

Feeding Ecology  
of the West Greenland Caribou  
(*Rangifer tarandus groenlandicus*)  
in the Sisimiut-Kangerlussuaq Region

by  
HENNING THING

Med et dansk resumé:  
Fourageringsøkologi for den  
vestgrønlandske vildren  
(*Rangifer tarandus groenlandicus*)  
i Sisimiut-Kangerlussuaq området

Резюме на русском языке:  
Экология фуражирования дикого северного  
оленя Западной Гренландии  
(*Rangifer tarandus groenlandicus*)  
в районе Сизимут - Кангерлуссуак

ISSN 0374-7344

COMMUNICATION NO. 190 FROM VILDTBIOLOGISK STATION  
Vildtbiologisk Station, Kalø, 8410 Rønde, Denmark  
1984

# DANISH REVIEW OF GAME BIOLOGY

The journal is published and distributed by the

**Game Biology Station, Kalø, DK-8410 Rønne, Denmark**

Each paper is issued separately. When a number of papers have appeared (comprising ca. 200 pages) these will be collected in a volume together with a table of contents. The price is 100 Danish kroner per volume.

Editor: Ib Clausager. – Assistant editors: Edy Bach Jensen and Else-Marie Nielsen. – Russian summaries: Axel Mortensen. – Linguistic consultant: Dr. Robert Russel. – Printed by Clemenstrykkeriet, Aarhus.

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## Abstract

A three-year study of West Greenland caribou focused on habitat and food selection in relation to various environmental factors. Seasonal habitat preference was closely attuned to plant phenology. High quality graminoid forage was available to caribou up to six weeks prior to calving. Arrival of pregnant cows on the calving ground was synchronized with this event. Graminoids dominated the diet year round. Fruticose lichens were scattered on both summer and winter ranges. In winter both foliose and crustose lichens as well as *Empetrum nigrum* were consumed. Caribou-induced plant succession resulted in formation of *Poa pratensis* greens with high quality forage in summer on the inland range. Feeding intensity peaked at the time of maximum forage quality during calving season. Highest cost: benefit ratios during foraging were observed in mid winter with extensive cratering activity. In July-August harassment by oestrid flies reduced feeding intensity by 70-90% for about 40% of the period. The 1980 stocking rate of < 1 animal/km<sup>2</sup> utilizable winter range appeared to prevent significant lichen resource recovery although herd size declined 90% in the previous decade. However, 4 animals/km<sup>2</sup> utilizable summer range were believed not to exceed carrying capacity of the inland area, but the potential of this range was strongly limited by oestrid fly harassment.

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## Introduction

The Caribou (*Rangifer tarandus groenlandicus*) is native to Greenland, and the main range at present is the west coast, from 62° N to 72° N. Because of natural topographical barriers (i.e. fiords and glaciers) the animals are actually split up into 8-9 sub-populations with apparently insignificant interchange (THING 1980b).

The Greenland climate has been described as undergoing large-scale fluctuations, and bird and mammal populations have in the past been unstable. Caribou exhibit considerable fluctuations in numbers (e.g. VIBE 1967, KELSALL 1968). Historical evidence and present knowledge indicate that on average there are about 60 years between two population peaks in Greenland.

The last population maximum occurred at the end of the 1960's and is estimated to have reached the 100,000 level (THING 1980a). Presently, Caribou are experiencing a rapid decline throughout most of their Greenland range (STRANDGAARD 1980). Aerial population censuses in March-April of 1977, 1978, and 1980 showed a total population size of 25-30,000, 18-20,000, and 7-9,000, respectively (HOLTHE & LASSEN unpubl.).

Because of considerable concern about the future development of the population which has provided a considerable annual harvest to native hunters, the Greenland government urged the Danish Ministry for Greenland to initiate a management research programme. In April 1977 a project was initiated to study population size, distribution, and dynamics as well as habitat and forage relationships. The Game Biology Station at Kalø directed this project, and after 3 years of field work most activities were brought to an end by April 1980.

Since *Rangifer tarandus* is an herbivorous species its success and prosperity are directly dependent on the quantity and quality of the available forage within its range. It has often been stated that the arctic ecosystem is very fragile and easily irreversibly altered (e.g. BLISS et al. 1973, KLEIN 1965, 1970a, 1970b, 1973, LUICK et al. 1975). The balance between the Caribou and its food resources appears to be rather delicate and once upset (e.g. by over-grazing) restoration usually is measured in decades. This is especially true for the traditionally favoured winter forage, fruticose lichens.

The aim of the present work is to describe and quantify the relationship between the Caribou and its food resources in a selected part of the Greenland range. Furthermore, the data are then applied to evaluate the relative importance of the forage parameters as factors regulating the population.

## Acknowledgements

The study was sponsored by The Ministry for Greenland's Commission for Scientific Research in Greenland and the Greenland Home Rule. The author is indebted to many Greenlanders and Danes for good advice and assistance during the years in Greenland. Furthermore the author wishes to thank colleagues from abroad and from Kalø for good company and inspiration in the field and for support and practical suggestions during the preparation of the paper.

## Study area

The study area is situated on the west coast of Greenland bounded by the Davis Strait to the west and the Inland Ice

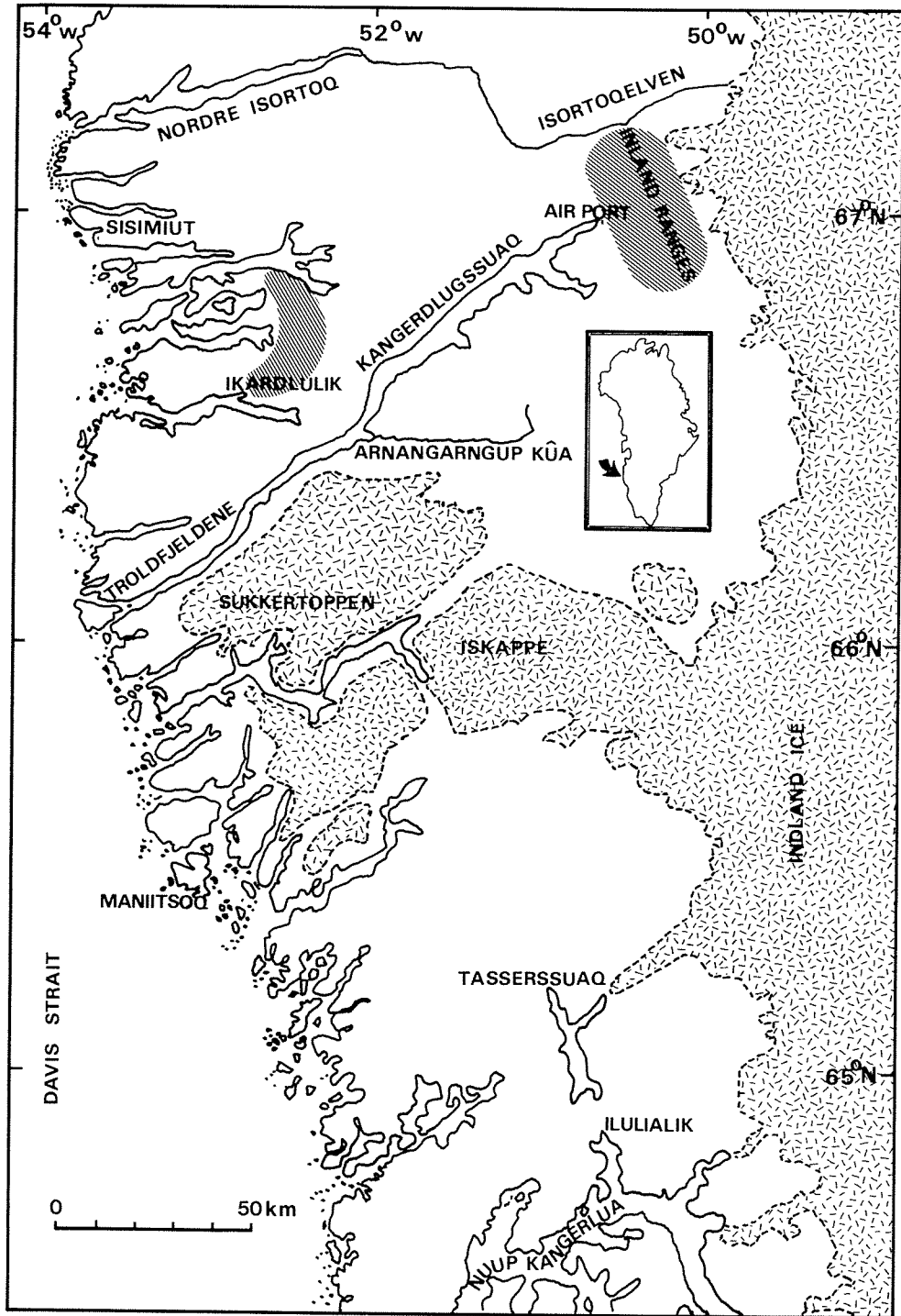


Fig. 1. Map of study areas on the west coast of Greenland.

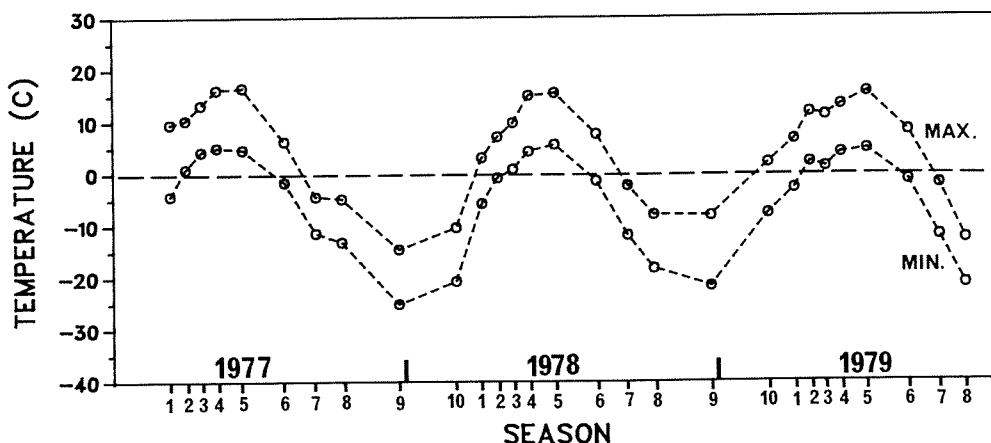


Fig. 2. Average maximum and minimum air temperatures at Kangerlussuaq Airport. Recorded by the Civil Aviation Airport Weather Service. (Season numbers refer to list p. 9.)

to the east. Most field work was conducted between Nordre Isortoq and Isortoq-elven to the north and Sukkertoppen Iskappe to the south, an area totalling 18,000 km<sup>2</sup>. Some additional data were collected further south, viz. Nuup Kangerlua – Ilulialik area (Fig. 1).

Traditionally the Sisimiut-Kangerlussuaq region has been considered one of the best Caribou ranges. Here the ice-free land edge is at its widest extending some 130 km from the Inland Ice to the coast of the Davis Strait. In 1967 the eastern third of the study area was designated a Caribou reserve and consequently no Caribou hunting has since been allowed. West of the reserve there are two hunting seasons: August 1 – September 30 (either sex) and February 1 – March 15 (bulls only).

### *Climate*

Throughout West Greenland a trend towards a more humid (oceanic) climate has prevailed since the turn of the century. The width of the ice-free land in the study area, however, allows for very significant climatic differences between the coast and the inland adjacent to the

ice cap. Coastal ranges receive relatively heavy precipitation compared to the inland ranges which have a continental desert-like climate. The climatic shift towards an increased annual precipitation may be illustrated by Sisimiut receiving an average of 270 mm annually during 1923-29 as opposed to an annual mean of 358 mm in 1961-76. Corresponding average figures from Kangerlussuaq airport are 126 mm annually in 1941-48, 152 mm annually in 1946-65, and 186 mm annually in 1977-79 (HASHOLT & SØGAARD 1978, DANISH METEOROLOGICAL INSTITUTE, unpubl. data). This means an increase in annual precipitation of 33% over 5 decades in the coastal range and of 50% over just 3 decades on the inland range.

Two major causes of the lower inland precipitation appear to be the glacier, Sukkertoppen Iskappe, and the mountain range, Troldfjeldene (see Fig. 1), extending from the Inland Ice to the mouth of Kangerlussuaq with elevations up to 1,800 m. These form a barrier for the frequent depressions moving towards the study area from the south-west. The humid air masses are therefore forced to



precipitate their water just south of the glacier and at the entrance to Kangerlussuaq (e.g. Maniitsoq 1977: 570 mm precipitation). Thus the Kangerlussuaq inland area is in a precipitation shadow.

The Davis Strait does not normally freeze in winter, and so the climate of the coastal zone is relatively warm. Sisi-miut had an annual mean temperature of  $-3.7^{\circ}\text{C}$  in 1961-1977 (HASHOLT & SØGAARD 1978), an average monthly minimum temperature in February of  $-18.0^{\circ}\text{C}$ , and an average monthly maximum in July of  $+9.6^{\circ}\text{C}$  (DANISH METEOROLOGICAL INSTITUTE, unpubl. data).

The proximity of the Inland Ice has a marked continental influence on the inland climate. The Kangerlussuaq inland range has been subject to an intensive study during this project and therefore deserves special attention regarding climatic conditions. Some temperature and precipitation parameters related to the Caribou seasons are presented (Table 1, Fig. 2).

A characteristic factor in the Greenland climate is the foehn wind which is a high velocity, warm (i.e. above  $0^{\circ}\text{C}$ ), and dry wind flowing from mountainous regions down into adjacent lowlands. Foehn winds usually originate on the Inland Ice and occur in any season. The shallow snow cover in winter in the Kangerlussuaq area facilitates complete thawing during foehn weather.

Climatic parameters relating to plant growth on the inland range are summarized in Table 2. The length of the snow free period is comparable with conditions on Reindeer ranges in northern Sweden, where for 160-170 days there is no snow cover (STEEN 1968).

### Vegetation

The climatic characteristics of West Greenland have important conse-

Table 1. Precipitation and temperature at Kangerlussuaq Airport. Annual mean temperature at recording site:  $-5.3^{\circ}\text{C}$ .

Year	Precipitation (mm)			No. precipitation days			% days above $0^{\circ}\text{C}$ max.			Mean depth of snow cover $\pm$ S.E. (cm)		
	77-78	78-79	79-80	77-78	78-79	79-80	77-78	78-79	79-80	77-78	78-79	79-80
Spring migration	1.1	17.0	8.6	3	13	5	96	76	96	0.5 $\pm$ 0.2	11.1 $\pm$ 1.8	< 0.1
Pre-calving	4.7	1.6	7.2	2	1	2	100	100	100	0	1.7 $\pm$ 0.5	0
Calving	24.2	6.2	33.5	9	10	14	100	100	100	0	0	< 0.1
Post-calving	3.4	5.7	38.0	2	4	6	100	100	100	0	0	0
Summer dispersal	11.3	60.1	15.6	5	18	9	100	100	100	0	0	0
Fall migration	31.3	56.1	30.5	13	14	8	93	89	95	0.8 $\pm$ 0.2	2.8 $\pm$ 1.1	0.1
Rut	8.2	23.6	9.4	4	9	8	40	44	35	2.9 $\pm$ 0.4	10.3 $\pm$ 1.7	2.6 $\pm$ 0.5
Early winter	48.8	14.0	13.1	16	8	8	28	35	3	28.0 $\pm$ 1.5	28.0 $\pm$ 0.8	7.4 $\pm$ 0.5
Mid winter	21.2	22.7	-	21	14	-	8	28	-	34.6 $\pm$ 0.2	13.5 $\pm$ 0.7	-
Late winter	4.5	9.2	-	6	7	-	15	68	-	38.2 $\pm$ 0.5	1.2 $\pm$ 0.3	-

Table 2. Some climatic parameters relating to plant growth on the Kangerlussuaq inland range.

Year	1977	1978	1979
Days without snow cover	151	135	183
Days of continuously frost free summer period	89 (May 27 - Aug. 24)	54 (Jul. 1 - Aug. 23)	87 (Jun. 8 - Sep. 3)
Days of max. temperature continuously above 0°C.	160 (Apr. 27 - Oct. 3)	140 (May 16 - Oct. 2)	151 (Apr. 30 - Sep. 28)
	1977/78		1978/79
Periods with max. temperature above 0°C, Oct. 15 - Apr. 15	13		22
Days above 0°C, Oct. 15 - Apr. 15	38		67

quences for the distribution of plant communities. The rich flora of the coastal mountains, mostly mesic species, continues to the entrance of Nordre Isortoq (TRAP 1970). The inland ranges around Kangerlussuaq airport and Nordre Isortoq are primarily covered by dwarf shrub heaths. However, a sub-arctic steppe vegetation may occur here and there, in a zone about 30 km wide adjacent to the edge of the Inland Ice. This xerophytic vegetation type is primarily distinctive on the south-facing slopes. The microclimate on these habitats is rather unique and in summer the daily temperature amplitude can exceed 50°C.

Habitat exposure has important consequences for the quality and quantity of the vegetation. The two extremes are the xeric south-facing slope and the north-facing densely-vegetated habitat with high standing crops of *Betula nana*, *Ledum palustre*, *Poa pratensis*, and *Calamagrostis* sp..

Two factors appear responsible for the differences. One is the generally sparse precipitation, the other the exposure-dependent soil decomposition rate. North-facing habitats experience much lower decomposition rates than south-facing

ones because of less insolation. Consequently, organic debris in general and inorganic nutrients in particular remain available for much longer to plants on the north-facing slopes.

Although snow accumulation and sparse insolation make the growing season short and the active soil layer shallow, these habitats produced a greater standing crop than the sunny but xeric vegetation type on the south-facing slopes.

