

CHAPTER 3 . Late spring

Calving grounds

Introduction

The critical nature of the calving grounds for large migratory caribou herds have long been recognized (Lent 1966; Skoog 1968; Kelsall 1968; Thomas 1969). In fact the fidelity of each population to this relatively discrete portion of their range led to the convention by caribou managers to name the herd after the geographical location of their calving grounds (Parker 1972).

Why are herds loyal to a unique calving ground? Many theories have been proposed, ranging from the ability of the parturient and lactating females to track the newly flushing, nitrogen rich vegetation (Klein 1970), the avoidance of insects, or the avoidance of high density predator populations (Kelsall 1968).

The calving grounds of most large migratory caribou herds tend to have at least one characteristic in common; they are generally found north of treeline at approximately the 0°C June 1 isotherm. During the onset and throughout the normal calving period these areas are characterized by a mosaic of newly flushing vegetation and melting snow patches. The annual variation in the pattern of snowmelt therefore has a large role to play in the exact location of calving (Lent 1980).

The exact location of the Porcupine caribou calving grounds has been determined only in the last 30 years. The Arctic Coastal Plain of Alaska and northern Yukon received little attention until coordinated surveys were initiated by the US Dept. of Agriculture and the Canadian Wildlife Service in the early 1950's. The «Porcupine Herd» was first named in 1953 after the river of the same name that best described the centre of habitation of a number of herds that were previously thought to be separate. As such the herd is not named after the location of their calving grounds.

Within the Yukon portion of the calving grounds of this herd, little human activity has disrupted the free movement of caribou during this critical stage in their life cycle. A proposal to construct a pipeline across the Yukon coastal plain linking gas reserves in Prudhoe Bay, Alaska with potential reserves in the Mackenzie Delta of the Northwest Territories, resulted in a number of investigations designed to document the movement patterns and extensive migration corridors of the Porcupine herd. The pipeline proposal was rejected by an inquiry in 1977 (Berger 1977). This and other proposals, however, caused concern among caribou researchers and managers and prompted a workshop in Fairbanks in 1978 to review our knowledge of large migratory caribou populations and suggest areas of research that should be conducted to better prepare ourselves for future development proposals (Klein and White 1978). Among the «first priority» recommendations of the workshop was the need to determine the «characteristics of caribou calving grounds» and the need to examine the «mechanisms of selection and factors governing selection of forage and habitats by caribou». This study was an attempt to fill in the knowledge gap in these two areas of concern.

The objectives of the present study were to;

- document the biophysical characteristics and annual variation of those characteristics on the area of most concentrated calving in the Yukon
- determine the patterns of range use exhibited by calving caribou in the area as reflected by habitat selection and food habits

- determine the energetic relationships of pregnant and lactating females as evidenced in activity budgets of the cow and the nursing behaviour of the calf.

Study area

The study area (Fig. 1.2) falls within the Northern Mountains and Coastal Plain Ecoregion, described by Oswald and Senyk (1977; Fig. 3.1). Annual precipitation in the region varies from 250 and 380 mm on the Arctic Plateau and British Mountains to about 125 mm along the Arctic Coast (Oswald and Senyk, 1977). Mean annual temperatures are about -10 to -11°C with extremes moderated by the coastal influence. The study area falls on the northern flank of interior mountains and is influenced by two maritime air masses that interact in the region. Pressure systems forming over the Gulf of Alaska frequently invade the area. However, because of the compact mountain barrier in Alaska, their access to the

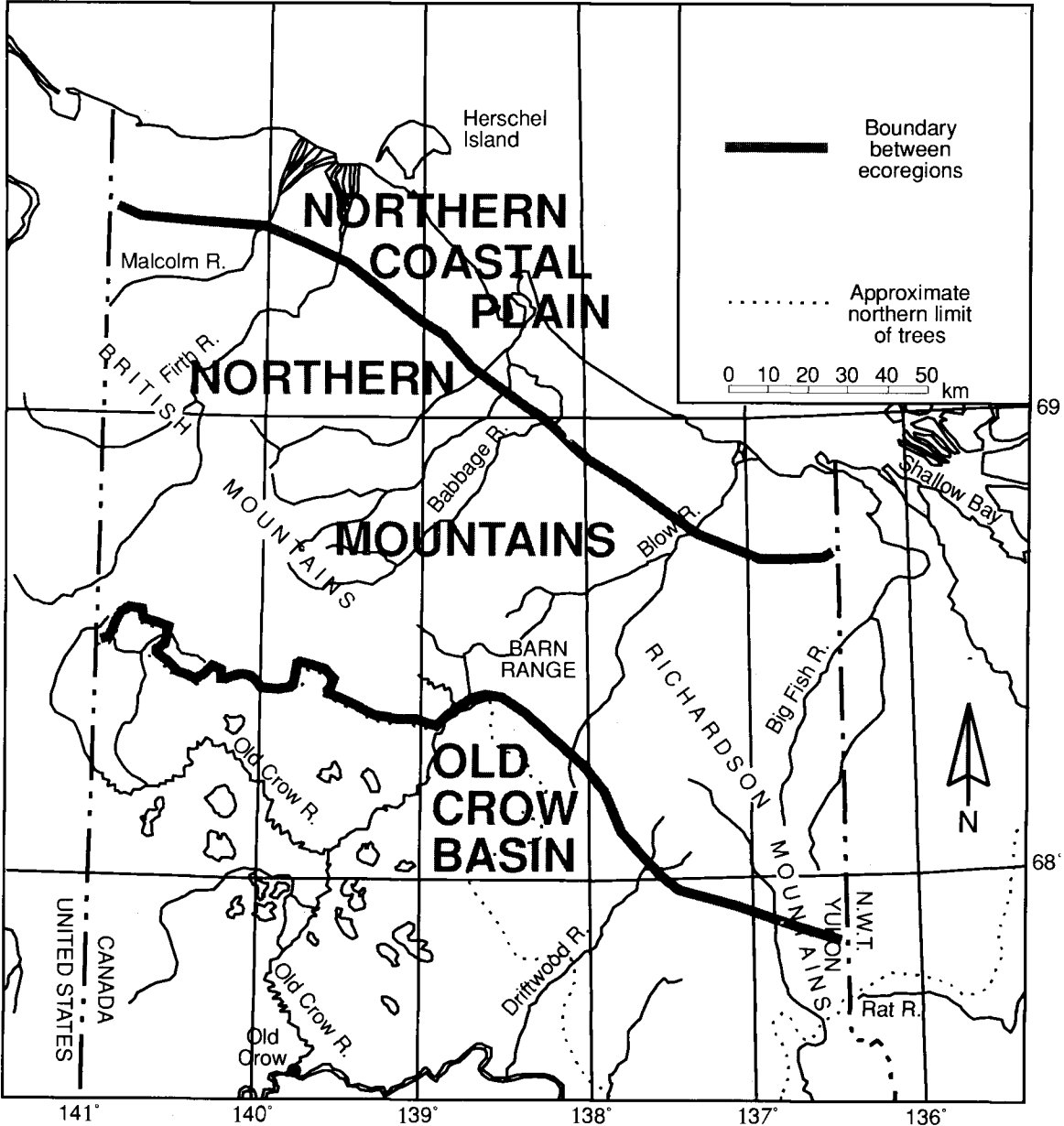


Figure 3.1. Ecoregions in the northern Yukon Territory.

northern Yukon is by sweeping along the coast. The second air mass is formed over the Beaufort Sea. This mass has a significant influence on the study area, but is barred from penetrating the interior by the mountain chain. The Beaufort Sea air mass introduces cold air to the region on its southerly course.

Within the Northern Mountains and Coastal Plain Ecoregion, Wiken *et al.* (1981) describe two ecodistricts that overlap our study area, the Komakuk Plains and Malcolm River Ecodistricts. In common with the entire Coastal Plain Ecoregion, the Komakuk Plains are characterized by their low altitude and subdued relief, and their abrupt termination along the foothills in the vicinity of our Camp 2 location. To the west the Plains continue into Alaska, while eastward there is a sharp change of geomorphology on to the King Plains Ecodistrict, which marks the extreme westward extent of the Quaternary glaciation. The Komakuk Plains are an unglaciated landform, covered by extensive fans and braided deltas, with low-lying areas covered with a blanket of patterned organic materials underlain with marine sediments. Soils are generally poorly weathered throughout the plains, primarily as a function of shallow depths to permafrost and the presence of free water in the active layer for prolonged periods. These soils tend to be acidic and nutrient poor, but rich in undecomposed organic matter (Wiken *et al.* 1981).

To the south of the Komakuk Plains lies the Malcolm River Ecodistrict, a region of highly variable relief. The generally rounded mountains of this ecodistrict offer a variety of geomorphic features. Bedrock summits, talus and solifluction slopes, fans, residual deposits, cryoplanation terraces, rock and gravel river terraces, and gravel-bed headwater streams abound. The majority of this ecodistrict is colluvium which is all but devoid of vegetation. Organic pediments form in lower slopes above the broad coarse-textured floodplains (Wiken *et al.* 1981).

Two camp locations were used during the study. The first, occupied in 1979 and 1980, was located approximately 20 km inland from the Beaufort Sea at 260 m elevation and observations were confined to 220 – 730 m elevation (generally under 350 m). The second camp, used in 1980 and 1981 was within 13 km of the coast at 140 m, with observations occurring between 120 – 470 m (generally under 250 m).

The vegetation of the study area has been described elsewhere (Russell *et al.* 1992a), together with the relative availability of the significant range types at the two camp locations (summary in Table 3.1).

Porcupine caribou calving distribution

The calving distribution of the Porcupine Caribou Herd over the last two decades was reviewed by Garner and Reynolds (1986). We have included much of their review while giving a more detailed account for the three years of our study. The calving grounds of the Porcupine herd are international, extending along the arctic foothills (up to 1,100 m elevation) and arctic coastal plain to the Beaufort Sea coast from the Babbage River in Yukon to the Canning River in Alaska (Fig. 3.2). Over the past 14 years in which similar data have been collected, substantial variation in the distribution of calving has occurred, while certain «core» areas have been used often. The location of the previous wintering area, weather and snow conditions encountered on spring migration, and the snow melt pattern encountered on the calving ground all affect the distribution of the herd at the peak of calving in any given year. In years of difficult snow conditions, parturient cows can give birth along the migration route, south and east of the normal calving grounds (Lent 1980). For example in 1972 and 1982, both years of deep spring snow and late snowmelt, significant levels of calving activity occurred in the Old Crow Flats, British Mountains and on the Coastal Plain east of the Firth River (Roseneau *et al.* 1974, Mauer *et al.* 1983, and Whitten and Cameron 1984). In 1975, when snow conditions along the migration route were light and snow melt within the calving grounds was early, nearly all of the herd calved in the extreme west of the traditional area.

The area of major concentration during the peak of calving is centred in the uplands of the Jago River, extending west to the Sadlerochit River and east to the Aichilik River (Fig. 3.2). Within Canada, the foothills region between the Firth River and the Alaska border has consistently incorporated some of the calving distribution of the herd. However the limited area between the coastal plain and foothills may limit the number of calving caribou this area can sustain.

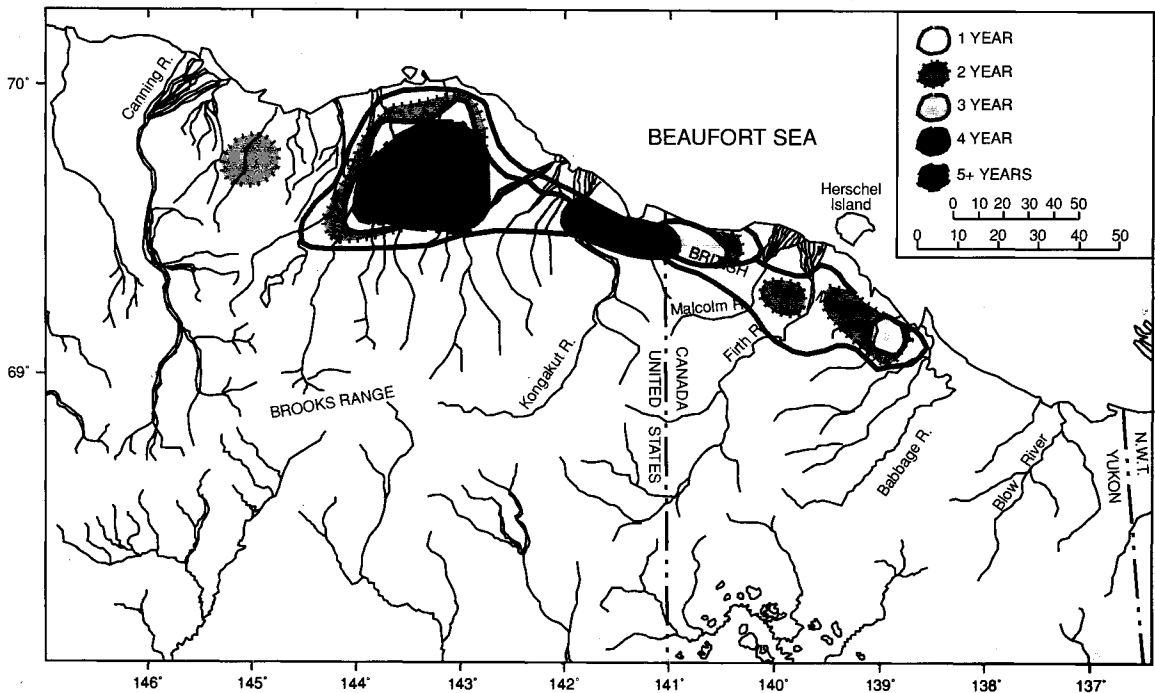


Figure 3.2. Porcupine Caribou Herd calving ground 1972-85

Movement of pregnant females to the «core» calving grounds is from the east and southeast along the foothills and mountain valleys where snow melts early. In years when snow melt is advanced, migration on to the calving grounds occurs along a more northerly, broad front across the foothills and coastal plain. Upon arrival within the core calving area, many caribou often move northward along corridors of early snow melt associated with major river courses.

The traditional calving ground of the Porcupine Caribou Herd is an area where snow melts early, along the foothills and the southern portion of the coastal plain from the Firth/Malcolm delta to the Canning River (Lent 1980). This area lies inland, is elevated sufficiently to experience frequent warming by spring-temperatures, and receives more solar radiation than the frequently fog-covered northern coastal plain.

Immediately after calving, the distribution of the nursery bands shifts northward, tracking the snow melt. The routes and patterns of movement are extremely variable. In general caribou that calve in Canada drift slowly, at first, westward toward the expansive coastal plains in the Jago region. Caribou that calve in the core Jago uplands tend to track the melting snow northward on to the coastal plain. Then, depending on the timing and intensity of insect harassment, the animals may move either to the Beaufort Sea shore (where caribou get some relief from insect harassment) or to the foothills and mountains returning to the coastal plain as harassment subsides.

In 1979, the calving distribution of the herd was very typical of the 14 year average (Russell *et al.* 1992b). Major concentrations of animals at the peak of calving were located in the Jago uplands and along the foothills from the Kongakuk River to east of the Clarence River (Fig. 3.3). Movement westward from the eastern concentration began about mid June and large aggregations formed in the region north of the Jago uplands. By the end of June the majority of nursery bands retraced their movements eastward, returning to Yukon in early July. Large aggregations were located at Demarcation Bay on July 4 and south of Komakuk Beach on July 5 (Fig. 3.3).

