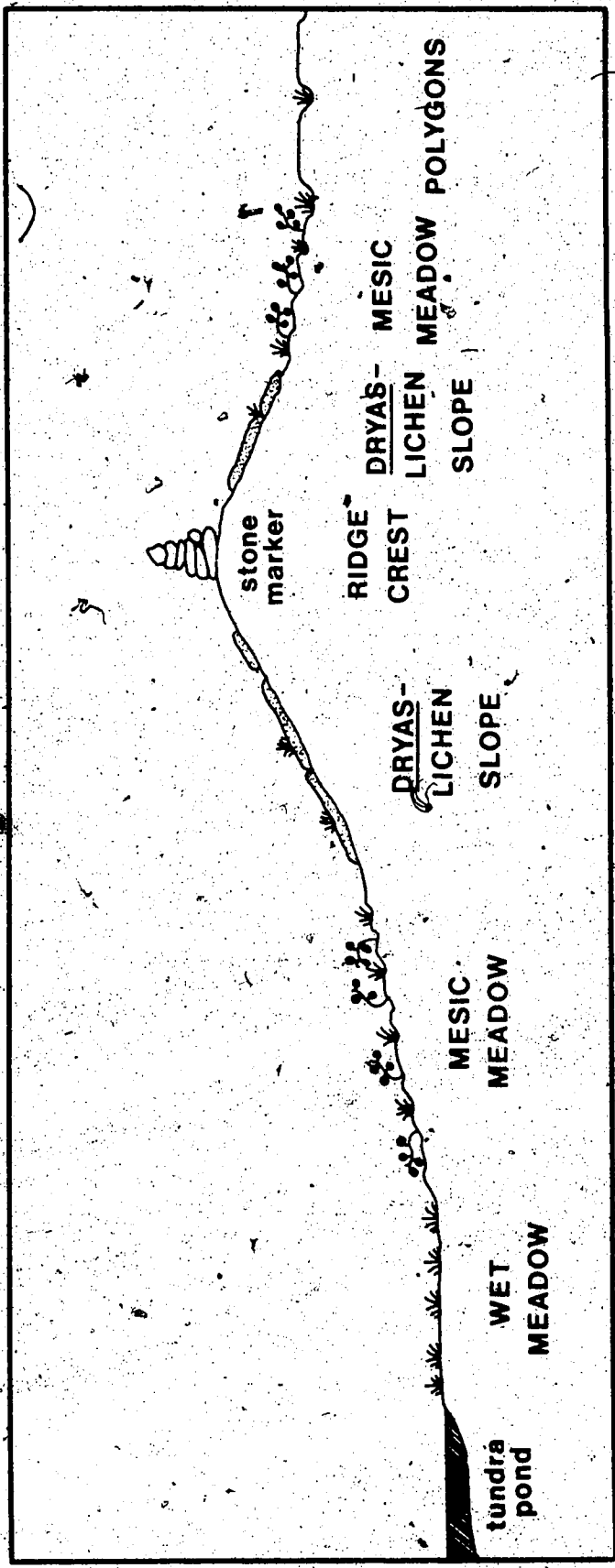


Fig. 2.1a. Profile of typical topography on coastal Coats Island.



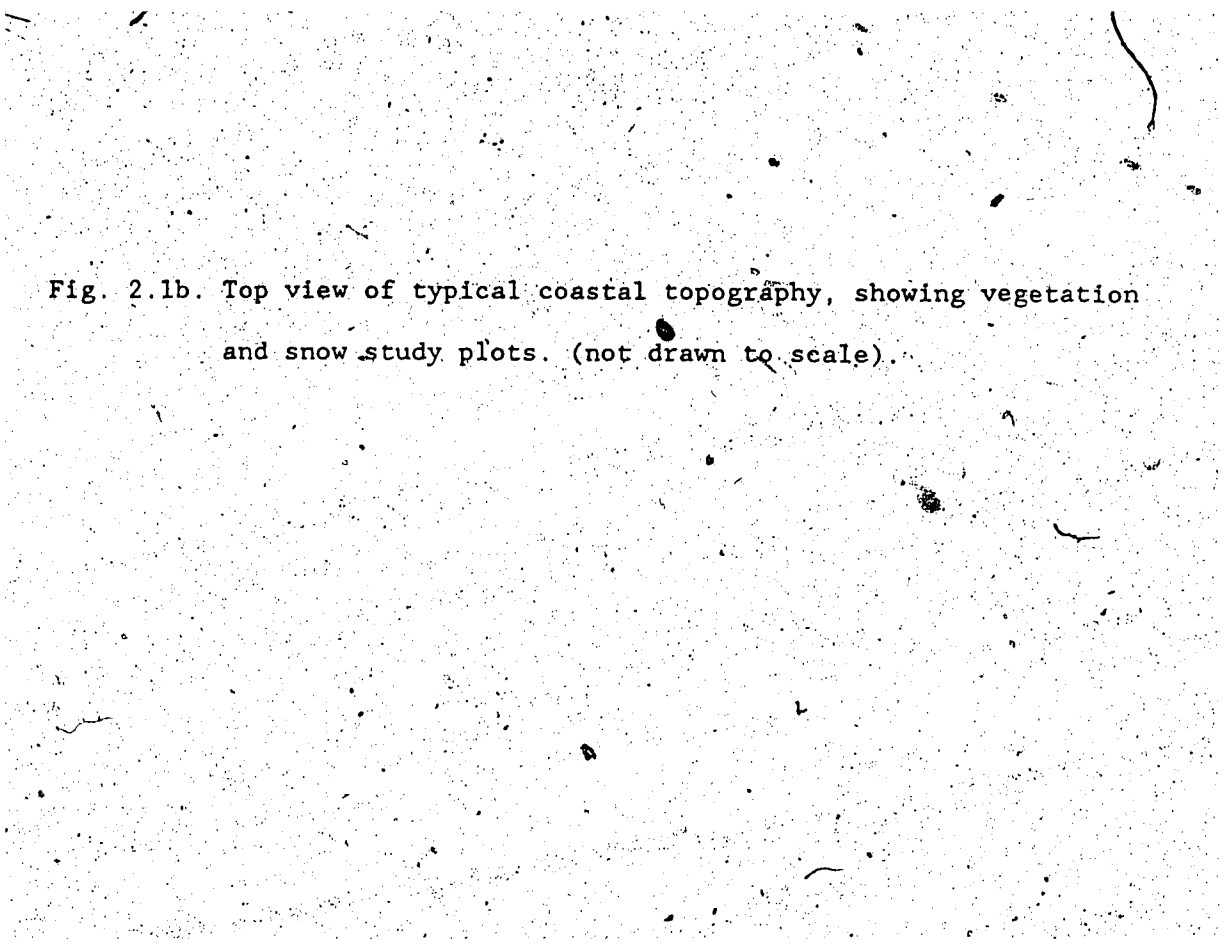
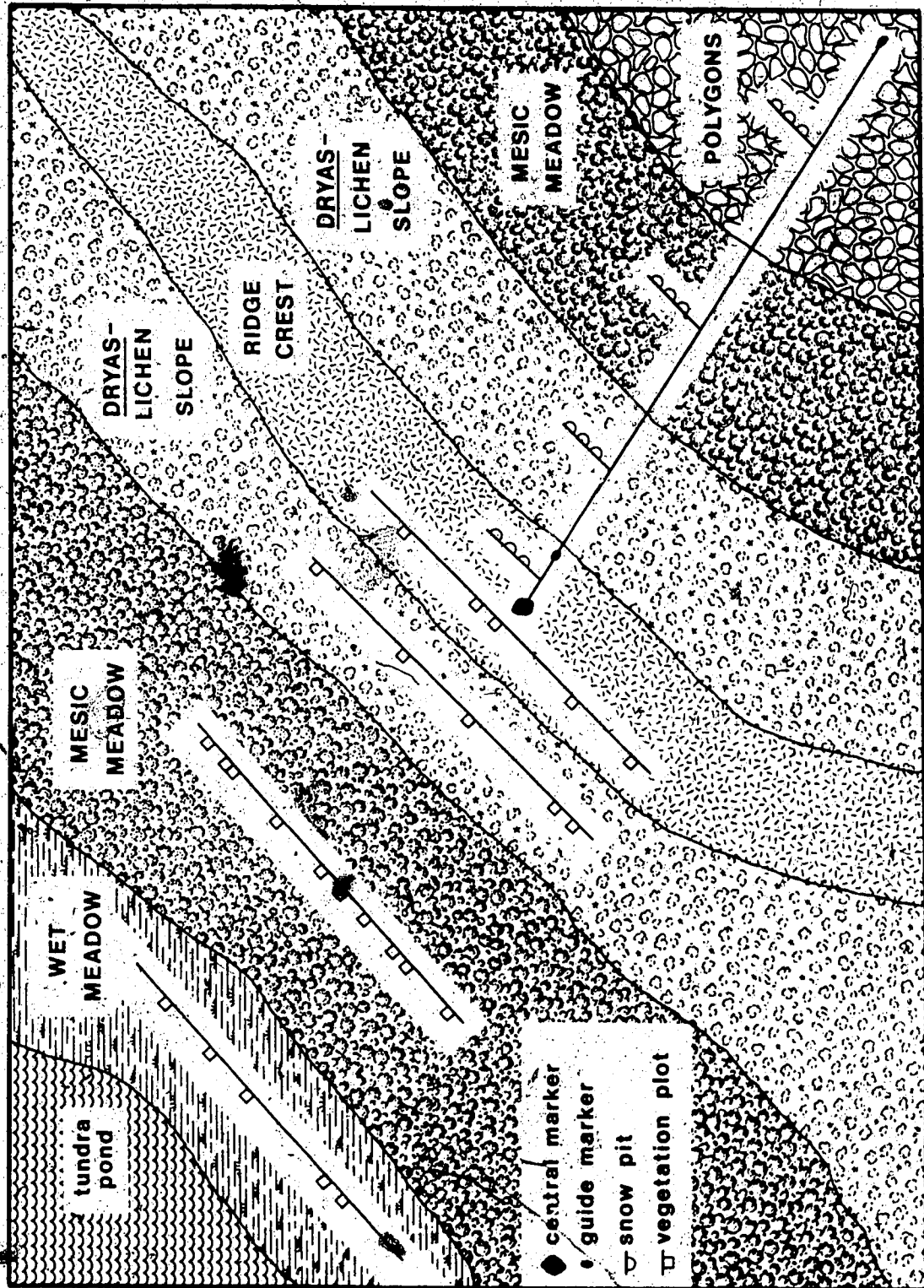


Fig. 2.1b. Top view of typical coastal topography, showing vegetation and snow study plots. (not drawn to scale).



spp.) and willows (Salix spp.) about equally dominant.

(4) Wet meadows - flat, wet, and sedge-dominated.

(5) Polygons - raised flat-topped peat polygons 2-7 m in diameter, poorly vegetated; separated by wet sedge-dominated ditches.

Eight study sites, each with 2 slopes containing most or all of the designated range types, were identified by stone markers in September 1982. Six representative slopes were chosen for the vegetation study from the 16 available. Sampling was carried out in late July and early August 1983, the expected time of peak standing crop. Within each range type, several 1 m<sup>2</sup> plots (5 or 10, depending on the diversity of the range type) were selected randomly along a 25 m transect. Cover of all plant types, bare ground, and open water was estimated visually in the plots using the Braun-Blanquet revised cover/abundance scale (Mueller-Dombois and Ellenberg 1974). The assigned values (ranges of percentages) were converted to cover values using the median percent in each category. Sedges and grasses were not identified to species due to the frequent absence of flowering parts. Standing crop of lichens and above-ground green biomass of vascular plants were determined from 0.1 m<sup>2</sup> plots (Daubenmire 1959) placed in the lower right-hand corner of the cover plots. All species were clipped at ground level except for larger willows, Dryas integrifolia, and Cassiope tetragona, for which dead material and large woody stems were discarded. Samples were stored in paper bags and weighed after drying at 65° C for 24 hours.



In August 1979, a vegetation study was carried out in north-central Coats Island (62° 30' N, 82° 30' W) and is presented here to compare with the more recent study. Standing crop of lichens and annual production of willows and sedges were clipped from 0.1 m<sup>2</sup> plots located randomly within the following vegetation types (defined after Parker 1975): raised Dryas barrens (Dryas-saxifrage-sedge barrens), flat Dryas barrens (Dryas-saxifrage-lichen barrens), patterned ground tundra, sedge-heath transition, sedge-willow bog, and sedge-willow meadow. Clip samples were weighed after air-drying for 14 days at 20°C. Raised Dryas barrens, sedge-willow bogs, and sedge-willow meadows of the 1979 study corresponded to ridge crests, wet meadows, and mesic meadows of the 1983 study, respectively. The sedge-heath transition and flat Dryas barrens of the 1979 study were combined under the Dryas-lichen slope type in 1983.

#### 2.2.2 Snow measurements

Snow measurements were made during early, mid-, and late winter (November, late-March/early April, and May) during winters 1982-83 and 1983-84. Five of the 8 vegetation study sites were used to study seasonally changing characteristics of the snow cover. Permanent transects were laid out along a slope using stone markers (Fig. 2.1b). At the midpoint of each range type, 3 snowpits were dug one meter apart, and a set of measurements was taken at each snowpit. Means for the 3 replicates were used in analysis. Since most

transects were used 3 times each winter, later snowpits were shifted a few meters laterally to undisturbed snow. At each band, snow cover was estimated visually by assigning 1 of 8 cover classifications (%): 0-5, 6-15, 16-25, 26-50, 51-75, 76-95, 95-99, and 100. The median values of these classes were used in further analyses.

At each snowpit, the "upslope" face of the pit was cut vertically and lightly brushed to expose individual snow layers. Total depth and thickness of the individual layers were recorded. The horizontal hardness of each layer was measured using Canadian hardness gauges (following Klein *et al.* 1950); 4 to 6 measurements were made in each layer and the means of these were used in further analyses. The presence of ground-fast ice and any other ice layers was noted.

### 2.2.3 Available biomass

Approximate estimates of green biomass available to caribou during summer were made as follows. Total land area of Coats Island, land areas covered by the Precambrian northeastern corner, flat wetlands (labelled "Tundra ponds"), central barrens, and coastal range were estimated by electronic planimeter from a 1:250,000 topographic map of Coats Island (Canadian Department of Energy, Mines and Resources, 1970). Areas of open water (rivers, lakes and ponds), ridge crests, bare ground (other than ridge crests), Dryas-lichen slopes, polygons, and meadows (wet and mesic meadows could not be separated) were outlined on 35 x 60 cm projections of 16 aerial photos taken during a flight over the southern coastal region of

Coats Island in July 1983. Percent coverage of each category was estimated for each drawing using an electronic planimeter. Mean cover estimates from these slides were multiplied by estimates of usable above-ground green biomass (from the vegetation study) to obtain estimates of island-wide available biomass. The Precambrian corner of the island and the central barrens are both very poorly vegetated and little used by caribou (Gates *et al.* 1986) and were excluded from these calculations.

The area covered by six vegetation types defined in the 1979 study was independently estimated by dot grid (precision = 90%) from 1959 aerial photos of Coats Island at a scale of 1:60,000. Water and the Precambrian upland were excluded from these calculations. These values were then multiplied by estimates of biomass to approximate available forage.

#### 2.2.4 Range use and diets

Seasonal range use by caribou was determined using pellet-group density, direct ground observation, and from observations during ground-based composition surveys in May 1983 and May 1984. Fecal groups (10 or more pellets in close proximity) were counted in July and August 1983 as they occurred on 1 m<sup>2</sup> vegetation cover plots. Observations during ground-based composition surveys in May 1983 and 1984 provided evidence of habitat use during late winter, and notes made during seasonal observations of activity budgets were used to determine habitat use.

Cratering depth was measured during mid- and late winter 1983-84. Measurements of maximum snow depth, to 1 cm, were made opportunistically at 88 feeding craters. Only 1 measurement was made at any crater, although some craters, shallow throughout, had been extended to cover several square meters.

Diet composition was estimated from preserved rumen contents of caribou shot during a concurrent study of body composition (Chapter 4). Eleven samples, each pooled from 4-9 mature females of one seasonal collection, were analysed at the Composition Analysis Laboratory, at Colorado State University. Food habits were analysed by microhistological analysis, 4 slides of 20 fields per sample.

Quality of seasonal diets was assessed using chemical analyses of dried rumen contents. Individual samples of rumen contents were frozen, dried to constant weight at 60°C, and ground in a coffee grinder. Samples were analysed for nitrogen by the Kjeldahl method (A.O.A.C. 1980) and for acid detergent fibre (ADF) and permanganate lignin following Goering and Van Soest (1970). Seasonal means were obtained for mature females and separately for calves (when collected). Samples of rumen contents were also analysed from 8 calf caribou found in March and April 1984 and presumed to have died of malnutrition (based on gelatinous red marrow in the long bones).

#### 2.2.5 Statistical analysis

Analysis of variance (ANOVA) was used to compare biomass components of the five range types, followed by SNK multiple range

comparisons (Steel and Torrie 1980) to compare individual range types. Values for ridge crests were excluded from analysis because only 2 of 30 plots had any measurable plant biomass. Analysis of cover data was limited to means and standard errors by cover type. Analysis of the 1979 vegetation data was also limited to means and standard errors.

Snow measurements were analysed using Harvey's least squares ANOVA (U.S.D.A. 1960), which permits missing cells; the effects of the two winters, three seasons, and five range types on depth, hardness, and cover were evaluated. Data for polygons were excluded from the ANOVAs because they rarely occurred in the intensive study area. Canadian hardness measurements were averaged to a single mean for each snowpit. Duncan's multiple range tests (Steel and Torrie 1980) were used to compare specific range means, and season-by-range cell means were compared with  $t$ -tests (Steel and Torrie 1980).

Dietary nitrogen, ADF, and lignin data were analysed by two-way ANOVA, with season and age (calves and adults) as main factors. Seasonal means for mature females were compared using SNK multiple range tests. Significant age-by-season interactions were explored using separate ANOVAs for the snow-free, winter, and June 1984 data sets.

All statistical analyses were carried out with SPSSx (SPSS Inc. 1983).

## 2.3 Results

### 2.3.1 Range characteristics in summer

Vegetation was sparse, with bare ground present throughout all five range types (Fig. 2.2). Most range types were dominated by a small number of species: Dryas integrifolia, 5 species of willow (Salix spp.), and a few species of sedge (Carex spp.) (Table 2.1a). Ridge tops were bare of vegetation except for Dryas integrifolia in 2 of 30 plots. Dryas-lichen slopes had significantly more total biomass than other areas ( $P < 0.05$ ) because of the widespread mats of Dryas integrifolia. There was significantly more Dryas, total lichens, and Cetraria lichens than on other range types ( $P < 0.05$ ). Mesic meadows contained significantly more willows ( $P < 0.05$ ) than other range types. Wet meadows had significantly less lichens, Dryas, and willows than mesic meadows ( $P < 0.05$ ), and significantly more sedge and grass ( $P < 0.05$ ) than other vegetation types. Polygons were poorly vegetated. Vegetation measurements from north-central Coats Island were similar and confirmed the low biomass present on all range types throughout Coats Island (Table 2.1b). Sedge-heath transitions were clearly the most important lichen-bearing range.

Mesic and wet meadows represented by far the greatest quantities of forage (Table 2.2). Dryas-lichen slopes had relatively high concentrations of biomass but much of it was Dryas integrifolia.

Fig. 2.2. Estimates of vegetative cover on five range types.  
on Coats Island.