*Carex supina* spp. *spaniocarpa* is common on steppe communities, and these dry habitats also may support significant densities of *Artemisia borealis*, *Potentilla hookeriana*, *Poa glauca*, and *Festuca brachyphylla*. With increasing soil moisture the vegetation becomes more dense and the dominant species are *Kobresia myosuroides*, *Calamagrostis lapponica*, *Betula nana*, *Hierochloa alpina*, *Poa pratensis*, and *Vaccinium uliginosum*. Because of the extremely low humidity, halophytic vegetation types such as salt-steppe and salt-meadows have developed in some lowlands. Permafrost is present throughout the study area, the depth of the active layer however being highly dependent on ex-

posure and the isolating effect of the vegetation mat.

In previous decades the study area apparently supported extensive lichen heaths with stands of fruticose lichens such as *Cladonia spp.*, *Cetraria spp.*, and *Stereocaulon spp.* (BÖCHER 1954, VIBE 1967). However, during the last 10 years especially this preferred Caribou forage has decreased tremendously in biomass. Fruticose lichens are rarely available in the inland region (1-10 g wet weight per m<sup>2</sup>) and in the coastal zone most areas now have heavily grazed and trampled lichen ranges which are low in standing crop (10-40 g wet weight per m<sup>2</sup>).

### *Caribou seasons*

The Caribou year is comprised of a total of 10 different seasons or sequences, each one being characterized by one or more important features in behaviour, population structure, group size or cohesion, etc. It should be emphasized that adult bulls (more than 3 years) tend to remain all year round on the inland range. Thus, their participation in migrations and activities on the coastal ranges are insignificant. During spring and summer they stay together in 'bachelor-groups'.

The transition between seasons is empirical, based on the average date of the first occurrence of a significant alteration in the characteristics of the preceding season. Between years these dates show only little variation.

1. Spring migration: most animals move towards calving and summer range. April 26-May 21.
2. Pre-calving: arrival on calving ground by cows and yearlings. May 22-May 28.
3. Calving: parturition. May 29-June 23. (65% of the calves born June 3-June 13.)

4. Post-calving: cows and neonates aggregate in large groups on certain localities. June 24-July 7.
5. Summer dispersal: small groups widely dispersed. During severe insect harassment formation of large aggregations. July 8-August 31.
6. Fall migration: bulls shed their antler velvet; mass movement of cows, sub-adults, and calves towards winter range. September 1-October 9.
7. Rut: harem formation and copulation. October 10-November 4.
8. Early winter: bulls start dropping antlers; cratering for food usually starts. November 5-December 15.
9. Mid-winter: very small group size; physical condition deteriorates quickly; December 16-March 15.
10. Late winter: widespread feeding on snow-free patches on ridge tops etc.; March 16-April 25.

### *Seasonal ranges and migration*

Fig. 3 depicts the situation of the primary and secondary summer (S1,S2) and winter (W1,W2) ranges of the population as well as migration routes. It should be noted that outside these areas and the routes of migration caribou are usually scarce but nevertheless present all year round.

The major calving area lies within the inland summer range S1 and is considered the centre of habitation of the Sisi-miut-Kangerlussuaq population. The summer range is occupied from the first half of May until the first half of September. The coastal winter range supports highest population densities in the months October-April. The length of each migration period is usually 2-3 weeks but is subject to variation according to snow conditions. The migration route is 50-70 km.

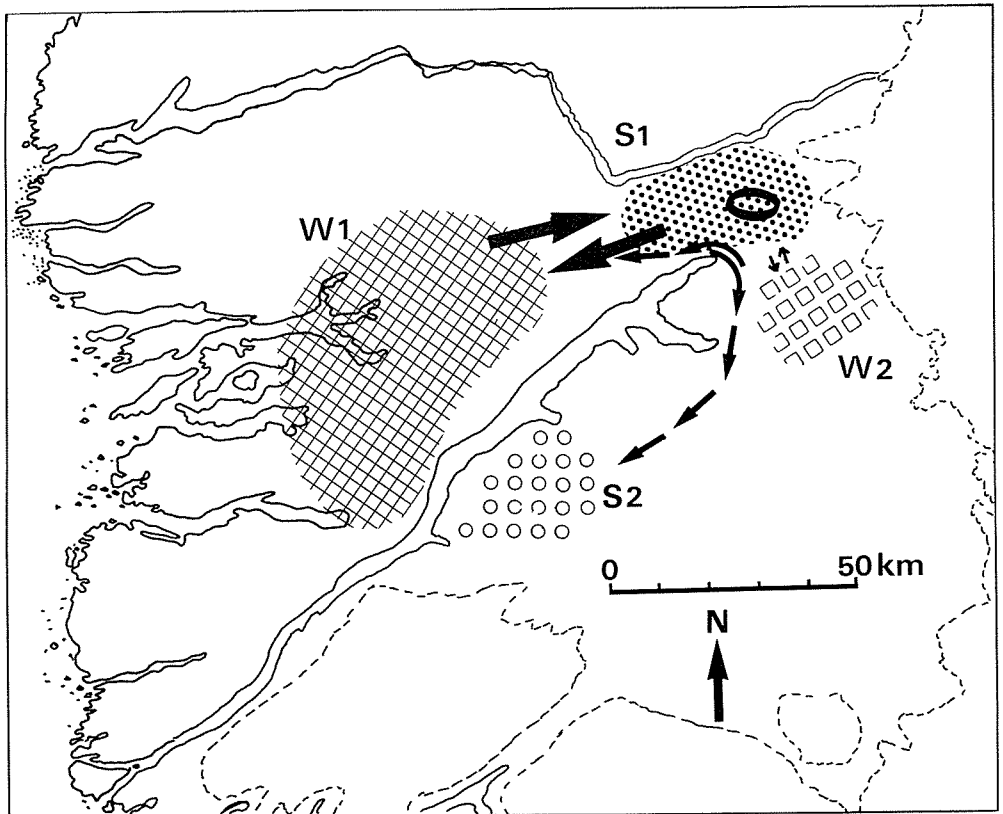


Fig. 3. The Sisimiut-Kangerlussuaq region showing winter and summer ranges and migration routes of the Caribou herd. W1 = primary winter range; S1 = primary summer range with the core calving area indicated; W2 = secondary winter range; S2 = secondary summer range. Size of arrows illustrates relative magnitude of migration.

That part of the population which spends the winter on range W1 north of Kangerlussuaq and the summer south of it (S2) has to cover a distance of 100 km or more. The magnitude of this migration has decreased tremendously during the last 7-8 years as a consequence of the population crash in the 1970's.

Little is known of the secondary summer range S2. However, some animals are believed to undertake only local migrations, remaining all year round on the southern side of the Kangerlussuaq. The rest apparently join the majority of the herd and winter on range W1. A small

scale migration takes place between the major summer range S1 and the secondary winter range W2; the distance and number of animals involved is, however, rather insignificant.

The pattern of the important migratory routes, as well as the two major distinct ranges used by the Sisimiut-Kangerlussuaq Caribou Herd, is similar to that of another major population in West Greenland, the Nuup Kangerlua-Tasserssuaq Herd.

Interestingly the herd of domesticated Norwegian Reindeer *Rangifer tarandus tarandus* L in the Nuuk region (see

THING 1980b) shows a contrary pattern, using coastal calving-summer ranges in the west and fall-winter ranges adjacent to the Inland Ice in the east (AASTRUP 1978, LASSEN & AASTRUP 1981). This difference is probably caused by several factors, e.g. husbandry, topography, grazing tradition, and current stocking rates.

## Materials and methods

In the snow-free seasons Caribou were located by hiking, and limited use of cross-country 3-wheeled motor bicycles. During winter skis, snow shoes, snow mobiles, ski plane, and helicopter were the major means of transportation in the field. Monthly aerial reconnaissance was conducted throughout the year using small fixed-wing aircraft for an average of 4 hours. These flights were made to record changes in occupancy and to locate concentrations of Caribou for ground observation. Groups or single Caribou were studied with the aid of 8 × binoculars and 15-25 × spotting scopes.

### *Feeding habitat preference*

To quantify the actual importance of the different habitat types for Caribou foraging the area, the distribution of the vegetation types in selected inland and coastal regions was determined. This involved limited use of aerial point estimates along non-random transects perpendicular to the longitudinal axis of the valleys, as well as extensive aerial photography using false colour infra-red film. The transparencies were converted to prints suitable for vegetation mapping (HOLT 1980, HOLT & THING 1979). Of the approximately 400 km covered by the aerial photos, about 25% was mapped

on the basis of actual ground observations and the rest by extrapolating from the experiences gained in interpreting the false-coloured spectra (HOLT 1983).

### *Utilization of winter feeding habitats*

On snow-covered winter ranges where cratering was a necessity, feeding craters selected at random were examined visually and exposed plant species recorded. No attempt was made to distinguish between forage and non-forage on the basis of the condition of the plants. A total of 1,706 feeding craters were examined.

Furthermore, non-random point estimates along parallel transects 5 m apart across cratered habitats were employed to quantify the use and disturbance of the feeding areas by Caribou. The procedure consisted of walking the transect lines and recording at every 5 m whether the snow just left of the observer's left foot in a plot 0.33 m × 0.33 m was disturbed by 1) a crater, 2) tracks, or 3) left undisturbed.

### *Feeding intensity*

Data on feeding intensity were collected from undisturbed feeding adults only, using a spotting scope and two cumulative stop watches. Feeding was divided into three sub-activities:

- a. ingestion (i.e. actual forage intake, head down, muzzle moving, mastication),
- b. searching (i.e. olfactory search for food, often in connection with walking), and
- c. cratering (i.e. pawing a hole in the snow layer to reach for forage).

The ratio of % ingestion / (% searching + % cratering) was used as an index of feeding intensity (equivalent to 'eating

time' defined by GAARE et al. 1970 & SKOGLAND 1974). Each animal was observed for approximately 5 minutes, since pilot tests showed no significant difference between data from 5, 10, and 15 minute observations.

### *Forage selection*

Information on the relative importance of different plant species as Caribou food was partly obtained through direct field observation of feeding animals. However, most knowledge of food preference was gained from analyses of rumen samples from specimens shot for research purposes. In addition supplementary data were furnished by analyses of rumina taken from carcasses of Caribou which had died from natural causes. Rumen samples (approx. 1,000 ml each) were preserved in 4% formaldehyde. In the laboratory 300 ml of each sample was washed through a sieve (mesh size 1 mm<sup>2</sup>) and the gross material was analysed macroscopically in a plastic tray (40 cm × 50 cm) divided into rectangles (each 7.8 cm × 4.6 cm).

The plant material was homogeneously distributed and % cover for each plant species determined in 10 randomly selected squares. Forage species with less than 5% coverage were registered as trace occurrence.

### *Forage quality*

In order to assess forage quality plants (minimum 25 g wet weight) were collected in most seasons. The material was air dried before being chemically analysed (using the proximate Weende method as well as the detergent analysis (VAN SOEST 1965)) for contents of N, P, Ca, CHO, NDF (neutral-detergent fibers), ADF

(acid-detergent fibers), fibre, lipids, ash. A total of 28 samples were analysed. Furthermore, 13 rumen samples were analysed for contents of nitrogen. This material was collected from September 1977 to March 1978.

### *Snow measurements*

To quantify the physical characteristics of snow, a dominant factor in the winter environment, standardized measurements were taken from early November 1977 until mid-April 1978.

A snow kit, consisting of 1 knife, 1 spring scale (0-1,000 g), 1 200 cm<sup>3</sup> snow sampler, 1 tape measure, 1 Rueger bimetal thermometer (-70°C - +40°C), and 2 spring penetrometers (model Eriksson 1976) (1 calibrated for 0-2,000 g and 1 for 0-20,000 g) with terminal discs of 1, 10, and 100 cm<sup>2</sup>, was used for this part of the study.

The following parameters were measured: depth (cm), horizontal and vertical hardness (g per cm<sup>2</sup>), density (g per cm<sup>3</sup>), temperature (degree C) at top, middle, and bottom of snow layer. The structure of the snow cover was also described. The Civil Aviation Airport weather service at Kangerlussuaq airport undertook daily registration of snow depth and duration of snow cover.

The regional distribution of snow cover was supervised using LANDSAT satellite imagery. In the period March-October black and white imagery from LANDSAT 3 channel 7 (Multispectral Scanner, MSS) was obtained once every 18 days. These pictures allowed an overall view of the Caribou ranges in scale 1:1,500,000 and a general assessment of snow conditions. However, because of the low angle of the sun during early to mid winter no imagery was processed for this period.

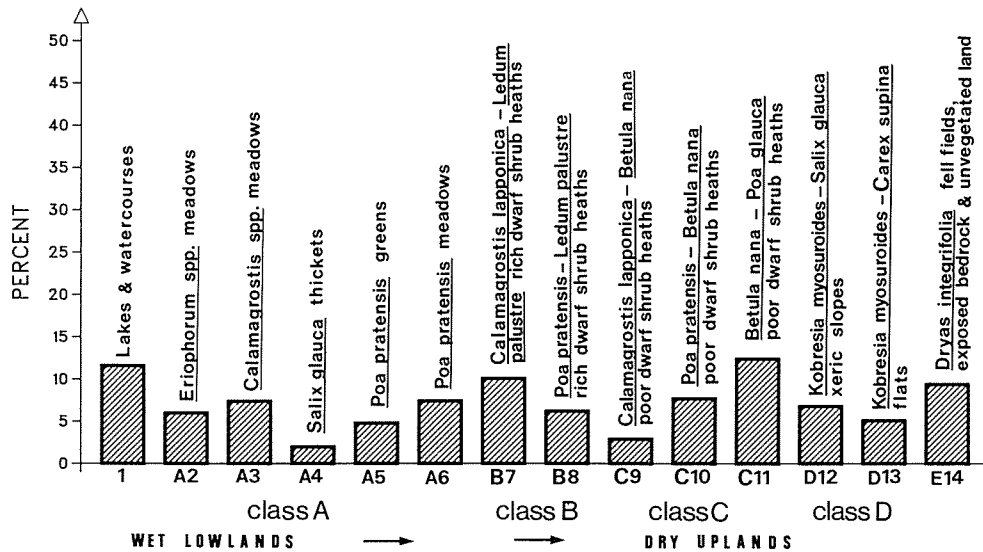


Fig. 4. Vegetation types and their frequency on the Kangerlussuaq inland range. Data based on aerial point transects; N = 646.

## Results

### Classification of vegetation

The study area has previously been subject to only limited botanical work, and the classification of vegetation types ('complexes') available in BÖCHER (1954) did not appear suitable for the purpose of classifying Caribou habitats from a management point of view. The vegetation cover of the inland summer range was divided into five main classes (A-E) with a total of 13 distinguishable vegetation types (excl. water bodies and man-made features), all listed in Fig. 4. This classification, as well as the area distribution of its components, formed the basis of the habitat related part of the present study.

As the inland range is dominated by graminoids the different vegetation types reflect this accordingly; only three (i.e.

A4, C11, and E14) have dominant species of shrubs or herbs (willow, birch, and *Dryas*), the rest having grasses or sedges as the dominant key species.

In the xeric environment of this region, the presence of soil moisture and amount of insolation are naturally factors of paramount importance in the formation of the vegetation types. Using these two as prime criteria in classification proved useful and relevant to Caribou usage.

The distribution of the vegetation types could be predicted to a certain degree from the topography of the area. Although generalized, Fig. 5 shows a schematic north-south transect with a typical distribution of the 14 habitat types recorded. The occurrence of these types in relation to physical characteristics such as slope and exposure has not been studied independently. Generally, type A2 represents the wettest vegeta-

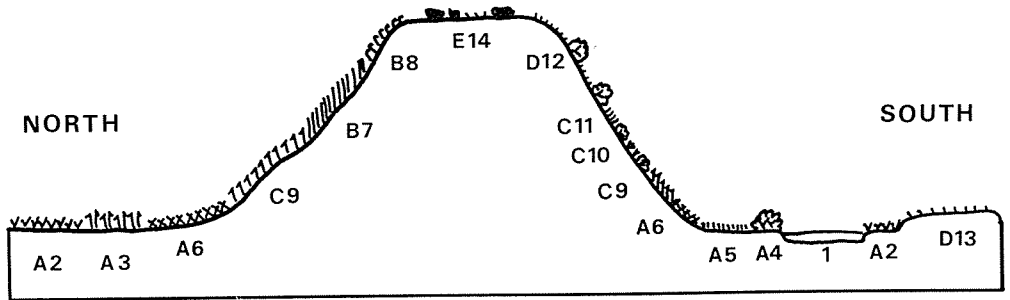


Fig. 5. Schematic example of the distribution of vegetation types on the Kangerlussuaq inland range. Code numbers refer to description in Fig. 4.

tion type and E14 the driest; between the two extremes there is a gradual decrease in soil moisture.

### *Seasonal variation in habitat selection*

Since exposure is a function of slope, it seems logical to regard these two parameters as integral parts of the physical description of habitats. However, for the sake of clarity in the figures, data on exposure and slope are presented separately but later discussed jointly.

Fig. 6 illustrates habitat exposure preference according to season. Level ground is preferred in calving, post-calving, and during summer dispersal as well as in the rutting season. North-northeast-facing habitats attract Caribou only in early winter. Sunny south-facing localities are most important to the animals during spring migration, pre-calving, fall migration, and late winter. All other aspects also receive some use, but no significant peak season is apparent. Similarly, the preference for slope is subject to changes between the seasons (Fig. 7). A mild inclination (1-10°) is preferred in summer dispersal, fall migration, early and late winter. Moderate slope (11-20°) appears to be favoured during spring migration and mid-winter

only, while preference for steeper slopes (>21°) is a feature limited to the pre-calving season. A general picture of the seasonal importance of habitat classes (cf. Fig. 4) is presented in Fig. 8; from this it is apparent that habitat classes A and B have well-defined peak seasons and that the two alternate in importance in summer and in winter respectively. Class C is of main significance as a feeding habitat in spring; the same is true for class D, while class E remains unimportant in all seasons.