In 1980, calving distribution appeared to be greatly influenced by deep snow and late snow melt over much of the traditional calving grounds. On 4 June about 85% snow cover existed on all of the coastal plain with the exception of a narrow band of snow free terrain between Fish Creek and the Clarence

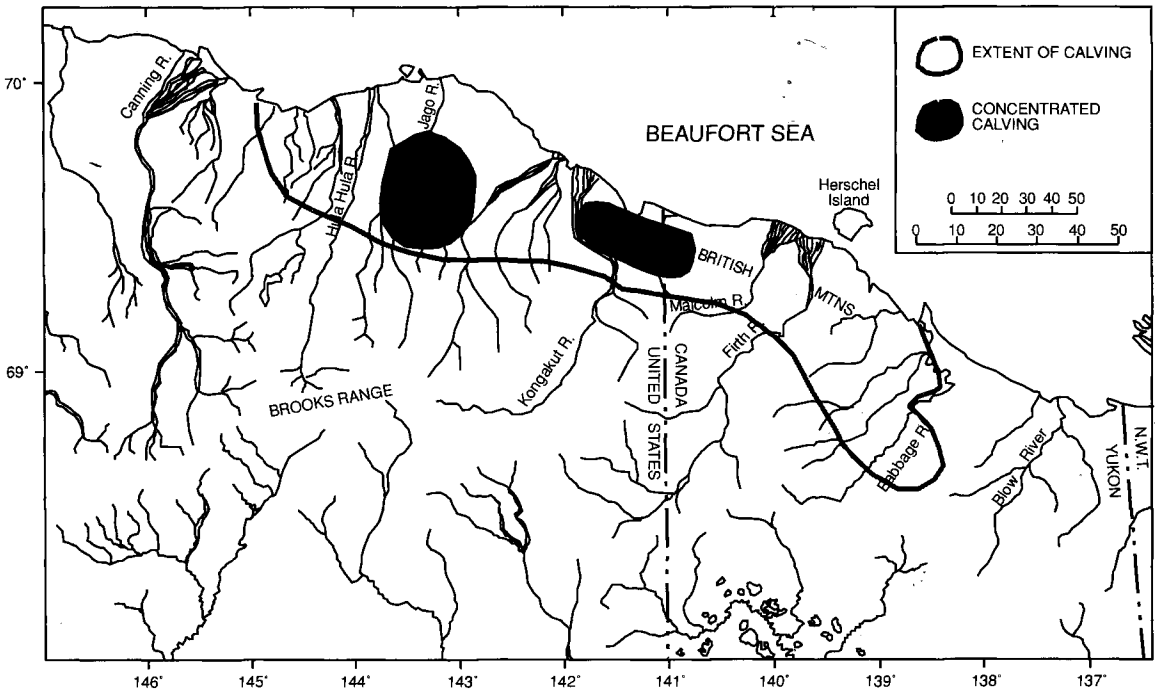


Figure 3.3. Porcupine Caribou Herd calving distribution, 1979.

River. The foothills regions along the north flank of the British Mountains and Brooks Range were relatively free of snow. The extent of calving corresponded closely to the snowfree areas, farther south and east than the usual concentration areas (Russell *et al.* 1992b). Areas of significant calving included the foothills reaches of the Trail, Crow, Spring and Firth Rivers, across the Fish Creek-Clarence River coastal

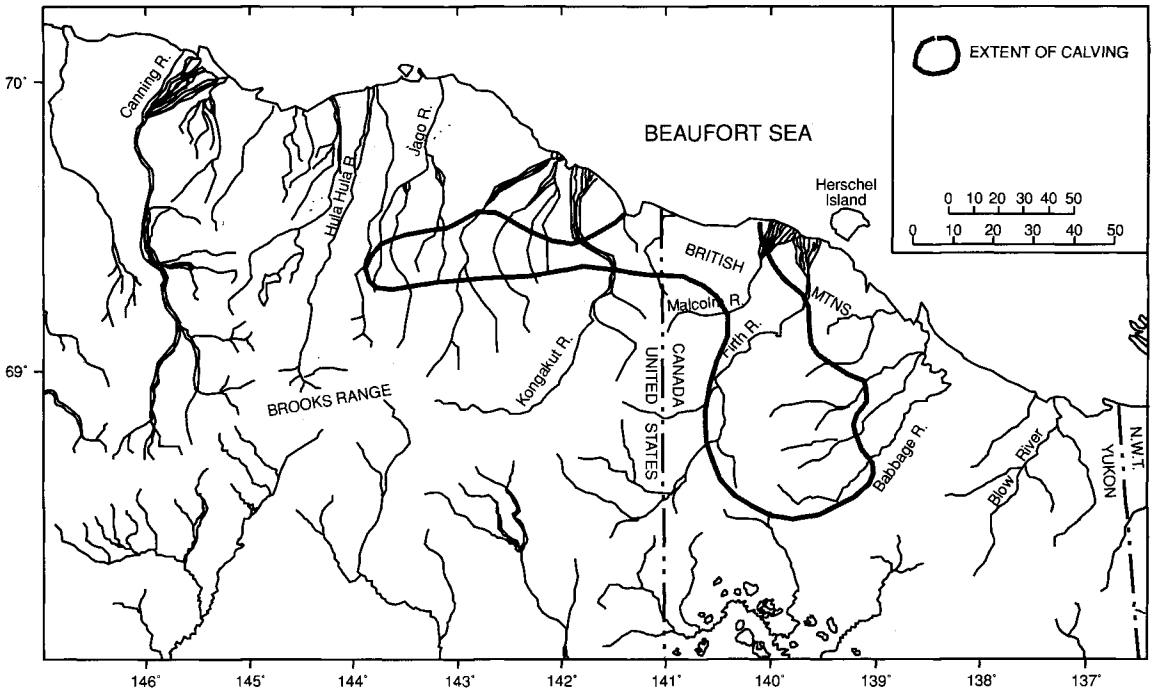


Figure 3.4. Porcupine Caribou Herd calving distribution, 1980.

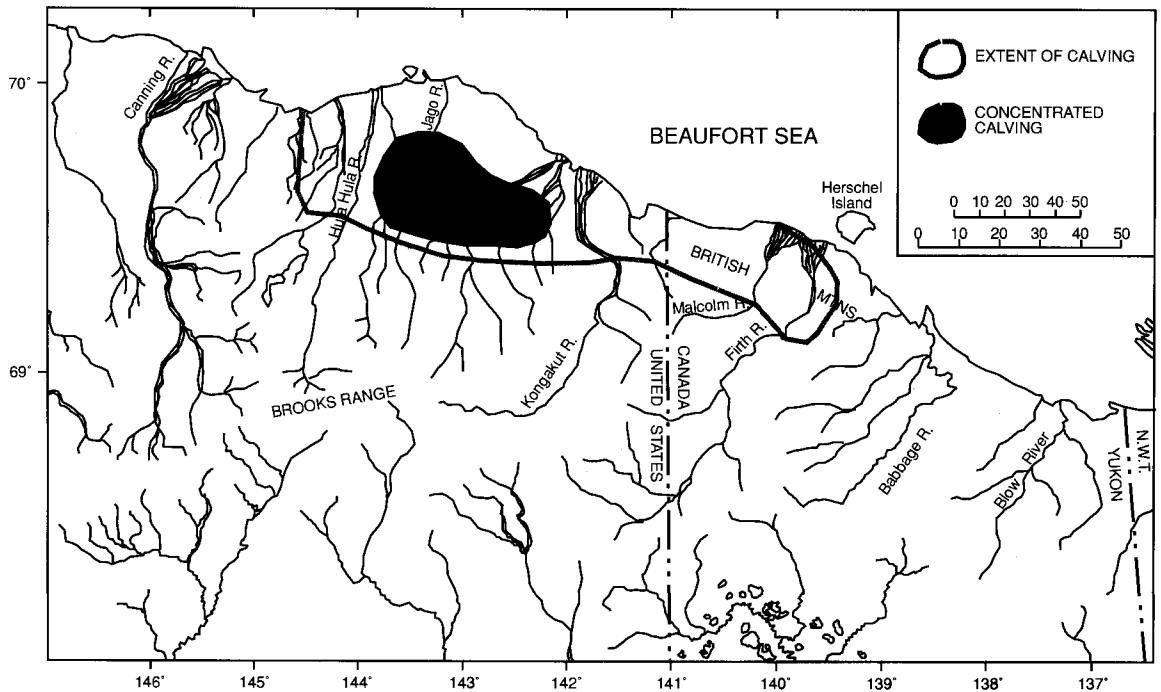


Figure 3.5. Porcupine Caribou Herd calving distribution, 1981.

plain area, into the Brooks Range foothills west to the Okpilak River (Fig. 3.4). After calving in 1980 the caribou moved swiftly westward and by late June the majority of the cows and calves were in the vicinity of the Jago River, drifting eastward along the foothills and coastal plain.

In 1981 most of the calves were born on the uplands of the Jago River in Alaska. The large concentrations there made extensive use of the foothills, primarily the dry snowfree uplands from the Okpilak River across the Jago River drainage to just east of the Egaksrak River in Alaska (Russell *et al.* 1992b). West of the Kongakut River, caribou bands appeared to consist almost exclusively of calving adult females, with few juveniles present. East of the Kongakut to the Firth River many more non-calving juveniles and a few bulls were mixed with the cows. Immediately after the peak of calving, movement of these eastern animals gradually drifted westward (Fig. 3.5). By June 29 the majority of the herd had moved from the Jago region to the northern foothills of the British Mountains, moving southeast from Alaska to the Yukon. Groups were scattered from the lower Firth River west to the lower Kongakut River (Fig. 3.5).

Characteristics of the range

Methods

Weather

Weather observations were made twice daily at approximately 0800 and 1600 hours. Temperature was recorded by maximum-minimum thermometers housed in a standard Stevenson screen and a thermograph mounted in the screen to provide a continuous measure of air temperature. Depth of fresh snow or the amount of rain from a standard rain gauge was recorded. Wind speed was measured from a totalizing anemometer mounted 1.5 m above ground surface. Weather observations were made at camp 1 in 1979 and 1980 and at camp 2 in 1981. Weather on the coast was obtained from Environment Canada records for Komakuk, approximately 26 km northeast of the study area.

Biomass

Biomass of fruticose and foliose lichens and new, green vascular matter was determined in the six major range types at 10-day intervals between 25 May and 15 July 1980. All vascular plants were clipped at moss or ground level in five 20 x 50 cm quadrats at 5 m intervals in each range type on each sampling date. Fruticose and foliose lichens were then collected from the clipped quadrats. One composite sample was made of each set of five quadrats. The vascular matter was then sorted to separate the new green biomass, floral parts and the lichens. It was not possible to separate «new green» leaves for some evergreen species (eg. *Ledum palustre*, *Vaccinium vitis - idaea*), therefore all green leaves were used. All materials were air dried in the field at approximately 40°C and later oven dried at 80°C until no further weight loss occurred, then weighed to the nearest milligram.

Tussock density

The density of cottongrass tussocks was determined in eight stands using the point-distance sampling technique (Batchelor 1971). In each stand 100 points were sampled at 2 m spacing. Distances to tussocks were not recorded if they exceeded 3 m. For each tussock the number of heads in flower, clipped by ptarmigan, or plucked by caribou were recorded. The proportion of tussocks covered with heath or heath-like species and the proportion grazed by small mammals were also estimated.

Phenology

The phenology of vascular vegetation was determined on 36 10x10 m permanent quadrats in the study area. Each range type in the study area was represented by three to 11 quadrats; larger numbers of quadrats were necessary for range types that varied dramatically in aspect. Eight quadrats were established at Clarence Lagoon for comparison. The phenology of all species present was determined at 10 - day intervals in nine classes: no development, flower buds, early flowering, full flowering, flowers senescing, seed or fruit, leaf buds, leaves unfolding, full leaf.

Nutrients

Twenty three species of plants were collected at ten day intervals between late May and early July 1980 to determine the level and change in the fibre and nutrient content of forage used by caribou. Each species was collected consistently from the same site and the portion of the plant collected mimicked that consumed by caribou. Samples were air dried in the field at approximately 40°C and later oven dried at 65°C until no further weight loss occurred (generally over 48 hours). A 7 g ground sample of each species collected was sent for analysis to the Plant and Soil Laboratory, University of Alaska, Palmer, Alaska. Samples were analysed for total nitrogen and phosphorus, acid detergent fibre, neutral detergent fibre, lignin, cellulose and residual and total ash.

Results and discussion

Weather

Mean daily air temperature increased gradually from the pre-calving period to the movement period, although there was significant between year variations. In all years the most dramatic increase in temperature occurred throughout the calving period (1-10 June) with mean values increasing approximately 1°C per day. Temperatures then oscillated lower and higher until the end of June. Only in 1981 did temperatures fail to recover to maximum calving period temperatures by the end of June. A significant warming period was observed in the pre-calving period in 1980 (Fig. 3.6). In general, 1980 was warmer than average throughout. In 1981 the calving period was cooler and the post-calving period warmer than 1979. The foothills were consistently warmer than the coast (Fig. 3.7), by 3 - 5°C during calving and post-calving.

In 1980 there was a significant increase in cumulative *degree days* in the foothills compared to the other years; no difference was apparent on the coast (Fig. 3.7).

In 1979 relatively high amounts of precipitation occurred from 20–25 May, from the 10–13 June and again from 20–25 June resulting in significantly higher levels of cumulative precipitation than in the other years, when the only period of high precipitation occurred in the calving period (Fig. 3.8).

Wind speeds varied considerably throughout the study, averaging approximately 8 km/h, with no general patterns emerging. The only noteworthy observations were the two peaks in wind speed recorded in the pre-calving (1980) and post-calving (1981) periods.

In summary, late spring in 1979 was wet and cool except during the calving period. In 1980, except for the calving period, temperatures were warm. The post-calving period in 1980 was very windy. The temperatures in 1981 were similar to 1979 except for a cooler calving and warmer and windier post-calving periods.

Phenology

Definite trends were found in the timing and progression of phenological changes in plants among range types, between the foothills and the coast and among years of the study. *Dryas* and *Vaccinium uliginosum* are indicative of the general trend. Flowering and seeding on the alpine barren were generally earlier than on alluvial and heath range and were latest on meadows.

In 1979 and 1980 *Eriophorum vaginatum* and most other species produced seeds at least 10 days earlier in the foothills than on the coast. In 1981 the difference in phenology between the coast and foothills was less, presumably due to the smaller disparity in temperatures between these two regions that year.

In 1980 phenology was most advanced in all communities and the transition from flower to seed was short. In 1979 flowering was early but the flowering period was elongated, possibly as a function of the cool, wet weather and almost constant cloud cover. In 1981, the flowering period was considerably later than in 1979 (Fig. 3.9).

Whitten and Cameron (1980) noted a similar trend in their latitudinal transect within the range of the Central Arctic Herd. They reported a 2–3 week advanced phenology in the southern foothills compared to coastal regions, with a strong south-north gradient along a 50 km transect.