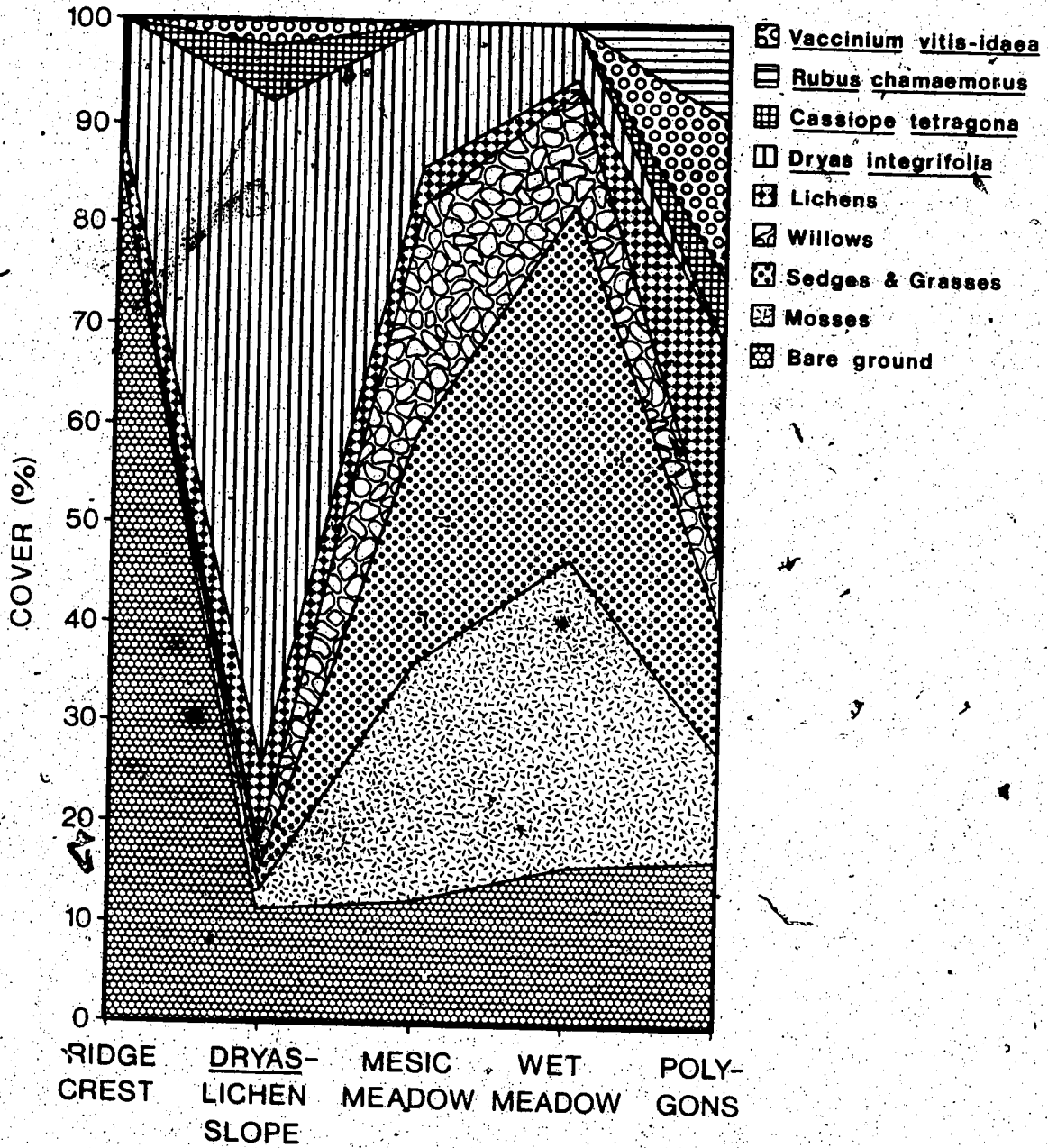




TABLE 2.1a. Green above-ground biomass (g DM/m<sup>2</sup>) on four range types of southeastern Coats Island, July-August 1983. Means ± standard errors.

Plant type	Range types			
	Dryas-lichen n=29	Mesic meadow n=39	Wet meadow n=25	Polygons n=20
<u>Dryas integrifolia</u>	78.5 (11.4)	13.3 (3.5)	-	-
Grasses & Sedges <sup>1</sup>	5.3 (1.7)	16.8 (2.0)	38.6 (6.2)	14.6 (6.2)
Lichens <sup>2</sup>	29.9 (3.7)	12.5 (2.0)	6.1 (1.8)	4.3 (1.7)
<u>Cetraria</u> spp. <sup>3</sup>	26.4 (3.7)	6.3 (1.0)	5.6 (1.7)	2.5 (1.0)
Willows <sup>4</sup>	3.3 (1.0)	17.2 (2.8)	0.7 (0.5)	1.2 (0.5)
<u>Cassiope tetragona</u>	15.6 (4.3)	0.2 (0.2)	-	-
<u>Vaccinium vitis-idaea</u>	-	0.4 (0.4)	-	11.1 (2.5)
<u>Empetrum nigrum</u>	-	-	-	5.1 (5.1)
<u>Rubus chamaemorus</u>	-	1.0 (0.4)	-	2.2 (0.5)
<u>Saxifraga hirculus</u>	-	0.2 (0.1)	0.1 (0.1)	-
<u>Cerastium</u> sp.	-	0.2 (0.1)	1.8 (0.9)	-
<u>Draba</u> sp.	-	0.5 (0.2)	1.3 (0.8)	-
<u>Polygonum viviparum</u>	0.2 (0.1)	0.1 (0.05)	-	-
<u>Tofieldia</u> sp.	1.0 (0.9)	-	-	-
<u>Equisetum</u> sp.	0.7 (0.7)	0.9 (0.5)	2.0 (0.8)	-
Total biomass	134.7 (11.8)	63.5 (4.9)	50.7 (7.1)	46.6 (7.5)

Table 2.1a continuedNotes

- 1 - ca. 80% of sedge and grass biomass consisted of sedges (Carex spp.)
- 2 - Cetraria spp., and Ochrolechia sp., Albctoria-sp., Thamnia vermicularis, Dactylina sp., Cladonia-sp., and Parmelia omphaloides
- 3 - Cetraria cucullata, C. islandica, and C. nivalis
- 4 - ca. 60% Salix reticulata, and lesser quantities of S. herbacea, S. arctica, S. lanata, and S. arctophila

Table 2.1b. Annual production of sedges and grasses and standing crop of lichens ( $\text{g DM/m}^2$ ) on vegetation of north-central Coats Island, August 1979. Means & standard errors.

Plant type	Vegetation type					
	Raised <u>Dryas</u> barrens n=30	Flat <u>Dryas</u> barrens n=30	Sedge- heath transition n=37	Patterned ground tundra n=60	Sedge- willow meadow n=45	Sedge- willow bog n=39
Sedges & grasses	0.007 (0.007)	0.37 (0.18)	5.78 (1.08)	3.00 (0.45)	24.17 (1.62)	30.75 (3.35)
Willows	0 0	7.40 (0.84)	2.35 (0.65)	6.60 (1.34)	13.47 (2.73)	1.55 (0.50)
Lichens	0.13 (0.13)	0.33 (0.32)	27.40 (6.08)	1.47 (0.89)	6.50 (1.52)	0 0
Total	0.14	8.10	35.5	11.07	44.14	32.3

TABLE 2.2. Estimates of island-wide available forage, Coats Island.

## A. Estimates based on the 1983 vegetation study.

(1) Areas of range ( $\text{km}^2$ ) estimated from 1:250,000 topographic map:

<u>Precambrian upland</u>	<u>Central barrens</u>	<u>Coastal range</u>	<u>Total</u>
353	1168	4153	5675

(2) Cover estimates (% means and standard errors) of terrain types from aerial photos over southern coastal range:

<u>Open water</u>	<u>Bare ground</u>	<u>Ridge crests</u>	<u>Dryas-lichen</u>	<u>Meadows</u>	<u>Polygons</u>
19 (3.4)	6.5 (3.4)	10.8 (4.9)	14.2 (3.7)	46.3 (7.1)	3.2 (1.8)

(3) Resulting estimates of area coverage ( $\text{km}^2$ ) by usable range types:

<u>Dryas-lichen</u>	<u>Polygons</u>	<u>Meadows</u>	<u>Total</u>
580	133	1922	2645

(4) Estimates of available green biomass (kg DM) on usable range:

<u>Dryas-lichen</u>	<u>Polygons</u>	<u>Meadows</u>	<u>Total</u>
7,906,000	625,000	10,955,400	19,486,500

(5) Estimates of available grass, sedge, willow and lichen (kg DM) only:

<u>Dryas-lichen</u>	<u>Polygons</u>	<u>Meadows</u>	<u>Total</u>
2,259,690	269,580	8,914,760	11,444,030

TABLE 2.2 (continued)

## B. Estimates based on the 1979 vegetation study.

(1) Areas of range (km<sup>2</sup>) estimated (+/- 10%) from aerial photos:

<u>Raised</u> <u>Dryas</u> <u>barrens</u>	<u>Flat</u> <u>Dryas</u> <u>barrens</u>	<u>Patterned</u> <u>ground</u> <u>tundra</u>	<u>Sedge-</u> <u>heath</u> <u>transition</u>	<u>Sedge-</u> <u>willow</u> <u>bog</u>	<u>Sedge-</u> <u>willow</u> <u>meadow</u>	<u>Total</u>
1094	640	881	183	676	968	4443

(2) Available standing crop of lichens and annual production of grasses, sedges and willows (kg DM) by range type:

<u>Raised</u> <u>Dryas</u> <u>barrens</u>	<u>Flat</u> <u>Dryas</u> <u>barrens</u>	<u>Patterned</u> <u>ground</u> <u>tundra</u>	<u>Sedge-</u> <u>heath</u> <u>transition</u>	<u>Sedge-</u> <u>willow</u> <u>bog</u>	<u>Sedge-</u> <u>willow</u> <u>meadow</u>	<u>Total</u>
15,316	512,000	975,260	649,650	2,183,480	4,297,920	8,634,016

### 2.3.2 Snow cover

Snow generally persisted from late October/early November until early to mid-June. Snow was consistently hard and wind-packed, deposited either during blizzards or re-deposited by nearly constant winds. Hardness measured using Canadian hardness gauges was significantly lower during the 2 early winter periods than during the 4 later ones ( $P < 0.05$ ) but did not vary significantly among range types or winters (Table 2.3). Layers of snow often varied greatly in hardness but there were very few pits without several very hard layers. Snow with hardness greater than  $10,000 \text{ g/cm}^2$  occurred at 29% snowpits during 1982-83 and at 41% during 1983-84. By April and May, the bottom 5-15 cm of snow often coalesced into an amorphous mass of large crystals and air near the ground.

Ice layers occurred rarely during the two winters of the study. Ice lenses between snow layers were never more than 1 mm thick, and ground-fast ice occurred at only 2% of snowpits during the first winter and at 5.2% during the second.

The crests of strand lines and raised beaches maintained significantly shallower snow cover ( $P < 0.01$ ) than other areas throughout the two winters of the study (Table 2.4); substantial bare ground was often visible. Dryas-lichen slopes had substantially deeper snow than crests, but the overall mean depth was significantly lower ( $P < 0.01$ ) than for meadows. Slopes and meadows showed little bare ground after early winter. The deepest snow was found on mesic and wet meadows, with the flat wet meadows having significantly

TABLE 2.3. Snow hardness on Coats Island, winters 1982-83 and 1983-84. Means and standard errors.

	<u>Winter 1982-83</u>					
	Early Winter (October-November)		Mid-winter (March-April)		Late Winter (May)	
Canadian hardness (g/cm <sup>2</sup> )	n=13	2012 (1391)	n=29	8034 (1105)	n=29	7514 (1101)
depth of snow (cm)		0		4.1		8.6
with hardness > 10,000 g/cm <sup>2</sup>		0		(1.0)		(2.1)

	<u>Winter 1983-84</u>					
	Early Winter (October-November)		Mid-winter (March-April)		Late Winter (May)	
Canadian hardness (g/cm <sup>2</sup> )	n=35	9319 (1469)	n=22	4465 (931)	n=29	5219 (948)
depth of snow (cm)		4.1		5.2		6.5
with hardness > 10,000 g/cm <sup>2</sup>		(1.2)		(1.8)		(2.6)

TABLE 2.4. Characteristics of snow cover on Coats Island during winters 1982-83 and 1983-84. Means & standard errors.

A. Depths

Range Type or Characteristic	n	Early Winter (October-November)	Mid-winter (March-April)	Late Winter (May)
		Mean Depth (cm)	n Mean Depth (cm)	n Mean Depth (cm)
<u>Winter 1982-83</u>				
Ridge Crest	10	0.5 (0.05)	6 8.9 (4.0)	6 6.3 (3.3)
Dryas-lichen- slope	10	2.1 (0.4)	6 43.8 (7.6)	6 54.4 (6.3)
Mesic meadow	10	3.9 (0.4)	6 47.4 (6.7)	6 70.5 (9.9)
Wet meadow	5	4.0 (0.7)	4 55.5 (8.7)	4 81.1 (9.7)
<u>Winter 1983-84</u>				
Ridge Crest	4	7.6 (2.9)	8 16.7 (3.1)	8 11.6 (3.9)
Dryas-lichen slope	3	8.0 (3.7)	8 49.8 (8.8)	8 55.5 (11.4)
Mesic meadow	4	12.9 (1.6)	8 64.5 (7.2)	8 72.3 (6.7)
Wet meadow	2	15.4 (4.1)	5 65.5 (8.7)	5 65.4 (3.4)



TABLE 2.4 continued

B. Estimated snow-free ground

Range Type or Characteristic	Early Winter (October-November)		Mid-winter (March-April)		Late Winter (May)	
	n	Estimated snow-free ground (%)	n	Estimated snow-free ground (%)	n	Estimated snow-free ground (%)

Winter 1982-83

Ridge Crest	10	42.9 (6.9)	6	18.7 (6.1)	6	16.5 (5.7)
Dryas-lichen slope	10	15.3 (3.1)	6	0 (0)	6	0 (0)
Mesic meadow	10	9.8 (2.1)	6	0.3 (0.3)	6	0 (0)
Wet meadow	5	9.0 (7.0)	4	0 (0)	4	0 (0)

Winter 1983-84

Ridge Crest	4	11.8 (3.3)	8	1.1 (0.4)	8	32.5 (7.5)
Dryas-lichen slope	3	5.3 (1.8)	8	0 (0)	8	2.4 (1.8)
Mesic meadow	4	5.3 (2.1)	8	0 (0)	8	0 (0)
Wet meadow	2	2.0 (0)	5	0 (0)	5	0 (0)

deeper snow overall than mesic meadows ( $P < 0.01$ ).

There were insufficient data for polygons to make statistical comparisons, but mean snow depth measured at 18 snowpits (6 slopes) during mid- and late winter was 32.2 cm (s.e. 5.0), while the comparable figures for ridge crests, slopes, mesic meadows, and wet meadows were 10.9 cm (2.5), 50.9 cm (4.1), 63.7 cm (4.3), and 66.8 cm (4.1). An estimated 8.7% (s.e. 2.9) of polygons remained exposed during these periods.

During early winter 1982-83, substantial bare ground remained on all range types. Snow cover remained minimal until early December; some 15-20% of the area occupied by ridge crests remained bare throughout winter. By contrast, snow cover was already significantly deeper during early November 1983 than during late November 1982 ( $P < 0.025$ ). A further heavy snowfall occurred just after data were collected in November 1983, creating a deep snow cover which was not re-distributed by winds; this buried all range types throughout the island (Table 2.5).

The two winters differed considerably during the final stages. Snow was significantly deeper during March-April 1984 than during March-April 1983 ( $P < 0.005$ ). Several major snowfalls in May 1983 significantly increased snow depth ( $P < 0.005$ ), and the proportion of bare ground remained virtually unchanged. The peak of snowmelt did not occur until the end of May. By contrast, mean depth of snow remained nearly unchanged from March-April to May in 1984, and there was a rapid increase of exposed areas. Caribou had ceased cratering

TABLE 2.5. Early winter changes in snow cover at one study site on Coats Island, November 1983. Means and standard errors.

	Ridge crest	Dryas-lichen slope	Mesic meadow
Date		Depth, cm	
November 3	15.2 (0.8)	11.2 (1.5)	14.7 (1.9)
November 7	30.7 (3.0)	21.0 (1.2)	21.3 (0.7)
	Estimated exposed ground, %		
November 3	2	2	15
November 7	0	0	0

by mid-May 1984, but cratered actively in late May 1983.

### 2.3.3 Habitat use and foraging behaviour of caribou

Throughout spring and summer, caribou fed only in low-lying meadows during 90 hours of observations. They moved little, often spending an entire day within an area of less than 2 km<sup>2</sup>. There was occasional use of raised areas during the peak of summer (late July-early August) to escape insects, but not to feed. Toward the end of summer (late August-early September), caribou occasionally fed on polygons and raised beach slopes and in a few cases dug into hummocks during feeding.

Winter brought a localized shift to areas with some relief. During the relatively snow-free beginning of winter (October-November), caribou seen feeding during 20 hours of observation were all in meadows. As snow accumulated, range types became impossible to identify, but all caribou feeding craters found during both winters were in areas of shallow snow. The vegetation at 88 craters was typical of Dryas-lichen slopes and polygons. Pellet groups were also concentrated in these areas: mean numbers of pellet groups/plot for ridge crests, Dryas-lichen, mesic meadows, wet meadows, and polygons, respectively, were 0.2, 1.2, 0.8, 0.1, and 2.7. Mean cratering depth at 88 craters in March and April 1984 was 14.9 cm (range 7-26, s.e. 0.4). These shallow craters were sometimes extended over 100-300 m along a slope. Cratering behaviour often consisted of fracturing the snow cover rather than digging through

it; caribou rarely used more than 3-4 strokes at one time.

Local shifts from meadows to adjacent relief areas also occurred on a larger scale: coastal flat areas where strand lines, raised beaches, and polygons were not present were devoid of caribou or any sign of caribou use when searched in May 1983, and May 1984.

Spring in June brought rapid snowmelt and a return to feeding in low-lying meadows even while much of the island was still snow-covered. The only time at which snow appeared to impede caribou locomotion occurred in late May and early June, when soft melting snow slowed caribou movement. At these times caribou concentrated their movements on ridges and other exposed areas.

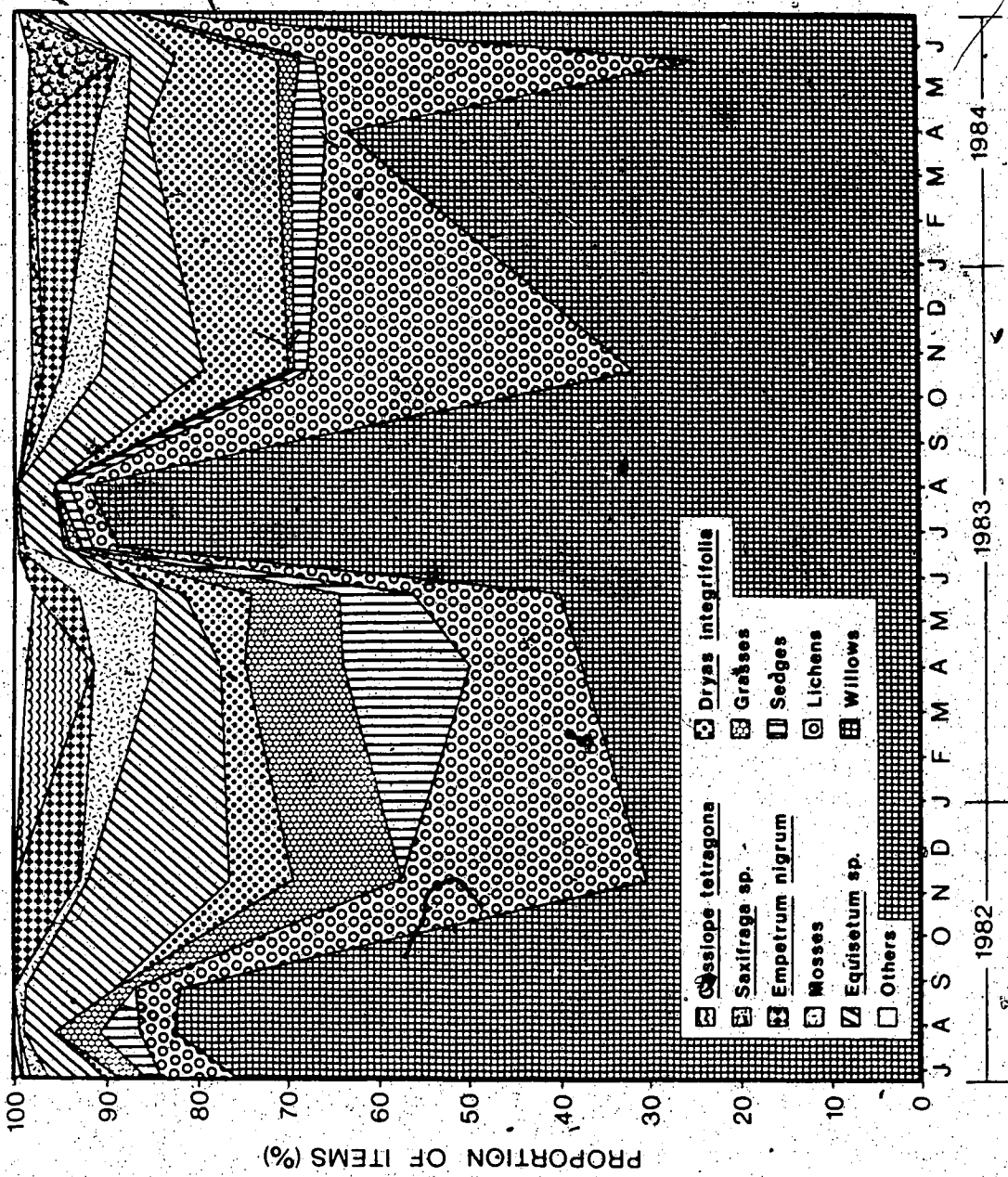
#### 2.3.4 Seasonal food habits

Patterns of diet selection were consistent among years within the summer, winter, and spring periods of the study (Fig. 2.3).