The histograms (Fig. 9) confirm the significance of

- 1) type D12, C11 and C9 during spring migration and pre-calving,
- 2) A2 during the calving season,
- 3) A5, A6, and C10 during post-calving and summer dispersal
- 4) B7, B8, and A3 during winter.

### *Habitat preference index*

To permit an assessment of observed habitat use in relation to the actual area distribution of vegetation types (Fig. 4), a preference index was calculated for each habitat.

The index was defined as (% of observed animals on vegetation type)/(% occurrence of vegetation type). Values > 1 indicate preference, i.e. concentra-



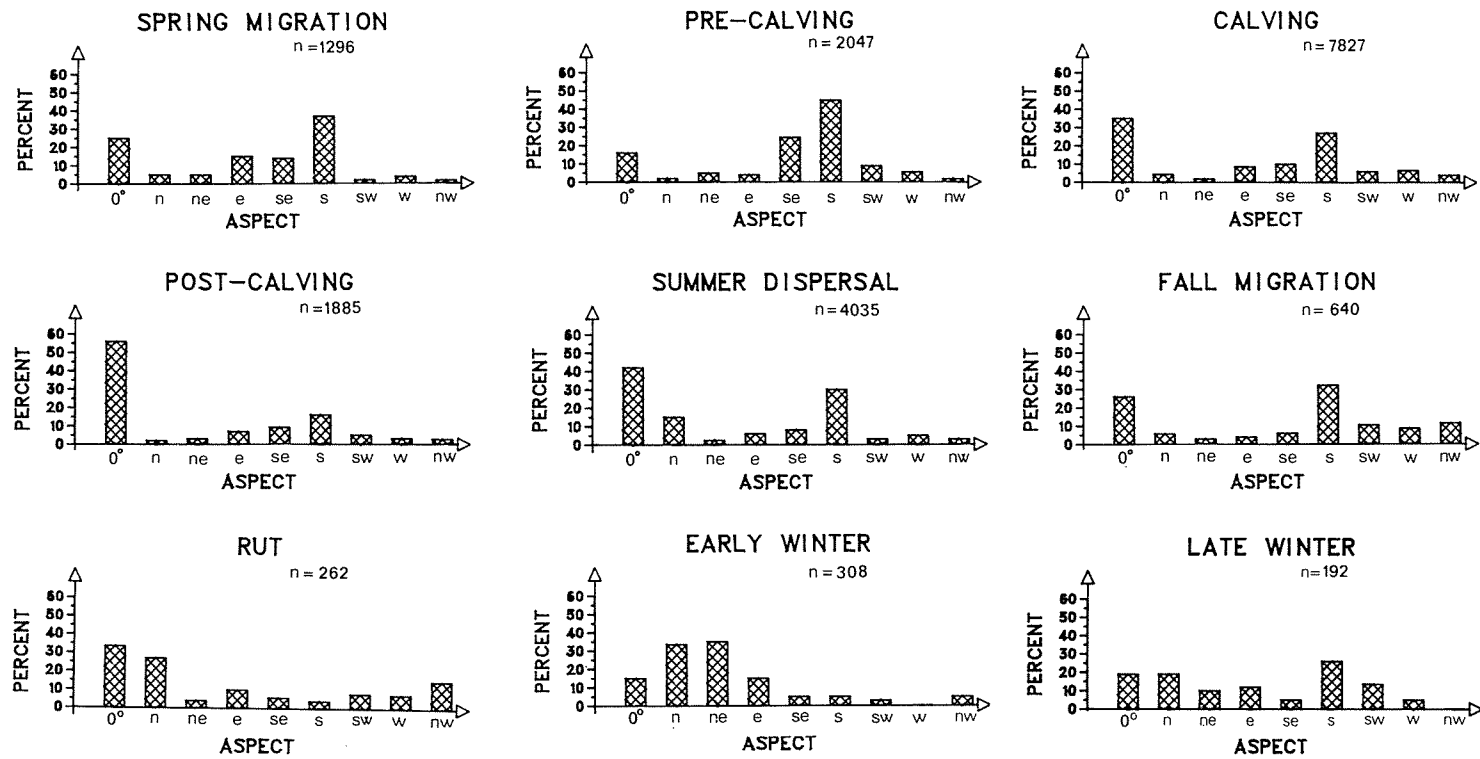


Fig. 6. Seasonal variation in the aspect of feeding habitats used by Caribou on the Kangerlussuaq inland range.

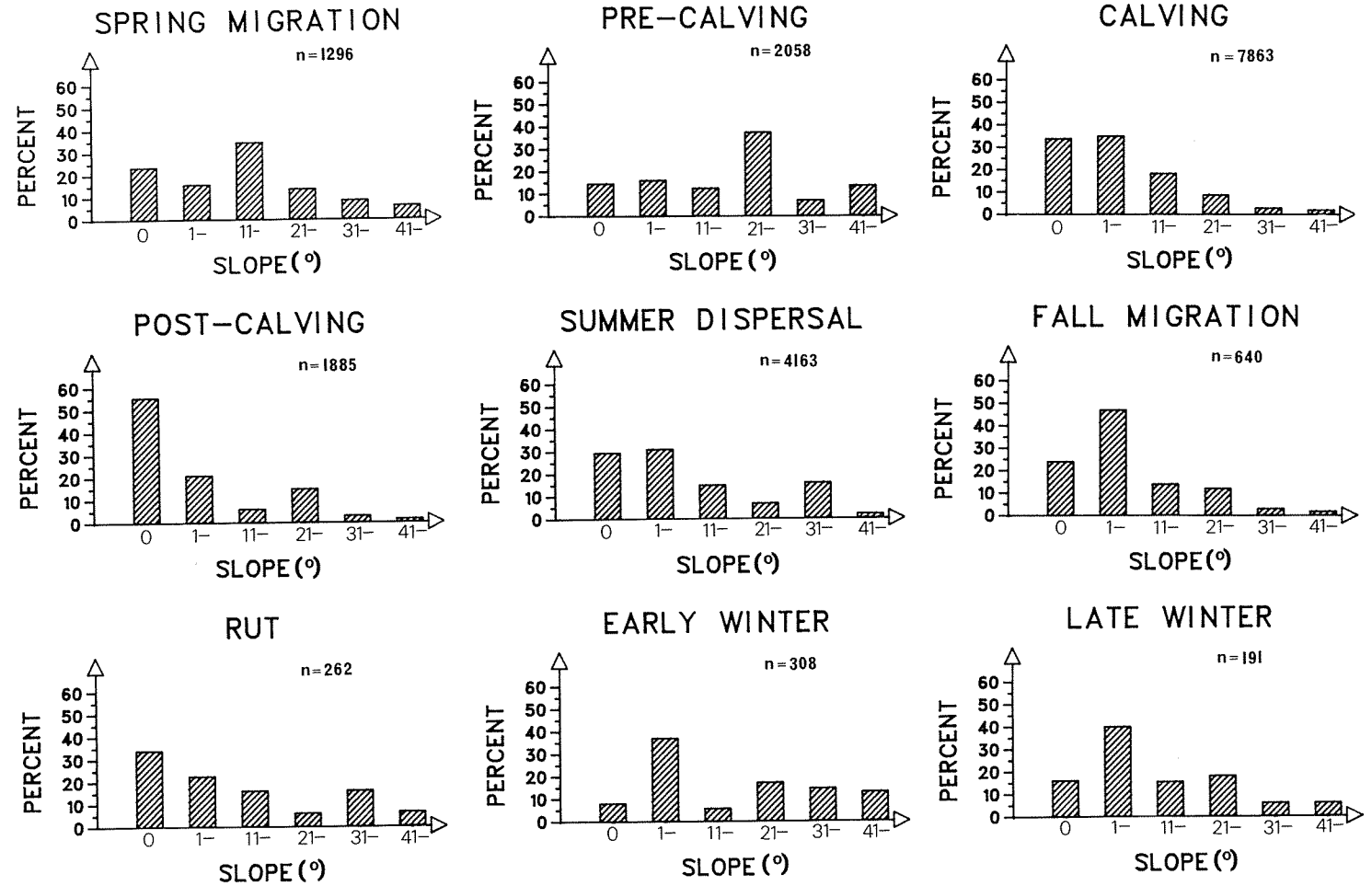


Fig. 7. Seasonal variation in the slope of feeding habitats used by Caribou on the Kangerlussuaq inland range.

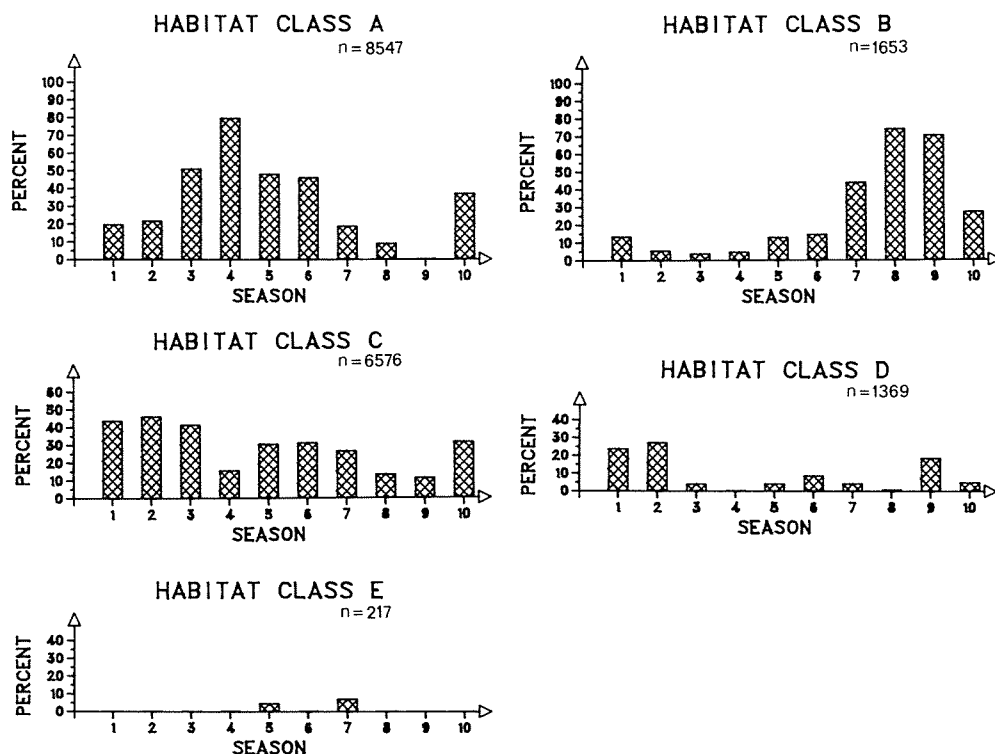


Fig. 8. Seasonal variation in the selection of habitat class by Caribou on the Kangerlussuaq inland range. (Season numbers refer to list p. 9.)

tion of Caribou on the vegetation type in question. Index value = 1 is use according to occurrence of vegetation type. Values 0-1 indicate avoidance of the habitat.

The interrelationship between use and total area reveals an annual pattern of habitat preference which furnishes valuable information on the seasonal significance of the vegetation types (Fig. 10). Class A habitats are especially in demand during calving and through the summer, while class B habitats attract up to 5 times the expected number of Caribou in winter. Habitats of class C receive twice the anticipated use by Caribou during the early growing season (spring migration to calving). The peak season for class D habitats is in the very begin-

ning of spring (i.e. spring migration and pre-calving), whereas the class E type never acquires the amount of use that its total area should permit. A detailed picture of habitat preference index for each season is shown in Fig. 11.

#### *Feeding behaviour and intensity*

The relationship between the sub-activities of 'feeding' has been studied and the data are presented in Fig. 12. This figure also includes variation in the feeding intensity index. The index is calculated as (% ingestion time)/(% searching time + % cratering time).

The most intensive feeding occurs in the calving season. The data from this

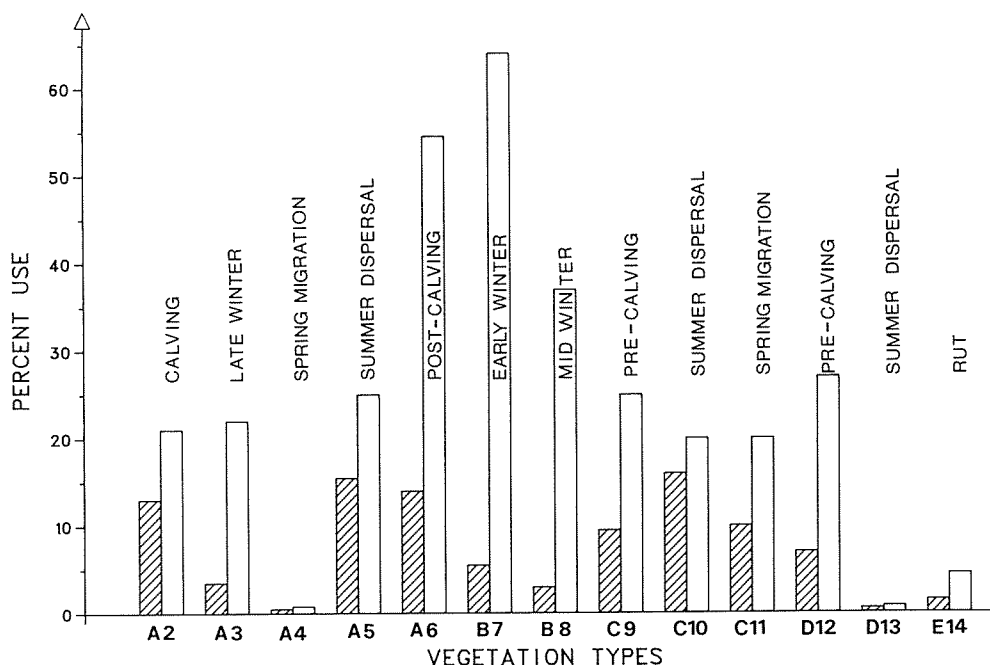


Fig. 9. Annual and peak season use of vegetation types on the Kangerlussuaq inland range; N = 18,375.

▨ = annual use; □ = peak season use.

season are based on observations of adult females and consequently the intensity peak during this period reflects the high physiological demands on the parturient and lactating Caribou cows.

### Feeding craters

During winter when plants are covered by snow, cratering is necessary to obtain otherwise unavailable forage. Information on available food in relation to actual selection can be gained by studying which plants are being exposed in feeding craters. The contents of a total of 1,706 craters were checked and the results should give a general idea of the forage available in the three winter ranges (Table 3). It should be stressed however that the table supplies only

quantitative data but nothing about the qualitative status of the plants.

The following significant difference between the ranges should be noted:

1. more dwarf birch *Betula nana*, very little willow *Salix spp.*, and no *Stellaria longipes s.l.* on the Ilulialik range;
2. graminoids are scarce in Ilulialik craters, but ubiquitous in Kangerlussuaq and common on the Ikarulik coastal range;
3. Kangerlussuaq craters rarely include any lichen whereas on the two other ranges lichens, especially fruticose species, are much more frequent.

### Winter habitat use

The degree of utilization of a feeding habitat in winter is reflected in the fre-

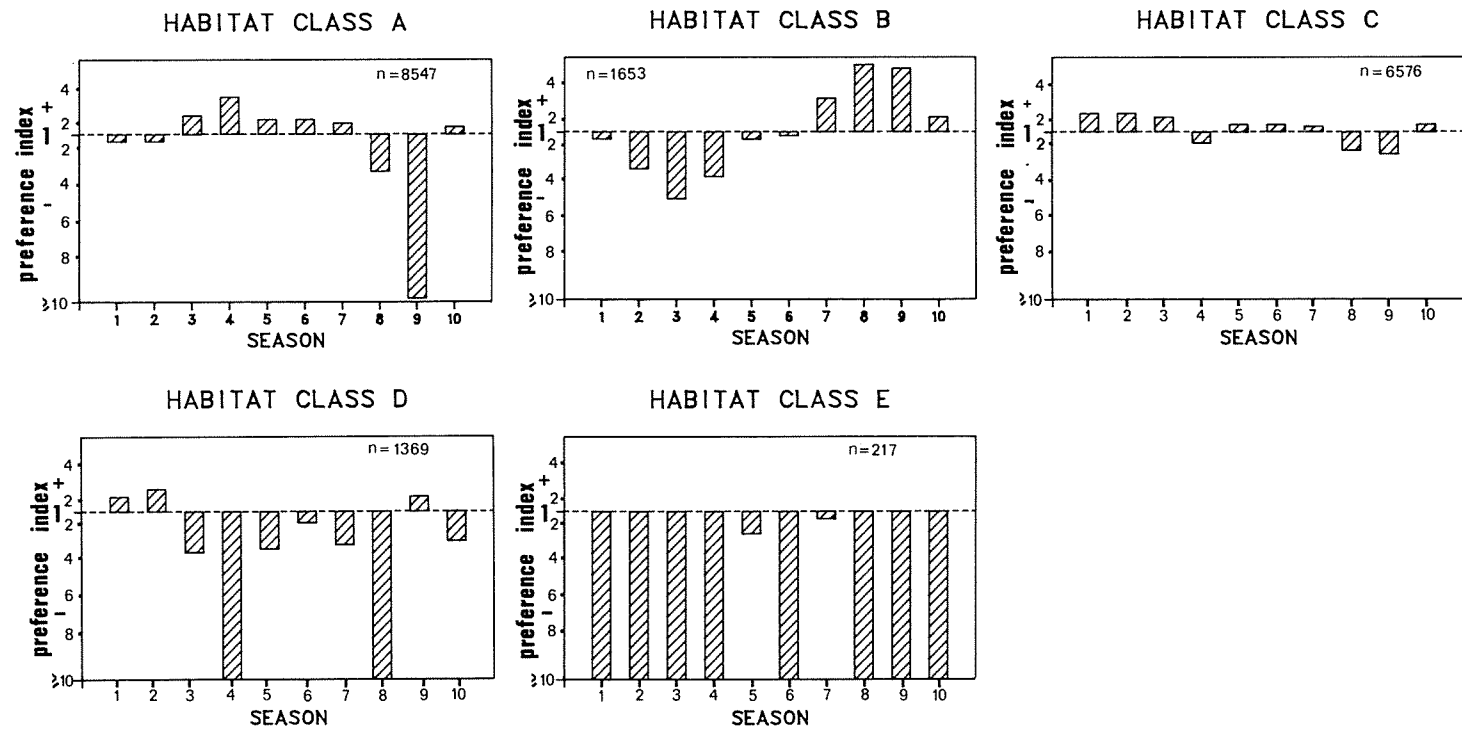


Fig. 10. Seasonal variation in habitat class preference index on the Kangerlussuaq inland range. (Season numbers refer to list p. 9.)