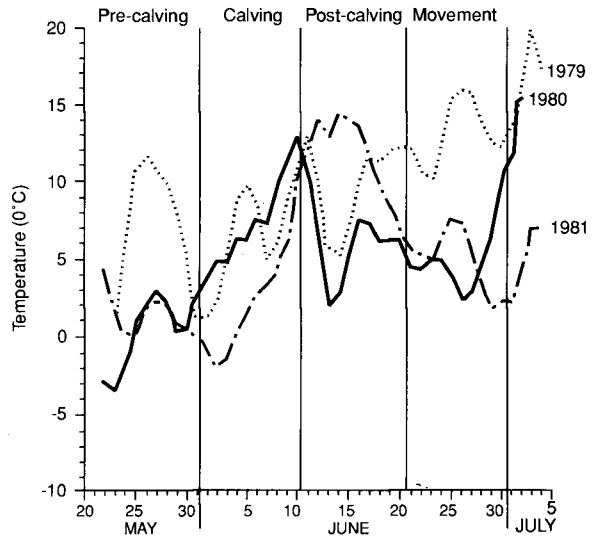


Figure 3.6. Mean daily air temperature recorded on the calving grounds of the Porcupine Caribou Herd, 1979–81.

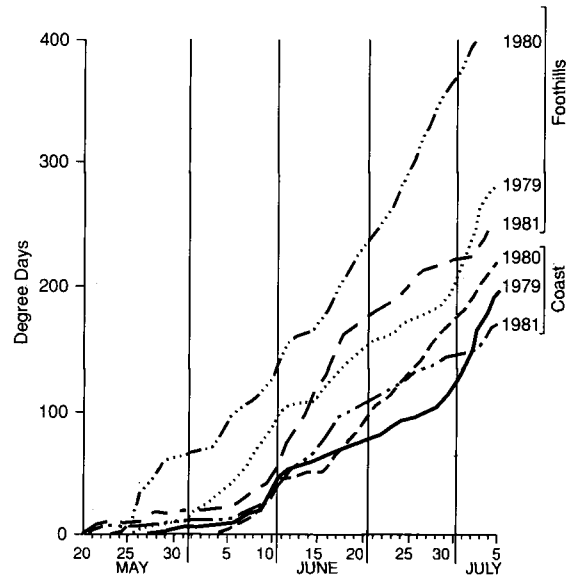


Figure 3.7. Cumulative degree days recorded on the Porcupine caribou calving grounds, 1979–81.

Biomass

The relative physiognomic composition of the major range types have been reported earlier (Fig. 3.10). Evergreen shrubs contributed most to total green biomass in the study area throughout the study period (Table 3.1). Deciduous shrubs contributed the most to new annual growth, followed by graminoids. Graminoids peaked in new annual growth by 25 June and forbs by 5 July. Deciduous shrubs had not yet peaked by the final collection on 12 July.

If we focus on the five major plant groups and the major range types within the study area (>5% of the study area, Table 3.2), each range type contributes a unique complex of plant groups. Mean lichen biomass was greatest in the alpine barren type (24 g/m²) with the remaining range types averaging about half (13 g/m², Table 3.3a – 3.3f). Graminoids were highest in the tussock tundra type throughout the sampling period, although biomass was low from late May to early June. Biomass of forbs appeared to peak in early July (Table 3.3). Most forbs were in the two heath communities and the alpine barren. The dwarf shrub heath type contained the highest biomass of deciduous shrubs in early June, but by mid June deciduous shrubs were found equally in all but the alpine barren range. After this period the tussock tundra community provided the highest biomass of shrubs.

Shrub biomass within wet sedge range types compared favourably to that measured in the Alaskan portion of the calving ground (Robus 1981) and both of these areas appear to have considerably higher *Salix* biomass than the calving grounds of the Western Arctic Herd (Kuropat 1984).

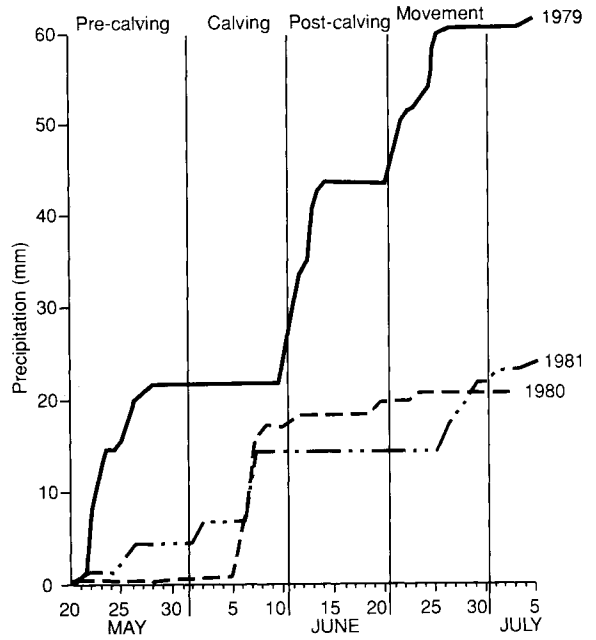


Figure 3.8. Cumulative precipitation recorded on the Porcupine caribou calving grounds, 1979–81.

Table 3.1. New green biomass (g/m²) on the Yukon calving grounds of the Porcupine Caribou Herd, 1980.

Plant group	Collection date					
	23 May	7 June	14 June	25 June	5 July	12 July
Lichens	9.00 ¹	21.17	9.73	14.39	13.30	17.84
Horsetails	–	0.09	0.03	1.03	0.97	0.88
Graminoids	3.40	7.35	19.23	30.02	32.18	34.47
Deciduous shrubs	–	0.78	4.13	20.15	23.92	46.55
Evergreen shrubs	41.78	46.21	50.83	64.41	69.56	69.56 ²
Forbs	0.23	1.30	2.45	7.88	13.79	10.46

1: weighted value reflected those communities snowfree on this date

2: adjusted value to reflect previous collection period (note low value recorded 12 July for tussock meadow community in Table 3.3c)

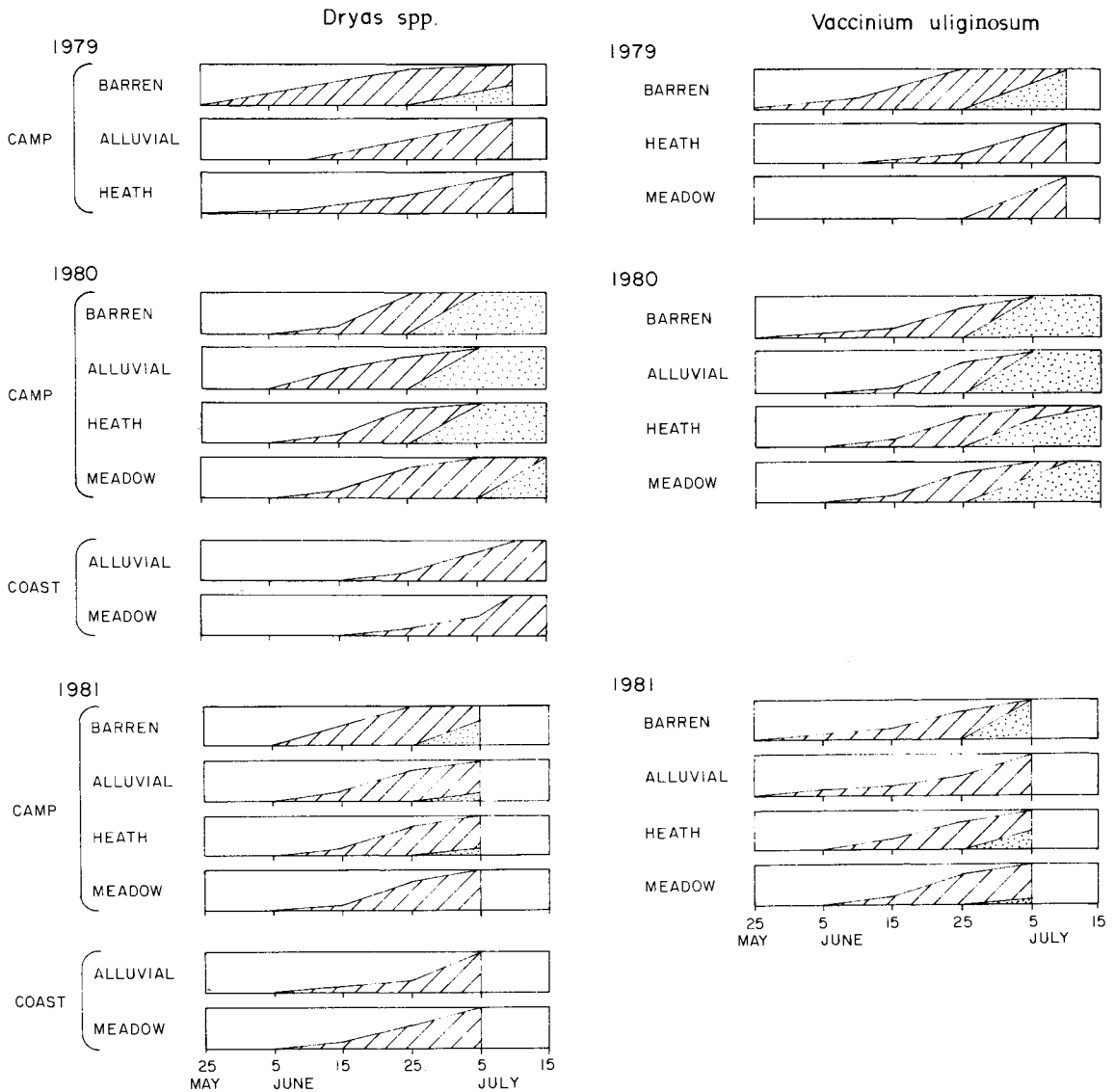


Figure 3.9. Phenological changes in key species over the three years of the study. Hatched area is proportion of sample flowering; stippled area is proportion in seed.

Tussock density

Eight stands were sampled to determine characteristics of tussocks in the study area; 4 in 1980, chosen to represent the wide range of tussock meadow communities, and 4 in 1981, chosen in large extensive meadows close to and on the coastal plain region. Stands sampled in 1980 tended to contain taller tussocks, with a lower heath component (except Stand 1) and fewer flower heads per tussock (except Stand 3, Table 3.4).

Within each stand, variables measured proved, at best, weakly correlated with the number of flowers produced per tussock (Table 3.5). Diameter and percent heath were the best predictors. Percent of the tussock grazed by microtines was significantly correlated to number of flowers in stand 6. Using multiple regression, the best model only accounted for 27% of the variability of total flowers (Stand 6, Table 3.6).

None of the stands chosen exhibited a strongly clumped distribution of tussocks; three (stands 1, 3, 4) tended to be uniformly distributed (based on an index of non-randomness of greater than 1.0, Table

Table 3.2. Percent coverage of range types on the calving grounds of the Porcupine Caribou Herd as determined from aerial photographs. Total area mapped (ha) in parentheses.

	Camp 1 (2563)	Camp 2 (3964)	Total (6527)
Alluvial gravel	2.8	4.1	3.6
Alluvial willow	0.8	2.6	1.9
Alluvial heath	3.7	15.4	10.8
Wet sedge meadow	1.4	8.0	5.4
Tussock meadow	32.5	53.3	45.2
Sedge heath	4.2	3.6	3.8
Dwarf shrub heath	13.4	4.6	8.1
Alpine barren	41.0	8.4	21.2

3.7, Pielou, 1977) while the rest tended to be slightly clumped (index less than 0.8). Bachelor's (1971) method of estimating density is not designed for stands with a uniform or close to uniform distribution of attributes. All of our estimates of tussock density, therefore, were based on all points sampled and varied between 1.62 m² (stand 1) to 5.89 m² (stand 8, Table 3.7). All stands sampled in 1981 contained a higher density of tussocks than those sampled in 1980.

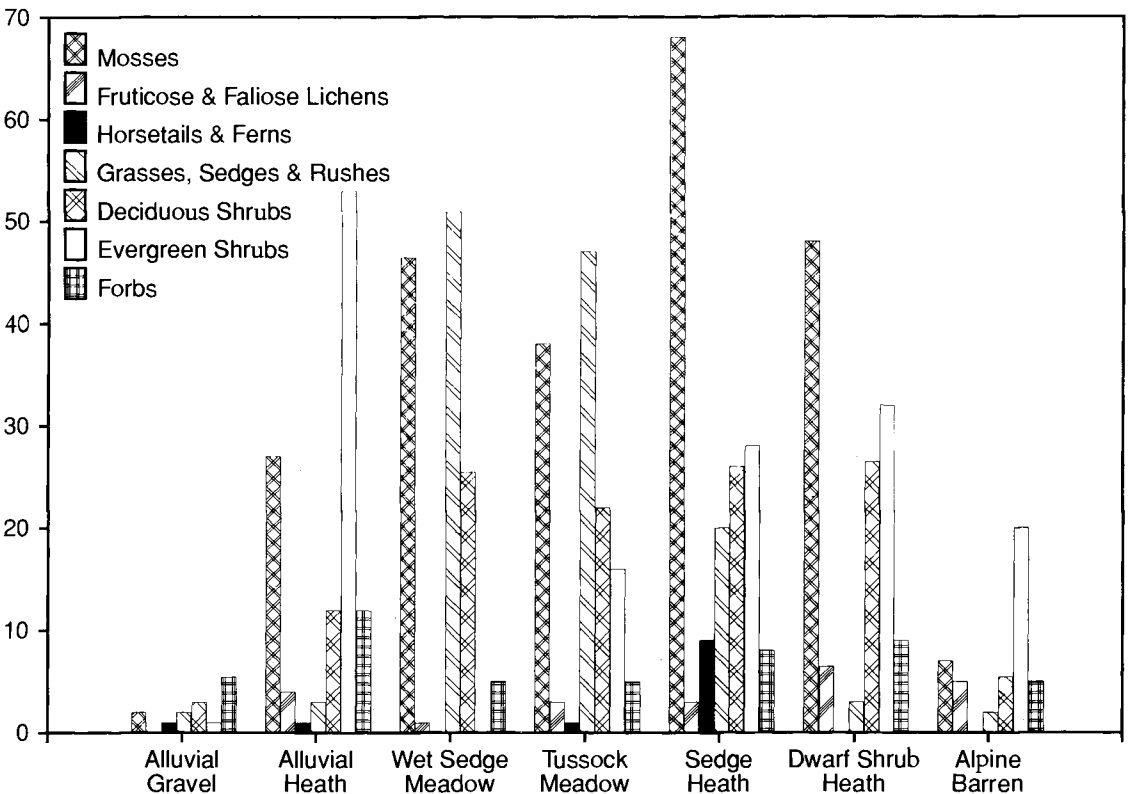


Figure 3.10. Physiographic composition of the seven range types encountered on the study area. Range type eight, *alluvial willow* was not sampled.

Table 3.3. New green biomass (g/m²) in different range types on the calving grounds of the Porcupine Caribou Herd in northern Yukon, 1980.