From the onset of spring in June until the beginning of September, caribou ate a very high proportion of willows. Visual examination of rumen contents suggested a high proportion of leaves.

Winter diets were more diverse, but willows continued to be the largest single item. In October-November, the dietary proportion of willow dropped to its lowest level (ca. 30%) as the proportion of lichens peaked (27-35%). Over winter, the use of willow gradually increased, particularly during the second winter, as did the use of sedges, Dryas integrifolia, and Empetrum nigrum. During winter, rumen contents were often brown and the material appeared woody.

Fig. 2.3. Seasonal proportions of plant types in rumen contents of Coats Island caribou.



Willow leaves were not readily distinguished. Mosses, Cassiope tetragona and Saxifraga spp. were minor components.

### 2.3.5 Nitrogen, ADF, and lignin content of rumen material

Means for nitrogen, ADF, and lignin content of rumen material from mature females were consistent within season (Fig. 2.4), although animals were shot at all stages of feeding cycles. Variability was highest in winter.

Nitrogen content of rumen material peaked during both summers in late July - early August. A rapid and significant ( $P < 0.05$ ) decline followed over summer to the start of winter (October-November). Nitrogen content continued to decline over winter and increased rapidly in spring ( $P < 0.05$ ). The lowest means occurred in May 1983 and March/April 1984, at 3.1 g/100 g DM. Lignin and ADF content of rumen material generally varied inversely with nitrogen content, peaking in winter and reaching lowest values in mid-summer.

Calves had mean nitrogen, ADF, and lignin values similar to those of mature cows. However, there was a significant age-by-season interaction ( $P < 0.01$ ) for all three indices. During spring, summer, and early winter, when diet quality was generally high, calves had significantly higher nitrogen, lower ADF, and lower lignin in their rumen contents (Table 2.6). During winter, however, when diet quality was poor, calves had values very similar to those of adult females. In June 1984, rumen contents collected from calves 7-10



Fig. 2.4. Seasonal changes in ADF, lignin, and nitrogen of rumen contents in Coats Island caribou females.

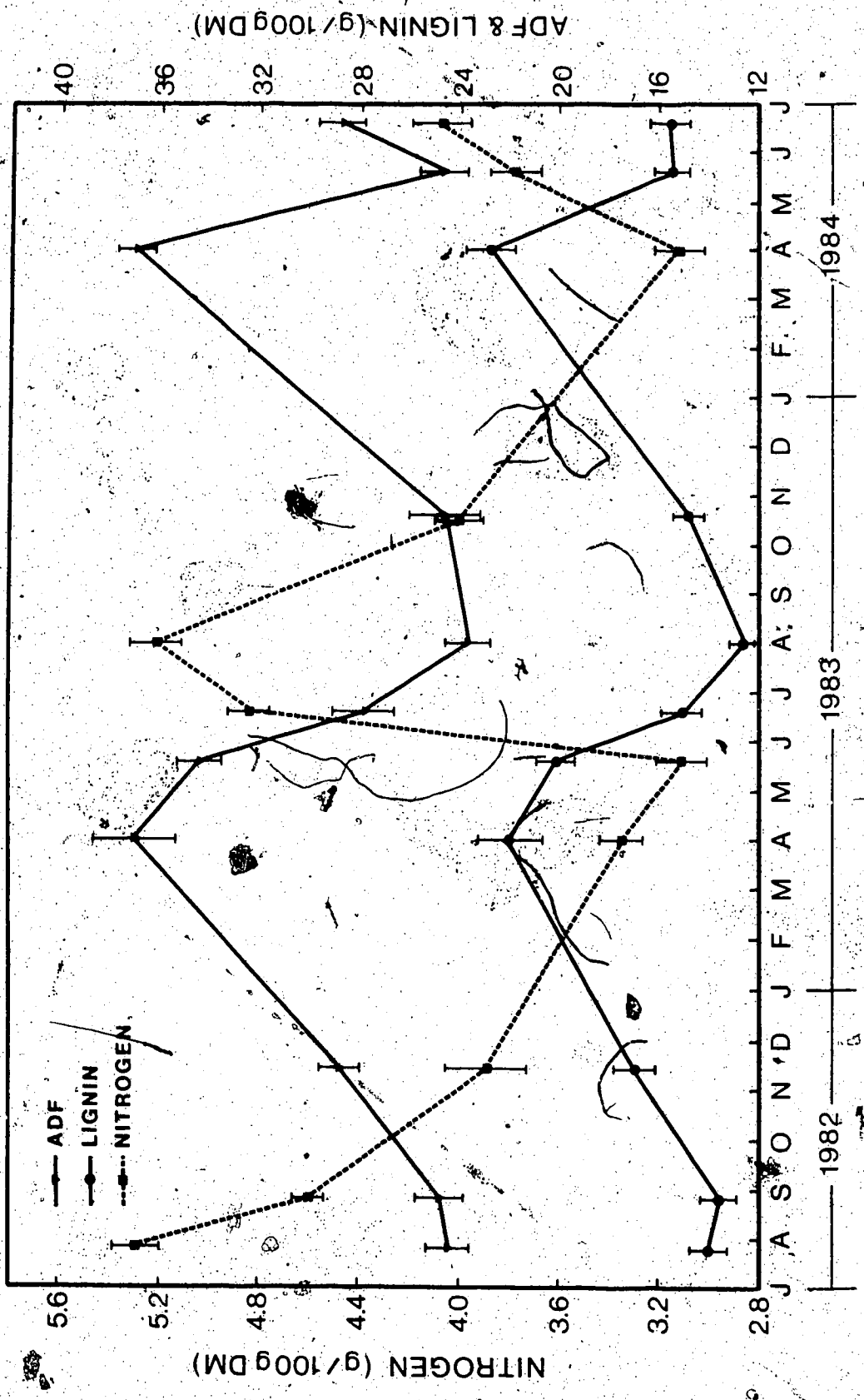


TABLE 2.6. A comparison of seasonal nitrogen, ADF, and lignin (g/100 g DM) of rumen contents for calf and adult caribou on Coats Island

Season	n	Mature females			Calves			
		nitrogen	ADF	lignin	nitrogen	ADF	lignin	
Spring, summer, and early winter	21	4.4* (0.1)	25.7** (0.6)	14.8** (0.4)	11	4.8 (0.1)	21.3 (0.9)	11.7 (0.6)
Winter	17	3.2 (0.1)	37.1 (0.9)	22.5 (0.9)	4	3.3 (0.1)	37.6 (1.9)	25.0 (1.8)
June 1984	9	4.1 (0.1)	29.3** (1.0)	16.1* (0.7)	5	3.7 (0.1)	36.4 (2.5)	22.2 (2.8)

\* - significantly different from corresponding calf mean (P < 0.05)

\*\* - significantly different from corresponding calf mean (P < 0.01)

days old (age judged by size, posture, and mobility) were significantly higher in ADF, lignin, and lower in nitrogen, than those collected from mature females.

Mean values for nitrogen, ADF, and lignin in rumen contents of 8 winter-killed calves were 3.2, 46.0, and 32.1 g/100 g DM. Nitrogen was comparable to the poorest winter values for shot animals, but the ADF and lignin values were significantly higher ( $P < 0.05$ ).

## 2.4 Discussion

### 2.4.1 Forage resources and nutrition during the snow-free season

Vegetation on Coats Island was low in density and diversity but provided a plentiful summer food supply of high quality. Above-ground biomass, particularly of lichens, was as sparse as on high arctic Devon Island (Muc 1977, Svoboda 1977) and lower than on Southampton Island (Parker 1975, Reznicek and Svoboda 1982). Low summer temperatures, strong winds, low soil moisture, and a short growing season - all found on Coats Island - tend to limit the productivity of tundra (Bliss *et al.* 1973, Svoboda 1977, Maessen *et al.* 1983). The island has only been deglaciated relatively recently (Gillett 1976) and few species of plants have colonized the island; organic layers have been slow to develop. Most useful forage - willows, sedges and lichens - was concentrated in meadows. Peak nitrogen and fibre of rumen contents (proportional to nitrogen and fibre in forage - Klein 1962, Staines and Crisp 1978) compared well

with summer means for several Aleut Island populations of reindeer and caribou (Klein 1981). Vegetation analysed for protein, fiber, ash, calcium, and phosphorus on neighbouring Southampton Island was of good quality (Parker 1975). Given an abundant food supply and little disturbance (Chapter 4), this large resource allowed caribou to grow and fatten rapidly and consistently (*op. cit.*). A similar situation prevails on Svalbard (Staaland 1984).

The strong preference for willow in summer may have been related to recovery of body protein. Mature female caribou may lose 30-35% of carcass muscle mass during winter in this population (Chapter 4). Extensive summer use of willows and other shrubs has been shown in several caribou and reindeer populations (Kelsall 1968, Parker 1978, Kuropat and Bryant 1980, Thompson and McCourt 1981, Boertje 1984). Mean crude protein content of the current year's growth of five species of Salix was 23.2 % on Southampton Island in August 1972, while current year's growth of five species of sedge and grass averaged 18.0 % and five species of lichens also found on Coats Island averaged only 2.3 % (Parker 1975). Willows likely provided the best dietary source of protein. The shift from a diet of an estimated 24% willow and 43% lichen in May 1984 to a diet of 82% willow and 6% lichen in June 1984 (before the peak of green-up) suggests the importance of dietary protein during late gestation and lactation. This shift carried the cost of increased ADF and lignin in the diet along with increased nitrogen.

By contrast, the increased use of lichens in fall during 1982 and

1983 coincided with a period during which carcass muscle levels had reached a plateau but fat levels were still increasing (Chapter 4). Verme and Ozoga (1981) have suggested that fattening may be obligatory during this period in white-tailed deer (Odocoileus virginianus). Lichens are well suited for fattening due to their high digestibility (Person et al. 1980, White et al. 1975, Thomas and Kroeger 1980) and low fiber and lignin content (Parker 1975, Person 1975).

#### 2.4.2 Snow cover and winter nutrition

Snow cover on Coats Island was consistently hard and wind-packed. Depth and hardness were comparable to those recorded for Peary caribou by Miller et al. (1982) and Thomas and Edmonds (1983). This snow put most vegetation beyond the reach of caribou and forced them to forage in areas where little of the preferred forage could be found.

Availability of forage under such deep hard snow was difficult to quantify, but clearly, vegetation buried under 60-90 cm of snow was unavailable when caribou cratered only in snow ca. 15 cm deep. Peary caribou also crater only to a depth of 10-20 cm (Thomas and Edmonds 1983). Like caribou on Coats Island, Peary caribou encounter snow orders of magnitude harder than snow in the taiga, where caribou may dig through 50-90 cm of snow (Pruitt 1959, Henshaw 1968, Laperriere and Lent 1977). Caribou on Coats Island sometimes fractured hard snow rather than digging through it; digging through snow with

hardness approaching 100,000 g/cm<sup>2</sup> would have been impossible.

During mid- to late winter, only those areas of range with topographic relief and shallow snow - the tops of Dryas-lichen slopes and polygons - presented opportunities for foraging. Over-grazing, particularly of lichens, may have occurred over time in these critical areas. Like Svalbard reindeer (Reimers 1977), South Georgian reindeer (Leader-Williams et al. 1981), and Peary caribou (Miller et al. 1982), caribou on Coats Island have rarely had the opportunity to over-graze range over much of the island.

Deep snow brought not only a major reduction in the quantity of forage available, but also (indirectly) a much poorer quality of food. While the spring-to-autumn changes in diet quality were mostly due to phenology, the overwinter changes were forced by snow accumulation. Caribou were much less selective and made increased use of Dryas integrifolia, senesced sedges, grasses, and willows, and even mosses, which tend to have low nutrient content (Parker 1975), and poor digestibility (White et al. 1975, Person et al. 1980, Thomas and Kroeger 1980, Thomas et al. 1984). A similar pattern has been shown in Peary caribou (Miller et al. 1982, Thomas and Edmonds 1983). While the decline in diet quality was not as rapid over winter as the summer-fall decline, White (1983) has demonstrated that small differences in digestibility and nutrient yield can have "multiplier effects" of considerable significance. Very high lignin concentrations radically reduce digestibility (Person et al. 1980, Van Soest, 1982). Eventually, body reserves dwindled under these

conditions (Chapter 4). Rumen full of woody brown material have been found in other dead caribou on Coats Island (Gates *et al.* 1986) and this pattern suggests that the quality of food eaten is normally the limiting factor in winter, rather than the absolute availability of forage.

Timing of major snowfalls and their distribution are likely critical factors for this population. The relatively snow-free early months of winter 1982-83 permitted caribou to choose preferred forage and conserve body reserves, while heavy early snows in October and November 1983 stressed caribou throughout winter. Ablation and a lack of additional snow in May 1984 allowed caribou to cease cratering and gain access to highly digestible lichens even though most vegetation was still buried. The blanketing nature of snowfalls in November 1983 was important, forcing caribou to crater for all food. Such conditions were unusual since ridge crests are normally exposed all winter (Gates *et al.* 1986). Thomson (1971) noted a similar topographic effect on forage availability for reindeer at Hardangervidda, Norway; the importance of wind-blown sites with shallow snow has been widely recognized in Canadian caribou (Bergerud 1974, Miller 1976, Miller *et al.* 1982).

#### 2.4.3 Consequences of diet selection by calves

Caribou calves selected diets of slightly higher quality than adults during the snow-free seasons of this study, assuming that rumen contents accurately reflected diet characteristics. Abundant



green forage and smaller absolute nutrient requirements may have permitted this luxury. This high quality of diet likely made possible their rapid growth (Chapter 4). Red deer hinds, smaller than stags and with higher proportionate nutrient requirements, tend also to select diets of higher quality (Kay and Staines 1981).

Ingestion of green food by calves no more than a week old emphasizes the importance of rapid ruminal development during the short arctic summer. The poor quality of the diet selected by young calves suggests that some learning is involved in the selection of forage.

Under severe winter conditions, calves were forced to use the same senesced lignified forage plants used by adults. Their higher relative nutrient requirements could not be satisfied by slowly fermenting forage, and this may have contributed significantly to their poor survival during severe winters. The remarkable enlargement of rumen volume in wintering calves (Chapter 4) appeared to be a compensatory mechanism.

#### 2.4.4 Range capacity and reduction in availability due to snow

A conservative calculation of range capacity (in the absence of snow) can be based on the two vegetation studies. Using a mean daily intake of 2.5 kg DM/day for a 90 kg caribou (based on White *et al.* 1975 and Arnold 1985), or 914 kg/year, annual production of sedges, grasses and willows alone could support 9500-12,500 caribou in one year, or 2850-3750 if caribou removed no more than 30% of the annual

production. The population has generally remained well below this conservative estimate (Gates et al. 1986). Clearly vegetation available in summer readily supports the present caribou population. Under average mid- to late winter conditions, we suggest the following reductions in availability for particular range types: Dryas-lichen slopes 85%, polygons 75%, and meadows 95-98%. Reduction in forage availability has been estimated at up to 97% for white-tailed deer (Odocoileus virginianus) (Moen and Evans 1971), over 90% in mule deer (Odocoileus hemionus) (Gilbert et al. 1970), and 82% in Soviet reindeer (Sablina 1961, quoted in Kelsall 1968) under severe winter conditions.

#### 2.4.5 Conclusion

Summer range on Coats Island provided a surplus of high-quality food for caribou. Over-grazing is unlikely to have affected range characteristics except on ridges and polygons, where small areas have been heavily used in winter.

Hard-packed deep snow reduced the forage available to caribou to a fraction of that available in summer, and forced caribou to feed in areas of shallow snow where vegetation was scarce and of low quality. Low quality of food appeared the proximal limiting factor in winter, rather than the absolute reduction of forage availability. Calves were particularly susceptible to malnutrition because of their higher relative nutrient requirements.

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## Chapter 3. Fat distribution and indices of carcass composition.<sup>1</sup>

### 3.1 Introduction

Coat Island, Northwest Territories (NWT) (62-63° N, 82-84° W), is a flat, rocky, poorly vegetated island of ca. 5600 km<sup>2</sup> in northern Hudson Bay (Gillett 1976). Barren-ground caribou (Rangifer tarandus groenlandicus) on this island are free of predation but they endure harsh winters during which wind-hardened snow may cause extensive malnutrition (Gates et al. 1986). Summers are short but favour rapid growth and replenishment of body stores. A study of the seasonal nutritional ecology of this population required rapid, accurate methods of determining body composition from indices readily measurable on a large number of shot caribou.

Dissectible bone, muscle and fat make up over 95% of the dressed carcass. Dissectible fat represents a large proportion of the reindeer's (R. t. platyrhynchus) stored fat and increases in relation to chemically extractable fat as fatness increases (Reimers and Ringberg 1983); muscle represents the animal's largest protein reserve. The proportion of total tissue contributed by each bone and

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muscle at any particular total tissue weight is relatively fixed (Berg and Butterfield 1976; Richmond et al. 1979; Butterfield et al. 1984a, 1984b) and can be used to predict total weight using allometric or rectilinear equations (Huxley 1932; Butterfield and May 1966; Price and Berg 1976, 1977). Fat, while more variable, also tends to be partitioned to various depots in a predictable manner (Davies and Pryor 1977, Jones et al. 1980, Jones 1982).

These proportionalities permit assessment of carcass bone, muscle, and fat using relatively simple indices. Ringberg et al. (1981) dissected 35 growing reindeer (R. t. tarandus) and established strong rectilinear regressions between total muscle weight and weights of indicator muscles (biceps femoris and gastrocnemius) and between total bone and indicator bones (femur and metatarsus). Dissectible fat is more difficult to predict from indices, in part because distribution among depots varies widely among species (Kempster 1981); and because fat depots may be variably affected by nutritional restriction and realimentation (Little and Sandland 1975, Murray et al. 1978). Reimers and Ringberg (1983) found depth of back fat (DBF) a useful predictor of dissectible fat in Svalbard reindeer, as has also been shown in cattle (Bos spp.) (Berg and Butterfield 1976) and pigs (Sus spp.) (Skelley and Handlin 1967).

This study was undertaken to determine indices useful for predicting dissectible bone, muscle, and fat, to quantify fat distribution among depots in caribou, and to examine the validity of these relationships for calves and adults varying from emaciation to high fatness. Results are compared with similar studies on Rangifer. An abstract of preliminary results will be published in conference proceedings (Adamczewski et al. 1986). The study area and population characteristics have been reviewed by Gates et al. (1986).

### 3.2 Materials and methods

#### 3.2.1 Collections

Twelve seasonal collections of female caribou (5-9 per collection) and their calves were made from June 1982 to June 1984. Collections during two seasonal cycles included spring (June), mid-summer (late July-early August), late summer (late August), fall or early winter (October-November), mid-winter (late March-early April), and late winter (May).

Carcass weights of harvested animals were determined as bled body weight less the following: head severed at the atlas, hide, viscera including kidneys, antlers, uterus and conceptus, and each limb severed at the distal end of the tibia or the radio-ulna.

#### 3.2.2 Dissections

As time permitted during the seasonal collections, carcasses

selected for a wide range in fatness and size, and with minimal shot damage, were cut along the spinal column in the median plane with a meat saw and the right side of the carcass was saved for dissection. Twenty-seven carcass sides were dissected from caribou ranging in condition from advanced malnutrition in May (no dissectible fat) to maximal fatness in fall. Ten sides, dissected were from calves varying in age, from 1 week to just under 1 year, 16 were from adult females (4 years old or older), and one was from a 2-year old female (treated here as an adult). Based on relative changes in fatness from one collection to the next, caribou were in poorest condition in late May and early June, gained fat from then until a maximum in October-November, and thereafter lost fat until the following spring (Chapter 4). Assuming these trends held for individual caribou in each collection, 5 calves, 10 adult females, and the one 2-year old female were losing reserves when dissected, and 5 calves and 6 mature females were either gaining reserves or at peak condition.