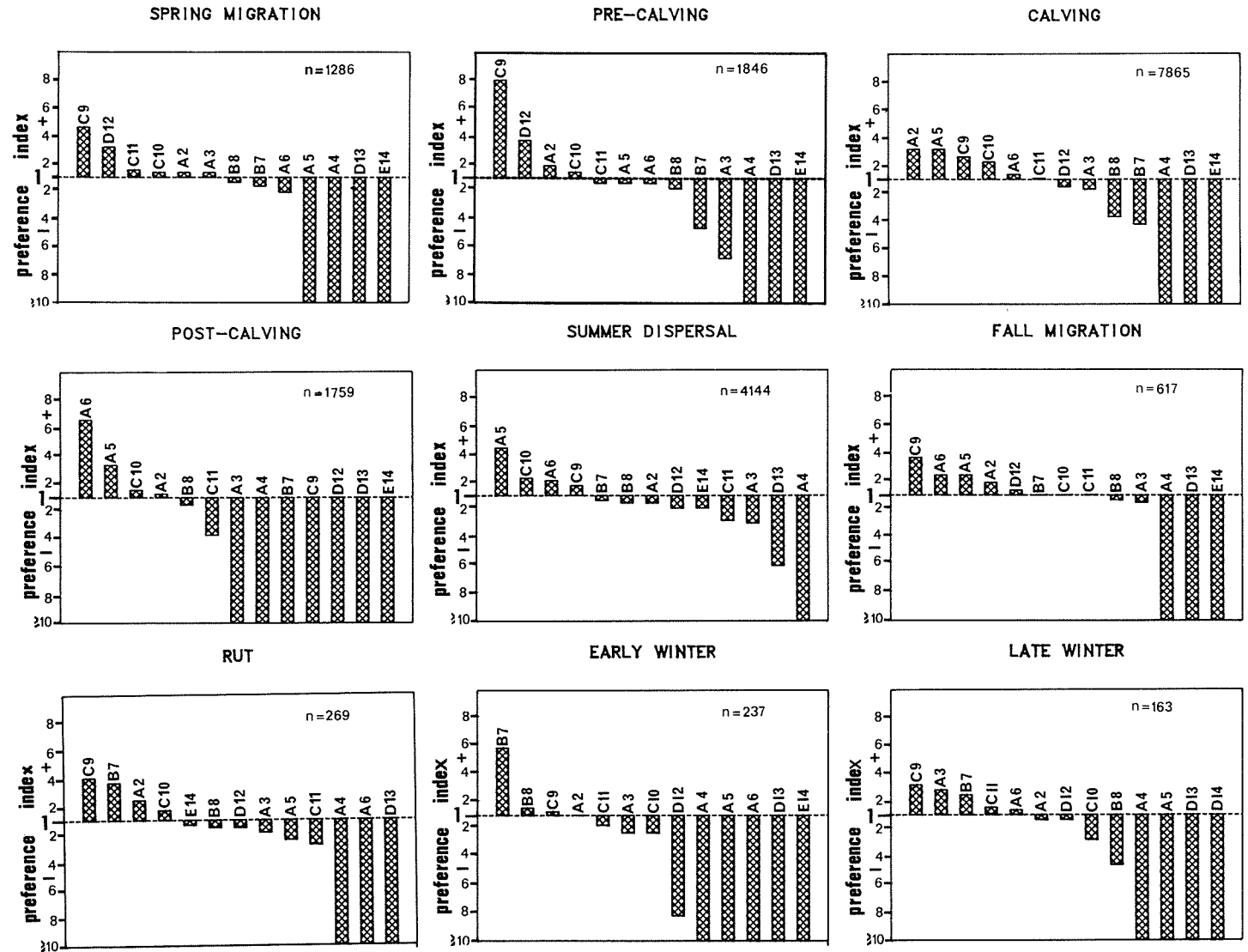


Fig. 11. Seasonal preference index of vegetation types on the Kangerlussuaq inland range. (Vegetation type codes refer to description in Fig. 4.)

## Feeding Ecology of the West Greenland Caribou

Table 3. Percent frequency of plant species in feeding craters on three winter ranges. N = 1,706 (+ indicates < 5%; - indicates not found).

Locality	Kangerlussuaq	Ikardlulik	Ilulialik
Year	1977-78-79	1978-80	1979
Season	Early-late winter	Early-mid winter	Late winter
N	681	602	423
<i>Artemisia borealis</i>	6	-	-
<i>Betula nana</i>	42	36	61
<i>Cassiope tetragonia</i>	+	9	-
<i>Empetrum nigrum</i>	+	33	10
<i>Ledum groenlandicum</i>	-	-	18
<i>Ledum palustre</i>	7	6	15
<i>Melandrium</i> spp.	5	-	-
<i>Polygonum viviparum</i>	6	8	-
<i>Pyrola grandiflora</i>	+	13	-
<i>Rhododendron lapponicum</i>	9	-	-
<i>Salix</i> spp.	12	26	+
<i>Stellaria longipes</i>	32	15	-
<i>Vaccinium uliginosum</i>	18	41	11
<i>Vaccinium vitis-idaea</i>	+	5	+
<i>Calamagrostis</i> spp.	56	-	-
<i>Carex</i> spp.	22	22	-
<i>Festuca brachyphylla</i>	16	-	-
<i>Kobresia myosuroides</i>	7	-	-
<i>Poa</i> spp.	32	6	-
Graminoids	19	32	12
<i>Equisetum arvense</i>	12	8	-
<i>Equisetum scirpoides</i>	15	+	-
Mosses	53	59	53
<i>Alectoria nigricans</i>	-	14	8
<i>Alectoria ochroleuca</i>	-	7	+
<i>Cetraria crispa</i>	-	6	+
<i>Cetraria cucullata</i>	-	36	9
<i>Cetraria nivalis</i>	+	33	39
'Cladinae' spp. §)	+	21	12
<i>Cladonia</i> spp.	+	37	41
<i>Dactylina arctica</i>	-	+	-
<i>Peltigera</i> spp.	12	+	5
<i>Sphaerophorus</i> spp.	-	+	+
<i>Stereocaulon</i> spp.	-	34	49
<i>Thamnolia vermicularis</i>	-	8	+
Crustose lichens	-	-	15

§) includes *Cladina stellaris*, *C. mitis*, and *C. rangiferina*.

quency of craters per area. To a limited extent this is illustrated by Table 4. Caribou seek forage on 30-40% of a habitat

and while searching they disturb just as much snow cover. The consequences of this will be discussed later.

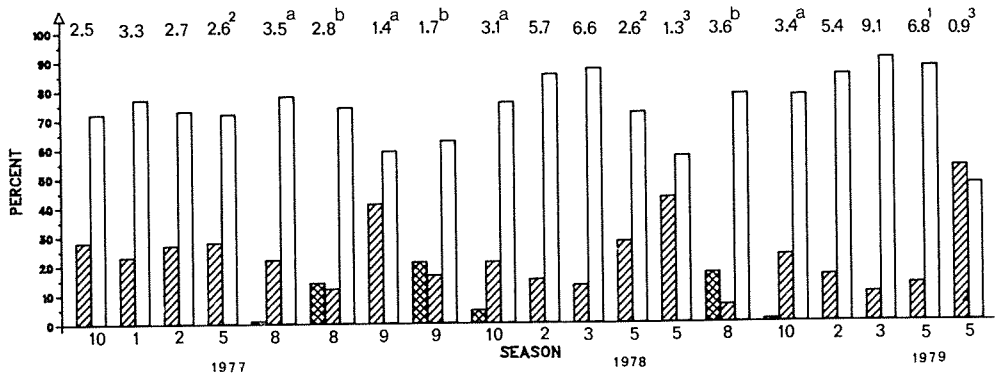


Fig. 12. Seasonal variation in feeding intensity. Numbers above columns are indices of intensity; N = 384. a = partial snow cover; b = full snow cover. 1 = no insect harassment; 2 = moderate insect harassment; 3 = severe insect harassment. (Season numbers refer to list p. 9.)

▨ = cratering time; ▧ = searching time; □ = feeding time.

### Snow measurements and monitoring

A knowledge of the characteristics of snow cover is essential in order to evaluate its effect on Caribou foraging. Some physical parameters of the snow layer are presented in Table 5. It should be added that snow was unusually plentiful in the winter of 1977-78, even in the normally dry regions around Kangerlus-

suaq Airport and in the Arnangarngup kua valley.

For the Kangerlussuaq inland area it is noteworthy that although the depth remains unchanged during the winter, both hardness and density increase significantly. The Arnangarngup kua valley has the softest and lightest snow cover for a mid winter season.

Additional information on winter distribution of Caribou, as well as their migration patterns in fall and spring was gained through a regional monitoring scheme using LANDSAT imagery initiated in late winter (March) 1979. Fig. 13 presents an example of 'Quick Look' hard copy prints giving as MSS (Multi-spectral Scanner) channel 7 (0.8-1.1 micrometer) image on a scale of 1:1,500,000.

Table 4. Habitat use and disturbance on the Kangerlussuaq inland range in late winter. N = 194.

Habitat class	A	A	B
Aspect/slope	0°	0°	0°
Snow depth (cm)	30	20	30
Snow cover (%)	100	100	100
N	60	48	86
% craters	38	33	43
% disturbed snow	45	34	40
% undisturbed snow	17	33	17

### Rumen samples

The most important method used to gain information on Caribou food selection was analysis of rumen contents. The



Table 5. Characteristics of the snow cover adjacent to feeding craters on three winter ranges. N = 99. (Mean  $\pm$  S.E.).

Locality	Kangerlussuaq		Ikardlulik	Arnangarngup kua
Year	1977-78		1978-79	1977-78
Season	Early winter	Mid - late winter	Early - mid winter	Mid winter
N	52	28	12	7
Depth (cm)	26 $\pm$ 0.2	26 $\pm$ 2.3	17 $\pm$ 1.4	14 $\pm$ 4.9
Max. horizontal hardness (g/cm <sup>2</sup> )	1512 $\pm$ 86	12238 $\pm$ 1707	8619 $\pm$ 4296	4000 $\pm$ 289
Max. vertical hardness (g/cm <sup>2</sup> )	2057 $\pm$ 872	9798 $\pm$ 1990	10325 $\pm$ 2651	1333 $\pm$ 371
Max. density (g/cm <sup>3</sup> )	0.28 $\pm$ 0.01	0.55 $\pm$ 0.1	0.42 $\pm$ 0.05	0.29 $\pm$ 0.02

most obvious result of these analyses (Table 6) is the amount of graminoids in the Kangerlussuaq diet as well as in the fall forage in the Nuup Kangerlua region. When the Kangerlussuaq animals feed on the coastal winter range graminoids occur 4-5 times less frequently in the rumen.

Fruticose lichens are not abundant in the winter diet, although they are twice as common on Ikardlulik coastal range as inland. Shrubs and herbs appear in minor quantities on all three ranges. The fraction of 'soil and unidentified organic material' is insignificant for the Kangerlussuaq inland range, but of importance

Table 6. Percent cover of plant species in rumen samples from three different ranges. Collected from killed animals; N = 67. Only plants of  $\geq$  5% cover in samples are included in the table. + indicates > 5% cover; -- = species not found. (Mean  $\pm$  S.E.).

Locality	Kangerlussuaq		Ikardlulik	Ilulialik
Year Month	1977-79 May-Sep.	1977-79 Oct.-Apr.	1978 Feb.-Apr.	1978 Sep.
N	20	10	18	19
Species:				
Graminoids	61.2 $\pm$ 5.1	57.9 $\pm$ 9.9	13.0 $\pm$ 1.8	47.2 $\pm$ 3.0
Betula nana	5.1 $\pm$ 1.1	+	+	+
Salix spp.	8.4 $\pm$ 2.2	+	+	7.4 $\pm$ 1.3
Empetrum nigrum	-	10.5 $\pm$ 6.0	+	+
Stellaria longipes	5.4 $\pm$ 2.3	5.6 $\pm$ 2.8	+	+
Crustose lichens	-	+	7.3 $\pm$ 2.5	+
Fruticose lichens	+	6.3 $\pm$ 5.9	14.2 $\pm$ 2.7	+
Soil & unidentified organic material	5.8 $\pm$ 1.2	+	60.0 $\pm$ 2.5	42.0 $\pm$ 3.9

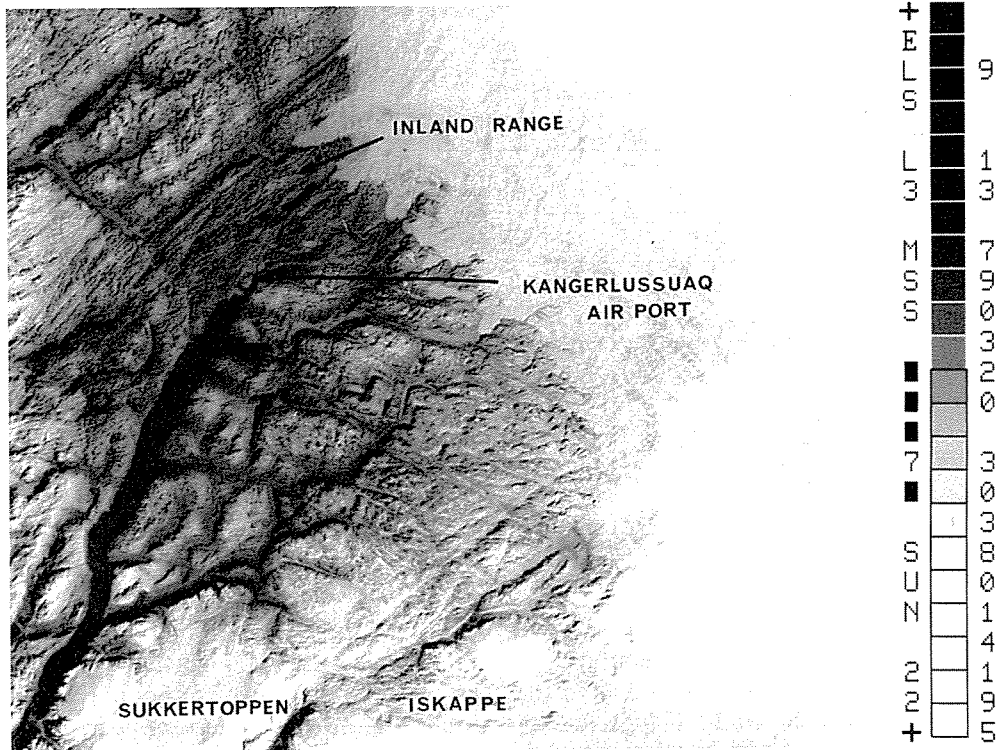


Fig. 13. LANDSAT-3 imagery of the Kangerlussuaq region March 20, 1979. Note the extensive snow free areas as the result of a foehn period. Scale = 1:1.5 million.

on the Ikarlulik coastal range. Animals on the latter range have a high portion of the rumen filled with ingested gravel, soil particles, and organic debris. The high proportion of unidentified organic material in the Nuup Kangerlua rumina is caused by inadequately preserved samples, leaving much of the contents unidentifiable.

#### *Chemical analysis*

As a supplement to the quantitative data of Table 6, a number of forage plant species have been chemically analysed for qualitative parameters relating to their nutritional value (Table 7).

The column 'crude protein' is of main

interest, being often used as an indicator of the general quality of a plant. The protein parameter varies considerably throughout the year. The 'lipids'-fraction (equivalent to 'ether extracts') includes fats, oils, waxes, organic acids, pigments, sterols, and vitamins A, D, E, K (HJELJORD 1975a). 'Ash' is the inorganic residue left after food material has been burned at about 600°C. This residue consists of different essential and non-essential minerals as well as some salts (MOEN 1973).

Of the organic material the non-nitrogenous substances besides lipids are listed in the last four columns. The soluble carbohydrates (i.e. nitrogenfree extracts) comprise the fractions CHO, ADF (acid-

Table 7. Chemical analysis of forage plants from the Kangerlussuaq inland range; N=28. Percent of dry matter.