Plant group	Collection date					
Alluvial heath						
	6 June	16 June	24 June	3 July	12 July	
Lichens	18.20	7.51	15.78	18.23	6.25	
Horsetails	0.15	-	-	0.22	-	
Graminoids	0.83	0.21	5.38	3.12	3.12	
Deciduous shrubs	-	2.11	26.32	13.31	39.00	
Evergreen shrubs	8.05	9.66	43.59	36.08	39.60	
Forbs	1.57	0.39	6.59	25.12	14.87	
Wet sedge meadow						
	6 June	16 June	24 June	3 July	12 July	
Lichens	9.26	-	3.15	3.71	17.04	
Horsetails	0.29	-	-	-	-	
Graminoids	21.87	57.23	70.88	65.48	91.48	
Deciduous shrubs	-	8.88	19.23	32.30	66.40	
Evergreen shrubs	0.37	-	0.54	5.88	-	
Forbs	0.18	0.23	5.47	9.47	1.35	
Tussock meadow						
	23 May	7 June	14 June	25 June	5 July	12 July
Lichens	7.31	22.59	8.36	10.51	8.19	18.87
Horsetails	-	-	-	-	-	-
Graminoids	7.12	11.45	31.24	49.83	54.22	56.05
Deciduous shrubs	-	-	6.03	30.57	39.87	76.77
Evergreen shrubs	87.41	83.30	82.93	86.10	93.49	22.68
Forbs	0.48	-	0.29	2.83	7.55	8.76
Sedge heath						
	9 June	14 June	27 June	6 July	13 July	
Lichens	3.73	5.56	-	4.28	0.06	
Horsetails	-	0.78	25.05	20.64	20.55	
Graminoids	7.98	10.86	18.92	18.08	34.71	
Deciduous shrubs	0.22	3.94	4.56	12.55	9.01	
Evergreen shrubs	10.48	44.05	11.47	39.41	28.99	
Forbs	3.22	6.28	10.31	12.50	8.80	

(Table 3.3. cont.d.)

Dwarf shrub heath

	9 June	18 June	26 June	6 July	13 July
Lichens	25.94	11.03	12.40	6.13	16.80
Horsetails	0.68	-	-	1.18	0.46
Graminoids	0.72	2.28	2.94	9.99	4.15
Deciduous shrubs	9.08	0.98	12.76	11.32	14.17
Evergreen shrubs	23.45	22.07	49.59	67.22	75.56
Forbs	4.27	4.14	21.32	22.43	22.24

Alpine barren

	8 June	18 June	27 June	6 July	14 July
Lichens	24.15	16.58	28.26	28.63	25.49
Horsetails	-	-	-	-	0.01
Graminoids	0.67	1.64	2.31	2.62	1.55
Deciduous shrubs	-	1.13	0.77	0.14	-
Evergreen shrubs	13.53	28.58	60.61	58.47	60.55
Forbs	2.76	7.35	14.41	19.44	10.03

Our tussock densities were consistent with those measured in other studies in the region. Shaver *et al.* (1986) determined that microsite or broad regional differences in *Eriophorum* flower production were less significant than annual differences. 1981 and 1983 were above average everywhere while 1980 and 1982 were below average everywhere. Kuropat (1984) found that on the calving grounds of the Western Arctic Herd, *Eriophorum* inflorescent density averaged 23.2 in 1977 and 22.7 flowers per m² in 1978. This compares with 13.6 in 1980 and 48.9 flowers per m² in 1981 in this study.

Table 3.4. Summary of tussock variables for the eight stands sampled on the calving grounds of the Porcupine Caribou Herd.

Variable	Stand								All ± SE
	1	2	3	4	5	6	7	8	
Sample size ..	261	300	297	297	300	300	300	300	2355
Diameter (cm)	30.8	26.8	28.4	28.2	26.8	23.4	22.5	25.3	26.4 ± 0.17
Height (cm) ..	18.7	20.4	18.9	20.4	15.0	11.3	13.8	16.5	16.8 ± 0.14
% heath	37.1	18.8	13.9	16.4	39.2	29.2	37.0	37.4	28.5 ± 0.54
% grazed	0.1	0.5	0.2	0.0	3.1	9.0	9.1	9.4	4.0 ± 0.25
Flowers	1.9	4.0	10.0	5.2	12.7	8.2	6.5	11.2	7.6 ± 0.19

Table 3.5. Correlation of variables measured during estimation of tussock density to the total number of flowers per tussock.

Variable	Stand							
	1	2	3	4	5	6	7	8
Diameter		*	***	***	***	***		**
Height	***	**					***	***
% heath ¹	***	**	**	**	***	***	***	***
% grazed ¹						**		

1: negative correlation

* p < 0.05 ** p < 0.01 *** p < 0.001

Table 3.6. Results of stepwise multiple regression and r² at inclusion of independent variable in the prediction of number of flowers.

Stand	Variable		
	1	2	3
1	Heath (0.05)	Height (0.09)	
2	Height (0.08)	Heath (0.11)	Diameter (0.13)
3	Diameter (0.13)	Heath (0.15)	
4	Diameter (0.06)	Height (0.13)	
5	Heath (0.17)	Diameter (0.23)	
6	Heath (0.11)	Diameter (0.25)	Grazed (0.27)
7	Heath (0.11)	Height (0.19)	
8	Diameter (0.09)	Heath (0.17)	Height (0.20)

Table 3.7. Estimate of tussock density, probable limit of error and Pielou's Index of Nonrandomness for the eight stands sampled.

Stand	Number of points	Density	Probable limit of error	Pielou's index
1	86	1.62	0.543	3.22
2	99	3.13	0.134	0.63
3	98	2.56	0.316	1.90
4	97	2.60	0.254	1.01
5	100	4.74	0.150	0.77
6	100	5.10	0.158	0.82
7	100	5.29	0.154	0.79
8	100	5.89	0.138	0.72

Nutrients

Appendix A describes the characteristics of plants collected for nutrient analysis in 1980 while Appendix B details the fibre, ash and nutrient content of the samples. General trends are evident if we use *Cetraria cucullata*, *Eriophorum vaginatum*, *Salix pulchra*, *Vaccinium vitis-idaea*, and *Pedicularis kanei* as repre-

sentative of the various plant groups. The proportions of lignin, cellulose and the ADF fraction increased later in the season while the proportions of nitrogen and phosphorus declined (Table 3.8). Total ash and NDF remained relatively constant (Table 3.8). The pattern and quantity of lignin reported for lichens is somewhat surprising since lichens do not contain lignin and this value must reflect an index of plant hardening in the analysis process. Lichens were characterized by low values for ADF, nitrogen, cellulose and phosphorus and high values for total ash. Graminoids contained high NDF, ADF and cellulose fractions, while deciduous shrubs exhibited high values for nitrogen and phosphorus early in the season and high lignin values later. *Vaccinium*, representing evergreen shrubs, showed the least seasonal variation in NDF, ADF, lignin and cellulose, with relatively low values for nitrogen throughout the sampling period. Forbs contained relatively high nitrogen and phosphorus and low NDF values throughout the season.

The magnitude of and trends in nutrient concentrations compare well with similar studies in areas to the west in northern Alaska (Robus 1981; Whitten and Cameron 1980; and Kuropat 1984; White *et al.* 1975). From our data it would seem that evergreen shrubs could prove to be a valuable constituent

Table 3.8. Fiber, ash and nutrient content (% dry weight) of key species collected in 1980.

Plant group *	Date	Fiber				Ash		Nutrients	
		NDF	ADF	Lignin	Cellulose	Residual	Total	Nitrogen	Phosphorus
Lichens	Pre-calving								
	Calving	31.8	5.2	4.0	1.2	0	11.7	0.4	0.1
	Post-calving	28.5	4.5	2.0	2.0	0.4	14.0	0.4	0
	Movement	28.9	5.6	3.0	2.0	0.9	13.1	0.4	0
	Early summer ..	30.9	6.4	5.0	1.0	0.4	12.8	0.4	0
Graminoids	Pre-calving	56.6	19.2	1.6	17.1	0.4	4.1	3.1	0.5
	Calving	58.2	19.6	1.7	17.1	0.8	4.2	2.5	0.4
	Post-calving	64.3	23.6	1.3	22.2	0.0	3.4	2.1	0.3
	Movement	64.1	25.4	2.1	23.0	0.4	3.3	2.2	0.3
	Early summer ..	63.3	27.6	3.5	23.8	0.3	3.4	1.9	0.3
Deciduous shrubs	Pre-calving								
	Calving								
	Post-calving	12.9	12.6	4.5	6.4	1.7	5.0	4.8	0.7
	Movement	16.6	14.8	6.3	7.3	1.2	4.2	3.9	0.4
	Early summer ..	19.4	15.0	5.7	9.3	0.0	3.6	2.5	0.2
Evergreen shrubs	Pre-calving	28.6	20.8	4.4	15.8	0.6	2.7	0.9	0.1
	Calving	30.0	20.4	6.4	13.7	0.3	2.4	0.9	0.1
	Post-calving	30.7	18.7	5.4	13.3	0.1	2.6	0.9	0.1
	Movement	31.3	18.6	5.5	13.4	0.0	2.5	0.9	0.1
	Early summer ..	33.7	21.1	6.3	14.8	0.0	2.6	0.9	0.1
Forbs	Pre-calving								
	Calving	17.5	14.1	2.5	11.3	0.4	7.1	3.5	0.5
	Post-calving	19.8	13.7	6.7	7.0	0.0	6.7	3.2	0.4
	Movement	20.2	15.7	3.8	11.5	0.4	6.6	2.7	0.4
	Early summer ..	37.5	23.0	3.0	19.7	0.2	5.1	3.6	0.3

* Lichens : *Cetraria cucullata*; Graminoids : *Eriophorum vaginatum* flowers; Deciduous shrubs : *Salix lanata* leaves; Evergreen shrubs : *Vaccinium vitis-idaea* leaves; Forbs : *Pedicularis kanei* flowers

of the diet in late spring, being high in biomass and cell solubles (100 – NDF). However, Kuropat (1984), points out that the leaves of evergreen shrubs can contain high levels of secondary compounds. These compounds can bind with endogenous and microbial protein and may cause an inhibition of rumen function, toxicity and/or lowered digestibilities (Trudell and White 1981). Kuropat and Bryant (1980) provide us with information on the trends and magnitudes of secondary compounds in the major plant groups, an aspect of forage chemistry that we did not document in our study. They found that new inflorescences and leaves (particularly *Salix*) were poorly defended by toxic compounds. They argue that the subsequent increase in concentration of secondary compounds and decline in nitrogen and phosphorus, require caribou to seek early phenological stages in plants.

Summary

The pre-calving to movement periods are by far the most dynamic time of the year in terms of nutrient dynamics within the calving grounds of the Porcupine Caribou Herd. Parturient females arrive on the calving grounds when a significant portion of the area is still covered with snow, when available nutrients are scarce and when they are at an energetic low in their annual energy and nutrient reserves. As well, once they have calved, the energetic demands of the animal are very high due to lactation.

Thus, calving occurs just prior to the period of maximum growth and nutrient dynamics in the vegetation. As we have documented, most changes in the vegetation occur between 4 June and 24 June, during the two week period after the peak of calving. The region chosen for the majority of calving in the Yukon, as represented by our study area, offers a diverse complex of range types from the alpine barren communities to wet sedge meadows, damping the between year extremes in timing of snowmelt and phenological development.

Within each range type habitat quality was a function of species composition, forage biomass, phenological development, and nutrient quality. In late May, snowmelt pattern and topography determined which range types offered potential forage. Digestible solubles were generally restricted to lichens, best provided by the alpine barren communities. Nitrogen sources were scarce until early June. Between 4 and 14 June graminoids were the best available source of both cell solubles and nitrogen. Thus the tussock tundra communities became the best range type to use. Between 14 and 24 June the emergence of deciduous shrubs and the declining importance of graminoids reduced the importance of tussock tundra. Although lower in biomass, the highly digestible, nitrogen-rich forb species gained in importance in the latter part of June, thus elevating the importance of heath type communities.

During the three years of this study, 1980 stood out as being advanced phenologically due to higher than average temperatures throughout the study period. Consistent with previous work in Alaska we observed an interesting carry-over effect of that good year; the apparent abundance of *Eriophorum* flowers in the next year. Shaver *et al.* (1986), also noted a good flowering year in 1981 and speculated that since flower setting occurred early in *Eriophorum*, the weather in the previous year may play an important role in determining flowering density in any given year. This carry-over effect can have important implications for the well-being of parturient females. In 1981, when *Eriophorum* flowering was high in spite of cool temperatures in May and early June, the density of flowers probably reflected the favourable conditions in 1980.

Habitat selection

Methods

We divided the area of each camp location into eight range types (Russell *et al.* 1992a), and determined the proportion of each type by plotting on aerial photographs (Table 3.1). During 15 minute scan observations, the habitat type occupied by the animals observed was recorded. Preference for a particular type

Table 3.9. Percent of animals observed in the eight range types on the Yukon calving grounds of the Porcupine Caribou Herd, 1979–81.

Period	Tussock meadow	Wet sedge meadow	Sedge heath	Dwarf shrub	Alpine barren	Alluvial heath	Alluvial gravel	Alluvial willow	Total caribou observed
<i>1979</i>									
Pre-calving	19.7	4.1	4.8	8.0	1.7	60.9	0.9	–	4823
Calving	17.6	0.9	23.2	4.6	2.7	46.6	4.4	–	2949
Post-calving	10.5	18.6	54.5	9.6	0.3	5.7	0.7	0.2	8095
Movement	12.0	0.1	23.4	38.8	12.4	13.2	–	–	4240
<i>1980</i>									
Pre-calving	87.9	1.6	2.3	0.4	1.2	6.5	0.3	–	39008
Calving	51.8	0.8	10.2	1.4	2.5	30.7	2.3	0.2	13134
Post-calving	38.4	29.7	20.6	0.5	0.1	9.1	1.1	0.5	60422
Movement	–	58.9	–	–	–	37.6	3.6	–	6515
<i>1981</i>									
Pre-calving	72.4	3.1	–	2.3	–	21.7	0.5	0.1	23973
Calving	80.1	8.8	–	2.4	–	8.2	0.4	0.1	4668
Post-calving	13.2	39.4	–	–	–	32.9	13.7	0.9	2774
Movement	31.6	56.9	–	–	–	2.2	1.2	8.2	1560

was calculated as the ratio (use-availability)/(use+availability). In 1980, when observations were made at both camp locations the contribution of each camp to the index was proportional to the number of animals observed. The biophysical characteristics in the location of the observations also were recorded (Appendix C).

Results and discussion

Over 50 percent of the animals used the tussock meadow community in each of the three years of the study (Table 3.9). Wet sedge meadows, alluvial heath and sedge heath were used by over 10 % of the animals (Table 3.9). In all years tussock meadows received the most use in the pre-calving and calving periods, declining later in June. Wet sedge meadows were used primarily in the post-calving and movement periods. Use of alluvial heaths showed no consistency (Table 3.9). Alluvial willows and alpine barren types were seldom used.

Selection for or against any community type was determined for all periods of the study (Table 3.10). In 1979, animals selected alluvial heath and sedge heath communities throughout the study period. They showed a strong preference for wet sedge meadows in the post-calving period and for dwarf shrub heaths in the movement period. In 1980, tussock meadows and sedge heaths were the only communities favoured from the pre-calving to the post-calving periods. Wet sedge meadows were strongly selected in the post-calving and movement periods in both 1980 and 1981. In 1981, tussock meadows continued to be preferred in the pre-calving and calving periods. Throughout the study alluvial willows and alpine barrens were strongly avoided by caribou.