Half carcasses were stored under plastic sheets for 1-3 days and were kept cold but not frozen. Each carcass side was separated into bone, muscle, and fat in a permanent field camp. Connective tissue, neural tissue, and glands were discarded. Dissected material was weighed to 0.1 g on a triple beam balance. The following weights and measurements were recorded during dissections:

### 3.2.3 Muscle

Carcass muscle weight included all muscular tissue, tendons, and

ligaments, doubled from the half-carcass. The gastrocnemius was weighed after being stripped of extraneous fat and tendons. The flexor digitorum superficialis, a smaller muscle virtually contained within the gastrocnemius, was separated (see Butterfield and May 1966).

#### 3.2.4 Bone

Carcass bone weight included all bones and cartilage, doubled from the half carcass. The femur, tibia, scapula, radio-ulna, and humerus were weighed after being individually stripped of tendons, ligaments, and articular cartilage.

#### 3.2.5 Fat

Dissectible fat included three carcass fat depots - subcutaneous, intermuscular and pelvic, and two visceral depots - omental and perirenal. Pelvic fat included fat lining the body cavity after removal of the viscera (including kidneys). Omental fat was the weight of the fresh omentum, including pockets around the omasum and abomasum. Perirenal fat was weighed both as total kidney fat and as kidney fat remaining after trimming according to Riney (1955). Additional fat indices measured were depth of back fat (DBF) and marrow fat in the femur (following Ransom, 1965). DBF was recorded along a cut ca. 2-3 cm from the midline of the spinal column and parallel to the spinal column, from the base of the tail cranially. This approach gave measurements identical with those by Riney's

(1955) technique in 30 animals tested.

Gastrocnemius muscles were retained for compositional analysis from caribou collected over six periods spanning the seasonal cycle. In two females of intermediate condition, additional samples of ca. 10 g. were taken opportunistically from six regions of the musculature (near the scapula, from the biceps femoris, from an intercostal muscle, near the pelvis, and near the metatarsus) to provide a general comparison with composition of the gastrocnemius. Muscle samples were autoclaved for 90 min at 120°C, homogenized, freeze-dried, and small subsamples were oven-dried to constant weight at 60°C to determine moisture content. Fat was extracted using chloroform-methanol-water in the ratio 1:1:0.9 following Atkinson et al. (1972).

### 3.2.6 Statistical methods

Data were analysed using APL Statpak (Smillie 1984) and SPSSx (SPSS Inc. 1983). Occasional damage occurred in the field and reduced the number of full data sets for fat analysis from 27 to 23, and also reduced the number of bones available for regression analysis. Least squares regression was used to evaluate relationships between index measurements and total tissue weights. Equations predicting dissectible fat from indices were developed using stepwise multiple regression. The effects of age (calves compared with adults) and condition (animals gaining fat or in peak fall condition, compared with animals losing fat) on the slopes of

regressions for muscle and bone were evaluated by covariance analysis. Multiple regression was used to test the effects of age and condition on equations for individual fat depots and predictive fat equations.

### 3.3 Results.

#### 3.3.1 Muscle

Weight of the gastrocnemius muscle was strongly related to carcass muscle weight (Fig. 3.1). Greater absolute variation was evident in adults (> 25 kg carcass muscle - Fig. 3.1), but age and condition had no effect on this regression ( $P < 0.01$ ).

Fat content of the gastrocnemius was lower in very lean caribou (young calves and malnourished females in late winter 1984) but showed little consistent pattern at other times (Table 3.1). Percentage fat in this muscle was weakly correlated with predicted dissectible fat weight ( $r^2=0.09$ ). Samples from five regions of the musculature showed that muscle tissue in caribou was generally lean (Table 3.2).

#### 3.3.2 Bone

Femur weight was strongly related to carcass bone weight (Fig. 3.2). Age and condition had no effect on this relationship ( $P < 0.01$ ). Of the five indicator bones, all but the scapula had allometric regressions less than 1 (Table 3.3).

Fig. 3.1. Carcass muscle weight in relation to gastrocnemius weight  
in caribou.

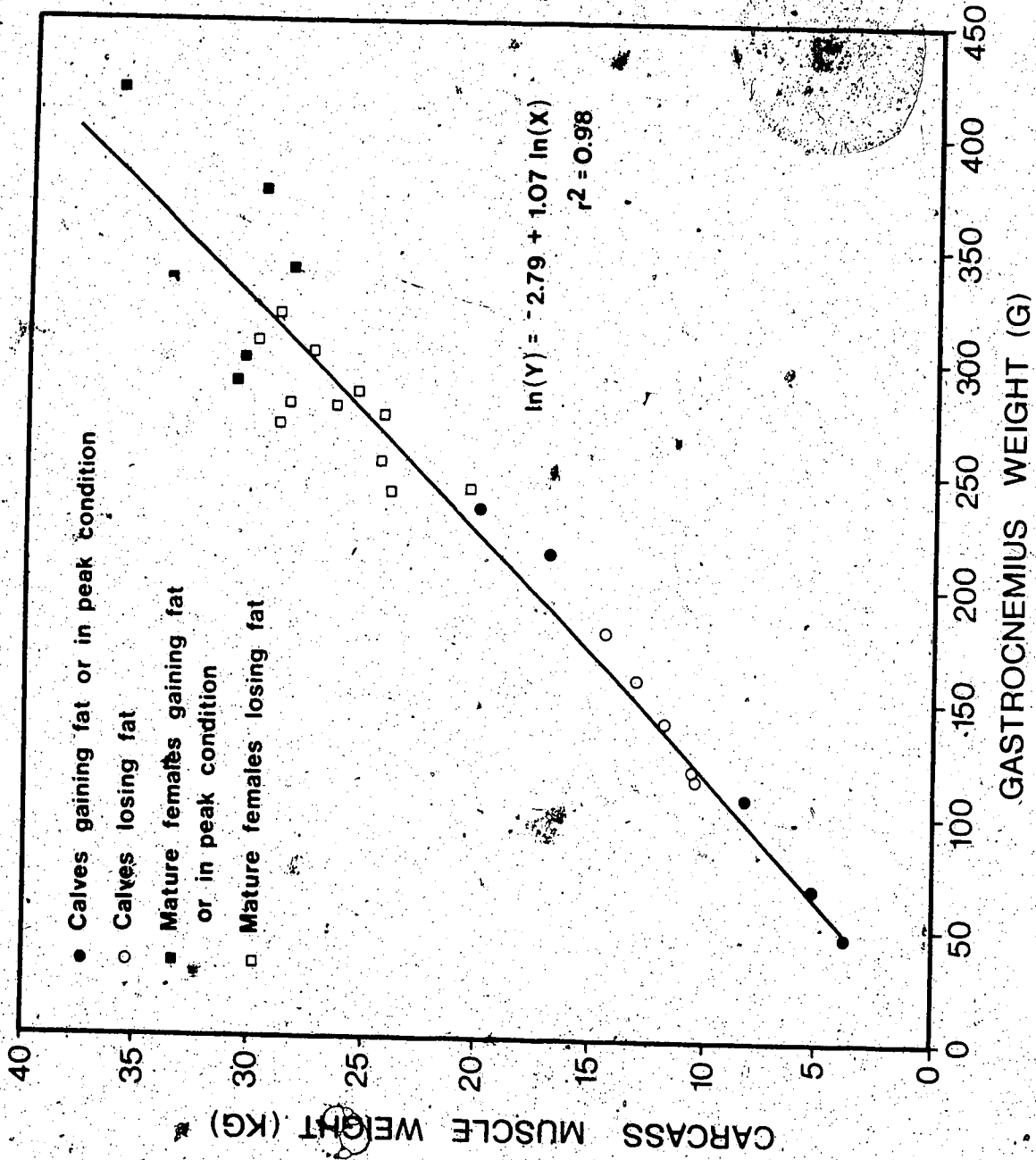




TABLE 3.1. Seasonal composition of the gastrocnemius muscle in Coats Island caribou. Means and standard errors (s.e.)

Season	Adults					Calves				
	n	DM (%)	s.e.	Fat (%)	s.e.	n	DM (%)	s.e.	Fat (%)	s.e.
mid-summer 1982	5	24.3	0.3	2.5	0.2	2	22.3	0.3	1.7	0.1
late summer 1982	9	24.6	0.3	2.1	0.1	4	23.6	0.1	1.8	0.1
early winter 1982	4	25.8	0.2	2.3	0.1	3	24.3	0.3	1.8	0.1
mid-winter 1984	8	25.0	0.2	2.3	0.1	2	19.5	0.2	1.1	0
late winter 1984	8	23.5	0.4	1.7	0.1					
spring 1984	8	24.2	0.4	2.2	0.1	5	22.0	0.7	1.8	0.1

DM - Dry Matter

TABLE 3.2. Dry matter (DM) and fat content of six muscle samples in two caribou. Means and standard errors (s.e.)

Anatomical location	DM (%)	s.e.	Fat (%)	s.e.
Near scapula	22.9	0.08	2.31	0.07
Biceps femoris	23.9	0.33	2.46	0.36
Intercostal	27.9	0.32	7.04	0.79
Near pelvis	24.2	0.04	3.51	0.12
Near metatarsus	24.9	0.06	1.87	0.23
Gastrocnemius	24.5	0.32	2.32	0.26

Fig. 3.2. Carcass bone weight in relation to femur weight in caribou.

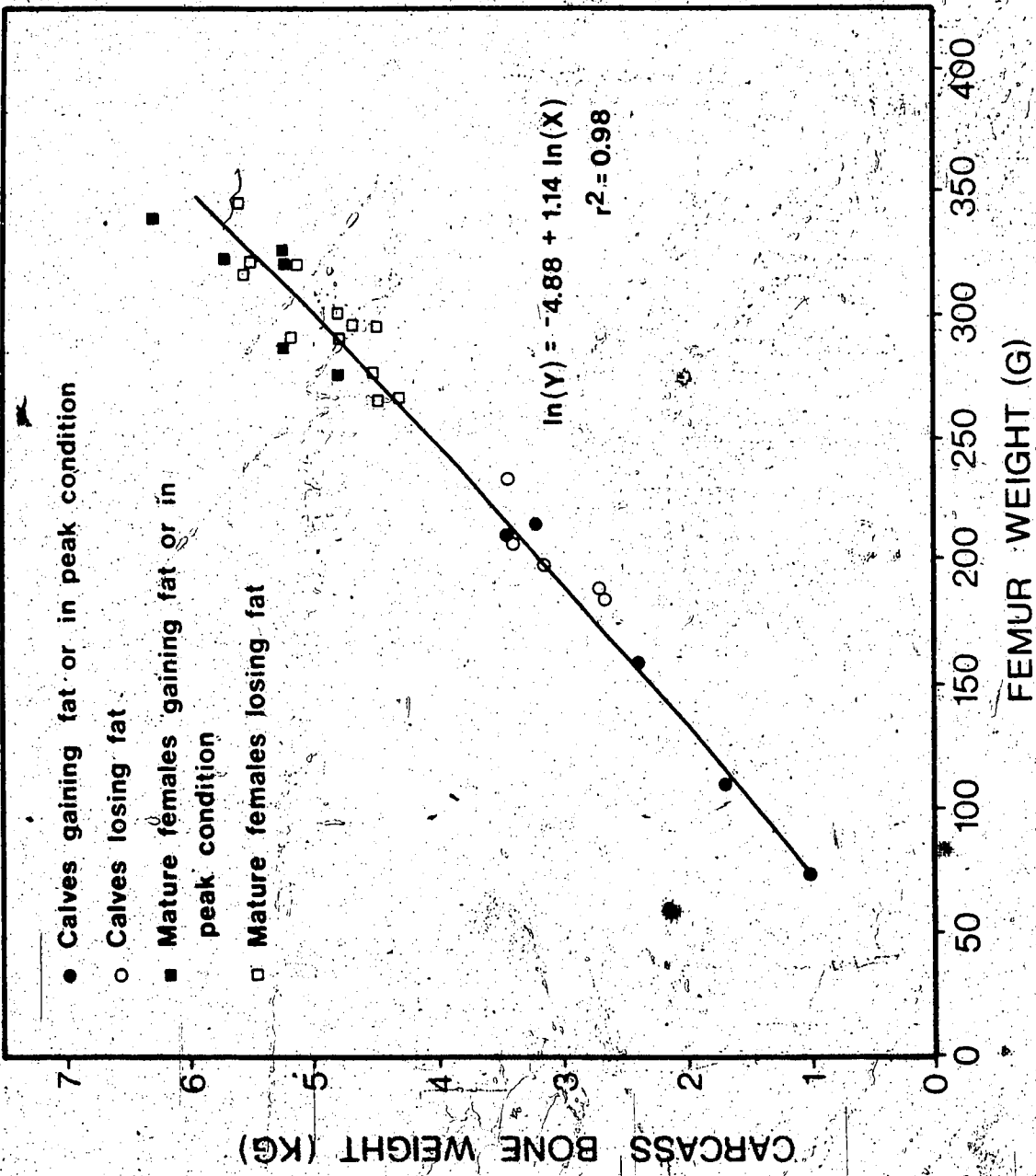


TABLE 3.3: Predictive equations for muscle, bone and fat in caribou on Coats Island.

<u>Muscle and bone</u> <sup>1</sup>					
Index tissue	Equation	n	r <sup>2</sup>	Allometric regression (b)	s.e.(b)
Gastrocnemius	$\ln(Y) = -2.791 + 1.071 \ln(X)$	27	0.98	0.91	0.028
Femur	$\ln(Y) = -4.878 + 1.137 \ln(X)$	27	0.98	0.86	0.024
Humerus	$\ln(Y) = -4.208 + 1.050 \ln(X)$	24	0.97	0.93	0.033
Radio-ulna	$\ln(Y) = -4.525 + 1.169 \ln(X)$	22	0.96	0.82	0.037
Tibia	$\ln(Y) = -4.823 + 1.160 \ln(X)$	18	0.98	0.84	0.033
Scapula	$\ln(Y) = -2.299 + 0.811 \ln(X)$	24	0.96	1.18	0.051

<u>Dissectible fat</u> <sup>2</sup>				
	Equation	n	r <sup>2</sup>	s.e.(est.)
with total kidney fat	$Y = -0.178 + 1.058 X_1 + 24.147 X_2$	23	0.98	0.547
with Riney-trimmed kidney fat	$Y = -0.246 + 1.151 X_1 + 26.401 X_2$	23	0.98	0.550

1 - Y is predicted weight of tissue in kg; X is weight of indicator tissue in g.

2 - Y is predicted weight of dissectible fat in kg; X<sub>1</sub> is DBF in cm, and X<sub>2</sub>

is weight of kidney fat in kg.

### 3.3.3 Fat depots

The subcutaneous and intermuscular depots were by far the largest in fat animals, while the three internal depots remained small (Fig. 3.3a). Subcutaneous fat was absent in very lean animals but increased quickly, and became the largest depot as dissectible fat approached 4-6 kg.

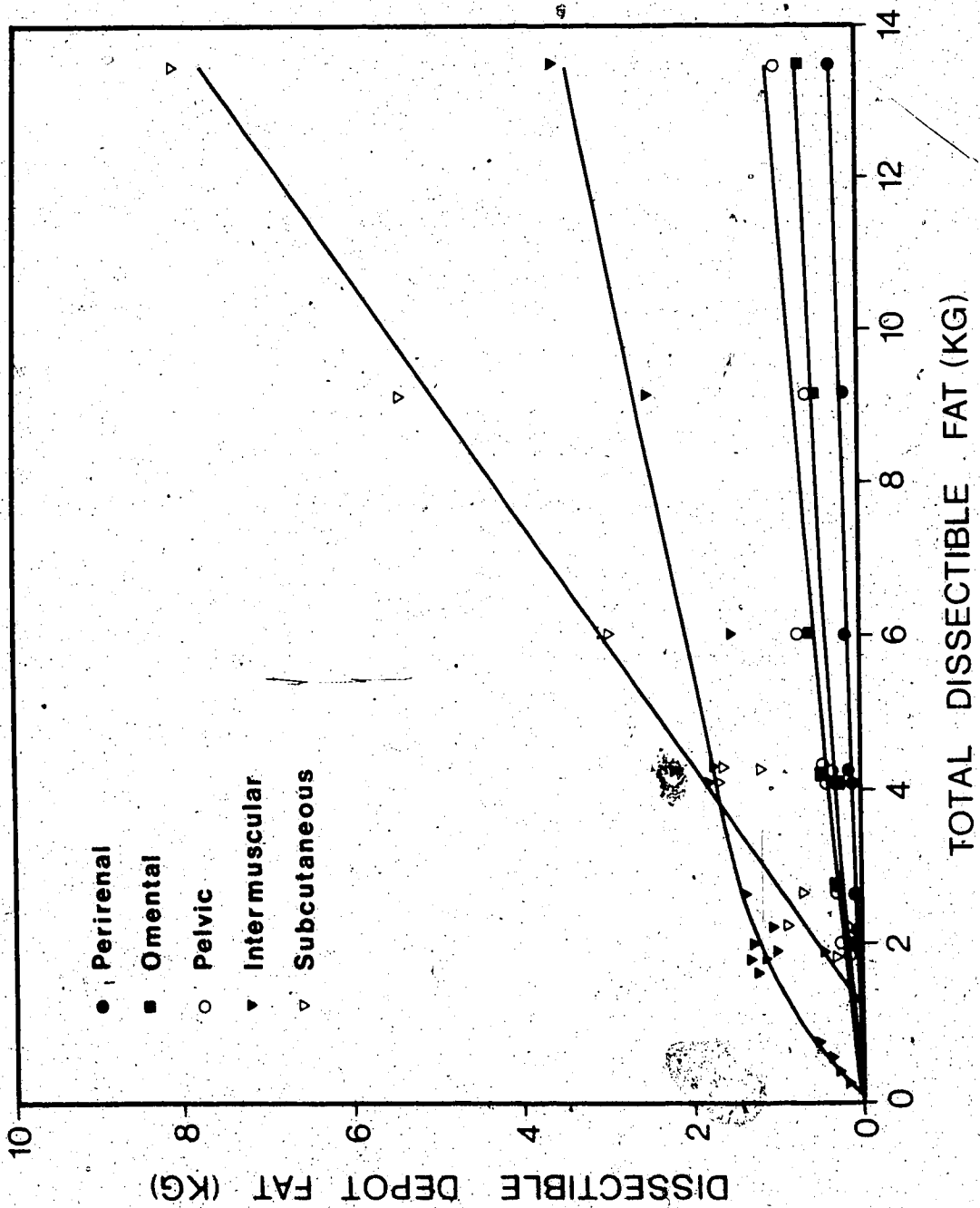
Subcutaneous and perirenal depots were related rectilinearly to total dissectible fat, while omental and pelvic depots were allometrically related to total fat, slowly decreasing as fractions of total fat (Fig. 3.3b). Changes in intermuscular fat appeared biphasic. Caribou losing fat tended to conserve it in the omental and pelvic depots, but there were few clear differences between calves and adults, and between caribou losing fat and those gaining fat or at peak condition.

### 3.3.4 Fat indices

Dissectible fat was accurately predicted from DBF and kidney fat (measured as total kidney fat or as trimmed according to Riney, 1955) (Table 3.3). Neither equation was affected by age or condition ( $P < 0.01$ ). Marrow fat was a poor overall predictor of fatness because it varied little with kidney fat except in very lean animals (Fig. 3.4). Omental fat also did not contribute significantly to the equations.

### 3.3.5 Comparison with other predictive equations

Fig. 3.3 (a and b). Changes in fat depots relative to total dissectible fat in caribou. X is total dissectible fat (kg); Y is fat in individual depot (kg). The equation for subcutaneous fat is based only on weights of subcutaneous fat > 0.