Species	Sample date	Crude prot.	P	Ca	Lipids	Ash	CHO	ADF	NDF	Crude fibre
<i>Artemisia borealis</i>	Nov. 19	8.1	0.2	1.0	2.7	16.6	-	-	-	36.9
<i>Betula nana</i>	Jul. 30	18.8	0.3	0.5	9.2	4.4	-	-	-	15.1
<i>Betula nana</i>	Oct. 27	8.1	0.1	0.3	11.0	4.0	-	-	-	22.5
<i>Calamagrostis lapponica</i>	Jul. 30	8.8	0.1	0.2	2.1	6.3	-	-	-	32.5
<i>Carex saxatilis</i>	Oct. 27	5.0	0.1	0.5	11.1	3.5	-	-	-	26.6
<i>Carex supina</i>	May 4	13.1	0.3	0.9	2.6	24.9	-	-	-	20.4
<i>Carex supina</i>	May 15	13.1	0.2	0.6	3.4	7.8	-	-	-	26.0
<i>Empetrum nigrum</i>	Nov. 1	8.8	0.2	0.4	2.9	5.9	-	-	-	30.1
<i>Equisetum variegatum</i>	Apr. 18	12.5	0.2	0.3	2.8	14.9	-	-	-	28.2
<i>Equisetum scirpoides</i>	Nov. 26	9.4	0.2	1.6	2.9	10.4	-	-	-	26.6
<i>Eriophorum augustifolium</i> *)	Oct. 6	7.8	0.1	-	-	5.1	17.3	35.0	60.9	29.9
<i>Festuca brachyphylla</i>	Apr. 18	10.0	0.2	1.3	3.4	20.6	-	-	-	22.8
<i>Festuca brachyphylla</i>	Jul. 30	11.9	0.2	0.6	3.5	8.4	-	-	-	31.0
<i>Hippuris vulgaris</i> *)	Oct. 6	16.1	0.2	-	-	0.6	22.8	19.1	28.1	18.4
<i>Peltigera aphthosa</i>	Apr. 18	13.1	0.2	1.3	3.4	20.6	-	-	-	22.6
<i>Peltigera aphthosa</i> *)	Oct. 6	12.5	0.2	-	-	21.8	4.0	35.7	65.9	13.9
<i>Poa glauca</i>	Apr. 30	11.9	0.2	0.3	2.8	21.8	-	-	-	24.6
<i>Poa glauca</i>	May 4	15.0	0.3	0.3	3.0	31.6	-	-	-	19.6
<i>Poa glauca</i>	Jul. 30	8.8	0.1	0.2	2.4	4.1	-	-	-	29.0
<i>Poa glauca</i> *)	Oct. 6	10.8	0.1	-	-	15.9	15.0	39.1	48.4	23.3
<i>Poa pratensis</i>	May 25	18.8	0.3	0.2	2.3	16.7	-	-	-	23.8
<i>Poa pratensis</i>	Jul. 30	21.3	0.3	0.6	5.0	10.6	-	-	-	17.6
<i>Potentilla hookeriana</i>	May 4	12.5	0.2	0.6	2.5	14.3	-	-	-	23.5
<i>Roegneria violacea</i>	May 25	18.8	0.4	0.2	3.3	14.9	-	-	-	27.4
<i>Salix arctophila</i>	Nov. 1	11.3	0.3	0.6	2.6	3.6	-	-	-	20.7
<i>Salix glauca</i>	Jul. 30	21.9	0.4	0.2	3.3	14.9	-	-	-	27.4
<i>Stellaria longipes</i> *)	Oct. 6	10.2	0.2	-	-	1.4	9.2	26.5	49.5	25.1
<i>Stellaria longipes</i>	Nov. 19	10.0	0.2	0.6	3.3	6.8	-	-	-	25.0

\*) indicates data from D.R. Klein, pers. comm.

detergent fiber), and NDF (neutral-detergent fiber). These primarily include starches and sugars which are highly digestible sources of energy, and minor quantities of organic acids, resins, tannins, pigments, and water-soluble vitamins (MOEN 1973, HJELJORD 1975a).

Crude fiber is the insoluble organic residue after successive boiling with acid and alkali. This material may not, however, be insoluble when exposed to the digestive process of an herbivore. This fraction contains cellulose, hemicelluloses, and lignin.

## Discussion

The aim of collecting the data presented was to permit an objective description of the interrelationship between the animal, its habitat, and its forage. Underlying this description is the assumption that an animal, being an integral part of its environment, has evolved its feeding behaviour to yield maximal energy input with a minimum of energy output.

### *Habitat selection and preference*

During classification of the vegetation of inland and coastal ranges, it was emphasized that only such habitats should be defined which 1) were readily recognizable by the researcher in the field and – while constituting a reasonable entity – 2) consider the natural complex mosaic so characteristic of the arctic plant cover (cf. BÖCHER 1954, BLISS et al. 1973).

The data presented in Fig. 4 were obtained following these principles. Only a brief key-word description of the vegetation is listed here; the reader is referred to HOLT (1980, 1983) for further information.

The number of vegetation types (excl.

water bodies and man-made structures) was kept at a low level (i.e. 13) which permitted relatively simple recording during field work, and subsequently a clearer picture of habitat use by the Caribou. Having few and rather broadly defined vegetation types was also advantageous, because it allowed for recording and mapping using remote sensing techniques such as aerial point transects and aerial photography (cf. HOLT 1980, HOLT & THING 1979).

PARKER (1975) recorded 13 habitat types during an investigation of Caribou range on Southampton Island, Northwest Territories, Canada, while JINGFORS (1980) described eight different vegetation types in relation to Muskox use in Northeast Alaska.

The preference regarding slope and aspect of habitats through the seasons (Figs. 6 and 7) reflects the topographical characteristics of the inland range. One modifying factor, altitude, is rather insignificant in this region, the landscape only varying between 200 and 550 m above sea level. Wide variation in topography on range allows for a longer period of young growth stages of plants, whereas uniform landscape results in uniform phenological progression of forage (KLEIN 1970a, SKOGLAND 1975, GAARE & SKOGLAND 1975). Therefore, any variation in exposure, slope, and altitude from a flat plain at sea level will alter phenological progression. In dry areas such as the inland range of Kangerlussuaq, the effect of exposure and slope is likely to be more directly related to seasonal availability of moisture for plant growth.

A characteristic feature of Caribou ecology on the inland range is that habitat selection is highly correlated with forage plant phenology. Where food species in early growth stages are available, Caribou tend to concentrate their feed-

ing on them. This behaviour is most pronounced during spring migration and pre-calving, when intensive foraging takes place on south-facing dry slopes which support an early emerging vegetation, particularly of *Poa glauca* and *Festuca brachyphylla*. These two tufted grasses have a patchy distribution on the C9, C10, C11, and D12 habitats, being concentrated around the scattered *Salix glauca* shrub.

As a consequence of the xeric conditions of the inland range and the subsequent early disappearance of the snow cover, especially on south-facing habitats, these species are available as young green forage to the Caribou as early as mid-April, i.e. up to 6 weeks prior to calving.

The affinity for more or less flat habitats is significant in the calving and post-calving seasons, as well as during summer dispersal. However, four different vegetation types are responsible for this preference (Fig. 11). In the calving season parturient and nursing cows and neonates concentrate on the flat wet sedge meadows (type A2) as well as the gently sloping dwarf shrub heaths dominated by *Poa pratensis* (type C10). The meadows have an abundant supply of emerging *Eriophorum spp.* at this time, whereas the main attraction of the heath apparently is the young *Poa spp.* leaves combined with the available *Stellaria longipes*, *Poa glauca*, and *Festuca brachyphylla*.

However, selection of the heath habitat may be partly due to a preference for using it during parturition and the subsequent period of initial *post partum* mother-infant relationships (THING 1980a).

In the short season of post-calving the A6 type, the *Poa pratensis* meadow, is the most important feeding habitat. This vegetation type is preferred in the period

of early phenological stages of the *Poa pratensis* plants before they reach anthesis and approach maturity. The concentration of animals on this habitat type is considerable, viz. > 7 times the expected level (Fig. 11).

During the main summer period, July-August, Caribou show the highest preference for the greens of vegetative *Poa pratensis* (type A5; Fig. 4). Actually a preference index of +5 (Fig. 11) indicates that about 25% of all animals are using this vegetation type for feeding. This is no doubt caused by the prevalence of immature *Poa* plants for a prolonged period due to special circumstances. These are quite interesting and will be dealt with in detail in a later section.

In the second half of the summer dispersal a much preferred food resource, mushrooms, become abundant and consequently Caribou are often observed on good mushroom habitats such as the *Poa spp.*-dominated poor dwarf shrub heaths (C10) and the *Poa pratensis* meadows (A6).

Of minor quantitative importance, but qualitatively significant is the behaviour of seeking steep north-facing shaded slopes on hot summer days. These habitats are mainly of the B7 and B8 type (rich dwarf shrub heaths) and besides functioning as relief areas during insect harassment they also offer forage in young phenological stages at this relatively late point. Because of the aspect and slope only little insolation is received. Consequently, snow melt and the following growth season are delayed, and slow in progress compared to other vegetation types.

At the beginning of September Caribou still select mushroom habitats, viz. type A6 and C9 as well as utilizing *Poa pratensis* greens and wet sedge meadows; other vegetation types are of insignifi-

cant importance. Although fruticose lichens are scarce on this range, some can be found, especially on the C9 habitats, and Caribou show a high preference for this food resource whenever it is available at this time of year.

An additional use of feeding habitats in this period is found among males, which can be frequently observed bush-thrashing and rubbing their antlers against any kind of shrub to clean them of the loosening velvet, as part of their pre-rutting behaviour.

During fall migration in September-October about 90% of the animals (viz. the majority of females and juveniles plus many young bulls) leave the inland summer range (THING 1982). In October-November the few Caribou left behind show a strong preference for B7 and C9 habitats with index values ranging around +4. Because the animals are then in rut the mature bulls try to maintain 'harems' of females, while younger and subordinate males tend to stay around these centres of activity.

Consequently, a major portion of feeding takes place on the rutting grounds which are frequently flat or slightly north-facing areas. From early November when the rutting season is over and until mid-March Caribou continue to prefer feeding on the rich dwarf shrub heaths (i.e. B7 and B8 habitats) as well as on the poor dwarf shrub heath (type C9).

The majority of these winter habitats are steep and face north or northeast. The late arrival of spring and subsequent slow phenological progression of food plants on these localities apparently still influence forage conditions in a beneficial way during early and mid-winter.

Following the spring equinox when insolation rapidly increases, southfacing and flat areas receive so much radiation that wide-spread melting of the snow

cover may begin. Such snow-free localities readily attract Caribou which will feed on the available plants. This is more often the case when vegetation type A3, A6, and C11 (Figs. 4 and 11) are used during late winter season. Frequently only limited quantities of forage can be found here, primarily species like *Calamagrostis spp.*, *Poa spp.*, and *Festuca brachyphylla*. However, as earlier in winter the B7 and C9 habitats are still in significant demand.

Limited observations (N=200) on habitat selection in early, mid, and late winter on the coastal Ikarulik range show that most animals prefer to feed on gently sloping (1-10°) mountainsides facing north-northwest in early winter and west in late winter. Feeding craters were observed from 100 m above sea level and up to 1,100 m but were by far most frequent between 400 m and 700 m. Apparently, animals primarily fed on wet sedge meadows as well as rich dwarf shrub heaths with relatively abundant lichens.

Snow cover is known to be an important modifying factor in relation to habitat selection during the winter seasons (cf. FORMOZOV 1963, ERIKSSON 1976, MILLER 1976, PRUITT 1959, SKOGLAND 1974). Habitats with relatively shallow and/or soft cover are preferred to areas with deep wind-packed or crusted layer. The average snow conditions on the inland range seem very favourable for Caribou feeding, the snow cover rarely exceeding 25-30 cm in depth. However, winter forage quality and diversity are probably inferior to that of the coastal range where the lichen cover, although heavily exploited, still furnishes more forage than on inland ranges.

To interpret the regional and seasonal distribution of the Caribou, information on extension and duration of the snow cover is valuable. Consequently, satellite

imagery of almost the entire west Greenland range has been used for a wider study of the above-mentioned parameters (Fig. 13). This method is mostly useful for monitoring arrival of significant snow cover in fall and snow conditions in late winter and spring. The latter season appears to be crucial to Caribou in relation to snow cover; a persistent hard snow layer is likely to have a strong detrimental effect on the animals, especially at the end of the winter.

Regional monitoring of the snow cover in Alaska has proved useful in predicting selection of major spring migration corridors as well as depicting locations for possible calving grounds (LENT 1980). Similar information appears to be obtainable from West Greenland. It is evident from Fig. 13 that snow may have almost disappeared as early as March 20 on the inland range, in the example shown the visible effect of a foehn period is striking, leaving the mean snow depth as low as 1.2 cm.

### *Food selection and preference*

Food is an essential parameter in studying *Rangifer* ecology and much research effort has been put into the aspect of forage selection and preference. The known selection of habitats naturally also reflects forage selection to a great extent. However, it is considerably more difficult to gather accurate information on the use of plant species as food, than to state which habitats have been utilized.

The principal method applied in this study of food selection, macroscopic analysis of rumen contents, is however biased because of several factors. As reported by various authors (e.g. COURTRIGHT 1959, ERIKSSON 1977, GAARE 1969, KLEIN 1962, SCOTTER 1967) use of gross particles alone to establish food selection of *Rangifer* may lead to an under-esti-

mation of the proportion of lichens in particular as well as over-emphasizing the importance of fungi and graminoids.

Secondarily, seasonal changes in food selection may not be as great as indicated by analysis of gross particles alone and differential rumen turnover rates of plant species create another problem, because dynamic ruminal processes are terminated at the moment of preservation of the sample, giving distorted proportions of the original forage intake at any one time (GAARE et al. 1977). Ranked according to increasing rumen turnover time, the relationship is approximately as follows;

Lichens – mosses – herbs – woody material – graminoids (GAARE 1969).

Despite the limitations in applicability, rumen content analysis is a widespread means of obtaining information on selection and preference of forage, and during the present study the method has been supplemented with data from direct observation of feeding animals.

The results presented in Table 6 are characterized by the dominance of graminoids in the diet of animals of the inland range of Kangerlussuaq and Ilulialik range. Dicotyledonous food is available and used, but not quantitatively dominant in any season. This compares to data from Peary Caribou on Banks Island, Northwest Territories, Canada (73° N) which specializes on upland monocotyledons. Graminoids are their most important forage, constituting 60% of their diet on an annual basis, while dicotyledons amount to only 17% (SHANK et al. 1978).

Monocots in demand on the inland range in spring and summer are: *Carex rariflora*, *Eriophorum angustifolium*, *Festuca brachyphylla*, *Poa glauca*, *Poa pratensis*, and *Trisetum spicatum* (Table 8). As the growth season progresses and winter approaches there is a gradual

Table 8. Seasonal use of food plants on the Kangerlussuaq inland range. Lines indicate species being selected as forage (non-graded use) as documented through rumen analyses and direct observations.

Season	Spring migr.	Pre-calving	Calving	Post-calving	Summer dispersal	Fall migration	Rut	Early winter	Mid winter			Late winter
	M	J	J	A	S	O	N	D	J	F	M	A
Artemisia borealis												
Betula nana												
Campanula gieseckiana												
Cerastium alpinum												
Draba spp.												
Empetrum nigrum												
Hippuris vulgaris												
Melandrium spp.												
Menyanthes trifoliata												
Pedicularis spp.												
Polygonum viviparum												
Potentilla hookeriana												
Pyrola grandiflora												
Salix arctica/arctophila												
Salix glauca												
Saxifraga tricuspidata												
Stellaria longipes												
Vaccinium uliginosum												
Vaccinium vitis-idaea												
Calamagrostis spp.												
Carex spp.												
Eriophorum angustifolium												
Festuca brachyphylla												
Poa glauca												
Poa pratensis												
Trisetum spicatum												
Equisetum arvense												
Equisetum scirpoides												
Fungi												
Crustose lichens												
Foliose lichens												
Fruticose lichens												

change towards supplementary use of other species like *Calamagrostis lapponica*, *C. purpurascens*, *Carex saxatilis*, *C. bigelowii*. These species are often readily available and abundant, and rumen contents from starved animals in late winter consist almost exclusively of withered *Calamagrostis* and *Carex*

leaves (> 95% cover; S. HOLT, pers. comm.).

Detailed information on graminoids in the diet in the Nuup Kangerlua region was not available and a comparison with the Kangerlussuaq conditions was therefore not possible.

Caribou wintering on the coastal



range of Ikarlulik obviously have a much smaller monocot component in their diet, apparently on the same level as fruticose lichens. The reasons for this appear to be the much lower frequency and biomass of graminoids than on the inland range, and the increased abundance of lichens and adverse snow conditions during the mid- to late-winter period. Unusually deep and crusted snow cover forced the Caribou to concentrate their feeding on wind-blown ridge tops, outcrops, and the upper zone of the chionophobous lichen heaths. These kinds of habitats all support only scarce vegetation cover and whatever fruticose lichens may be found are mostly scattered fragments less than 2 cm. The crustose lichens, primarily of the genera *Cetraria*, *Parmelia*, and *Umbilicaria*, occurring on the outcrops are also consumed. Similar data are reported from domesticated Swedish Reindeer and wild Reindeer on Hardangervidda, Norway in late winter; selection of this kind of forage is often associated with imminent starvation (STEEN 1968, SKOGLAND 1974). However, actual starvation did not seem to be common on the winter range in 1977-1978, but the physical condition of the Caribou did appear to be very poor. This is substantiated by the dominant fraction (60%) of the rumen contents being 'soil and unidentified organic material'. The inorganic part was the more frequent, with particles ranging from < 0.5 mm up to gravel size: 5 mm. The rest was organic debris (i.e. mostly woody fragments), probably ingested while feeding on the minute fruticose lichen resource scattered among the gravelly soil, as well as 'gnawing' the crustose lichens off the rock substrate.

The available fruticose lichen species on the Ikarlulik range are primarily *Cladonia mitis*, *Stereocaulon paschale*, *Ce-*

*traria nivalis*, and *C. cucullata*, as well as less abundant *Cladonia alpestris*, *C. rangiferina*, *Cetraria crispa*, *Alectoria nigricans*, and *A. ochroleuca*.