Phenologically, 1980 was the most advanced year and 1981 the most retarded. Density of *Eriophorum* flowers was greatest in 1981. These observations may help explain the early preference for tussock tundra communities in 1980 and 1981. The tussock tundra communities, although least advanced phenologi-

Table 3.10. Habitat preference of animals observed in the eight range types on the calving grounds of the Porcupine Caribou Herd, 1979–81.

Period	Tussock meadow	Wet sedge meadow	Sedge heath	Dwarf shrub	Alpine barren	Alluvial heath	Alluvial gravel	Alluvial willow
<i>1979</i>								
Pre-calving	-0.25	0.48	0.06	-0.25	-0.92	0.89	-0.52	-1.00
Calving	-0.30	-0.23	0.69	-0.49	-0.88	0.85	0.22	-1.00
Post-calving	-0.51	0.85	0.86	-0.17	-0.99	0.21	-0.60	-0.60
Movement	-0.46	-0.87	0.69	0.49	-0.54	0.56	-1.00	-1.00
<i>1980¹</i>								
Pre-calving	0.32	-0.55	0.25	-0.90	-0.89	-0.26	-0.84	-1.00
Calving	0.06	-0.75	0.45	-0.70	-0.78	0.47	-0.22	-0.81
Post-calving	0.08	0.68	0.69	-0.88	-0.99	-0.10	-0.53	-0.59
Movement	-1.00	0.83	-1.00	-1.00	-1.00	0.55	-0.00	-1.00
<i>1981</i>								
Pre-calving	0.15	-0.44	-1.00	-0.33	-1.00	0.17	-0.78	-0.90
Calving	0.20	-0.05	-1.00	-0.31	-1.00	-0.30	-0.82	-0.90
Post-calving	-0.60	0.66	-1.00	-1.00	-1.00	0.36	0.54	-0.36
Movement	-0.26	0.75	-1.00	-1.00	-1.00	-0.75	-0.55	0.62

Note: preference was determined as (use-availability)/(use+availability)

1: in 1980 availability was calculated as the average of the two camps, weighted by the number of animals observed at each camp.

cally compared to other range types in any given year, offer the highest concentration of cell solubles and nitrogen in the pre-calving and calving period. In 1980 this community was well advanced and used early by the caribou. In 1981, the unusually abundant *Eriophorum* inflorescences, along the edge of the retreating snow, may have attracted the large numbers of caribou observed.

In 1979, alluvial heaths were much more preferred in the pre-calving and calving period, perhaps due to the unavailability of the tussock meadow type (due to snow cover) and the abundance of lichens and mosses in this heath type.

Although the alpine barren community contains relatively high biomasses of lichens, its low relative use in the early part of the season may be due to the lack of other vegetative cover in this type. Caribou must be able to maintain a full rumen and if little else is available will fill the rumen with poorly digestible forage types such as moss. The alpine barren community (*Dryas/Vaccinium uliginosum*) contains only 4% cover of moss and only 31% cover of total vegetative matter.

Another reason for not utilizing lichens in the alpine barrens may be the low moisture content. Trudell and White (1981) reported an avoidance of sites with dry lichens, even though lichens formed a major constituent in the diet of their animals. They attribute this avoidance to severe lip abrasion from ingesting dry lichens.

In the post-calving and movement periods, the preference for wet sedge meadows may be associated with the abundance of freshly flushing willow and the emergence of young basal shoots of *Eriophorum angustifolium* and *Carex aquatalis*, a species which reaches its greatest abundance in wet sedge communities.

The early season use of tussock meadow communities has been documented in most range studies of caribou in spring and early summer (Skoog 1956; Lent 1966; Kelsall 1968; White *et al.* 1975; Kuropat 1984). The traditional calving grounds of the Western Arctic Herd contain a complex of vegetation types similar to those we have described, though our study area contained more alpine barren and less tussock meadow (Kuropat 1984). Kuropat (1984) reported that, following anthesis of *Eriophorum*, caribou moved from the lowland tussock communities to drier upland meadows to take advantage of new forb growth, particularly *Lupinus*. When *Salix* leaves began to unfold, they shifted to the lowland wet meadows, high in *Salix* biomass. We also noted a shift to wet meadows following the calving period in all years except movement period 1979.

The avoidance of the alluvial willow community may be a result of predator avoidance. Other authors have noted the reluctance of caribou to enter tall willow communities, which provide excellent ambush cover for wolves and grizzlies (Roby 1978; Boertje 1981; Kuropat 1984). The avoidance of the alluvial willow type also may be related to the poorer quality of willow leaves in these communities compared to those species present in the meadows (*Salix pulchra* versus *S. glauca* and *S. alexensis*).

Food habits

Methods

We collected composite fecal samples throughout the study area during five life cycle periods over the three years; precalving (n=7), calving (n=4), post-calving (n=5), movement (n=4) and early summer (n=5). The methods of analysis of fecal fragments and statistical treatment of the data were described earlier. We submitted two identical samples for analysis on four separate occasions and four replicates on one occasion.

Results

Effect of analysis at different times

The frequency of discerned plant fragments in replicates analysed at one time compared with those sampled at different times was significantly different for deciduous shrubs in the 1979 sample (Table 3.11). For most species, samples analysed at different times tended to have a much higher coefficient of variation than those analysed at the same time. This was particularly true for moss (1979 and 1980), *Eriophorum* (1979), deciduous shrubs (1979) and evergreen shrubs (1979 and 1980). Only *Cladonia*-type lichens, *Dryas* and forbs showed relatively similar coefficients of variation. They are therefore the only foods that can be statistically compared with confidence between times of analysis (Table 3.11).

Differences between periods

Several significant differences occurred between periods. Moss, *Vaccinium*, and *Eriophorum* were significantly higher in pre-calving and calving than in later periods, while lichens and *Equisetum* were significantly higher in pre-calving compared to post-calving, movement and early summer. *Dryas* was significantly higher in the pre-calving period than all other periods and *Salix* was significantly higher after the calving period (Table 3.12).

Differences among years

Recognizing the limitations of comparing samples analysed at different times, we did note some striking differences among years for some of the plant groups. Graminoids comprised over 30% of the fecal fragments from the pre-calving to the movement period in 1981, but were virtually absent from the diet after the calving period in the other two years (Table 3.13). Deciduous shrubs did not become the dominant component in fragments until the movement period in 1981, compared to the post-calving period in the other two years. In 1980, moss was represented in over 50% of fragments in the pre-calving and calving period, nearly twice as often in the other two years.

Table 3.11. Average percentages and coefficients of variation (CV) of discerned plant fragments in replicates of caribou fecal samples that were analysed at one time (O) and replicates that were analysed at different times (D).

Plant genus or group	21–28 May 1979					28 May 1980				
	Mean		CV		Ratio	Mean		CV		Ratio
	O	D	O	D	CV(D)/ CV(O)	O	D	O	D	CV(D)/ CV(O)
Moss	13.5	30.9	13.8	60.4	4.4	27.1	25.6	18.0	50.4	2.8
Lichens	10.8	6.6	48.0	48.1	1.0	25.4	32.3	20.6	35.0	1.7
<i>Cetraria</i> -type	2.7	1.1	57.2	86.4	1.5	4.9	4.7	61.4	71.1	1.2
<i>Cladonia</i> -type	6.8	4.9	62.5	47.9	0.8	15.9	24.1	27.7	45.1	1.6
<i>Stereocaulon</i>	1.3	0.5	51.2	68.1	1.3	4.6	2.6	69.0	133.6	1.9
<i>Peltigera</i>	–	0.2	–	206.3	–	–	1.0	–	123.4	–
Horsetails	8.6	9.1	33.8	58.4	1.7	20.9	11.4	39.3	32.6	0.8
Graminoids	12.3	18.5	17.3	36.7	2.1	9.4	12.6	37.4	36.5	1.0
<i>Carex</i>	4.0	2.2	74.5	123.4	1.7	1.3	2.9	16.1	81.5	5.1
<i>Eriophorum</i>	7.4	16.0	15.3	58.5	3.8	7.5	9.0	38.5	47.0	1.2
Deciduous shrubs*	42.6	14.7	16.1	107.4	6.7	5.3	4.1	33.3	59.7	1.8
Evergreen shrubs	11.3	19.6	23.0	61.2	2.7	10.5	12.6	16.7	50.3	3.0
<i>Dryas</i>	6.0	5.3	28.7	26.0	0.9	1.7	4.0	53.0	43.6	0.8
<i>Vaccinium</i>	5.0	14.1	36.2	92.6	2.6	7.0	7.6	38.3	62.5	1.6
Total shrubs	53.8	34.4	8.7	58.3	6.7	15.9	16.7	4.6	26.0	5.7
Forbs	1.0	0.5	106.4	67.6	0.6	1.3	1.4	94.9	75.4	1.3
Total vascular	74.9	62.5	6.8	25.8	3.8	47.5	42.1	14.5	4.3	0.3

Significant differences between means indicated by an asterisk (*= $p < 0.005$).

Fecal sample versus ingested diet

Fecal samples from Duquette's trials using a summer diet similar to that observed in this study and analysed in Colorado were used to assess the over or under estimation of certain components of the summer diet. Compared with actual ingested diet, fecal analysis significantly under-estimated lichens, mushrooms and forbs while over-estimating deciduous shrubs (Table 3.14). The apparent high digestibility of forbs probably influences the estimation of the other components of the diet. Therefore, to correct the diet to better reflect actual intake, we applied correction factors to lichens and to evergreen and deciduous shrubs and assigned the remaining portion of the diet (to add to 100%) to forbs (Table 3.15). These correction factors were based on regressions of actual versus fecal-estimated diet for both summer and winter trials.

Discussion

The progression of diet change over the five periods measured in this study indicate that the caribou are rapidly changing diet as the quantity and quality of foods change. Between year comparisons indicate that the animals are taking advantage of annual variations in forage as well. In an average year, when the pregnant cows reach the calving grounds, many of the communities are unavailable due to snow cover, especially the widespread tussock tundra community. The objective at this time of year is to fill the rumen with whatever is digestible, and if digestible forage is unavailable, to fill the rumen with anything else. Thus we see the use of lichens, evergreen shrubs and mosses in the pre-calving and calving period in

Table 3.12. Average percentages (\pm SE) of discerned plant fragments collected from the calving grounds of the Porcupine Caribou Herd, 1979–81

Species name	Season				
	Pre-calving n = 7	Calving n = 5	Post-calving n = 5	Movement n = 4	Early July n = 5
Moss	32.4 \pm 8.19	49.5 \pm 8.78	5.6 \pm 4.56	0.3 \pm 0.14	-
<i>Selaginella</i>	8.9 \pm 2.13	4.6 \pm 0.95	1.0 \pm 0.50	0.1 \pm 0.07	0.1 \pm 0.05
Total mosses	41.3 \pm 7.06	49.1 \pm 7.85	6.5 \pm 5.02	0.5 \pm 0.17	0.1 \pm 0.05
<i>Cetraria</i> -type	1.7 \pm 0.99	0.4 \pm 0.20	0.1 \pm 0.13	-	<0.1 \pm 0.04
<i>Cladonia</i> -type	7.8 \pm 3.49	1.2 \pm 0.66	0.2 \pm 0.12	-	0.1 \pm 0.08
Total lichens	10.8 \pm 4.81	2.0 \pm 0.84	0.5 \pm 0.24	-	0.1 \pm 0.09
<i>Equisetum</i>	2.6 \pm 1.05	0.7 \pm 0.31	0.3 \pm 0.34	0.2 \pm 0.08	<0.1 \pm 0.04
Total horsetails and ferns	2.6 \pm 1.05	0.7 \pm 0.31	0.3 \pm 0.34	0.2 \pm 0.08	<0.1 \pm 0.04
<i>Carex</i>	2.3 \pm 0.78	2.5 \pm 1.34	0.9 \pm 0.47	0.3 \pm 0.32	0.2 \pm 0.10
<i>Eriophorum</i>	17.2 \pm 5.17	20.7 \pm 9.71	6.8 \pm 6.67	1.3 \pm 0.75	0.1 \pm 0.05
Total graminoids	20.0 \pm 4.77	23.9 \pm 8.09	7.7 \pm 7.08	1.6 \pm 0.66	0.4 \pm 0.07
<i>Salix</i>	5.0 \pm 1.58	6.8 \pm 3.24	80.0 \pm 13.72	96.3 \pm 1.50	98.0 \pm 0.22
Total deciduous	5.0 \pm 1.58	6.8 \pm 3.24	80.1 \pm 13.71	96.3 \pm 1.50	98.0 \pm 0.22
<i>Dryas</i>	4.4 \pm 0.76	0.9 \pm 0.48	1.3 \pm 0.90	0.6 \pm 0.54	0.7 \pm 0.11
<i>Vaccinium</i>	14.7 \pm 6.11	16.0 \pm 4.51	2.8 \pm 1.52	0.9 \pm 0.40	0.5 \pm 0.17
Total evergreen shrubs .	19.7 \pm 6.17	16.9 \pm 4.50	4.1 \pm 1.87	1.6 \pm 0.91	1.2 \pm 0.22
Total shrubs	24.7 \pm 5.24	23.7 \pm 3.22	84.2 \pm 12.39	97.8 \pm 0.65	99.2 \pm 0.23
Total forbs	0.6 \pm 0.17	0.7 \pm 0.31	0.8 \pm 0.39	0.1 \pm 0.06	0.2 \pm 0.11
Total vascular content .	47.9 \pm 6.54	48.9 \pm 8.34	93.0 \pm 5.23	99.5 \pm 0.17	99.8 \pm 0.10

1: *Sphagnum*, *Peltigera*, *Stereocaulon*, *Arctagrostis*, *Dupontia*, *Festuca*, *Luzula*, *Poa*, *Ledum*, *Artemisia*, *Astragalus*, *Draba*, *Lupinus*, *Saxifraga*, and unknown forbs occurred at average frequencies of less than 1.0 % in some seasons.

most years. In 1979, a normal to poor year for *Eriophorum* flower production, animals utilized the most available digestible forage, lichens and ingested significant quantities of moss and evergreen shrubs. In 1980, with early phenological development, animals were able to utilize a wider variety of forage types, including early flowering *Eriophorum* and deciduous shrubs. The relatively high moss intake recorded in the pre-calving and calving period in 1980 may indicate that the animals were selecting roughage to offset the highly digestible forage available early in the season. In 1981, with the excellent production of *Eriophorum*, animals quickly focussed on graminoids, evergreen shrubs and moss.

As snow melts, the first component of fresh vegetation is the heads of *Eriophorum*, high in cell solubles, nitrogen and phosphorus and with significant biomass. Other forage such as forbs are of high quality but scarce early in the season. In 1981, a year of very abundant flowering of *Eriophorum*, caribou ate the heads of this species early in the pre-calving period and continued its use longer than in 1979 and 1980.

As deciduous shrubs and forbs become more available, animals quickly shift to the freshly unfurled leaves of *Salix*. These leaves are high in digestible cell solubles, phosphorus and nitrogen at a time when these components in the *Eriophorum* heads are rapidly declining in value. In 1980, a year of early snowmelt and advanced phenology, caribou began shifting to *Salix* in the calving period compared to a shift in the post-calving period in 1981. Deciduous shrubs and probably forbs (based on corrected diet, Table 3.15), remain the main component of the diet into July as the sequential leafing and blooming of different species of these plant groups become available.

Table 3.13. Annual differences in the major food types based on discerned plant fragments for the Porcupine Caribou Herd, 1979-81.