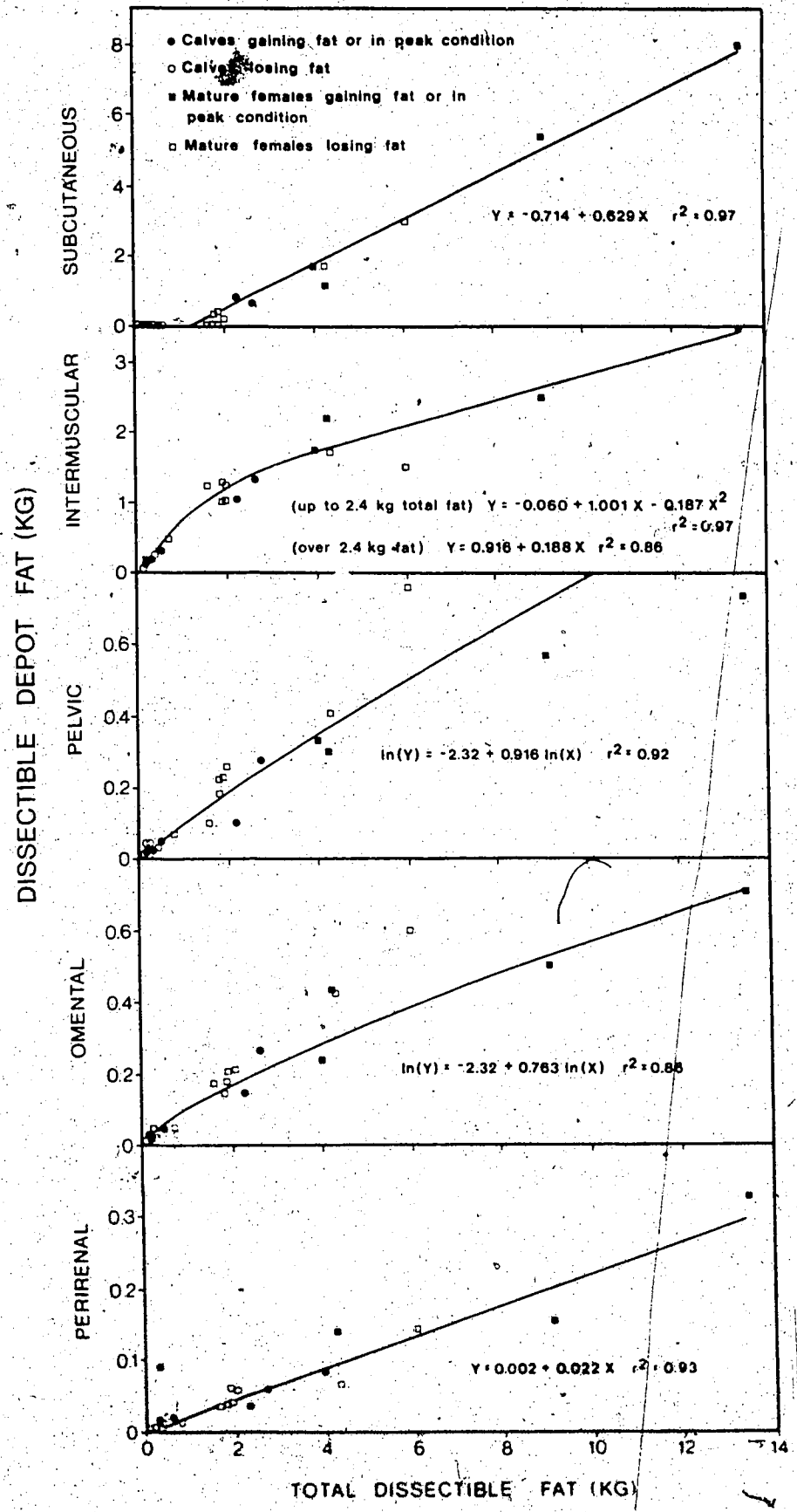
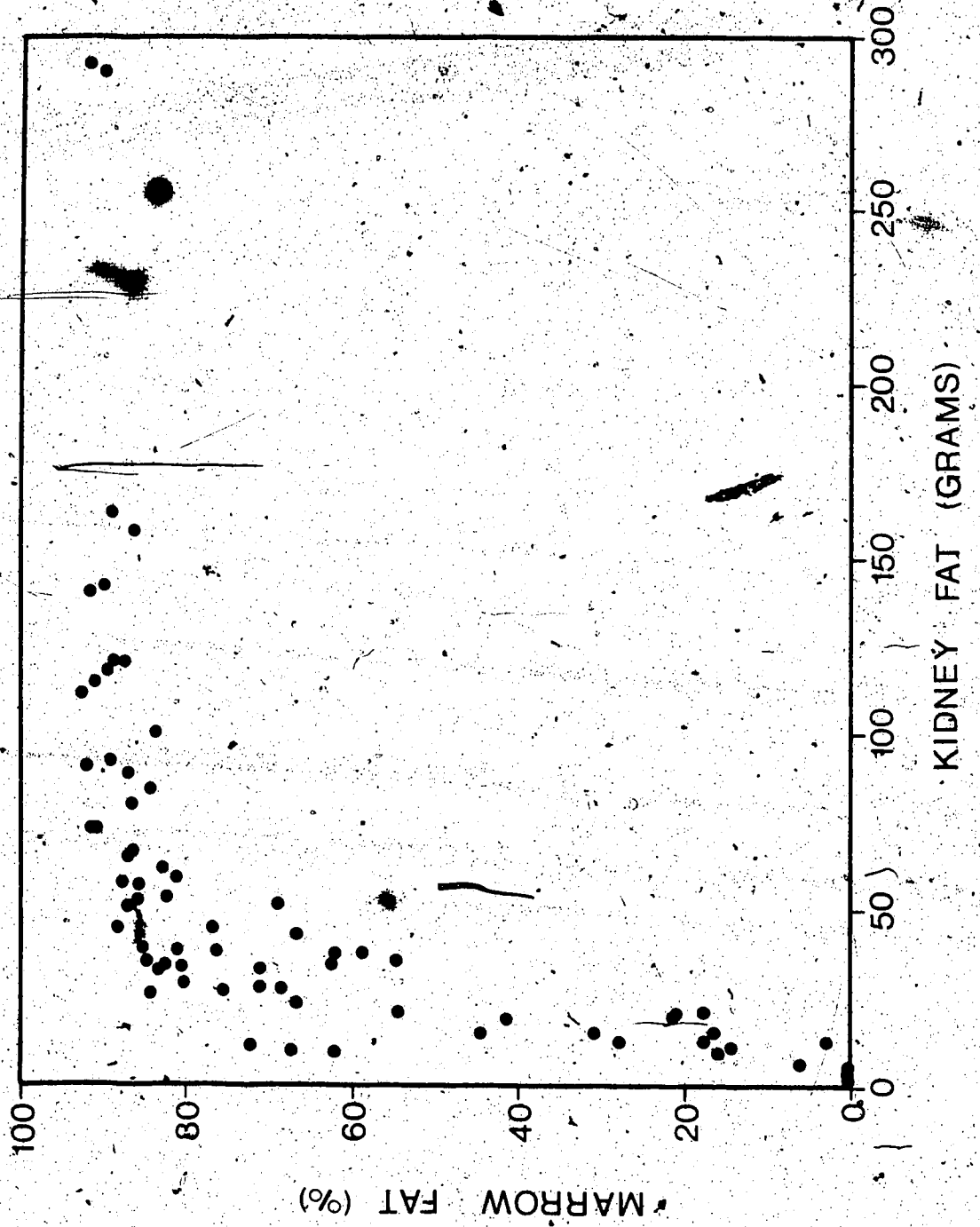


Fig. 3.4. Changes in femoral marrow fat in relation to kidney fat in caribou.



Predictions of dissectible muscle, bone, and fat from this study were compared with predictions of carcass muscle from weight of the gastrocnemius, carcass bone from weight of the femur (Ringberg et al. 1981), and dissectible fat from DBF (Reimers and Ringberg 1983) by entering identical index values in the related equations and comparing with values from actual dissections (Table 3.4). These comparisons are discussed below.

### 3.4 Discussion

#### 3.4.1 Muscle

A strong relationship existed between the weight of the gastrocnemius and carcass muscle weight for caribou at any body weight, and the relationship was not affected by sex (Ringberg et al. 1981). Similarly, distribution of weight among the muscles remains generally constant relative to total muscle weight in cattle through nutritional restriction and compensatory growth; early-maturing muscles (such as the gastrocnemius) lose the least weight during nutritional restriction and recovery of muscle weight during compensatory growth follows the normal pattern of growth (Butterfield 1966). Although all muscles maintain a strong allometric relationship with total muscle (Berg and Butterfield 1976), the gastrocnemius was particularly useful because it is small, readily identified, and its removal does not cause major damage to the carcass.

Seasonal changes in muscle weight of caribou on Coats Island can

TABLE 3.4. Comparison of predicted carcass tissue weights in Rangifer

<u>Muscle</u>				
Animal size	Predictor gastrocnemius weight (g)	Predicted muscle Ringberg <i>et al.</i> 1981 (kg) <sup>1</sup>	Predicted muscle, this study (kg)	Actual muscle (kg)
calf	119.5	9.8	10.3	10.7
adult female	320.8	26.8	28.7	29.1

<u>Bone</u>				
Animal size	Predictor femur weight (g)	Predicted bone Ringberg <i>et al.</i> 1981 (kg) <sup>2</sup>	Predicted bone, this study (kg)	Actual bone (kg)
calf	110.8	2.17	1.62	1.71
adult female	321.1	6.94	5.38	5.49

<u>Dissectible fat</u>				
Animal fatness	Predictors DBF (cm) & kidney fat (g)	Predicted fat Reimers & Ringberg (1983) (kg)	Predicted fat, this study (kg)	Actual fat (kg)
Lean	0.9, 39	1.3	1.8	1.9
Fat	3.3, 112	6.2	6.5	6.0

1 - adjusted upward due to use of extra muscle by Ringberg *et al.* (1981) (see text)

2 - Ringberg *et al.* (1981) included weights of metacarpi & metatarsi in carcass bone.

be large: four calves collected in October 1983 had a mean predicted muscle weight of 19.4 kg (s.e. 0.68); while two calves collected five months later had a mean predicted weight of 11.3 kg (s.e. 0.68) (Chapter 4). Reimers and Ringberg (1983) found comparably large overwinter changes in lean body mass of Svalbard reindeer. Perhaps more consideration should be given to evaluation of muscle as a protein reserve in wild ungulates, as protein is a major factor in seasonal weight change and constitutes an important reserve. (Torbit et al. 1985).

3.4.2 Bone

Carcass bone weight was accurately predictable from femur weight for caribou at all stages of growth and weight loss. The strength of the allometric equations for the five bones measured demonstrates the constancy of these anatomical relationships from birth to maturity. The consistency of the relationships may, however, mask large changes in marrow composition (from 0 to ca. 90% fat) and in density of mineral salts with nutritional status (Hyvarinen et al. 1977).

Allometric slopes less than 1 are characteristic of early-maturing tissues (Berg and Butterfield 1976) and thus the femur, humerus, radio-ulna, and tibia are early-maturing in the caribou while the scapula is late-maturing. These results are consistent with results of Richmond et al. (1979) in pigs, and Jones et al. (1978) in cattle, and reflect priority in functional development.

Bone weight changes little in animals losing or gaining reserves (Price 1976, 1977). Bone lengths and their ratios have been used in comparisons of population nutrition (Klein and Strandgaard 1972, Klein 1981). Weights of indicator bones may be useful in this context.

### 3.4.3 Fat

Caribou, like Svalbard reindeer (Reimers and Ringberg 1983), deposit relatively little fat internally and subcutaneous fat is by far the largest depot in fat animals. The late development of the subcutaneous depot suggests that insulative value of subcutaneous fat is not essential and that fat around major blood vessels and organs has a higher priority, perhaps to permit localized increases in metabolic rate (Frisch 1984). The general pattern of depletion/repletion is consistent with results for wapiti (Cervus elaphus canadensis) (Flook 1970), thar (Hemitragus jemlahicus) (Caughley 1970), and caribou (Dauphine 1976). Although the depots varied in rate of maturation, there was no discrete "sequence" of mobilization.

The inherently more complex nature of distribution among fat depots (compared with muscle and bone) is indicated by the variety of curves fitted to individual fat depots in Fig. 3. Fat allocation does not follow allometric rules in marrow and muscle, and the convenient depot designations used may not reflect actual biological priorities in fat distribution. Fat was lost most rapidly during

nutritional stress from those depots which were latest to mature, as found by Butterfield (1966) in cattle. Both subcutaneous and internal depots have been suggested as disproportionately susceptible to undernutrition (Murray *et al.*, 1975, Little and Sandland 1975).

Ideally, indices of fatness should approximate a rectilinear relationship with total fat over its entire range (Robbins 1983). The best estimators of dissectible fat in this study were kidney fat weight and DBF, both of which have rectilinear or near-rectilinear relationships with dissectible fat. The equation using Riney-trimmed kidney fat may be preferable since this method of designating perirenal fat is repeatable, while identification of total perirenal fat can be relatively subjective in fat animals. Huot and Goudreault (1984) did not consider DBF a useful correlate of fatness in caribou since it was not measurable in very lean animals ( $< 6\%$  body fat) but noted its possible use in fatter animals.

By contrast, marrow fat in the caribou, as in white-tailed deer (*Odocoileus virginianus*) (Ransom 1965) and wildebeeste (*Connochaetes taurinus*) (Sinclair and Duncan 1972) is depleted late and replenished early. It is a useful measurement in lean animals. Similarly, chemical fat in the gastrocnemius was a useful predictor of dissectible fat only in very lean animals. Huot and Goudreault (1984) reached a similar conclusion, while Ringberg *et al.* (1981) found chemical fat in the gastrocnemius strongly correlated with overall fatness in lean growing reindeer.



#### 3.4.4 The kidney fat index in caribou

The kidney fat index (KFI = weight of kidney fat as a percentage of weight of kidneys without fat) has been widely used with many variants. Assessments of its validity have been similarly varied (Riney 1955; Anderson *et al.* 1972; Monson *et al.* 1974; Finger *et al.* 1981). This index is a valid measure of body fatness if kidney weight consistently reflects body weight, and if kidney fat weight is strongly proportional to total fat. Although kidney fat weight is strongly proportional to dissectible fat weight in caribou, kidney weight in caribou fluctuates seasonally and may not reflect body weight accurately (Dauphine 1975). On Coats Island, mean weight of both kidneys in adult female caribou varied from 332 g. (n=5, s.e.=0.9) in July 1983 to 166 g (n=8, s.e.=9.4) in May 1984 while body weight changed from 87.5 kg (s.e.=3.5) to 76.7 kg (s.e.=3.2) (Chapter 4). The use of kidney fat weight as a measure of fatness (Dauphine 1976), is preferable to the use of KFI in caribou, because kidney weight is a poor correlate of body weight. This index should be used with caution in any species for which these relationships are unknown, as suggested by Van Vuren and Coblenz (1985).

#### 3.4.5 Comparison of predicted bone, muscle, and fat weights

Total muscle weights predicted from the weight of the gastrocnemius using equations of Ringberg *et al.* (1981) and this study compare favourably. Ringberg *et al.* (1981) included weight of the flexor digitorum superficialis with the "gastrocnemius"

(Ringberg, pers. comm.), which represents an increment of 33.9% over the weight of the gastrocnemius ( $n=33$ ,  $s.e.=0.45$ ; Adamczewski, unpublished data).

The gastrocnemius declines slightly as a proportion of total muscle weight with maturity (allometric slope  $< 1$ ) as shown by Berg and Butterfield (1976) in cattle. This slow decline may not have shown in the data range of Ringberg *et al.* (1981a) because their study was limited to growing reindeer.

Carcass bone weights predicted from equations of Ringberg *et al.* (1981) and this study are somewhat less comparable, perhaps because their "carcass weight" included the skull, metatarsi, tarsi, metacarpi, and carpi (not included in this study). Inclusion of skull and mandible weights would likely have decreased differences in predicted carcass bone weight.

Predictions of dissectible fat weight from the equation of Reimers and Ringberg (1983) and this study compare favourably but show the variability inherent in prediction of fatness. Dissectible fat measured by Reimers and Ringberg (1983) included some fat not measured in this study, but internal depots in caribou and reindeer are small.

These comparisons suggest that proportions between weights of individual bones, muscles, fat depots, and their respective total weights are relatively constant among subspecies of Rangifer, given that most differences in predicted values were due to methodology. Similarly, breeds of cattle varying widely in size and apparent body

conformation rarely show significant differences in distribution of weight among bones, muscles, and fat depots (Berg and Butterfield 1976).

#### 3.4.6 Conclusión

Dissectible fat, muscle, and bone were readily predicted from simple indices of each tissue in caribou. Allometric relationships within tissues appeared to hold for different subspecies of Rangifer and were largely unaffected by age, sex, and condition. The variability of predicted values compared with actual values, particularly for dissectible fat, suggests that predictions from these indices can best be used in comparing groups of animals and in comparing individuals differing substantially in condition and weight.

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Chapter 4. Seasonal changes in body composition of mature female  
caribou and calves.<sup>1</sup>

4.1 Introduction

Overwinter losses of body reserves strongly influence mortality and reproduction in insular populations of reindeer (R. t. tarandus) (Klein 1968; Leader-Williams and Ricketts 1982; Reimers et al. 1982). Calves of Svalbard reindeer (R. t. platyrhynchus) typically deplete reserves by late winter and their survival during severe winters is poor (Reimers et al. 1982; Reimers 1984). Adult female Peary caribou (R. t. pearyi) and Svalbard reindeer survive winter better, but poor nutrition during late winter may adversely influence fetal growth, survival, and adult size (Thomas 1982; Skogland 1983; 1984). During exceptionally severe winters, extreme loss of body reserves is associated with heavy mortality of reindeer and caribou in all age classes (Klein 1968; Thomas et al. 1976).

Full recovery of body reserves during the short arctic summer is essential for winter survival and reproduction. Summer recovery is

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rapid in Svalbard reindeer despite severe depletion of reserves and a short growing season (Reimers et al. 1982; Reimers 1984), but disturbance by insects can severely limit summer fattening in barren-ground caribou (Kelsall 1968). An upper limit to fatness may be determined by a seasonally varying set point (Ryg 1983) but few wild reindeer and caribou approach such fatness.

Protein also decreases substantially in nutritionally stressed mule deer (Odocoileus hemionus) (Torbit et al. 1985) as does lean tissue in wintering Svalbard reindeer (Reimers et al. 1982). However, little is known of seasonal dynamics of muscle mass and of their importance in wild ruminants. Muscle catabolism may occur in reindeer eating lichen diets even under conditions of positive energy balance (Nieminen 1980). Large changes in rumen fill and size of internal organs characterize seasonal cycles in red deer (Cervus elaphus) (Mitchell et al. 1976). Such changes may have a large effect on total body weight in sheep (Ovis aries) and cattle (Bos taurus and Bos indicus) (O'Donovan 1984) and provide indirect evidence of nutritional quality.

Barren-ground caribou (Rangifer tarandus groenlandicus) on Coats Island, Northwest Territories, are isolated and free of predation. They fatten far more by late summer than most mainland caribou (Parker 1975) but extensive winter malnutrition and poor productivity

have occurred frequently (Gates et al. 1986). Calf production has nearly ceased following severe winters on Coats Island (Gates et al. 1986). In the absence of predation, population dynamics in this population are clearly dependent on the depletion of body reserves and properties of nutrition during winter, and on the ability of caribou to recover these reserves during summer.

This study was undertaken to analyse changes in body composition of mature female caribou and calves on Coats Island during two successive summers and winters from 1982 to 1984. Dynamics of fat and muscle were compared between females and calves, and related to fetal and calf growth and calf survival.

## 4.2 Materials and Methods

### 4.2.1 Study area and population

Coats Island is a flat sparsely vegetated island of ca. 5600 km<sup>2</sup> in northern Hudson Bay (Gillett 1976). There is an elevated area of granite and gneiss at the northeastern end, but much of the interior is composed mainly of shattered limestone and resembles flat polar deserts (Svoboda 1977) on high arctic islands. Coastal areas are primarily lowlying wetlands with myriad small lakes and ponds, interspersed in some areas with a network of old strand lines and raised beaches. Summers tend to be short and cool due to the marine environment, which brings frequent fog, rain, wind, and 24-hour mean temperatures rarely exceeding 5-7°C in summer. Persistent snow

cover begins in October/November and the peak of snowmelt usually is in early or mid-June.