The same diversity was apparently present on the Ilulialik winter range except for *Cetraria cucullata* being much less, and *Stereocaulon sp.* much more, abundant in the feeding craters (Table 3). However, only a single animal was sampled in late winter on that range; analysis of its rumen contents showed (% cover): 1. fruticose lichens 48%, 2. graminoids 19%, 3. *Betula nana* 9%, 4. *Vaccinium uliginosum* 6%, and 5. other species < 5% each, which may indicate a considerably greater available fruticose lichen biomass as compared to the Ikarlulik range. Snow and feeding conditions appeared similar on the two ranges with the majority of feeding taking place on the wind-blown upper zone of the lichen heaths.

The Ilulialik and Ikarlulik winter ranges apparently offer better lichen resources than the Kangerlussuaq inland range. Accordingly, the diet of Caribou wintering on the latter range consists of a quantitatively insignificant amount of fruticose lichens (about 6%, primarily *Stereocaulon spp.* and *Cetraria nivalis*).

The foliose lichen *Peltigera aphthosa*, which is fairly common on the Kangerlussuaq range, is an interesting forage species. It is actually the lichen most frequently exposed in feeding craters (Table 3). It is consumed from October until mid-April, but never in quantities exceeding 3-4% cover of the total rumen contents. However, it is significant that the species is selected at all, since it has been shown for several other ranges that *Rangifer* actively reject this lichen (LUICK 1979, KELSALL 1968) or feed on it only in periods of extreme shortage of forage (LARIN et al. 1937). Thus, the use of *Peltigera* is presumably yet another

indicator of depleted winter forage conditions.

Dicotyledonous plants play only a secondary role as forage on the Kangerlussuaq range. On an annual basis herbaceous and woody species comprise 25-30% of the Caribou diet in relation to quantity. No significant quantitative difference was found between the seasons, although different plant species were selected in summer and winter.

Caribou may be characterized as having a versatile broad-spectrum dicot diet in spring and summer (Fig. 8). Only two species receive year-round attention; *Betula nana* and *Stellaria longipes*. Dwarf birch is stripped of its leaves in summer, and in winter the terminal twigs are sometimes taken whereas the animals eat the whole *Stellaria* plant, which remains green over the winter, at least in the basal half.

Five species *Artemisia borealis*, *Empetrum nigrum*, *Melandrium triflorum*, *Saxifraga tricuspida*, and *Vaccinium vitis-idaea* are eaten in winter only. *Artemisia* and *Melandrium* occur primarily on dry south-facing slopes and are usually easily available to Caribou which consume the withered inflorescence and stem leaves of *Artemisia* as well as the basal rosettes of wintergreen leaves of *Melandrium*. *Saxifraga* spp. are mainly found on or adjacent to the upper zone of the chionophobic lichen heaths, and are generally an unimportant food resource with little exploitation (KELSALL 1968, ROBY 1978, SKJENNEBERG & SLAGSVOLD 1968). However, Peary Caribou in the Canadian High Arctic use *Saxifraga oppositifolia* heavily in winter (PARKER et al. 1975).

The dwarf shrubs *Empetrum nigrum* and *Vaccinium vitis-idaea* are apparently only eaten in winters with an unusually thick snow cover. Whole stems with leaves of the former are consumed

whereas the latter is only stripped of leaves. Similarly, STEEN (1968) reports that under adverse snow conditions in late winter domesticated Swedish Reindeer are often forced to eat shoots of *Empetrum nigrum* and *Vaccinium vitis-idaea*. Data from starving Reindeer during the population crash on St. Matthew Island indicated that *Empetrum nigrum* was the only forage available and eaten in any quantity (KLEIN 1968). These observations suggest that *Empetrum* is likely to be consumed only in marginal forage situations, and its presence in the diet in quantity may therefore be used as an indicator of famine conditions. However, the growth season May-August is the most important period for dicots in the Caribou diet. Up to 80% of the forage species are utilized during spring and summer (Table 8), and furthermore 65% of these are being consumed exclusively in this period.

Two of the latter species – *Potentilla hookeriana* and *Hippuris vulgaris* – appear to have an extraordinarily early and late season of use, respectively. *P. hookeriana* is an inhabitant of the xeric south-facing slopes with D12 vegetation, and flowering may start as early as the first week of May. Caribou select the young flowers, and usually not the leaves.

*Hippuris vulgaris* is a fresh water plant like *Menyanthes trifoliata* but its use as forage is extended into early November because the green rhizomes and winter buds are much preferred by Caribou, and dug out along the banks of the smaller ponds and lakes. During the summer whole plants of both *Menyanthes* and *Hippuris* are grazed down by Caribou wading through the stands along the shores. Should an extra dry summer drain smaller water bodies, the exposed *Hippuris* vegetation attracts

Caribou which readily eat down this forage.

Of the remaining summer food species, the following selective use has been observed:

*Campanula gieseckiana*: flowers (mostly eaten by calves)

*Cerastium alpinum*: flowers and young leaves

*Draba spp.*: inflorescence or whole plant

*Pedicularis spp.*: flowers and young leaves

*Polygonum viviparum*: bulbils or whole plant

*Vaccinium uliginosum*: young leaves

Finally, three species are used both in spring and again during fall or winter: *Pyrola grandiflora* possesses relatively large winter-green leaves and these are fed upon to some extent during their emergence in June-July. Again in mid-winter they may form part of the diet for Caribou (especially mature bulls) which expose the often lush *Pyrola* stands in feeding craters. Two prostrate willow species, *Salix glauca* and *S. arctophila*, are important to Caribou during June-July when the animals feed on the young leaves.

The catkins do not appear to be taken to any extent. The growth form of the plants does not allow for stripping of the leaves (as is the case when feeding on tall-growing *Salix glauca*) but rather selective grazing on individual leaves. In early and mid-winter Caribou have often been observed to dig down to living stems and dormant buds, and feed on this food resource.

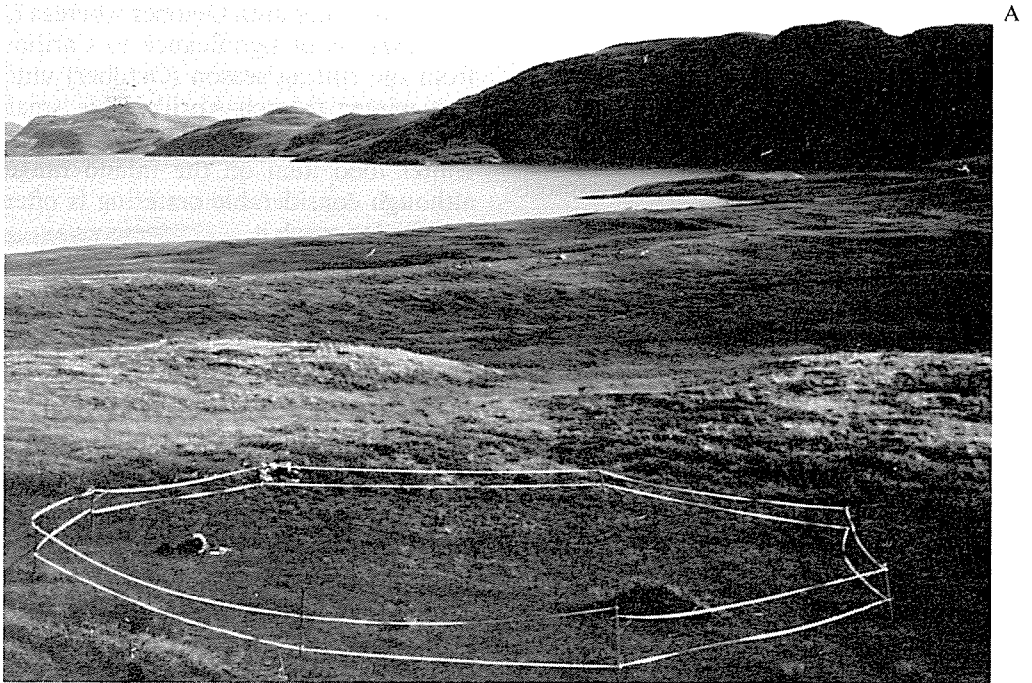
Cryptogams form the last but interesting part of the Caribou diet. The two species *Equisetum arvense* and *E. scirpoides* alternate as forage, the former having green vegetative parts only in summer and the latter staying green over winter. Consequently, *E. arvense* is fed

upon from July until October whereas *E. scirpoides* is of significance to Caribou from the rutting season (October) until late winter (March-April). This small prostrate species is a highly preferred winter food item on the inland range, although considerable cratering is often required to reach it.

Similarly, wintering Caribou in northern Alaska have a strong affinity for areas with good cover of the small, evergreen *Equisetum variegatum*, which was heavily fed upon in winter and early spring (ROBY 1978). *E. arvense* has its main occurrence on the steep north-facing rich dwarf shrub heaths and on disturbed sites, e.g. along gravel roads etc. However, on an annual basis the use of this species is insignificant. The sporophylls of the fertile part have not been observed to be consumed.

For a couple of months following mid-summer, when most fungi start to develop, feeding Caribou can frequently be seen selecting good mushroom habitats in order to maximize their dietary intake of this forage which throughout *Rangifer* ranges in the Holarctic has been reported as a much favoured food resource (e.g. KELSALL 1968, SKJENNEBERG & SLAGSVOLD 1968, SKOGLAND 1974). Although the dry climate inland is probably not optimal for the edaphic requirements of mushrooms, they seem to be ubiquitous on the meadows and the poor dwarf shrub heaths. The most preferred species are apparently *Leccinium scabrum*, *Agaricus spp.*, and *Calvatia spp.*

Mosses are infrequently found in rumen contents and are believed to be ingested incidentally with other food items. This is in agreement with the findings of AHTI (1959) and BERGERUD (1972). Generally, *Rangifer* does not possess the ability to digest moss efficiently and in only one range of the Hol-



arctic are mosses known to be deliberately consumed. This exception is Svalbard where the Reindeer (*R.t. platyrhynchus* Vrolik) successfully utilizes mosses especially during the long winter periods (EKERN & KILDEMO 1978, HJELJORD 1975b).

#### *A Caribou induced plant succession – cause and effect*

Grazing is one of the important modifying forces in the environment of Caribou. Grazing pressure affects the subsequent yield of the range by affecting the physiological systems of plants and their local environment. Caribou, like other herbivores, tend to aggregate in favoured habitats, and their feeding appears to be beneficial for the primary production of graminoids. A high density of grazing Caribou may therefore cause graminoids to spread by preventing regrowth of shrubs (e.g. willow and birch), so that

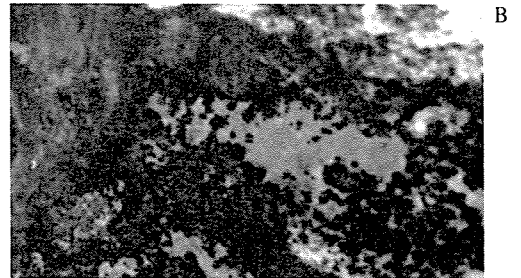


Fig. 14. Aerial view of the same *Poa pratensis* green in 1978 (A) and in 1962 (B). Primary production of the green was studied in 1978. Note the scattered *Salix glauca* shrubs on the habitat of photo B. (Aerial photo (B), Geodetic Institute, Copenhagen (266Å, no. 66, 1962). Reproduced with G.I. permission A.539/80. Copyright.)

when the mature woody component of the vegetation dies there is no replacement until the local environment is eventually altered due to a significant decrease in herbivore density, e.g. during a population minimum. When considerable parts of a range are reduced to such short grass habitats it can be taken as an

indication that full utilization of the range has been achieved.

Habitat-herbivore relationships have been studied in numerous areas around the world. Although it is beyond the scope of this presentation to summarize these data, the reader is referred to the following examples: DE VOS 1969, ELLISON 1960, VESEY-FITZGERALD 1965, CRISP 1964, BLISS 1971, CHAPIN 1980.

A case in point of this dynamic relationship is the *Poa pratensis* green of the Kangerlussuaq inland range. The green (type A5; Fig. 4) is commonly situated in minor depressions of the landscape or in connection with meadows (HOLT 1983) so that water supply (i.e. surface water) normally does not become a limiting factor for plant growth during the summer. This vegetation type has been found mainly in the eastern half of the

inland range and is especially common in the core calving area (Fig. 3). It covers around 5% of this part of the range and the area of each habitat unit rarely exceeds 100 m<sup>2</sup>. Detailed studies of older aerial photos (available from the Danish Geodetic Institute) and research at specific localities make it apparent that this vegetation type is created by intensive foraging by Caribou (Fig. 14). The apparent successive stages of the plant cover are:

1. Healthy stands of *Salix glauca* and *Betula nana* are supported by the locality during low Caribou density in the area.
2. With increasing Caribou numbers, browsing pressure is intensified during leaf emergence in post-calving and summer dispersal. This browsing consists of stripping the branches of

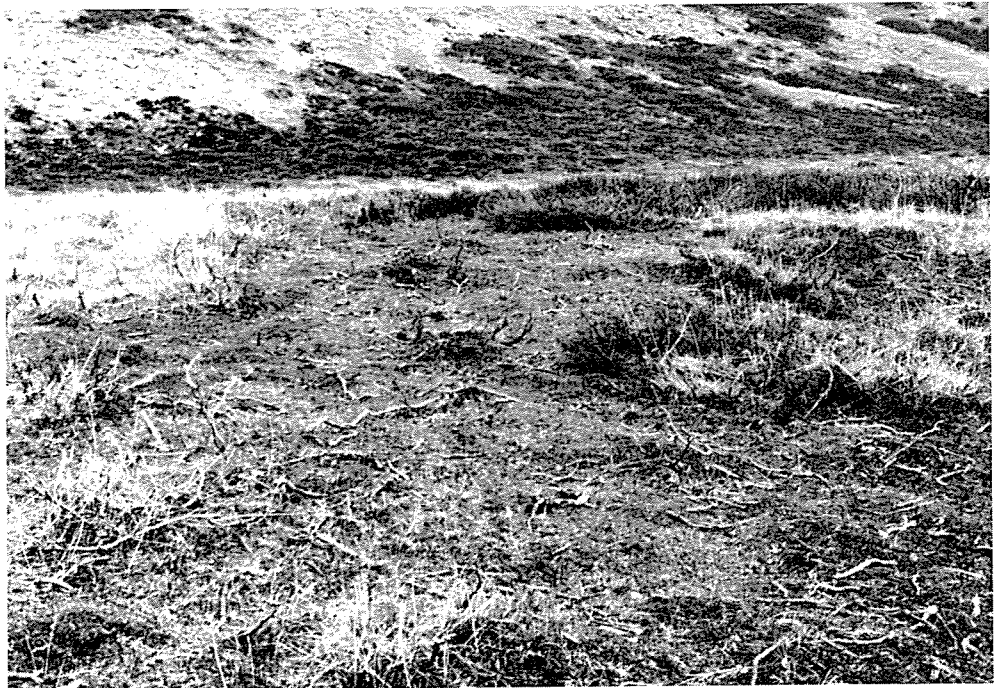


Fig. 15. *Salix glauca* – *Betula nana* shrub dying back due to heavy grazing pressure (stage 4). Kangerlussuaq inland summer range, July 1978.



Fig. 16. A fully developed *Poa pratensis* green (stage 6). Kangerlussuaq inland summer range, July 1979.

the leaves and removal of terminal twigs.

3. The effect of intense browsing for several consecutive summers eventually means destruction of the shrub and its subsequent disappearance (Fig. 15).
4. During phase 2 and 3 foraging Caribou fertilize the locality with urine and faeces. These products in turn favour lush growth of some grass species of which *Poa pratensis* is one of the most nitrophilic.
5. Young green grasses are an added forage attraction of the locality, and a positive reinforcing process is begun with more Caribou concentrating on the preferred food supply. Consequently, the substrate receives heavier fertilization which further enhances the growth of *Poa*.
6. Eventually, the green develops among the dying stumps of willow

and birch. The grass cover is kept in a vegetative state due to intensive cropping (Fig. 16).

7. Following a population peak the decreasing Caribou density and grazing pressure on the habitat allow for an initial alteration of *Poa pratensis* green towards a biotope of mature, sexually propagating individuals. This change is visible as a dominance of inflorescences in the area and a subsequent modification of the habitat towards a heterogenous botanical composition. The above description of the succession is substantiated by data by HOLT (1983) and REHDER (1981) on phenology, primary production, and pellet counts on the greens (Table 9).

Preliminary analyses indicate that the succession of *Salix glauca* – *Betula nana* shrub – *Poa pratensis* green – *Salix*

Table 9. Weight of Caribou fecal pellets on *Poa pratensis* greens; N = 15. Weight is calculated as: no. of pellet groups (i.e.  $\geq 11$  pellets in aggregation)  $\times$  approximated wet weight of 50 g.

Locality	Sample date	Sample area (m <sup>2</sup> )	A	B	C
			Weight of pellet groups from present year (kg/100m <sup>2</sup> )	Weight of pellet groups from previous years (kg/100m <sup>2</sup> )	Total weight of pellet groups (kg/100m <sup>2</sup> )
1	21.06.78	75	3.0	22.3	25.3
2	21.06.78	60	2.8	—	—
3	29.06.78	30	0.7	11.5	12.2
3	25.08.78	30	1.2	—	—
4	29.06.78	33	1.4	10.3	11.7
5	29.06.78	33	1.4	10.5	11.9
5	25.08.78	33	2.0	—	—
5	03.06.79	30	3.3	15.3	18.6
6	29.06.78	50	1.1	9.1	10.2
6	03.06.79	50	3.2	9.2	12.4
7	24.08.78	50	2.7	14.7	17.4
8	25.08.78	60	5.0	—	—
9	03.06.79	95	3.5	15.5	19.0
9	09.08.79	95	4.4	—	—
10	08.08.79	38	—	—	16.6
			$\bar{x}=2.6 \pm 0.3$		$\bar{x}=15.5 \pm 1.5$

*glauca* – *Betula nana* shrub has been repeated several times during the past, presumably reflecting long term climatic fluctuations. Although Caribou generally can be considered 'nervous' feeders (KLEIN 1970a), moving frequently during foraging, animals feeding on the *Poa pratensis* greens are remarkably stationary, using but an insignificant part of their time searching and selecting food. This is evidenced by the average feeding intensity being as high as  $89.2\% \pm 1.4$  on the greens compared to  $75.3\% \pm 2.7$  on all other vegetation types during July-August.