Study period	n	Plant group						
		Graminoid	Lichen	Forbs	Deciduous Shrub	Evergreen Shrub	Moss	Horsetail
<i>1979</i>								
Precalving	1	11.4	31.4	0.6	1.2	22.0	22.9	8.7
Calving	-	-	-	-	-	-	-	-
Post-calving	1	0.4	0.6	0.1	97.5	1.1	0.3	0.0
Movement	-	-	-	-	-	-	-	-
Early summer	1	0.6	0.4	0.6	97.0	0.9	0.1	0.0
<i>1980</i>								
Pre-calving	4	15.1	8.6	0.6	8.3	11.3	54.0	2.1
Calving	2	9.9	1.9	1.1	12.4	11.6	61.9	1.1
Post-calving	4	1.0	0.6	0.9	90.3	3.7	2.1	0.6
Movement	2	0.8	0.1	0.1	97.9	0.7	0.5	0.0
Early summer	4	0.4	0.1	0.1	98.1	1.3	0.1	0.1
<i>1981</i>								
Pre-calving	2	34.1	3.8	0.8	0.4	35.3	25.3	1.0
Calving	2	37.8	2.1	0.3	1.2	22.1	36.3	0.3
Post-calving	1	36.2	1.3	1.3	27.3	8.1	26.1	-
Movement	2	2.4	0.0	0.0	94.6	2.5	0.4	0.2
Early summer	-	-	-	-	-	-	-	-

Table 3.14. Average percentages of actual intake and average percentages of discerned plant fragments in fecal samples from feeding trials on captive caribou and reindeer at the University of Alaska in 1982 by L. Duquette.

Plant group	Actual intake $\bar{x} \pm SD(\text{range})n=8$	Fecal estimate $\bar{x} \pm SD(\text{range})n=8$	Correlation coefficient*
Moss ¹		0.3	-
Lichens ²	18.1 ± 4.8(14-28)	4.8 ± 1.5	0.72
Mushrooms	3.1 ± 0.6 (2-4)	0	-
Graminoids ³	5.4 ± 2.9 (2-11)	3.4 ± 2.4	-0.54
Deciduous shrubs ⁴	43.1 ± 2.5 (41-47)	90.3 ± 2.8	-0.74
Evergreen shrubs ⁵	2.5 ± 0.5 (2-3)	1.2 ± 0.8	-0.12
Forbs ⁶	27.6 ± 2.6 (22-30)	<0.1 ± 0.1	-

1: *Hylocomium splendens*; 2: *Cladina stellaris*, *C. rangiferina*, *Cetraria nivalis*; 3: *Bromus*, *Carex aquatilis*; 4: *Salix alexensis*, *S. lanata*; 5: *Vaccinium vitis-idaea*; 6: *Epilobium latifolium*, *Medicago falcata*, *Trifolium repens*.

* $p < 0.05$

Table 3.15. Adjusted diet of the Porcupine Caribou Herd, adjustment based on correction factors derived from Table 3.14.

Plant group	Pre-calving	Calving	Post-calving	Movement	Early July
Moss	41	49	6	<1	<1
Lichens	27	15	13	12	13
Horsetails	3	1	<1	<1	<1
Graminoids	20	24	8	2	<1
Deciduous shrubs	1	1	38	46	47
Evergreen shrubs	9	8	3	2	2
Forbs	0	2	32	38	38

Regressions used;

Lichens (n=16) Actual = 12.44 + 1.33 estimate R=0.96

Evergreen shrubs (n=16) Actual = 1.91 + 0.34 estimate R=0.90

Deciduous shrubs (n=16) Actual = -1.2 + 0.49 estimate R=0.99

Forbs 1.00 – sum of rest.

Caribou activity

Methods

Scans – see methods described in Winter Activity budget section.

Focal animal – In 1980 and 1981 we watched focal animals to determine the individual variation in active and bedded cycles, nursing behaviour of the calves and to document how individuals partitioned their active time. Only complete active and bedded cycles were used in the analysis. Activity criteria follow from the activity scans. We further divide feeding into;

feed – standing in one place with head to the ground ingesting forage,

graze – head down ingesting forage while walking, and

search – head down or moving from side to side but not ingesting forage.

A successful suckle was considered any suckle lasting at least five seconds. Suckling duration and time between successful suckles were recorded.

Results

Band size

Mean band size weighted by period was 69.1 ± 15.01 (mean \pm SE, Table 3.16). The maximum group size was generally in the movement period and the minimum in the calving period. In 1979, animals tended to stay in smaller groups until the movement period when considerable aggregation occurred.

Movement rate

Caribou tended to reduce their movement rate from pre-calving to the calving period and increase again after the post-calving period. Animals tended to have higher movement rates in 1980. The reduced rate in the pre-calving period for 1979 is noteworthy (Table 3.17).

Active and bedded cycles

Total cycle lengths (active + bedded) increased from the pre-calving to post-calving periods and then declined sharply in the movement periods, largely as a result of the significant decline in the active cycle length (Table 3.18).

Table 3.16. Group sizes of the Porcupine Caribou Herd during different periods of the life cycle, 1979-81.

Study period	n	Group size		
		Mean	SE	Range
<i>1979</i>				
Pre-calving	52	17.1	2.00	2 - 64
Calving	29	13.3	2.22	2 - 50
Post-calving	24	36.8	8.28	5 - 163
Movement - early July .	7	192.8	103.41	5 - 550
<i>1980</i>				
Pre-calving	73	77.5	9.61	6 - 442
Calving	61	30.9	4.34	6 - 232
Post-calving	59	142.3	28.53	8 - 1168
Movement	7	127.1	28.53	23 - 202
<i>1981</i>				
Spring migration	13	90.9	20.16	3 - 239
Pre-calving	25	73.8	22.51	8 - 578
Calving	18	37.9	5.51	4 - 110
Post-calving	7	31.0	9.75	5 - 81
Movement	5	85.4	28.99	14 - 152

Table 3.17. Movement rate of the Porcupine Caribou Herd based on scans from pre-calving to early July, 1979-81.

Study period	n	Movement rate (km/h)	
		Mean	SE
<i>1979</i>			
Pre-calving	278	0.20	0.031
Calving	177	0.20	0.029
Post-calving	232	0.20	0.028
Movement	19	0.45	0.171
Early July	15	0.31	0.131
<i>1980</i>			
Pre-calving	533	0.97	0.060
Calving	571	0.25	0.024
Post-calving	629	0.53	0.032
Movement	44	0.98	0.184
<i>1981</i>			
Spring migration	134	0.24	0.276
Pre-calving	187	0.59	0.077
Calving	168	0.24	0.043
Post-calving	109	0.25	0.073
Movement	35	0.40	0.145

Table 3.18. Summary of average active and bedded cycle lengths for the Porcupine Caribou Herd during the late spring – early summer, 1979–81.

Study period	Cycle lengths	
	Active (n, mean ± SE)	Bedded (n, mean ± SE)
Pre-calving	(13) 86 ± 8.0 a,b*	(29) 88 ± 5.6 a
Calving	(17) 99 ± 7.4 a	(37) 75 ± 5.4 a
Post-calving	(35) 102 ± 8.1 a	(55) 83 ± 3.9 a
Movement	(4) 42 ± 7.2 b	(7) 66 ± 8.6 a

* periods with the same suffix (a, b) are not significantly different.

Activity budgets

The proportion of time spent feeding declined from the pre-calving period through to the movement period. The magnitude of this decline was greatest in 1979 and least in 1980. In all years the proportion of time spent feeding was lowest in the movement period, but not significantly lower in 1980. In all years, the decline in feeding from post-calving to movement period was marked by a concurrent increase in the proportion of time spent walking. In 1979, the decline in feeding from pre-calving to calving was associated with an increase in lying time (Table 3.19). In 1980 and 1981, lying time increased from pre-calving to calving, while walking time decreased.

In 1979 and 1980 lying time increased from the pre-calving to the post-calving period, then declined in the movement period. The proportion of time spent walking declined from pre-calving to post-calving and increased in the movement period (Table 3.19). The proportion of time spent walking was notably low in the pre-calving period of 1979.

Focal animal observations

No significant differences were measured among the classes of adults. Within an active cycle, adults spent a significantly higher proportion of time grazing, while calves spent a higher proportion of their active time running (except post-calving) and standing (except pre-calving, Table 3.20). In the pre-calving period adults spent a significantly higher proportion of time walking while calves walked more in the post-calving period.

Adults spent a higher proportion of active time grazing in the calving and post-calving periods compared to the pre-calving period, and a higher proportion of time walking in the pre-calving period compared to the post-calving period. Calves spent the highest proportion of time grazing in the calving period and the lowest proportion in the pre-calving period, and all periods were significantly different from each other (Table 3.20). Feeding intensity (graze-search/100) was extremely high throughout the seasons (0.98 for adults and 0.99 – 1.0 for calves).

Due to their skewed frequency, the mean length of active and bedded cycles are misleading (Tables 3.21 and 3.22). The median lengths of the active and bedded cycles, probably a more appropriate measure, increased for both adults and calves from the pre-calving to the post-calving period (Tables 3.21 and 3.22). The most dramatic increase for both adults and calves was from the pre-calving to the calving period, possibly due to the pregnant females preparation to give birth and/or the constant interruption from nursing and the calves frequent nursing bouts (see next). Adults had much longer median active and bedded cycles than calves.

Nursing

We analysed 386 bouts of nursing behaviour involving 39 different individual calves. We noted a decline in bout frequency from pre-calving to post-calving (significant between pre-calving and calving) and

Table 3.19. Summary of activity budgets of the Porcupine Caribou Herd in late spring and early summer, 1979-81.

Study period	n (groups)	n (animals)	Activity (mean ± 95%CL)				
			Feed	Lie	Stand	Walk	Trot
<i>1979</i>							
Pre-calving	52	4823	.58 ± 0.042	.28 ± 0.057	.03 ± 0.006	.11 ± 0.025	.01 ± 0.008
Calving	29	2961	.48 ± 0.061	.34 ± 0.086	.02 ± 0.006	.15 ± 0.049	.02 ± 0.011
Post-calving	24	8143	.44 ± 0.045	.45 ± 0.045	.01 ± 0.005	.08 ± 0.024	.01 ± 0.013
Movement*	5	4240	.30 ± 0.135	.20 ± 0.084	<.01 ± 0.001	.48 ± 0.175	.02 ± 0.022
<i>1980</i>							
Pre-calving	73	39015	.56 ± 0.040	.20 ± 0.082	.01 ± 0.003	.23 ± 0.063	<.01 ± 0.000
Calving	61	13363	.54 ± 0.055	.35 ± 0.071	.01 ± 0.003	.10 ± 0.027	.01 ± 0.007
Post-calving	59	60380	.56 ± 0.053	.37 ± 0.051	.01 ± 0.003	.06 ± 0.015	<.01 ± 0.002
Movement	7	6515	.44 ± 0.024	.32 ± 0.178	<.01 ± 0.003	.22 ± 0.173	.02 ± 0.014
<i>1981</i>							
Pre-calving**	38	23973	.59 ± 0.048	.21 ± 0.079	.01 ± 0.004	.19 ± 0.095	<.01 ± 0.002
Calving	18	4668	.60 ± 0.055	.30 ± 0.072	.02 ± 0.006	.07 ± 0.027	.01 ± 0.019
Post-calving	7	2774	.51 ± 0.037	.39 ± 0.069	.01 ± 0.004	.08 ± 0.038	.01 ± 0.005
Movement	5	1560	.36 ± 0.059	.49 ± 0.121	.02 ± 0.011	.13 ± 0.094	<.01 ± 0.001
<i>All years</i>							
Pre-calving	163	67811	.58 ± 0.028	.21 ± 0.055	.01 ± 0.003	.21 ± 0.050	<.01 ± 0.001
Calving	108	20992	.54 ± 0.040	.33 ± 0.050	.01 ± 0.003	.10 ± 0.020	.01 ± 0.006
Post-calving	90	71297	.54 ± 0.048	.38 ± 0.044	.01 ± 0.002	.07 ± 0.013	<.01 ± 0.002
Movement	17	12315	.38 ± 0.075	.30 ± 0.115	.01 ± 0.003	.29 ± 0.163	.01 ± 0.009

* contains some observations in early July.

** contains some observations in mid May.

Table 3.20. Summary of caribou activity based on continuous observations of active individuals for the Porcupine Caribou Herd, late spring to early summer, 1978-83.

Activity	Pre-calving		Calving		Post-calving	
	Calves	Others	Calves	Others	Calves	Others
	n= 171	n=54	n=64	n=35	n=34	n=12
Feeding	<.01 ± .002	.30 ± .051	.20 ± .026	.57 ± .064	.10 ± .027	.70 ± .080
Walking	.37 ± .028	.25 ± .039	.22 ± .026	.19 ± .037	.31 ± .043	.05 ± .014
Standing	.47 ± .028	.42 ± .051	.46 ± .038	.24 ± .054	.49 ± .050	.25 ± .086
Running	.05 ± .013	<.01 ± .002	.04 ± .013	<.01 ± .001	.01 ± .004	<.01 ± .001
Nursing	.08 ± .013	-	.04 ± .013	-	.10 ± .031	-
Other*	.03 ± .013	.02 ± .016	<.01 ± .001	<.01 ± .001	<.01 ± .001	<.01 ± .001

n = number of complete cycles observed.

* other activity includes sparring, swimming, drinking, etc.

Table 3.21. Frequency of complete active cycles for calves and adults of the Porcupine Caribou Herd, late spring – early summer, 1978–83.

Cycle length	Calves			Adults		
	Pre-calving	Calving	Post-calving	Pre-calving	Calving	Post-calving
<10 min	170	52	33	35	14	3
11 – 30 min	1	9	1	3	2	2
31 – 50 min	–	2	–	5	2	–
51 – 70 min	–	1	–	7	5	2
71 – 90 min	–	–	–	4	8	2
91 – 110 min	–	–	–	–	–	1
111 – 130 min	–	–	–	–	2	–
>130 min	–	–	–	–	2	2
median value (min)67	1.4	2.6	2.5	44.7	67.7

an increase in bout duration from pre-calving to calving (significant only based on bouts). The percent of active time spent nursing declined from calving to post-calving (Table 3.23).

Discussion

At our camp location, pre-calving cows were either still migrating west to calving sites in Alaska or were in preparation for calving within our study area. In 1979, concentrated calving occurred in the study area (Fig. 3.3). In the pre-calving period cows tended to have lower movement rates, lower proportion of time walking and smaller group sizes than the other two years. Although calving did occur in the study area in 1980 and 1981, most animals present in the study area in the pre-calving period appeared to be moving into Alaska. Animals that did calve in the area in 1980 and 1981 were those further back on migration during the pre-calving period.

Table 3.22. Frequency of complete bedded cycles for calves and adults of the Porcupine Caribou Herd, late spring – early summer, 1978–83.

Cycle length	Calves			Adults		
	Pre-calving	Calving	Post-calving	Pre-calving	Calving	Post-calving
<10 min	156	36	19	35	11	1
11 – 30 min	9	12	12	13	8	2
31 – 50 min	5	10	4	4	4	3
51 – 70 min	1	3	2	7	8	1
71 – 90 min	–	2	–	3	5	4
91 – 110 min	–	2	–	3	4	–
111 – 130 min	1	–	–	–	3	1
>130 min	1	1	1	2	–	1
median value (min)	1.1	8.2	10.2	7.6	45.3	55.0

Table 3.23. Frequency and duration of nursing bouts of calves of the Porcupine Caribou Herd, late spring – early summer, 1979–81.