Caribou are generally found on the island's periphery, with no distinct subpopulations. Southampton Island to the north is the nearest and likeliest historic source of the population (Gates *et al.* 1986). Wolves have never colonized the island, and despite significant hunting by Inuit from Coral Harbour on Southampton Island in recent years, winter mortality has been the major force in population dynamics (Gates *et al.* 1986). A large die-off in 1974-75 eliminated two thirds of the population (*op. cit.*) and some winter mortality occurred in 1979-80, 1981-82, 1983-84, and may occur to varying degrees every year (*op. cit.*).

#### 4.2.2 Collections

Twelve seasonal collections of mature female caribou (4-9 per collection) and their calves were conducted from May 1982 to June 1984 (Table 4.1). In the second seasonal cycle, the late summer collection was omitted and the early winter collection was made in October. A final collection was made in June 1984.

The study area centered on a permanent camp built near Cary's Swan Nest (62° 5' N, 83° 11' W) at the southern end of Coats Island. Animals were collected within a 15-20 km radius of this camp, typically over a 10-day period. Tissue samples were frozen in a propane-powered freezer. Animals were aged using annuli in the cementum of incisors (Miller 1974).

TABLE 4.1. Numbers of mature females, calves, and yearlings collected during 1982-1984 on Coats Island, N.W.T.

Collection period	Season	Mature females	Calves	Yearlings
mid-June 1982	spring	4	1	-
late July - early August 1982	mid-summer	5	2	-
late August 1982	late summer	8	4	-
early November 1982	early winter	5	3	-
late March - early April 1983	mid-winter	8	3	-
mid-May 1983	late winter	8	1	-
mid-June 1983	spring	4	3	1
late July - early August 1983	mid-summer	5	4	1
mid-October 1983	early winter	7	4	2
late March - early April 1984	mid-winter	8	2	-
mid-May 1984	late winter	8	-	-
mid-June 1984	spring	9	6	-
Totals		79	36	4

#### 4.2.3 Linear Measurements

Measurements to the nearest 0.5 cm included total body length and body length to base of tail (Langvatn 1977), head length (Krog et al. 1976), mandible length, chest girth (Langvatn 1977), shoulder height to base of dew claw (Dauphine 1976) and to hoof tip (Krog et al. 1976), foreleg and hindleg length, and femur length (Langvatn 1977).

#### 4.2.4 Weights

The entire animal was weighed (except blood loss from shooting), skinned, and eviscerated. Carcass weight (dressed carcass remaining after removal of head, skin, lower legs severed at distal ends of metacarpi and metatarsi, viscera including kidneys with fat, and gravid uterus in pregnant females) was recorded. Other measurements recorded were weight of the skin, antlers, reticulo-rumen with and without contents, remaining full gastrointestinal tract from omasum to anus, liver, kidneys, and heart (without pericardium, stripped of blood, with the major vessels severed at the tops of the auricles). In pregnant females, the gravid uterus, fetus, and stripped uterus were weighed; presence of lactation was noted during summer and fall collections.

#### 4.2.5 Dissectible tissue weights and indices of condition

Anatomical dissections were carried out on 27 caribou carcass sides to calibrate predictor indices of dissectible tissues (Chapter 3). Regression equations from these dissections (all with  $r^2$  of

0.98) were used to predict weights of dissectible bone, muscle, and fat from weight of the femur, weight of the gastrocnemius muscle, and depth of back fat (DBF) and weight of Riney-trimmed kidney fat, respectively (indices measured on every animal). Dissectible fat included fat of the carcass and the internal omental and perirenal depots. Percentage of fat in the femoral marrow (Adamczewski *et al.* 1987) was also determined. Marrow fat, depth of back fat (DBF), and weight of kidney fat have been reported in addition to dissectible fat weight.

#### 4.2.6 Statistical methods

Analysis of variance (ANOVA) was used to establish the significance of seasonal changes in mean weights, followed by multiple range comparisons (SNK) (Steel and Torrie 1980) of seasonal means in adult females and calves. Least squares regression and correlation (*op. cit.*) were used to establish relationships between maternal condition and fetal weight. A comparison between lactating and non-lactating females was made for summer and fall data using an ANOVA to test for the effect of month (July, August, and October/November) and year, followed by a least-squares ANOVA (U.S.D.A. 1960; used due to unbalanced data) to test for the significance of lactation and month. Statistical analyses were made with SPSSx (SPSS Inc. 1983).

### 4.3 Results

Numbers of mature females, calves, and yearlings collected are shown in Table 4.1. Results for 2- and 3-year-old females were insufficient for analysis. Data for calves were few but variability (standard errors of means) was consistently low. Females four years old and older were referred to as mature or adults.

#### 4.3.1 Linear measurements

Growth was rapid in calves from birth until October-November, but then slowed to near zero until spring (Fig. 4.1). Rapid growth resumed in the second summer. Growth achieved by the two calf cohorts during their first summers was compared by pooling data for both winter periods. Shoulder height from hoftip was significantly greater ( $P < 0.01$ ) in 1983-born calves than in 1982-born calves (87.6 cm vs 79.4 cm), and metatarsal length was also significantly greater (31.3 cm vs 29.9 cm,  $P < 0.025$ ). Males, which would be expected to be larger, made up 4 of the 7 calves in 1982, and 2 of the 6 in 1983.

Linear measurements for females 4 years old and older (Fig. 4.1) were grouped since they changed little after that age. Linear measurements compared by year of birth showed no significant trends.

#### 4.3.2 Body and carcass weight

Carcass weight of mature females decreased markedly over winter and increased rapidly during summer, but total body weight showed

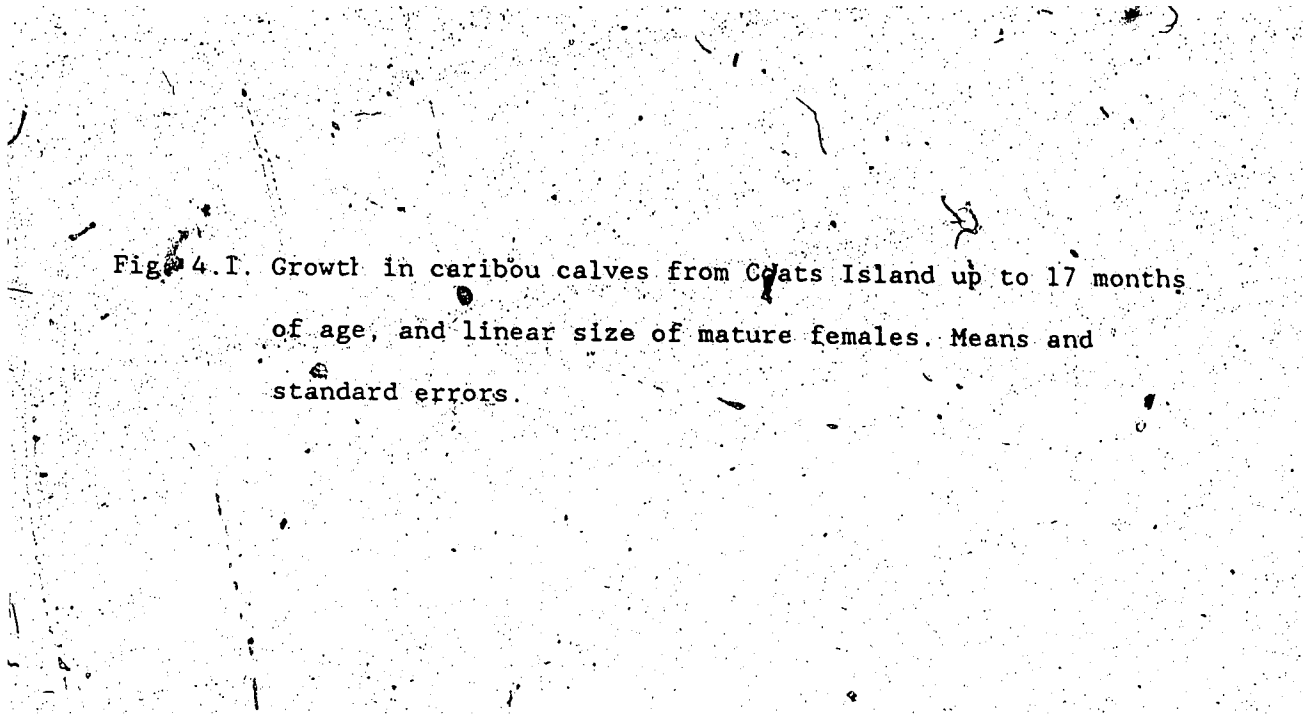
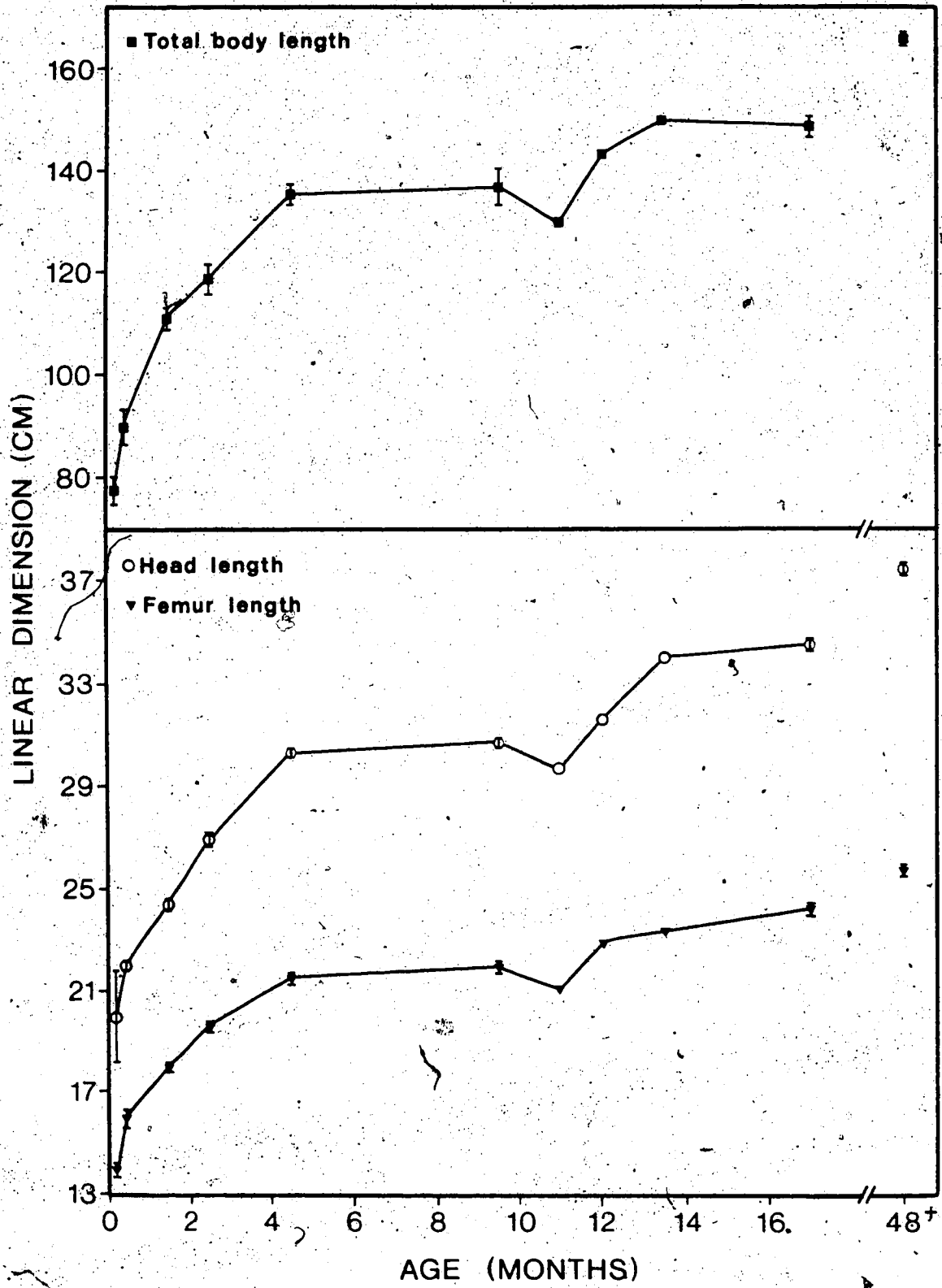


Fig. 4.1. Growth in caribou calves from Coats Island up to 17 months of age, and linear size of mature females. Means and standard errors.





less fluctuation (Fig. 4.2). Carcass weight was weakly related to total body weight ( $r^2=0.66$ ); correcting total body weight for weight of the conceptus improved the  $r^2$  to 0.81. Similar peak total and carcass weights were reached in fall/early winter of 1982 and 1983. Overwinter loss of carcass weight was 38% from October 1983 to June 1984. Parturition occurred between the May and June collections.

Growth of calves was a rapid 390 g/day from calving in mid-June to late July (Fig. 4.3) assuming a birth weight of 5 kg (Reimers 1983). Growth rate slowed to 270 g/day over the August-October period. Total body weight in calves showed little of the severe overwinter losses in carcass weight (Fig. 4.3).

#### 4.3.3 Digestive tract

Changes in weight of reticulo-rumen contents were a major factor in the relative composition of total body weight. The weight of rumen contents in mature females was highest in winter (Fig. 4.2), with a maximum in March/April 1984 and a minimum in October 1983. These two extremes were significantly different ( $P < 0.05$ ) from the weights at all other seasons. Weight of the reticulo-rumen contents increased even more markedly over winter in calves (Fig. 4.3).

Empty reticulo-rumen weight was significantly higher in July 1983 than at any other season, ( $P < 0.05$ ), coinciding with peak summer plant growth. The weight of the remaining digestive tract (omasum to anus) also peaked in July 1983 (Fig. 4.2). Empty reticulo-rumen

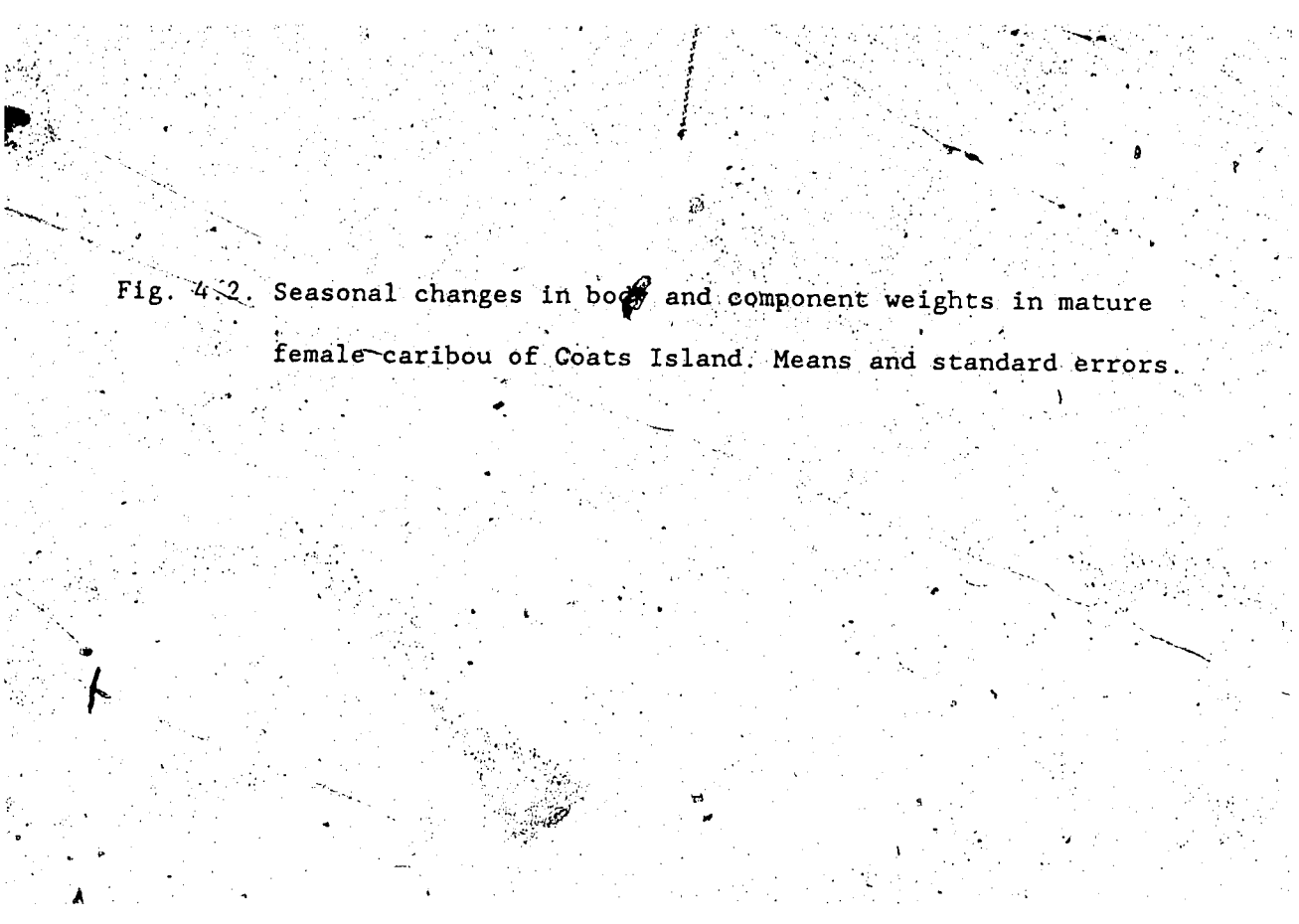
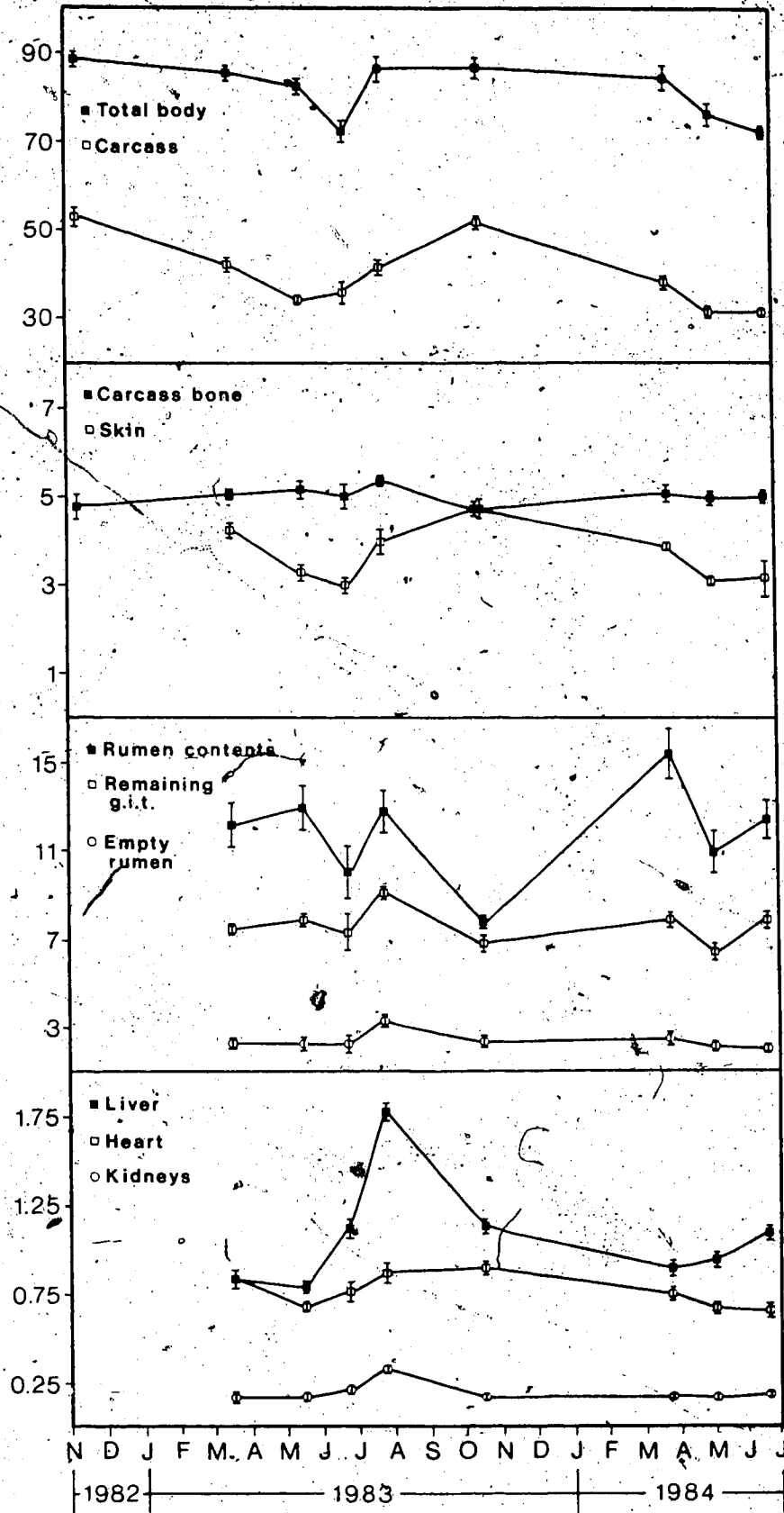


Fig. 4.2. Seasonal changes in body and component weights in mature female caribou of Coats Island. Means and standard errors.