Accordingly, young phenological stages of *Poa pratensis* are available to Caribou throughout the summer, a fact which is responsible for the importance of this vegetation type as a food resource.

The data presented in Table 9 illustrate the amount of fertilizer passed on to some selected greens currently used

by Caribou. A general idea of the rate of macroscopic decomposition of pellet groups might be obtained by dividing column B values by A values. Thus  $B/A = 7.2 \text{ years} \pm 1.3$  (N=9) before pellets are disintegrated into microscopic components. The average monthly increment of pellet groups over the summer (May 25 – September 15) equals  $0.62 \text{ kg} \pm 0.2$  per  $100 \text{ m}^2$  (N=5).

A decomposition rate of 7.2 years appears relatively rapid considering the xeric environment of the region. However, the greens are situated in comparatively moist locations and a high moisture level in the substrate enhances the rate of decomposition. This compares with data by FERGUSON (1955) and VAN ETTEN & BENNETT (1965) cited in NEFF (1968) from studies of mule deer pellet groups in USA. Here 6-7 years of disintegration were required to make the faecal pellets undetectable to the observer.

Pellet-group counts were made on south-facing dry heath habitats, i.e. type D12. These habitats are primarily used during 6 weeks in spring, and a total pellet group wet weight of 0.5 kg per 100 m<sup>2</sup> was found (HOLT 1983).

Although *Poa pratensis* greens have a longer season of intensive use, viz. 8-9 weeks in summer, the amount of faeces accumulating on the two vegetation types puts the utilization of the greens in proper perspective, the two values differing by a factor of 30, i.e. 15.5 kg per 100 m<sup>2</sup> versus 0.5 kg per 100 m<sup>2</sup>. An average total pellet group weight of 15.5 kg per 100 m<sup>2</sup> is however an insignificant quantity compared to temperate regions (e.g. Denmark) where an annual application of 300-400 kg of livestock manure per 100 m<sup>2</sup> does not create any ecological difficulties (KOFOED 1980).

In Sweden Reindeer ranges have been fertilized with urea and NPK fertilizer (Nitrogen, Phosphorus and Potassium). The effect of urea application increased over a 5 year period and was especially beneficial to the grasses which became much more abundant. The weight of applied urea varied between 1 and 3 kg per 100 m<sup>2</sup>, equivalent to 0.46 and 1.38 kg N per 100 m<sup>2</sup>, respectively (ANDERSSON 1971). Some domestic sheep ranges in southern Greenland have been subject to experimental fertilization, increasing their frequency and coverage very significantly on the test areas. Species like *Phleum pratense*, *Poa pratensis*, and *Festuca rubra* thrive particularly well following application of nitrogen to crofting land (THORSTEINSSON 1980).

An apparent detrimental consequence of the high pellet group density on the greens is believed to be the facilitation of the spreading of a lethal calf disease (*Escherichia coli* - polyarthritis) in summer because of frequent incidental ingestion of contaminated pellets by

young calves inexperienced in food selection (CLAUSEN et. al. 1980, THING & CLAUSEN 1980).

### *Feeding behaviour*

In earlier sections efforts have been made to give a qualitative description of the feeding habitats and behaviour of the Caribou. This kind of information is valuable, but additional data should also be obtained by a quantitative study of the behaviour itself, and its relation to various factors.

The combination of snow cover and the rigorous winter climate itself suggests that Caribou must have evolved some special types of behaviour in order to survive these severe conditions and to thrive as a species. An obvious adaptation to snow is cratering to obtain food from beneath it. The snow cover encountered by Caribou on winter ranges may be characterized by some parameters important to feeding animals (Table 5).

Caribou wintering on the inland range in 1977-78 experienced the same snow depth from November to April although approx. 75 mm (water equivalent) precipitation accumulated in that period. This was caused by settling of the snow due to wind-packing and above-freezing weather, resulting in a doubling of the density from early to late winter. Similarly, snow hardness increased by a factor of 5-8 which strongly influenced the feeding behaviour of the Caribou (Fig. 12). It should be emphasized that precipitation during the winter of 1977-78 was far above average.

The traditional winter range near Ikarlulik only had shallow snow cover in 1978-79. However, the area was exposed to strong winds and the cyclonic weather situations of the coastal region, and con-



sequently the snow was very hard-packed with frequent but thin icy layers.

At the same time a very different situation was found in the valley of Arnangarngup kua where about 100 Caribou spent mid-winter. In the relatively shallow layer of snow, density and hardness remained at low levels indicating much more favourable cratering conditions for the animals here than in Kangerlussuaq. The valley is sheltered by high mountains in all directions, and high winds and thaw were apparently infrequent in this locality.

Limited observations of use and disturbance of feeding areas (Table 4) during the first feeding sequence in late winter on the inland range indicated that when cratering for food, the animals disturbed just as much snow cover at the same time by their activity in the area, incidental to cratering leaving only about 25% of the habitat undisturbed. This is comparable with data on late winter conditions for Alaskan Caribou (THING 1977). The significance of this is that by disturbing 70-80% of the snow cover in forage areas the Caribou decrease their own chances of effectively feeding again in the same area. The value as a feeding area apparently decreases with increased previous use, a fact that makes Caribou extensive rather than intensive feeders, and helps to prevent over-grazing of the forage species. Quantification of *Rangifer* activity in general is a fairly recent phenomenon. Considerable amounts of data have nevertheless already been accumulated (CURATOLO 1975, REIMERS 1980, ROBY 1978, 1980, ROBY & THING 1983, THOMSON 1971, 1973, 1977, and WHITE et al. 1975).

In the present chapter only feeding activity is discussed.

The seasonal differences observed in feeding intensity (Fig. 12) may be explained by both physiological and en-

vironmental factors. As the data relate almost exclusively to adult females the variations in spring and summer may to a wide extent reflect the energy requirements for pre-partum foetal development, parturition, and milk production.

During pre-calving and calving the animals use only little time searching for food, indicating that the selected forage is easily available. This is especially important for parturient cows which primarily feed on the *Eriophorum-Poa pratensis* communities. Thus an intensity index of 7-9 in the calving season shows that the energetically least-demanding foraging coincides with the time of maximum graminoid quality (Fig. 17) and the highest level of physiological stress in the animal.

When snow cover necessitates cratering the cost:benefit ratio during feeding increases (THING 1977). In habitats with full snow cover, 15-20% of a feeding period is used in cratering, in addition to the time devoted to searching thus reducing the intensity index to a minimum level of 1-4. In late winter Caribou show a strong preference for feeding on partially snow-covered habitats, presumably because less cratering is required to reach the forage. Because searching in snow-covered habitats takes up an increasing part of the feeding activity as the winter progresses (from 6-12% in early to 20-22% in late winter) a reduction in cratering time in March-April only means that the time available for ingestion would be back to the early winter level. In mid-winter feeding on snow-covered habitats requires considerably more cratering than earlier e.g. in November. However, on the inland range even in mid-winter, more or less snow-free habitats are available but scattered; feeding on these does not involve cratering.

A most important environmental fac-

tor influencing feeding behaviour of the animals in summer is the harassment by biting or parasitic insects (*Diptera*), viz. mosquitos (*Culicidae*), black flies (*Simuliidae*), and oestrid flies (*Tabanidae*), i.e. the warble fly (*Oedemagena tarandi*) and the nostril fly (*Cephenomyia trompe*). Mosquitos and black flies first emerge around June 20 (i.e. at the very end of calving), and parasitic flies during the first week of July. The dry inland climate appears unfavourable for development of great numbers of mosquitos and black flies whereas the oestrid flies seem to thrive frequently experiencing air temperatures above their minimum for flying activity (i.e. 13-15°C and low wind velocities; SKJENNEBERG & SLAGSVOLD 1968). The greatest effect on the Caribou comes therefore from warble and nostril flies. About 40% of the days in the summer dispersal season (July 7 – August 31) involved moderate to severe insect harassment (THING & THING 1983).

The presence of harassing insects causes a marked reduction in the time devoted to ingestion, with a concomitant increase in searching (including insect avoidance behaviour like walking, stamping, shaking, and bunting). During severe harassment the two sub-activities are equally time-consuming (Fig. 12). Expressing the state of disturbance as an index of feeding intensity during no, moderate, and severe harassment gives a value of 6.8, 2.6, and 0.9-1.3, respectively.

This 5-6 fold insect-induced change in activity not only has an immediate effect (viz. reduced food intake and increased energy output for movement), but also a significant long-term effect. A close negative correlation between frequency and intensity of harassment during summer and the probability of surviving the following winter has been found both in Norway and Canada (THOMSON 1977,

KELSALL 1975). Increased insect harassment leads to increased winter mortality, especially if the food resource of the winter range is inadequate. The reason for this is the decreased possibility of acquiring sufficient fat deposits during summer to last through the winter. This is especially critical for cows and calves. Bulls are apparently harassed to a lesser degree, and their fat reserves are primarily used during rutting. The prerequisites for such a harassment-mortality relationship are obviously present in the Sisimiut-Kangerlussuaq area but remain undocumented.

### *Quality and adequacy of the forage*

The metabolic processes of a ruminant are fairly complex, and a simple approach to the relationship between forage nutrients and animal requirements may not be justifiable. However, various physiological studies have clarified significant metabolic processes and pathways in both *Rangifer* and ruminants in general, and circumstantial evidence accumulated during forage related field studies (especially in Norway and Alaska) permits meaningful nutritive evaluation of a food plant, based on analysis of its chemical components.

Several factors affect the nutritive quality of plants available to Caribou. The more significant ones are listed below (BISSELL 1953, BLISS 1962, 1971, CHAPIN 1980, JOHNSTON et al. 1968, OELBERG 1956, REIMERS 1972, REIMERS & GAARE 1969):

1. Stage of maturity of vegetation with the highest nutritive quality coinciding with initiation of growth.
2. Edaphic influences such as soil type, quality, and exposure.
3. Macroclimate, especially temperature, precipitation, and insolation.

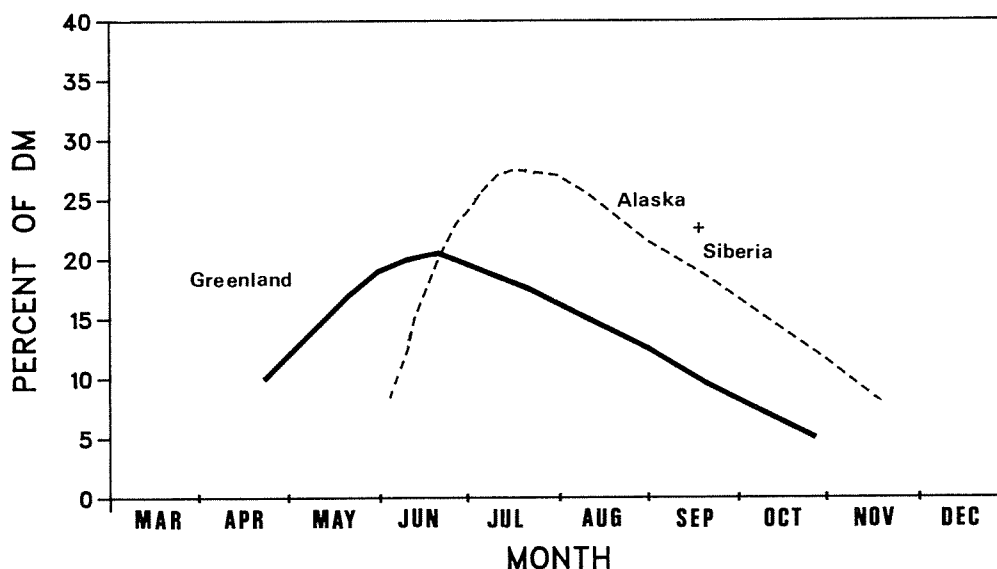


Fig. 17. Trends in amount of crude protein (% of DM) in Reindeer/Caribou graminoid forage. Based on this study and data from D.R. KLEIN (pers. comm.) and COURTRIGHT (1959).

4. Intraspecific qualitative variation due to translocation of energy pools in the plants.
5. Range condition, i.e. intensity of previous animal use.

The dietary quality of the Sisimiut-Kangerlussuaq food resources has received only limited attention during the present study. There is a need for future research in seasonal intraspecific variation of quality, as well as a comparative study of winter and summer food quality. The conclusions drawn in this study will therefore be of a preliminary character.

Since the proximate analysis of food plants has been a widely-used method in studies of ungulate forage quality, it was desirable that one of the parameters analysed could be selected as a reasonably accurate measure of quality. The crude protein (or nitrogen) fraction has proved to be such a factor. A high content of protein in plant samples is interpreted as indicating high dietary quality, and vice versa for low protein content. However

this relationship is probably altered in winter, when available energy (e.g. starch) is more important. The quality is influenced by components like lignin and tannins, as well as the ability of the animal to digest the forage. Despite its limitations the crude protein level is an accepted indicator of quality which will also be used in the following discussion.

At the onset of spring the initiation of plant growth causes a considerable increase in protein levels in growing tissues. Highest protein values are reached when the phenological stage of rapid cell growth is at its maximum, and before any sign of maturation is apparent. This usually coincides with the time of anthesis. Subsequently protein content declines during the summer, and stabilizes at a low winter level around rutting season in late fall – early winter. This general pattern applies to various groups of forage plants (viz. shrubs, herbs, and graminoids) although different levels of protein content are apparent between

species and ranges. Fig. 17 illustrates the seasonal trends in content of crude protein and permits a comparison between Greenland graminoids and species from Alaska and Siberia.

There are three obvious differences:

1. Greenland graminoids commence growth in the second half of April, 5-6 weeks before herbs and graminoids initiate their growth in Alaska;
2. The maximal level of crude protein in Greenland graminoids is reached at calving time (i.e. the first 3 weeks of June), whereas the protein content in Alaskan-Siberian graminoids peaks subsequent to calving;
3. Greenland samples remain at a lower protein level than Alaskan-Siberian samples, the latter being about 50% higher on average from June until October.

Lichens show a totally different pattern because they do not have any significant seasonal variation in protein, nor in any other of the chemical components. Year round fruticose species hold about 3% DM (Dry Matter) of protein (COURT-RIGHT 1959, SCOTTER 1965). It is obvious that fruticose lichens would not be consumed for this reason, but rather because of other components found in larger amounts, such as carbohydrates.

However, as Caribou are capable of selecting the most nutritious plants within a species as well as the portions of plants which are of highest quality (KLEIN 1970b) the actual diet may well be of a higher quality than the present data indicate, but the general trend in quality/digestibility still exists.

The utilization of *Poa pratensis* greens is an example of selectivity for high protein forage. In late May analysis shows a protein level of 18.8% DM. Frequent leaf regeneration in *Poa* favours availability of high quality forage for a prolonged period, substantiated

by 21.3% DM protein at the end of July – a value well above average.

The data presented indicate that although graminoids as the primary food source contain only about half the amount of protein available to some Alaskan Caribou, a compensatory effect may be achieved by being able to consume green forage 4-5 weeks earlier than Alaskan animals. This is an obvious advantage for pregnant females which experience high physiological requirements for the foetus in the last month before parturition (DAUPHINÉ 1976). These animals are the first to arrive at summer and calving areas, starting in early April but not in considerable numbers until the latter half of the month. Their arrival seems to be very well synchronized with growth initiation of graminoids on dry south-facing slopes. Whether there is an adequate supply of high quality forage on the range to balance the energy demands of the cow and foetus remains to be determined. However, the average total body weight of neonates (0-2 days old; 4.8 kg  $\pm$  0.2; N = 8) does not differ significantly from birth weights in Canadian barren-ground Caribou populations like the Beverly and Kaminuriak herds (MCEWAN 1968, DAUPHINÉ 1976), which may indicate that pregnant females in the study area manage to stay in sufficiently good condition during the last few weeks of pregnancy.

Nevertheless, following parturition the observed nursing/suckling behaviour in cow/calf pairs makes it likely that parturient Caribou females often do not have a positive energy balance until the end of July because of the increased energy requirements for milk production, and insect-related avoidance behaviour (THING 1980a, THING & THING 1983).

Additional forage samples from dicotyledonous plants do not permit any

evaluation of their quality in relation to other ranges, because of too small a sample size. However, none of the few shrub and herb sample analyses from Greenland differ significantly from the average Alaskan samples (COURTRIGHT 1959, D.R. KLEIN pers. comm.) in the parameters analysed when related to phenological stages.

For most native *Rangifer* populations lichens constitute an essential part of the winter diet, but play a minor role in the summer (KLEIN 1982). Prior to the recent population peak in West Greenland, Caribou supposedly consumed a variety of fruticose lichens on the winter ranges. Because of the subsequent depletion of this food resource the present diet included only an insignificant amount of lichens.

Generally speaking fruticose lichens of the genera *Cladonia*, *Cetraria*, and *Stereocaulon* have a higher palatability for Caribou than any foliose or crustose species (LARIN et al. 1937). However, they also have a lower protein content (2-4% vs 7-8% DM) (COURTRIGHT 1959). It still remains something of a paradox that fruticose lichens are more highly preferred to any nutritionally superior food source available during the winter months. This strong preference for a seemingly nutritionally inadequate diet is hard to explain in relation to natural selection. However, findings by CAMERON & LUICK (1972) suggest that daily water flux in the animals is considerably diminished during winter. This would mean that the survival value of a smaller dietary protein intake such as fruticose lichens may be attributed to body water and body heat conservation, by decreasing the amount of water required to eliminate metabolic nitrogen. The apparent reason for the importance of fruticose lichens to *Rangifer* is the high starch content, which the animals are

especially adapted to utilize as a primary energy source during the long winters.