Study period	Time observed (h)	(n)	Frequency ¹ (bouts/100min) mean ± SE	Duration (sec) mean ± SE	% time nursing
<i>Based on bouts</i>					
Pre-calving	27.6	120	7.2	23.3 ± 2.13 a	2.8
calving	70.3	193	4.6	37.8 ± 2.66 b	2.9
post-calving	41.6	73	2.9	32.9 ± 3.68 b	1.6
<i>Based on calves</i>					
pre-calving		11	9.7 ± 1.92 a ²	26.2 ± 5.46 a	4.2
calving		16	5.1 ± 0.87 b	39.9 ± 5.56 a	3.4
post-calving		12	3.8 ± 1.13 b	36.7 ± 5.36 a	2.3

1: bouts > 5 sec duration.

2: Values with the same suffix (a, b) are not significantly different.

The period of calving was characterized by a reduction in movement (both rate and proportion), smaller group sizes, and an increase in lying time. Although group cycle lengths, based on scans, did not differ from the pre-calving to the calving period, focal animal investigations indicated a tendency toward longer median active and bedded cycles. The high frequency of short cycles shown by focal individuals would be masked by the synchronous alteration in active/rest cycles dictated by groups.

The post-calving period was marked by a further increase in lying time, a reduction or maintenance of movement rates and/or proportion of time walking and an increase in the median length of active and bedded cycles. Activity budgets did not differ significantly between the calving and pre-calving periods.

The movement period showed the most dramatic change in the activity of the animals. Group sizes increased dramatically, the proportion of time and rate of walking increased significantly, the proportion of time spent feeding declined significantly and the alteration between active and rest cycles was significantly reduced. In 1980, group sizes had already increased in the post-calving period. This was associated with an increase in rate of movement, which indicated that animals moved from the study area earlier than in previous years (although this is not reflected in an increase in the proportion of time spent walking).

Individual calves decreased the frequency of nursing bouts and increased the duration of an individual bout within a few weeks of birth. In the pre-calving period all the calves seen were probably less than a week old. In the calving period we were observing calves from newborn to two weeks old and in the post-calving period from newborn to three weeks old. The increase in bout duration and decrease in bout frequency would be much more pronounced for an individual calf than our data suggest. Using a captive herd in which individuals were marked, Parker *et al.* (1990) reported an exponential decline in the frequency of feeding bouts with age of calf while bout duration remained relatively constant.

Few data exist on the activity of newborn caribou calves. Our data agree well with those presented by Parker *et al.* (1990), who observed that calves spent less than 1 % of the day grazing post-partum, increasing to between 10 – 20 % by the end of one month of life. The percent of day spent lying (bedded cycle length/(bedded+active cycle length)) varied between 65 – 85%, comparing favourably with the observations of Parker *et al.* (1990). They also noted a sharp decline in the time spent running from birth to one month of age, similar to our findings.

Summary discussion

In 1979 pregnant cows moved out of wintering areas in northcentral Yukon along the ridges of the Old Crow route. Snow was relatively deep in the forested habitats below the ridges. Once on the north slope animals dropped out of migration randomly and occupied calving areas by late May. The two regions of concentrated calving were the foothills areas between the Kongakuk and Malcolm rivers and the uplands of the Jago River. Weather conditions in late May prevented early exposure of the tussock tundra communities; precipitation was high 20–25 May and temperatures were coldest among the years recorded in this study. As a result of the late snowmelt and cool temperatures the timing of flowering in the key forage species was late. Once on the core calving area for that year, many females remained, not moving further west. Movement rates were slow, and group sizes small as animals fed primarily on lichens, evergreen shrubs and *Equisetum* available in sufficient quantities in the alluvial heath communities. These habitats open up early compared to the tussock tundra communities. Lichens at that time in 1979, provided necessary digestible solubles while moss and evergreen shrubs provided roughage to maintain a full rumen.

Weather remained cool and wet throughout the calving period. As vegetation became available, animals switched to a graminoid based diet and then to deciduous shrubs by mid June. Habitats primarily utilized were the sedge heath communities, a range type with abundant willows and sedges. By mid June animals began to bunch up and move west towards Alaska, reflected by an increase in movement rate, group size, and proportion of time spent walking in the last 10 days of June.

In 1980, spring migration was greatly slowed by the deep snow and late snowmelt along the migration routes. The area of snow free habitat was limited up to early May, but subsequent warm weather from the middle to the end of May resulted in early snowmelt in the foothills. Animals that occupied the study area in mid May continued westward to the foothills habitats of Alaska. Thus the pre-calving period was characterized by relatively large group sizes, high movement rates and a high proportion of time spent walking, in direct contrast to the same period in 1979. These animals were able to take advantage of the early melt in the tussock tundra communities along the foothills and the resultant early phenology. Diet in late May was primarily moss, evergreen shrubs, and graminoids. It was a poor year for the production of *Eriophorum* flowering due to the inclement weather in 1979. The tussock tundra communities were the favoured type in the pre-calving to calving period. By calving, early phenological changes were evident and we noted an early shift from graminoids to deciduous shrubs associated with a shift to the wet sedge meadow communities, abundant in deciduous shrubs.

In the post-calving period the animals began early aggregations with group sizes of over 1000 animals recorded. The movement rate, date and radio-tracking information (Russell *et al.* 1992b) indicated that the animals moved rapidly and early (after the peak of calving) to Alaska. This movement was further evidenced by the high rate of movement in the post-calving period. Although the proportion of time spent walking (based on scans) did not show an increase in the post-calving period, evidence from the focal animal studies indicate that animals in the grazing period tended to move while feeding much more than in 1981. Therefore we suggest that during the important post-calving period nursery bands displayed highly oriented feeding rates towards Alaska. We further suggest that this rapid movement from our study area may have been due to the compressed flowering period compared to other years. If phenology was progressing rapidly in 1980 and if animals were attempting to track phenology then the logical movement was north and west. We would suggest therefore that early and rapid phenological development, although beneficial in late May and early June may prove detrimental later as key forage species decline quickly in nitrogen and phosphorus and lignify earlier.

The warm weather in 1980 resulted in a very high production of *Eriophorum* in 1981. The progress and timing of spring migration was relatively normal in 1981 and animals arriving on the calving ground appeared to be continuing on to core calving areas in the Jago River region of Alaska, similar to 1980 and in contrast to 1979. The weather in 1981 was cool and plant growth was slowed and prolonged com-

pared to 1980. The normal snowmelt and high production of *Eriophorum* flowers resulted in the early exploitation of tussock tundra communities with animals able to pluck newly exposed flowers at the edge of the snow. Use of *Eriophorum* continued into the post-calving period, and thus the use of *Salix* was delayed compared to previous years. This prolonged use of graminoids may be due to the abundance of *Eriophorum* flowers and/or the retarded phenological development of the willows. Similar to 1980, the animals switched from a preferred tussock tundra community before calving, to the utilization of the wet sedge communities after it.

Movement from the calving area westward was a slow drifting compared to the rapid movement in 1980. The prolonged phenology may have been an important factor. Continuous observations of calves in 1981 indicated that there was an increase in the proportion of active period spent nursing from the calving to the post-calving period (compared to a decline in 1980). In both years the proportion of the adult's active period spent standing mirrors the proportion of the calves active period spent nursing indicating that the frequency and duration of nursing has an effect on the activity budget of the female. Perhaps this is the reason for the high frequency of short active and bedded periods observed with focal adults in the pre-calving and calving periods; the frequent nursing bouts constantly interrupted the activity of the female. These shorter cycles were not evident in the scan observations of the groups. Group activity better reflects the overall alternation of ingestion (or movement) and digestion.

In all years we noted a decline in the length of both active and bedded cycles in the movement period and we have evidence that this phenomenon occurred early in 1980. The use of willow and forbs in the latter part of June may help to explain this sharp reduction in cycle lengths. White and Trudell (1980) noted that the rate of dry matter disappearance was highest for forbs followed by deciduous shrubs. Thus the rate of digestion and passage would increase and lying periods would be reduced. White and Trudell (1980) and Kuropat (1984) reported a relationship between increased biomass and increased bite size and bite rate and this was most pronounced with forbs (*Luninus*) and shrubs (*Salix*). Kuropat (1984) contrasted the high eating rates on forbs (8.2 g per min) and deciduous shrubs (6 g per min) with the lower values for *Eriophorum* (1.7 g per min). White *et al.* (1975) indicates that a curvilinear relationship exists between biomass and intake in some of the key plant groups and further that the slope of the line for forbs is particularly steep because animals can increase the effective biomass of forbs by walking while grazing and consuming almost all of the aerial biomass. Thus the short active cycles in the movement period may not reflect a reduced intake but may reflect a combination of higher intake rates and higher rates of digestion and passage.

Our data suggests that calving caribou are able to react rapidly to the quickly changing environment experienced in the month between arriving on the calving grounds and leaving. They are able to track rapidly the quantity and quality of vegetation as dictated by weather and terrain. The fact that they do react quickly suggests that uninterrupted movement in response to these changing conditions is an essential element in the survival of the calves and in the ability of females to regain reserves depleted over the winter and throughout spring migration. The transition from post-calving to the movement period appears to be the time of most dramatic change for the animals, a time when they attempt to maximize nutrient intake and minimize energy output. Our observations were conducted on animals that move westward after calving to the post-calving aggregation sites in the Jago region of Alaska. For that reason the activity budgets of our animals after mid June may not be indicative of those animals that reach the Jago region in the calving period. We would suspect that the high movement rates and low feeding rates, that we measured during the movement period, would not necessarily occur in the core calving regions of Alaska. We suspect that these latter animals would be able to enjoy a more energetically beneficial «movement» period. In fact their activity budgets may suggest that a prolonged post-calving period may extend to the end of June and that no «movement» period exists.

Spring range of bulls

Introduction

The general pattern of spring migration involves pregnant cows migrating early from wintering grounds to calving sites north of treeline. Meanwhile males, juveniles and non-pregnant females remain on the wintering areas until early May. Therefore, during calving, and for a variable period before and after calving, males are segregated from females. It has been suggested that this segregation occurs because males follow the northward initiation of growth of forage while pregnant females move quickly to the calving grounds for other reasons, such as predator avoidance (Whitten and Cameron 1980). Recent proposals for a seaport, quarries and roads in northern Yukon in the area used intensively by males in early summer have focused attention on the need for information on that component of the herd.

Study area

Investigations were conducted in northern Yukon, north of the Porcupine River (Fig. 1.2 and 3.11). The area can be divided from south to north into three broad ecoregion bands: Old Crow Basin, Northern Mountains and Northern Coastal Plain (Wiken *et al.* 1981; Fig. 3.1). These ecoregions will be described in some detail in Chapter 4.

Three campsites were used for observing caribou in 1983: Sam Lake, 21 May – 12 June; King Point, 13 – 21 June; Firth River, 22 – 30 June (Fig. 3.11). The Sam Lake camp was at the southern edge of the Barn Mountains and overlooked rolling, tundra-covered pediments. The King Point and Firth River camps both lay on the coastal plain in rolling arctic tundra. Sites for documenting plant phenology (Fig. 3.11) were established on the Old Crow pediments (Sam Lake, Bonnet Lake), in the intermountain basins (Cottonwood Creek, Anker Creek), on the inner coastal plain (Crow River, Walking River) and at the coast (Stokes Point, King Point).

Methods

Distribution

To follow the movements of caribou, radio transmitters on collars were placed on animals on the winter range. Between five and 15 caribou were available for relocation each year (1981 – 5; 1982 – 5; 1983 – 15). In 1981 and 1982, four relocation surveys were flown between 3 and 28 June and in 1983 six surveys were flown between 8 May and 1 July. In addition to the locations of radio-collared animals, the locations of all male caribou observed on aerial surveys and reported by other researchers were plotted on maps.

Activity

See methodology described in Winter activity budget section.

Phenology

We observed snowmelt and the development of vegetation in eight relatively flat cottongrass (*Eriophorum vaginatum*) tussock meadows (Fig. 3.11). We estimated the relative stage of development of the flowers of *Eriophorum vaginatum* (flower bud, early flower, full flower, past flower, seed) for 24 tussocks at approximately 5-m intervals along a transect at each site. Along the same transect we also documented the relative stage of development of the leaves of 24 plants of *Salix pulchra*, *Betula glandulosa* and *Ledum palustre* (leaf bud, leaf unfolding, full leaf).

Habitat selection

We divided the area of observation at each campsite into six distinct habitat types and determined the extent of each by mapping them on aerial photographs. These types were similar to those described in the Calving Ground study with the addition of an open White Spruce type. We also documented the use of late snow patches and sandy beaches at some camps. The areas observed at campsites appeared

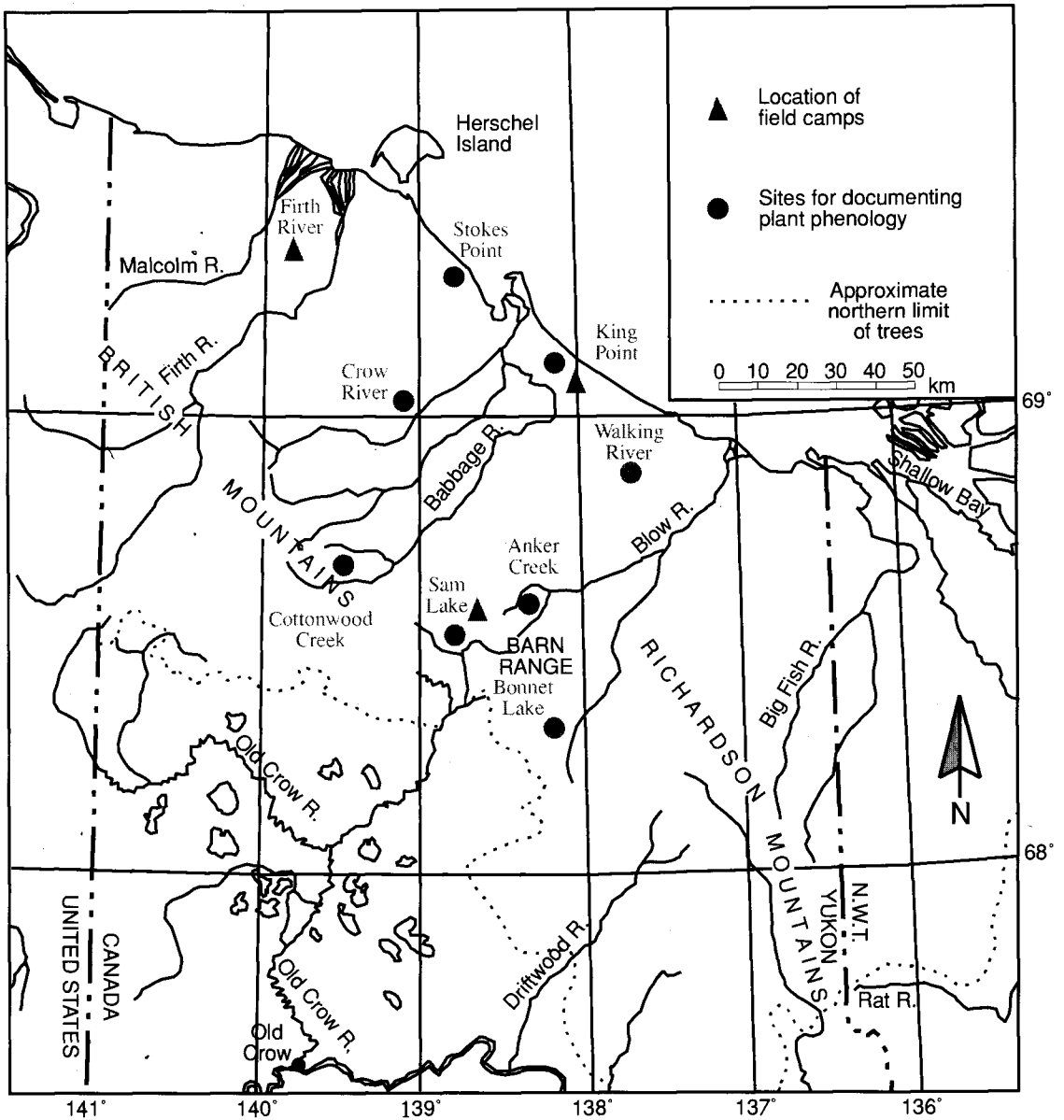


Figure 3.11. Location of study of males in spring, showing camp sites and phenological plots, 1983.

to be representative of much wider areas based on examination of aerial photographs and observations from aircraft.