WEIGHT (KG)



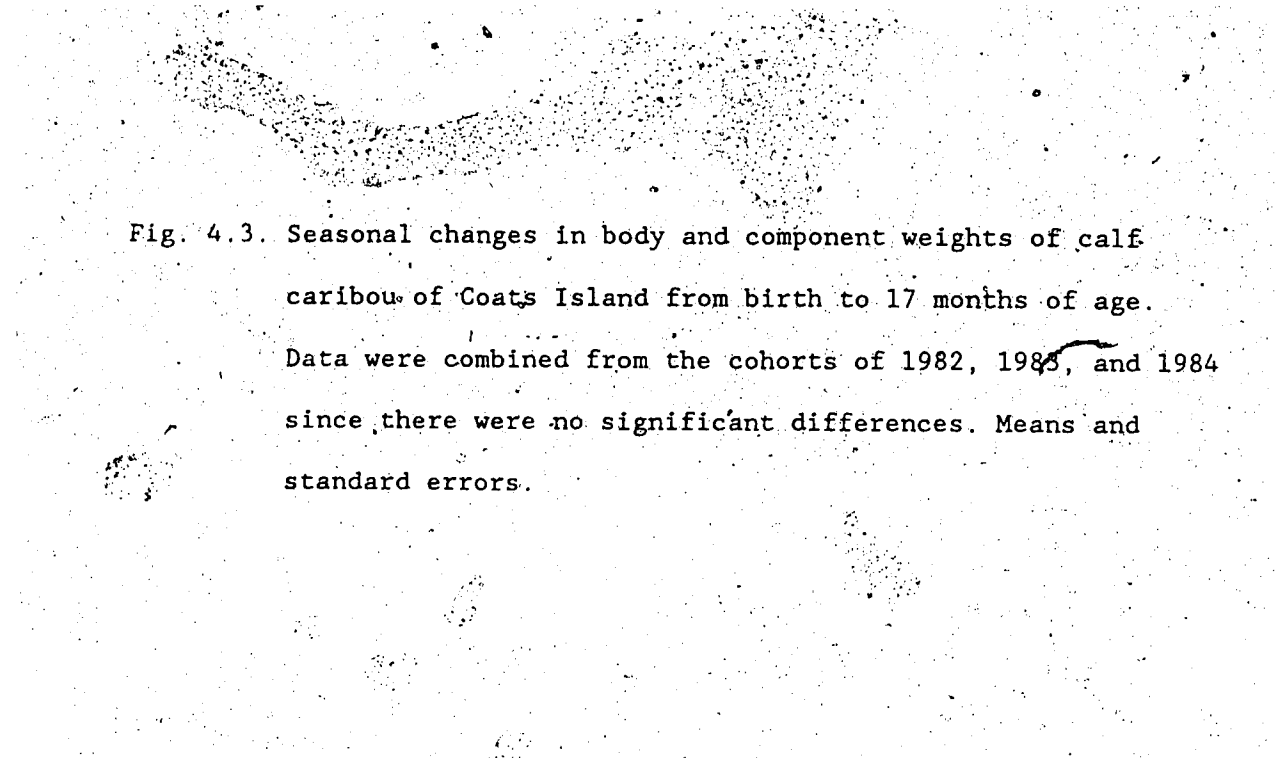
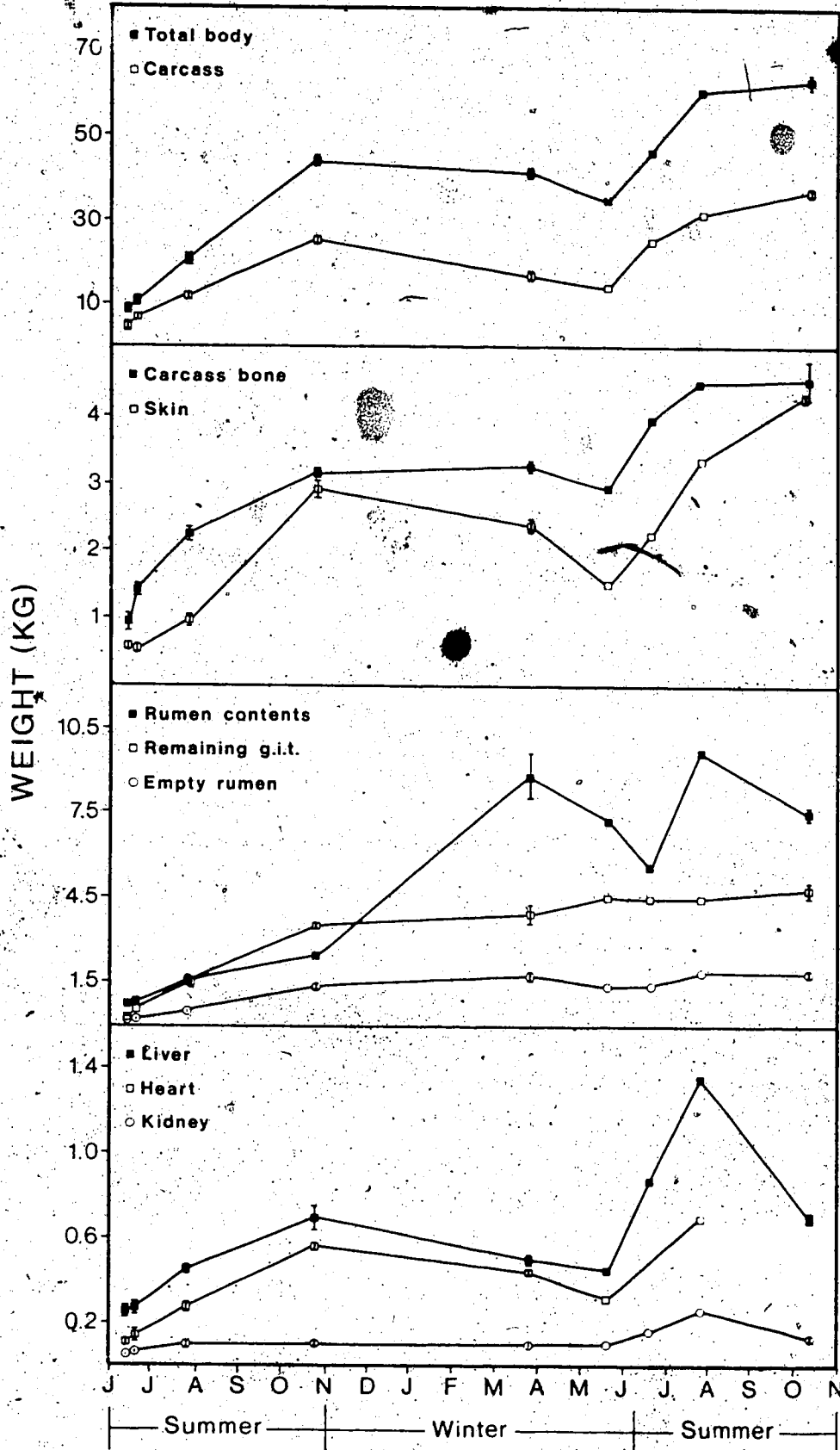


Fig. 4.3. Seasonal changes in body and component weights of calf caribou of Coats Island from birth to 17 months of age. Data were combined from the cohorts of 1982, 1983, and 1984 since there were no significant differences. Means and standard errors.



weight increased marginally over winter in calves.

#### 4.3.4 Internal organs

Weights of the heart, liver, and kidneys changed widely with season in mature females and calves. The liver and kidneys reached maximal weight in mature females at peak summer plant growth in July 1983, when they were more than double the weight of the same organs in May 1984 (Fig. 4.2). Weights of these organs were poorly related to carcass weight: the liver represented 4.2% of carcass weight in July 1983 and 2.2% of carcass weight in October 1983. The heart, by contrast, remained close to 2.0% of carcass weight through the year.

Changes in liver, heart, and kidney weights in calves showed the same pattern as in adults (Fig. 4.3) although the sharp July peak in liver and kidney weight was obscured by rapid growth of calves. Organ weight changes in caribou in their second season of growth approached those in adult females (Fig. 4.3).

Weight of the hide fluctuated in concert with carcass weight (Figs. 4.2, 4.3).

#### 4.3.5 Dissectible fat

Fattening of mature females was rapid but dissimilar between the summers of 1982 and 1983. Females began summer 1982 in poorer condition than in 1983 (Figs. 4.4, 4.5). They gained fat most rapidly during the early part of summer 1982, while most of the fattening in 1983 came late in the season after a slow start.

Fig. 4. Seasonal changes in dissectible fat and carcass muscle in adult female caribou. Fat and muscle weights were standardized to a mean carcass bone weight of 5.0 kg, to standardize frame size of animals compared. Muscle (left axis) and fat (right axis) weights have been arranged so that minima of both are level. Means and standard errors.



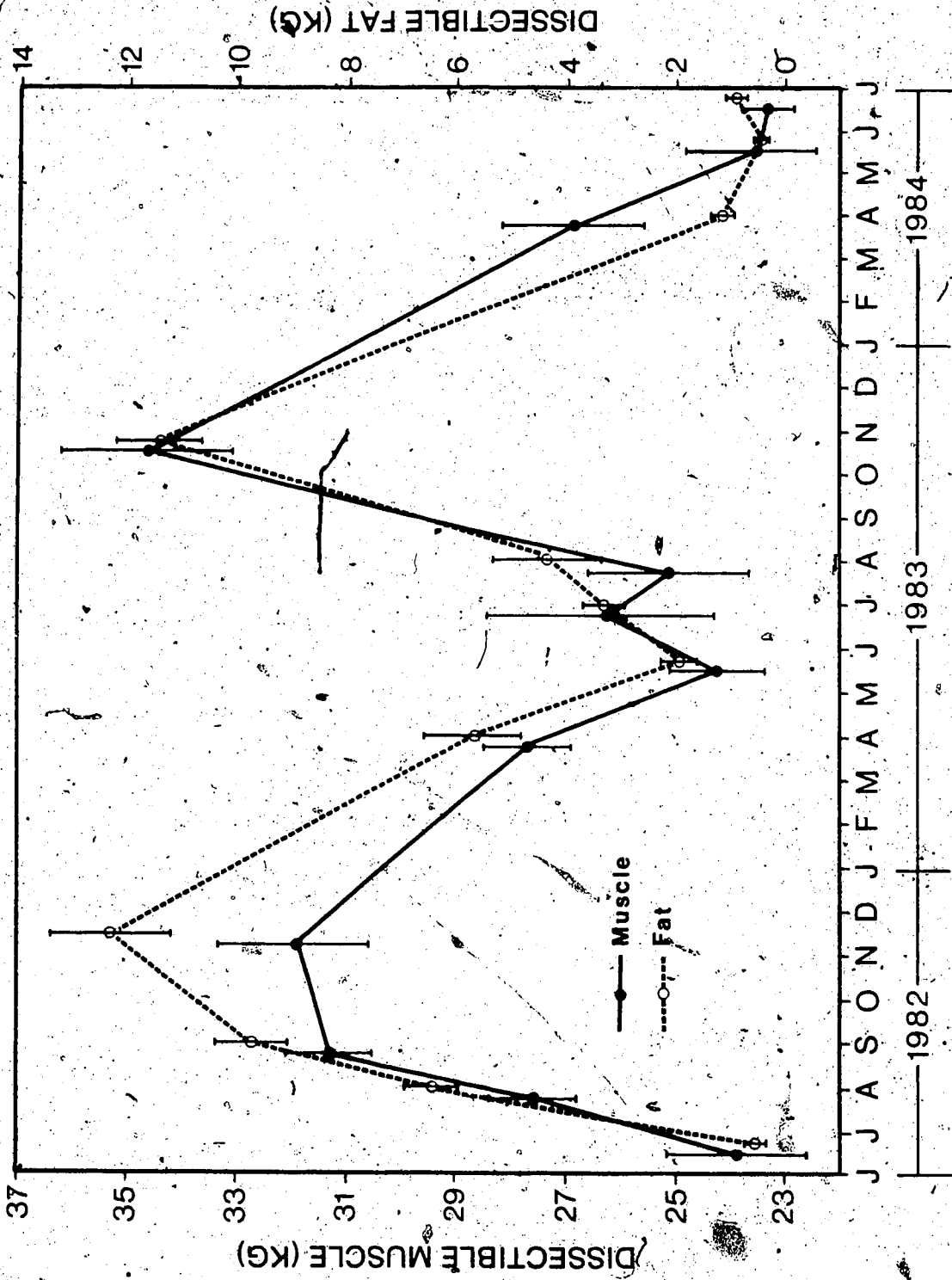
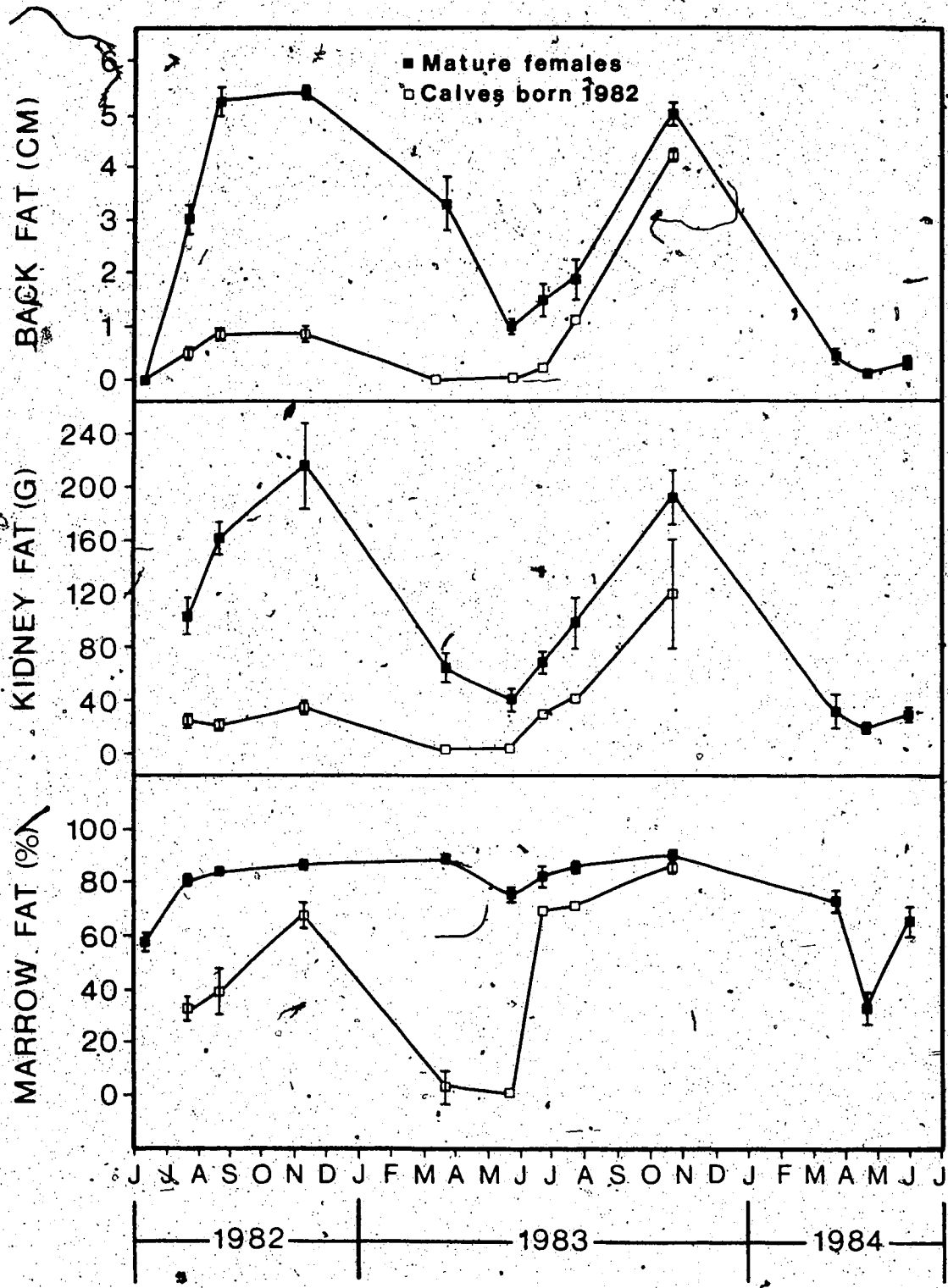


Fig. 4.5. Seasonal changes in fat indices in mature females and calves born 1982 on Coats Island. Means and standard errors.



Similar peak fatness occurred at the beginning of winter during both years.

Mobilization of fat in mature females differed between the two winters in magnitude and timing. Fat was lost from November 1982 to March/April 1983, with a rapid decrease in fatness during the final weeks of winter (Fig. 4.4). Females were significantly leaner ( $P < 0.05$ ) in March/April 1984 than a year earlier, and had little fat to lose over the final weeks of winter. Overall losses were more severe during 1983-84, with most females in June 1984 having significantly less dissectible fat than in June 1983, ( $P < 0.05$ ).

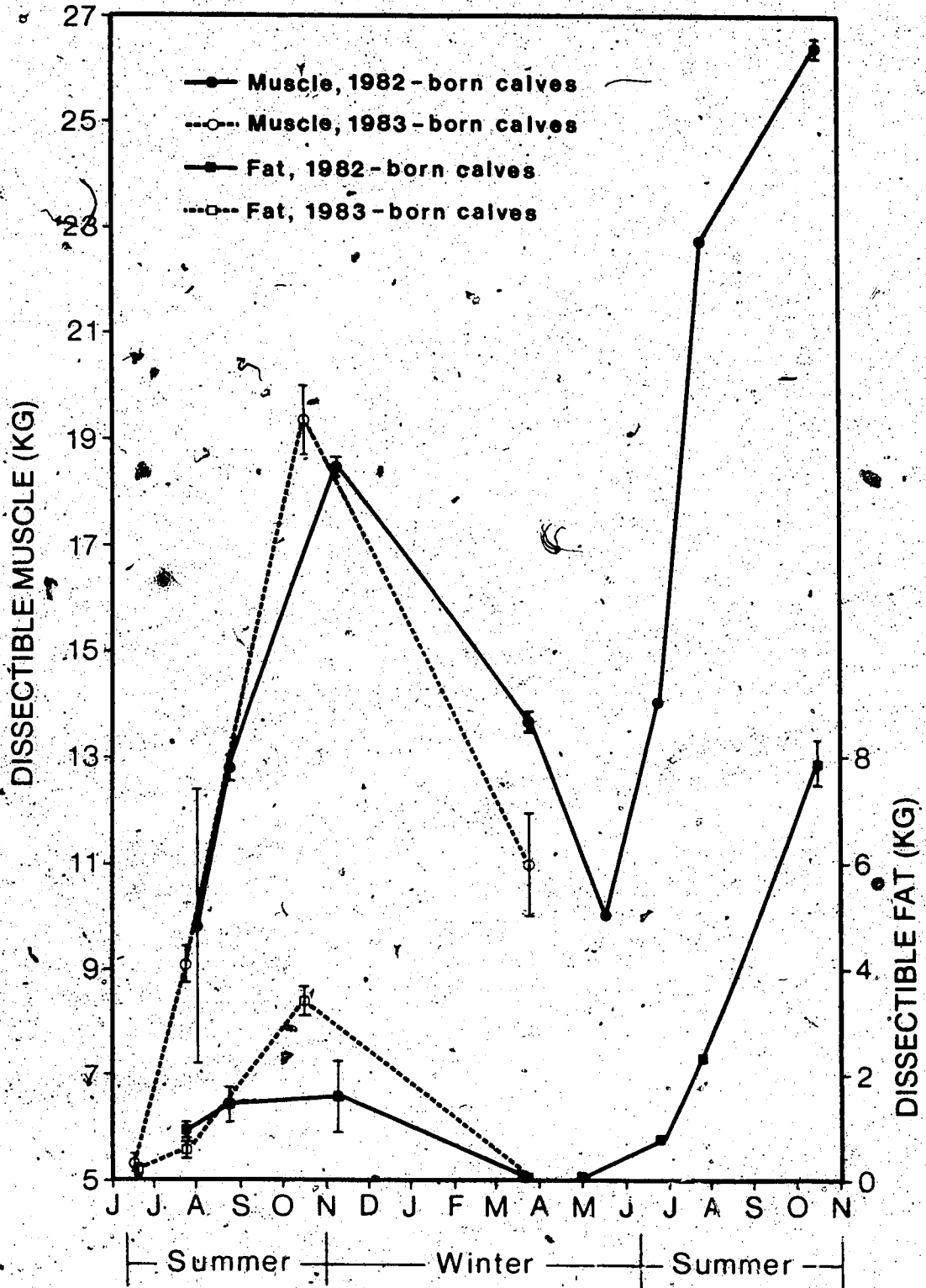
Calves were lean during their first summers in both years, and deposited proportionately far less fat in fall than adults (Figs. 4.5, 4.6). Calves born in 1983 were significantly fatter at the end of the growing season than calves born in 1982 (3.4 kg vs 1.6 kg,  $P < 0.05$ ). Females were fatter than males in both years at the same carcass bone weight, but the difference was not significant (1.32 kg vs 0.81 kg,  $P = 0.06$ ).