As heavy over-grazing of the Sisimiut-Kangerlussuaq ranges has almost completely deprived the Caribou of this diet, the animals face a marginal winter situation because no other forage has a similar chemical composition and digestibility. Low quality senescent graminoids and herbs, as well as foliose and crustose lichens are essentially all that is available to them, and these provide inadequate energy and other nutrition, therefore the inevitable result for wintering Caribou is poor physical condition or even starvation.

Although only a minimum of protein is ingested with food during fall-midwinter (5-10% DM; cf. Fig. 17) the protein content of the rumen is considerably higher (20.0%  $\pm$  1.9 DM; N=13). The increase of protein in the rumen over that of the ingested material is a consequence of the fact that part of the ammonia formed by protein digestion is recycled to the rumen via the liver and saliva. On a low-protein diet this additional supply of ammonia helps to promote an active microbial population with a concomitant increase in the synthesis of microbial protein. This requires an adequate energy supply in a readily digestible form, e.g. starch. The real significance then of the fruticose lichen diet is to supply energy. On depleted winter ranges energy input fails to maintain an optimal microbial activity in the rumen, and the subsequent lowering in production of digestible proteins is a hindrance to normal physical condition and activity.

On ranges in northwest Alaska with an adequate supply of fruticose lichens, the late winter level of ruminal protein is significantly higher (viz. 25.6%  $\pm$  0.6 DM, N=13, D.R. KLEIN, unpubl. data), and Caribou are found to be in good con-

dition throughout the winter.

Caribou wintering on the inland range or in the valley of Arnangarngup kua are known to starve on a diet of withered graminoids. If a Caribou consumes a large amount of such species, digestive disturbances may apparently develop due to malfunction of the ruminal contractions and a drastic irreversible reduction in ruminal microbes (KURKELA 1976, NAGY et al. 1964). This was observed during early and late winter in the two areas where some of the starving animals had very intense diarrhoea caused by the diet.

A ruminant feeding on low quality forage can compensate by eating more only if the food has a sufficiently good dry matter digestibility (i.e. 40-45%, WHITE 1975). Poorly digestible forage results in a decreased food intake because the limits of the ruminal capacity are reached before the energetic demands of the animal are satisfied.

However, not all ruminants can digest and utilize the same forage equally efficiently. The ability to digest a poor-quality forage is positively correlated with the capacity of the rumen-reticulum. Comparison of stomachs among adult ruminants reveals major size differences in relation to body weight; this may indicate that Caribou in West Greenland are able to cope with rather poor quality food.

On the winter range available forage is frequently very fibrous, causing an increased rumen turnover time. Therefore, an energy requirement per unit time exceeding that which the food can supply with a filled rumen puts the animal into a negative energy balance.

### *Status and perspective of the range*

The present condition of the Sisimiut-Kangerlussuaq range is obviously due to

over-grazing. The herd reduction in the last decade mostly resulted from winter range depletion and consequent starvation, but has not significantly alleviated grazing pressure on the range.

Over-stocking is not just a matter of absolute numbers but rather of density in relation to the carrying capacity of the range. On the over-populated range, Caribou which have survived starvation may still be too many for the range to support. Even with few animals per km<sup>2</sup> a stocking rate exceeding the carrying capacity will continue to prevent recovery of the range, causing increased range depletion. To evaluate such circumstances current range conditions and trends must be established.

### Coastal range

At the beginning of this study (April 1977) Caribou density on the major winter range W1 (Fig. 3) was 4-5 animals per km<sup>2</sup> utilizable range (i.e. total area excl. water bodies and barren mountain ridges). The following winters showed a reduced density, viz. 1978, 2 per km<sup>2</sup> and 1980, less than 1 per km<sup>2</sup>. The size of the herd a decade earlier is estimated at around 40,000 with a maximum winter range density of 13-14 animals per km<sup>2</sup> utilizable range. Despite this drastic decline in stocking rate on the coastal winter range there is so far no sign of recovery of the plant resources.

Of the forage species present in the area those with the highest and lowest preference rating are especially useful as indicators of the balance between Caribou stocking density and range condition. The highly preferred fruticose lichens have decreased dramatically in biomass, partly because of the cratering activity of the animals and partly due to trampling. During winter foraging, in addition to the amount of lichens con-

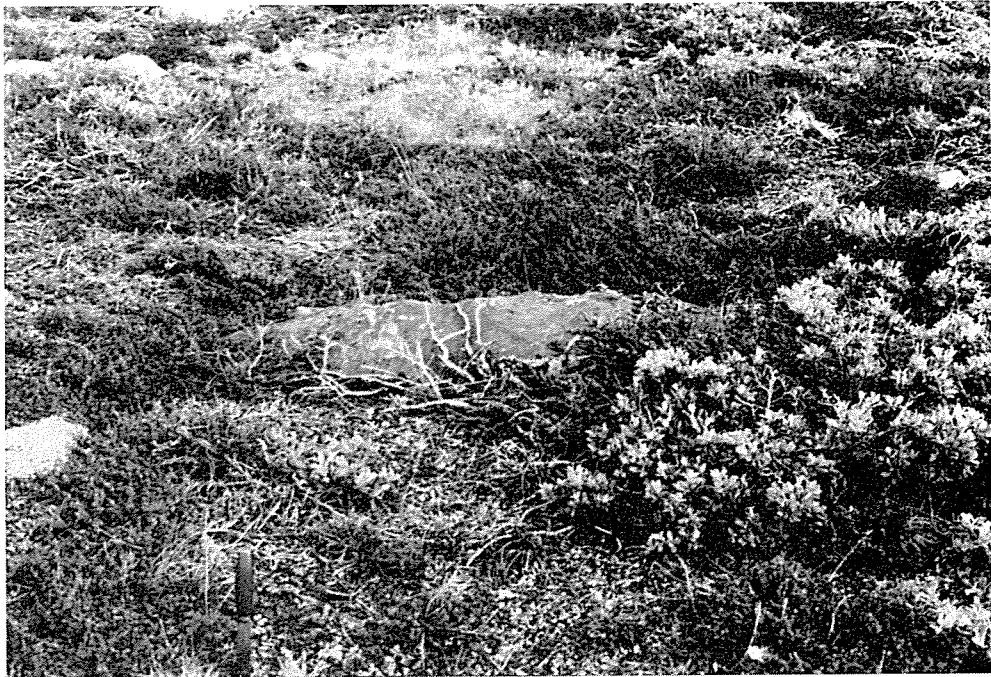


Fig. 18. Plant succession with grasses and mosses invading exposed soil formerly covered by fruticose lichens. The coastal winter range, August 1978.

sumed a spillage factor of about 10 should be included in the total biomass removed from the habitat (GAARE & SKOGLAND 1975).

Concomitant with the disappearance of most of the fruticose lichen cover, grazing pressure has brought about an increase in the relative abundance of neglected or avoided species of graminoids and mosses (especially of the genera *Calamagrostis*, *Hierochloa*, *Polytrichum*, and *Dicranum*), establishing themselves on the newly exposed substrate (Fig. 18).

A similar succession has been observed on various other *Rangifer* ranges following over-grazing, viz. Eurasian (LARIN et al. 1937, GAARE 1968, OKSANEN 1978), North American (PALMER & ROUSE 1945, MILLER 1976), and sub-Antarctic (LINDSAY 1973, LESEL & DERENNE 1975).

LARIN et al. (1937 citing SOCHAV 1932) distinguish between the following stages of winter grazing pressure according to the effects on the vegetation:

1. Moderate grazing; only the completeness of the lichen cover is broken.
2. More intense or unseasonal grazing; *Cladonia* abundance is decreased and replaced by *Cetraria nivalis* and *Stereocaulon* spp. A rest period for several years is necessary in order to restore the former cover.
3. Disappearance of fruticose *Cladonia* species; presence only of *Cetraria*; increase of mosses and development of grass cover. Restoration possible after several decades of rest.
4. Complete disappearance of all lichens; they are restored only with much difficulty after many decades.

At present the coastal Ikarlulik range is at stage three, and interest is focused on

possible perspectives for the area. Studies of other ranges in the world (e.g. GAARE 1968, LINDSAY 1973, PEGAU 1975, OKSANEN 1978, LEADER-WILLIAMS 1980) have revealed the delicacy of the *Rangifer*-lichen balance, and that restoration is a long-term task. Experience gained in other regions of the Holarctic may be most valuable for present management plans for the West Greenland Caribou and their winter ranges.

A useful aid to management is the establishment of exclosures (excluding Caribou from an area) and monitoring vegetational trends within them. The development of plant cover inside and outside the exclosures can then be compared and evaluated in relation to the present stocking rate.

A recent example of this comes from the Nelchina range, Alaska (PEGAU 1975) where the condition of a climax lichen cover of *Cladonia alpestris* began to degenerate after only 2-3 years of use. Even after 15 years in exclosures lichens had just started to recover reaching a height of about 2 cm. Outside exclosures lichens continued to deteriorate even with a marked reduction in Caribou winter use. It was concluded that the range required 25 years or more of total protection to reach climax conditions again, yet it took only 5-8 years to destroy this condition.

To evaluate future winter grazing pressures a 10 m × 10 m exclosure and a similar unfenced control area were established on the coastal Ikarlulik range. The site is presumed to be representative of the dry lichen heaths of the range (estimation based on personal knowledge of the area and aerial infrared photos) with the following vegetational composition (in % cover): live whole lichen thalli 1-5% (mostly *Cladonia mitis*, *Cetraria nivalis*, and *Stereocaulon paschale*); dead lichen bases + fragmentary

thalli 10-20%, mosses 3-5%, other plants 3-5%; and dead organic material + exposed soil 75-80% (REHDER 1979).

Differential development of plant cover in the exclosure and control area will be monitored and used as a range recovery indicator. Recovery of the fruticose lichens is mainly dependent on their growth rate; the latter varies in relation to climatic factors, especially precipitation, but even under optimal conditions lichens are very slow growing organisms indeed.

*Cladonia mitis* is one of the most rapid growing species, with a maximum annual growth under optimal conditions of 5-6 mm in length; other species like *Cladonia rangiferina* and *Stereocaulon paschale* may achieve around 4 mm a year. Slowest growing of the fruticose lichens is *Cladonia alpestris* with about 2 mm annual length increment (LARIN et al. 1937, KOSMO 1973).

It is generally recognized that the lichen cover of an area ought to have a minimal height of 20 mm before any foraging is recommended. Furthermore, the present condition of the range necessitates that additional years should be allowed for re-establishing and initial growth of the fragmented thalli. Assuming an optimal climate for lichen growth, recovery to a height of 20 mm would probably require something like 10-15 years, even if no Caribou were present in the area. However, as the latter assumption is only hypothetical, a considerably longer period would be required to reach a final balance in the lichen-Caribou relationship. If the present stocking density of about 1 animal per km<sup>2</sup> utilizable winter range is maintained through an applied harvest policy, the lichen cover of the coastal ranges can be expected to recover within the next 30-40 years.

Although comparison with other



*Rangifer* ranges should be treated with caution because of differences in climatic and biological conditions, the following data may be useful in relating the Sisimiut-Kangerlussuaq range situation to past examples and experience in other regions:

a. A density of 1.5 animals per km<sup>2</sup> utilizable habitat is recommended for the semi-domesticated Itinnera herd (Nuuk region, West Greenland) on the inland winter range which is presently in prime condition (Aastrup 1978).

b. In Norway over-grazing is usually the consequence of a stocking density exceeding 2 animals per km<sup>2</sup> utilizable habitat (Reimers 1977).

c. In the Canadian high arctic archipelago Peary Caribou, which exist on ranges almost devoid of lichens, occur in densities of less than 1 animal per km<sup>2</sup> in late winter (Miller et al. 1977).

d. Further south (viz. Southampton Island) in the Northwest Territories, Canada, Parker (1975) recommends a maximal Caribou stocking rate of 2.8 animals per km<sup>2</sup> winter range.

#### Inland range

The current status of inland habitats is similarly a reflection of the past and present stocking rates of Caribou. However, interest has focused on coastal ranges because most animals winter there, and the winter season is considered the critical forage period of the Caribou year. The fruticose lichen cover on the inland range has disappeared almost completely (1-10 g wet weight per m<sup>2</sup>) and trampling and over-grazing have presumably been the major causes for this disappearance.

This primary summer range (S1, Fig. 3) had in 1980 a Caribou density of about 4 per km<sup>2</sup> utilizable habitat, compared to about 10 per km<sup>2</sup> utilizable habitat 3

years earlier. Assuming the limits of the summer range were similar a decade ago, stocking rate in the peak years must have been in the order of 25 per km<sup>2</sup> utilizable habitat.

The high densities brought about certain changes in the vegetation, but currently the range carrying capacity does not seem to be exceeded. Caribou summering on the inland range may recover fully from the hardships of the winter, and build up energy reserves within the period May-September if no disturbing factors in the environment interfere.

However, the presence of introduced oestrid flies limits the potential of the range; through harassment the energy budget of the Caribou is affected so significantly that the fall physical condition of the animals is generally far from optimal. Therefore because of this harassment factor, the importance of a good winter range is emphasized.

The anticipated continued decline of the herd in the near future and the concomitant decrease in grazing pressure is likely to result in a regeneration of *Salix glauca* and *Betula nana* stands, making these species relatively more abundant. With low Caribou numbers recovery of the fruticose lichens is expected, but because of differences in stocking density and the precipitation regime of the region, regeneration of a lichen cover on the inland range will presumably require more time than on the coastal range.

## Dansk resumé

### Fourageringsøkologi for den vestgrønlandske vildren (*Rangifer tarandus groenlandicus*) i Sisimiut-Kangerlussuaq området

Gennem en treårig undersøgelse af Vestgrønlands vildrener er dyrenes valg af habitat og føde blevet studeret og sat i forhold til forskellige miljøfaktorer. Det årstidsbestemte valg af habitater var i nøje overensstemmelse med fødeplanternes vækststadier. I op til seks uger før kælvningen kunne rensdyrene fouragere på forskellige græsser med et højt næringsindhold. Især de drægtige simler havde afpasset deres ankomst til kælvningsområdet til fremkomsten af denne føderessource.

Græsser og halvgræsser udgjorde den største del af renerens føde på alle årstider. Rensdyrlaver forekom kun meget sparsomt både på sommer- og vinterområderne. Revling (*Empetrum nigrum*) samt blad- og skorpeformede laver blev i nogen grad anvendt som vinterfoder – et sikkert tegn på »nedslidte« fødereserver og en overhængende fare for sultedød.

Den mest intense fouragering fandt sted i kælvningsperioden, hvor fødeplanternes næringsindhold var maksimalt. Største energikrav var forbundet med fourageringen i midvinter perioden, hvor dyrene måtte grave i sneen efter føden. I juli-august forårsagede forstyrrelse fra de parasitiske fluer (renbremser) en nedgang i dyrenes fourageringsintensitet på 70-90% i ca. 40% af perioden.

I 1980 var tætheden af dyr kun ca. 1/km<sup>2</sup> udnyttbart vinterområde, men det syntes stadigvæk at forhindre bevoksningen af rensdyrlaver i at regenerere, til trods for en bestandsnedgang på 90% i det sidste tiår. Imidlertid syntes en nuværende tæthed på 4 dyr/km<sup>2</sup> udnyttbart sommerområde ikke at overskride indlandets bæreevne, men dette områdes muligheder blev dog stærkt begrænset på grund af tilstedeværelsen af de generende renbremser.

Резюме на русском языке:

Экология фуражирования дикого северного оленя Западной Гренландии  
(*Rangifer tarandus groenlandicus*)  
в районе Сисимут – Кангерлуссуак

В течение трехлетнего исследования диких северных оленей Западной Гренландии изучался выбор этими животными местообитания и пищи, зависимо от разных условий среды. Зависимый от времени года выбор мест обитания точно соответствовал стадиям роста кормовых растений. В течение до шести недель перед телием, северные олени могли фуражировать на разных травах высокой питательности. В особенности, стельные самки приспособляли время прибытия в район телиения так, что оно совпадало с появлением этих пищевых ресурсов.

Во все времена года, преобладающую часть пищи северных оленей составляли травы и травоподобные растения. Олений мох как в летних, так и в зимних районах встречался только скудно. В качестве зим-

ней пищи до некоторой степени служили медвежья ягода (*Empetrum nigrum*), а также листообразный и чешуйчатый мох – верный признак "изношенных" пищевых резервов и грозящей опасности голодной смерти.

Самое интенсивное фуражирование происходило в периоде телиения, когда содержание питательного вещества в пищевых растениях было максимальным. Наивысшие требования энергии предъявляло фуражирование в среднем периоде зимы, когда животные были принуждены выкапывать пищу из-под снега. В июле-августе животным мешали паразитные мухи (оленьи оводы), что в продолжение прибл. 40% этого периода вызывало понижение интенсивности фуражирования в 70 – 90%.

В 1980 г. густота популяции составля-

ла только около одной особи на км<sup>2</sup> пригодного зимнего пространства, но казалось, что это всё-еще препятствует восстановлению поросли оленьего моха, несмотря на 90-процентное сокращение популяции за последнее десятилетие. Однако кажется, что теперешняя густота – 4 животных на км<sup>2</sup> пригодного летнего пространства – не превышает поддерживающую способность внутренней части страны, но возможности этого района сильно ограничиваются наличием мешающих животным оленьих оводов.

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