Over winter, calves lost fat earlier and more completely than adults (Fig. 4.6); by March-May, they had virtually no marrow fat left (Fig. 4.5). For calves that survived winter, fat deposition during the second summer approached that in adults (Figs. 4.5, 4.6).

#### 4.3.6 Muscle

Females gained muscle rapidly during the summer of 1982, reaching a plateau in late summer (Fig. 4.4). As with fat, peak weights of

Fig. 4.6. Seasonal changes in dissectible fat and carcass muscle  
in calves born 1982 and 1983 on Coats Island. Means and  
standard errors.



muscle were comparable between years despite a lower starting point in 1982 and a slow initial gain of muscle in 1983. Maximal losses of muscle weight were 24.5% during winter 1982-83, and 32.8% during 1983-84 (Fig. 4.4). Muscle losses appeared most rapid at winter's end in both years.

Calves gained muscle rapidly throughout their first growing season, even after adult muscle weight had stabilized (Fig. 4.6). Both absolute and relative gains and losses of muscle were much larger in calves than in adults.

Muscle and dissectible fat weights generally declined and increased concurrently in mature females but their relative rates were not necessarily similar. During late summer 1982, fat gains apparently continued when muscle weight had reached a plateau (Fig. 4.4). During winter, rates of fat loss and muscle loss also were not identical; muscle catabolism in late winter 1984 appeared to increase as fat exhaustion approached (Fig. 4.4). The pattern in calves was generally similar but muscle weight changed considerably more than fat over winter (Fig. 4.6).

#### 4.3.7 Bone

Carcass bone weight varied little about a mean of 5.0 kg in mature females, with no clear seasonal variation (Fig. 4.2). Bone growth was substantial in calves during the first summer (Fig. 4.3), with the largest increases occurring early. Bone weight was static during winter, but increased again early in the second summer.

4.3.8. Fetal growth, pregnancy rate, and effect of lactation on condition

All 16 mature females shot in March, April, and May 1983 were pregnant, as were 14 of 16 females a year later.

The products of conception grew rapidly from March/April to May during both years (Table 4.2). Fetal weight was comparable between the two March/April collections, but was significantly lower ( $P < 0.05$ ) in May 1984 than in May 1983, even though the May 1984 collection was conducted a week later.

Maternal body condition was significantly related to fetal weight in May, but not in March/April. There was a significant ( $P < 0.05$ ) positive correlation between dissectible fat weight of the mother and fetal weight in May 1983 ( $r^2=0.50$ ). A significant positive correlation ( $P < 0.025$ ) between independent variables marrow fat and weight of dissectible muscle, and dependent variable fetal weight was found for the May 1984 collection ( $r^2=0.63$ ).

Birth weight of calves could rarely be measured. In June 1982, one healthy neonate weighed 5.0 kg and a second, found dead, weighed only 2.7 kg. Peak calving was estimated at between June 16 and 18 in 1982. All calves shot in late June 1983 were at least 1-2 weeks old. In June 1984, calving peaked about June 15. One female shot on 20 June contained a 5.78 kg fetus, while two neonate calves weighed 4.32 kg and 6.16 kg, giving an approximate birth weight for 1984 of 5.4 kg (s.e. 0.56).

During July, August, and November 1982, 7 of 17 mature females



TABLE 4.2. Weights (kg) of the fetus and uterus in pregnant females on Coats Island, 1983 and 1984.

	1983		1984	
	late March early April n=8	mid-May n=8	late March early April n=6	mid-May n=8
Gravid Uterus	4.3	9.0	4.8	8.0
s.e.	0.4	0.6	0.2	0.5
Stripped Uterus	0.83	1.50	0.92	1.51
s.e.	0.08	0.09	0.04	0.06
Fetus	1.41	5.10	1.56	4.17
s.e.	0.26	0.35	0.06	0.32

were lactating; all 12 females shot in July and October, 1983 were lactating. Lactating females had significantly less dissectible fat (7.7 kg vs. 10.3 kg,  $P < 0.025$ ) than non-lactating females over this period, but nearly the same muscle weight (30.9 kg vs. 31.2 kg). Data for 1982 and 1983 were pooled since there were no significant differences between years.

#### 4.4 Discussion

##### 4.4.1 Body weights, digestive tract, and internal organs

Total body weight was a weak predictor of body condition, particularly in calves. This was largely due to variability in rumen fill, a phenomenon commonly observed in other ruminants (O'Donovan 1984). Carcass weight, by contrast, clearly reflected seasonal trends in reserves of fat and muscle.

Winter increases in rumen fill appeared to be a compensatory response to an increasingly fibrous diet. Snow conditions forced caribou to use foods high in acid-detergent fiber and lignin (Chapter 2). Similarly large compensatory rumen fill has been found in red deer (Milne 1980), chamois (Rupicapra rupicapra) (Hofmann 1982), cattle (Bos indicus) (Mould et al. 1982), and sheep (Ovis aries) (Weyreter and Engelhardt 1984). The high rumen fill maintained in winter suggests that absolute quantity of forage available was not limiting for these caribou.

The high weight of the empty rumen in July 1983 may have been due

to increased papillation of the ruminal mucosa, in response to high rates of volatile fatty acid production. Forage quality was highest during late July/early August (Chapter 2), and studies summarized by Hofmann (1985) have shown large seasonal changes in ruminal papillary development of the chamois, roe deer (Capreolus capreolus), red deer, and other ruminants.

Changes in liver, kidney, and heart weights reflected their physiological functions. Liver and kidney weights were greatest in July when forage quality was highest (Adamczewski et al. 1986b) and energy expenditures and intermediary metabolic processes presumably were at high levels. Functional hypertrophy of the liver in response to diet quality has been suggested in cattle (Bos taurus) (Leche 1973) and red deer (Mitchell et al. 1976), while large seasonal variation in kidney weight has been found in red deer and caribou (Mitchell et al. 1976, and Dauphine 1975, respectively). Liver weight as a fraction of carcass weight could serve as an index of recent nutrition, as suggested by Mitchell et al. (1976), in contrast to fat and muscle which are cumulative measures of nutrition. The heart serves all body tissues, and therefore maintains a strong proportionality to empty-body or carcass weight.

#### 4.4.2 Fat

The amplitude of the cycle of fatness was considerably larger in this population than that observed in mainland barren-ground caribou (Dauphine 1976) and approached the extreme cycle in Svalbard reindeer

(Reimers et al. 1982, Reimers and Ringberg 1983).

Winter fat losses reflected changes in diet forced by hard-packed snow cover, which restricted caribou to foods of very poor quality (Chapter 2). During winter 1982-83, fat losses were initially slow due to a relatively mild early winter period of little snow, but a late winter increase in snow depth (op. cit.) coincided with late gestation to force an increased use of fat during the last weeks of winter. Heavy snowfalls early in the second winter (op. cit.) reduced available diet quality and produced a more rapid loss of condition.

Recovery of fat during both summers was complete despite severe depletion. Good quality summer forage and few impediments to feeding are essential to growth and fattening (Reimers 1980). Caribou on Coats Island fed on high quality foods, mostly willow (Salix spp.) during summer, and moved little (Chapter 2). The only restriction to feeding was disturbance by mosquitoes (Aedes spp.) and warble flies (Oedemagena tarandi). While lactation apparently slowed fattening during early summer 1983, females were able to compensate in late summer and reached a similar fatness by October 1983 as during the previous fall.

Disturbance by insects may also have contributed to slow initial fattening in summer 1983. Insects disturb grazing in Rangifer tarandus most on hot, calm, sunny days (Kelsall 1968; White et al. 1975), conditions that rarely occur on Coats Island due to its marine environment. Abnormally dry warm weather during late July and

early August 1983 (Adamczewski, unpubl. data) would have fostered insect activity. Indeed, the mean number of warbles in adult females was significantly higher ( $P < 0.01$ ) during late winter 1983-84 (mean 61.3, s.e. 8.4) than during the previous winter (26.9, s.e. 4.8), which followed a cooler, wetter summer (op. cit.). Hot weather and insect harassment have been linked to considerable summer weight loss in mainland caribou (Kelsall 1968), while Svalbard reindeer, which encounter no insects at all (Reimers 1984), fatten rapidly throughout summer (Reimers et al. 1982, Reimers and Ringberg 1983).

#### 4.4.3 Muscle

Changes in muscle weight were a major factor in seasonal weight dynamics of Coats Island caribou. Svalbard reindeer (Reimers and Ringberg 1983) and white-tailed deer (Odocoileus virginianus) on Anticosti Island (Huot 1982) also show large seasonal changes in lean body mass.

Muscle in caribou, particularly calves, represents a significant energy source which increases in importance as fat is depleted. The importance of amino acids as an energy store, particularly contributing gluconeogenic precursors, is well known and has been demonstrated by Torbit et al. (1985) in mule deer. However, skeletal muscle is also a nitrogen store. Changes in body protein are not entirely dependent on changes in fat and energy balance (Orskov 1982). It is possible to induce positive nitrogen balance during negative energy balance (Orskov 1982); conversely, reindeer on

low-nitrogen lichen diets may degrade muscle despite abundant digestible energy (Nieminen 1980). Similarly, the composition of empty body weight gain in sheep and cattle depends to a considerable extent on protein concentration of the diet (Andrews and Orskov 1970; Byers 1980). Protein accretion and loss in the ruminant depend most on a supply of microbial protein adequate to maintain tissue (Orskov 1982). Body muscle may be built or used depending on this supply.

Dietary nitrogen may be a limiting factor for Coats Island caribou in addition to energy. Caribou recycle urea efficiently (Wales *et al.* 1975) but during late winter, the level of nitrogen in the rumen of Coats Island caribou was low (Chapter 2) and females lost muscle mass during late gestation in April-May despite an apparent increase in diet quality in late winter 1984 (*op. cit.*). Similarly, cats may deplete body protein at the end of pregnancy in spite of a high-quality diet (Naismith and Morgan 1976).

#### 4.4.4 Evidence for a set point in body composition

Ryg (1983) provided evidence of a seasonally varying set point for body fatness in reindeer, as has been suggested in domestic ruminants (Baile and Forbes 1974; Forbes 1977) and other mammals (Mrosovsky and Prowley 1977; Mrosovsky and Sherry 1980). There was circumstantial evidence from measures of body fat, muscle, and rumen fill that mature female caribou in this population were at, or near, set points in body fat and muscle in October/November 1982 and 1983. They had similar (and seasonally maximal) levels of body fat and

muscle in October 1983 and November 1982 despite a poorer "starting" condition in 1982, and slow gains of fat and muscle in early summer 1983. At their set point in body energy, ruminants are expected to decrease intake and rumen fill to a maintenance level (Baile and Forbes 1974). Rumen fill maintained by female caribou was considerably lower in October 1983 than at any other season, although diet quality was similar to that in spring (Chapter 2), when rumen fill was much greater. Body fat and protein levels appear to be the seasonal targets rather than body weight itself.

#### 4.4.5 Calf survival

Poor fattening in calves was likely a major handicap to their survival. Calves in this population grew rapidly (compared with other Rangifer - Reimers, 1983) during their first summer, but little fat was deposited until late in the growing season. This pattern is also typical of red deer (Drew 1985) and cattle, which normally do not fatten substantially until a certain lean body growth has been achieved (Berg and Butterfield 1976). In contrast to mature females, which demonstrated some degree of flexibility in their summer compensatory growth, calves used the entire snow-free season to gain weight. The greater fat reserves of 1983-born calves on Coats Island occurred because they had already achieved a greater lean body size. Calves of Svalbard reindeer fatten almost as quickly as adult females, perhaps in part because lean body size is smaller in Svalbard reindeer (Reimers et al. 1982, Reimers 1984). The

consistently better survival of female calves than males on Coats Island (Gates *et al.* 1986) may also be related to their smaller mature lean body mass and apparent tendency to fatten slightly more than male calves; male caribou/reindeer take longer to reach their larger mature size (Dauphine 1976, Timisjarvi *et al.* 1982).

Under conditions of deep, hard snow, forage available to Coats Island caribou tends to be of very poor quality (Chapter 2). Such food ferments slowly in the rumen, and calves, with their higher relative energy requirements due to smaller body size, are at a disadvantage. Given a presumably poor ability to supply energy from food and smaller body reserves, poor winter survival would be expected in caribou calves under severe winter conditions. In fact, extensive starvation of calves was found in March and April 1984, well before snowmelt, while no dead mature females were found that year (Gates *et al.* 1986).

#### 4.4.6 Nutrition, reproduction, and linear growth

Excellent summer recovery of body reserves and high pregnancy rates suggest that females were not vulnerable to undernutrition until late winter.

Poor maternal condition apparently retarded fetal growth and reduced production of viable calves during late winter 1983-84. The retarding effects of poor maternal condition on fetal growth have been shown in sheep (Palsson and Verges 1952), white-tailed deer (Verme 1963), and reindeer (Skogland 1984). The percentage of



neonatal calves in the population in late June 1984 was well below its potential, and has been as low as 7:100 following more severe winters (Gates et al. 1986). While lactation may delay fattening in females, they are clearly able to recover condition by fall and the cost of rearing a calf does not apparently carry over to the next year.

Light birth weight and poor lactation may reduce subsequent survival of calves. Two emaciated females shot in June 1982 on Coats Island had both given birth, but had regressed mammaries and no milk. The depressing effect of poor maternal condition on milk production is well known in sheep (Doney et al. 1981). The combined effects of light birth weight and poor early lactation might then hinder calves from achieving a growth stage at which substantial fat could be deposited. The greater fatness and larger fall size achieved by calves born in 1983 to relatively fat mothers, relative to calves born in 1982 to emaciated mothers, support this suggestion. Poor survival of calves below a threshold birth weight has been documented in red deer (Blaxter and Hamilton 1980).

Light weight at birth and poor early lactation may also affect eventual mature size. Skogland (1983) and Clutton-Brock et al. (1982) have shown that mature body size of reindeer and red deer, respectively, is most vulnerable to stunting during the late fetal/neonatal stage. Total body length in mature females on Coats Island was nearly identical to that in mainland Kaminuriak barren-ground caribou females (Dauphine 1976), but shoulder height and metatarsal length were less in Coats Island females. These

differences were similar in magnitude to those between the 1982 and 1983 calf cohorts on Coats Island, and may indicate a large number of mature caribou stunted during the critical neonatal/late fetal stage. Severe winters are common on Coats Island, and several winters more severe than 1982-83 and 1983-84 have been documented (Gates et al. 1986). Shorter extremities may also be an indication of slight racial (genotypic) differentiation on Coats Island.

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## Chapter 5. General Discussion and Conclusions

Winters 1981-82, 1982-83, and 1983-84 severely stressed caribou on Coats Island despite excellent nutrition in summer. Winters considerably more severe than these have been documented on Coats Island (Gates *et al.* 1986), yet mature females catabolized nearly all dissectible fat and a substantial portion of skeletal muscle during these three winters. Mature females, of all classes, are least stressed nutritionally by winter in white-tailed deer (Huot 1982), wapiti (Flook 1970) and Svalbard reindeer (Reimers 1984). Adult female caribou apparently can withstand remarkable depletion of reserves over winter. However, since they seem to frequently approach the nadir of their reserves in late winter, fetal growth and the production of healthy calves may often be vulnerable. Consistent calf production seems unlikely in this population. Once spring arrives, female caribou regain reserves at a rapid rate, achieving maximal pregnancy rates at the beginning of winter.

Body composition and forage quality were strongly correlated. With little disturbance and a good supply of nutritious willows, sedges and grasses, the vegetation available in summer readily supported the low density of caribou on Coats Island and permitted rapid fattening. During mid- and late winter, however, caribou had to rely on a food base reduced in some areas to less than 5% of the biomass available in summer, and with quality reduced by senescence and poor availability. Energy and nutrients not available from food



had to be supplied from tissue reserves: snow cover influenced diet quality directly and body reserves indirectly.

Calves were far more susceptible to nutritional stress in winter than adults, due to higher proportionate energy requirements, a poorer ability to fatten, and the same sparse, lignified forage used by mature caribou. With a proportionate energy requirement approximately 20% higher than in adults, calf survival over winter was precarious. During winter 1983-84, heavy calf mortality was found in March and April, well before mature females were strongly stressed. Consistently poor calf survival could help stabilize this population, but surveys from 1975 to 1984 suggest at least a few winters of good calf survival.

Insular populations of reindeer and caribou vary widely in density. Coats Island is characterized by a vegetation much sparser than is found on most parts of Svalbard (Reimers 1982) and South Georgia (Wiegolaski *et al.* 1982), which tend to support correspondingly higher densities of reindeer. Both the diversity and the density of vegetation on Coats Island are low; the island could not support a high density of caribou even in the absence of snow. The harsh, high-arctic climate (Parker 1975) will not permit it.

Stability of insular populations of reindeer and caribou probably

depends most on (1) a resilient forage resource, and (2) the variability of severe winter weather. Caribou on Coats Island, like those on South Georgia (Leader-Williams et al. 1981) and Svalbard (Reimers 1977) depend primarily on vascular vegetation. Such vegetation can resist grazing and as on Svalbard and South Georgia (op. cit.), long winters with extensive hard snow or ice prevent over-use. Peary caribou also seem to share this characteristic (Miller et al. 1982).

The population on Coats Island has few buffers against severe winter weather; this study suggests there may be few "easy" winters, and many severe ones. Calf survival is often poor, and more importantly, it is inconsistent (Gates et al. 1986). The exceptionally large representation of mature females in the population (op. cit.) and their consistently high pregnancy rates add to the apparent instability by providing the potential for rapid increases in population numbers. Survival among mature females is much better than among calves. However, the frequently large overwinter reduction in the reserves of mature females, with its potential effects on fetal growth, suggests high variability in calf production. This has been documented (op. cit.). Svalbard reindeer sometimes end winter in good condition (Reimers 1984), and the sex ratio does not appear as skewed as on Coats Island. Calf survival among Svalbard reindeer is poorer than for adults (Reimers and Ringberg 1983) but they appear to fatten relatively well compared to calves of caribou on Coats Island. At present, the population of

caribou on Coats Island is susceptible to winter weather every year; no stable cycles seem likely. A similar situation may prevail with Peary caribou on much of their range (Gunn *et al.* 1981). Caribou on Coats Island most closely approximate pattern C (Chapter 1) - well established, but unlikely to achieve either high density or any predictable pattern.

In summary, this study supports the following conclusions:

1. Summer forage is sparse, but is of good quality and readily permits rapid growth and fattening in the present population.
2. Hard deep snow makes much of the vegetation unavailable in mid- and late winter, and results in a very poor quality of diet for caribou.
3. Mature female caribou achieve high pregnancy rates in fall, but lose most of their body reserves by late winter, when nutritional stress may threaten calf production.
4. Calf survival is generally low due to poorer fattening, low-quality food in winter, and proportionately higher energy requirements.

5. The population will likely continue its erratic trends because of inconsistent calf survival, poor nutrition in winter, and highly variable calf production.

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