Food habits

We collected composite fecal samples at Sam Lake (22 May, 4-5 June, 12 June), King Point (15-17 June), Firth River (26-27 June) and Stokes Point (15 June, 27 June). The method of fecal analysis and statistical treatment of the data follow those described in the Winter Food Habits section.

Data analysis

For the purpose of comparison, data analysis was consistent, in terms of time periods, with the calving ground study (Table 1.1).

Results and discussion

Distribution

Male caribou follow the females on spring migration along essentially the same routes leading from the two principal wintering areas, the Ogilvie Mountains of north-central Yukon and the Arctic Village region of northeastern Alaska. Females reach the calving grounds in mid to late May while males fan out in the rolling pediments north and east of the Old Crow Flats and into the wide basins near the headwaters of the Firth River (Fig. 3.12A). In early June, at the time of calving, males are distributed in a broad crescent south and east of the calving grounds (Fig. 3.12B). By this time, if not earlier, males from both the Alaskan and Yukon wintering areas are well mixed. Males then move eastward south of the British Mountains and northwestward from the Richardson Mountains. By mid June large aggregations begin to form in the intermountain basins near the headwaters of the Spring, Trail, Babbage and Running Rivers, and, in some years, on the Firth River (Fig. 3.12C). By late June males are found moving westward and northwestward towards the coast of the Beaufort Sea near the Alaska-Yukon border (Fig. 3.12D). At this time, band sizes frequently number in the thousands and smaller bands which have lingered behind move quickly to join the larger concentrations. Most males meet and mix with females and young on the Alaska-Yukon coastal plain by early to mid July before returning eastward to the Richardson Mountains.

Males, therefore are essentially segregated from females during May and June. The consistent pattern of distribution and movements among years and the formation of aggregations in mid June prior to joining females and prior to the insect season suggest a response to food resources combined with a form of social facilitation.

Activity

In late May, at Sam Lake, many females were moving through the area and males occurred in both male-dominated and female-dominated bands. Therefore, observations included both types of bands. After that time, only male-dominated bands were observed. The average size of bands was relatively constant from late May to mid June but increased significantly in late June (Table 3.24).

There was no significant difference in the proportion of time spent feeding or trotting/running among observation periods (Table 3.25). In mid June the proportion of time spent lying was significantly higher, and the proportion of time spent walking was significantly lower, than during other periods. The proportion of time spent standing was significantly lower in late June. The rate of movement (Table 3.24) mirrored the proportion of time spent walking (Table 3.25) and was conspicuously low during mid June.

It is not possible to make precise comparisons of activity budgets among studies because of differences in methods of calculation. In general, for the same season, Roby (1978) found that male caribou in north-central Alaska spent less time feeding (39%) and more time lying (47%) than males we observed.

Table 3.24. Size and rate of movement (km/h) of bands of male caribou in northern Yukon in 1983

Period	Size		Rate	
	(n)	$\bar{x} \pm SE$	(n)	$\bar{x} \pm SE$
Pre-calving	45	17.5 \pm 1.78a ¹	574	0.35 \pm 0.26a
Calving	55	24.2 \pm 2.90a	730	0.54 \pm 0.025b
Post-calving	65	19.9 \pm 4.47a	1088	0.15 \pm 0.007c

1: Means with same suffix (a, b) are not significantly different ($p=0.05$).

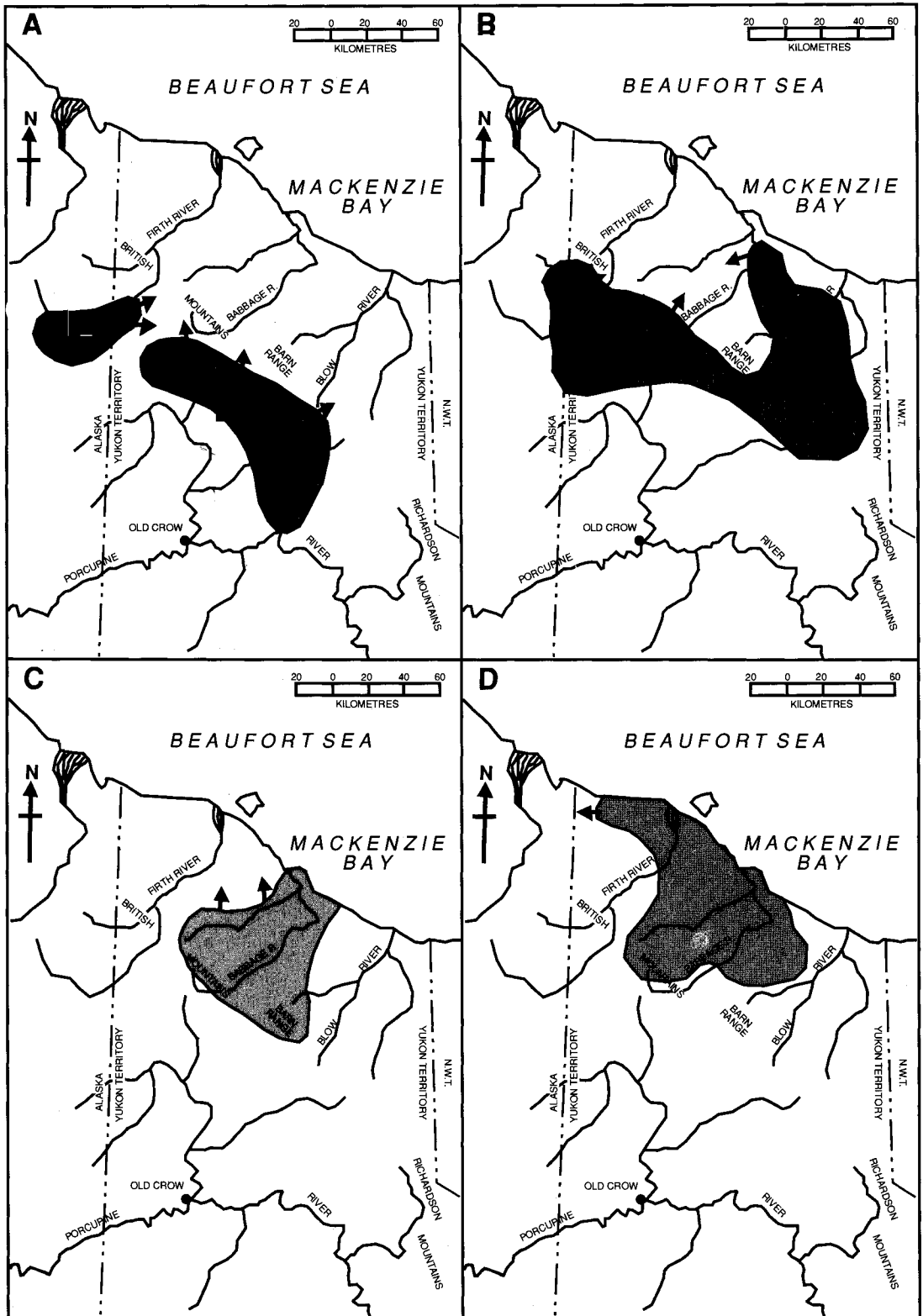


Figure 3.12. General distribution and direction of movement of male caribou in northern Yukon in late May (A), early June (B), mid June (C), and late June (D).

Table 3.25. Daily activity budgets (% time \pm estimated 95% confidence intervals) for male caribou in northern Yukon in 1983.

Date	Pre-calving	Calving	Post-calving	Movement
Number of observations .	619	787	1,153	330
Number of bands	45	55	65	29
Number of individuals . . .	8,443	14,498	19,554	25,592
Feeding	51.0 \pm 4.0	47.6 \pm 3.4	52.0 \pm 3.0	49.0 \pm 2.8
Lying	31.1 \pm 6.4	31.9 \pm 5.0	40.4 \pm 3.3	25.4 \pm 4.3
Standing	1.8 \pm 1.1	0.9 \pm 0.3	0.9 \pm 0.2	0.4 \pm 0.1
Walking	14.8 \pm 4.9	19.1 \pm 2.4	6.3 \pm 0.9	24.1 \pm 5.6
Trotting/running	1.2 \pm 1.1	0.5 \pm 0.3	0.3 \pm 0.3	1.0 \pm 0.4

The mean length of both active and resting periods declined significantly from late May to late June (Table 3.26). The decrease from mid June to late June was particularly conspicuous. The mean length of the active period that we observed late May to mid June (112 minutes) was shorter than that reported for male reindeer in summer (135 minutes; Segal (1962)), while the mean length of the resting period (104 minutes) was nearly identical (reindeer; 105 minutes).

Table 3.26. Length (minutes) of active and resting periods ($\bar{x} \pm SE$) for male caribou in northern Yukon in 1983. (Samples sizes).

	Pre-calving	Calving	Post-calving	Movement
Active period	(7) 118 \pm 18.4a ¹	(10) 111 \pm 12.9ab	(29) 110 \pm 6.4ab	(5) 78 \pm 11.0b
Bedded period	(23) 103 \pm 6.9a	(34) 98 \pm 5.2a	(46) 109 \pm 4.7a	(12) 69 \pm 6.5b

¹ Means with same suffix (a, b) are significantly different (p=0.05).

Phenology

On 18-19 May 1983, the Old Crow pediments were about 80% snow covered farther north all sites were about 95% snow covered. By 3 June the snow cover had declined to less than 5% on the Old Crow pediments and on the coast but was about 50% (30-70%) between those sites. By 10 June the intermountain and inner coastal plain sites were 10-20% snow covered and by 17 June all sites were essentially snow-free.

In general, the development of vegetation was most rapid on the Old Crow pediments (Table 3.27). In early June, the development of *Eriophorum vaginatum* was more advanced on the coastal plain than at inland sites but by mid June plant development on the coast was behind that at other sites and remained so. This was probably due to the temperature gradient which develops between the coast, strongly influenced by the ice-covered Beaufort Sea, and the thermal basin surrounding the Old Crow Flats (Pearson and Nagy 1976). In general, plant development on the Old Crow pediments was at least a week in advance of that on the coast.

Habitat selection

Tussock Tundra was weakly selected in late May and early June while Wet Sedge Meadow was strongly avoided until late June (Table 3.28). Dwarf Shrub Heath began to be avoided weakly after late May and Alluvial Willow shifted from being avoided in late May and early June to being selected in mid June and late June. Other habitat types were too poorly represented to compare.

Table 3.27. Phenology of vegetation in northern Yukon in 1983. The percent of plants in each stage of development is presented in sequence. Blank spaces indicate that the plant had not yet begun to develop.

	Date				
	June 3	June 10	June 17	June 24	July 1
<i>Eriophorum vaginatum</i> .	B/E/F/P/S ¹	B/E/F/P/S ¹	B/E/F/P/S ¹	B/E/F/P/S ¹	B/E/F/P/S ¹
Coast	0/33/67/0/0	0/6/92/2/0	0/0/0/100/0	0/0/0/0/100	0/0/0/0/100
Coastal plain	0/48/52/0/0	0/0/88/12/0	0/0/0/100/0	0/0/0/0/100	0/0/0/0/100
Mountain basins	0/88/12/0/0	0/2/67/31/0	0/0/0/90/10	0/0/0/0/100	0/0/0/0/100
Pediments	0/60/40/0/0	0/4/46/50/0	0/0/0/0/100	0/0/0/0/100	0/0/0/0/100
<i>Salix pulchra</i> ³	B/U/L ²	B/U/L ²	B/U/L ²	B/U/L ²	B/U/L ²
Coast	100/0/0	0/100/0	0/96/4	0/0/100	
Pediments	58/42/0	38/62/0	0/10/90	0/0/100	0/0/100
<i>Betula glandulosa</i>			B/U/L ²	B/U/L ²	B/U/L ²
Coast			56/27/17	2/54/44	0/0/100
Coastal plain			46/50/4	0/0/100	0/0/100
Mountain basin			48/38/14	0/0/100	0/0/100
Pediments			2/29/69	0/0/100	0/0/100
<i>Ledum palustre</i>					B/E/F/P/S ¹
Coast					86/14/0/0/0
Coastal plain					80/20/0/0/0
Mountain basin					66/34/0/0/0
Pediments					0/0/100/0/0

1: flower bud/early flower/full flower/past flower/seed.

2: leaf bud/leaf unfolding/full leaf.

3: *Salix pulchra* was not sufficiently abundant to tally on the inner coastal plain and intermountain basin sites.

Food habits

In late May *Cladonia*-type lichens and *Vaccinium* (likely *V. vitis-idaea*) were the most important components of fecal samples (Table 3.29). Those species continued to be important in early June, although *Eriophorum* (likely *E. vaginatum*) was the most important item. *Eriophorum* predominated in the samples in mid June but declined sharply in late June. *Salix* increased markedly from early June to mid June and dominated the samples in late June.

There were no marked differences in diet, as reflected in fecal samples, at the two sample sites in late June. In mid June the proportion of *Eriophorum* increased from Sam Lake (50%) to King Point (61%) to Stokes Point (91%) while evergreen shrubs declined over the three sites (25%, 3%, 1%, respectively). *Salix* was highest at King Point (32%), lower at Sam Lake (16%) and lowest at Stokes Point (1%). Those variations did not appear to be precisely related to either availability or phenological stage.

Thompson and McCourt (1981) reported that *Eriophorum* (56%) and lichens (37%) were the most important components in fecal samples of the Porcupine Caribou Herd in late May and that samples were dominated by *Eriophorum* (77%) in early June and by *Salix* (99%) in late June. Although the proportions of lichen in late May and *Salix* in late June are consistent with our findings, the proportions of

Table 3.28. Availability (A, % area), utilization (U, % caribou) and selection (S)¹ of habitat types by male caribou in northern Yukon in 1983. Approximate area observed at each campsite in parenthesis.

Habitat type	Sam Lake (29 km ²) Pre-calving			King Point (26 km ²) Calving			Post-calving			Firth River (23 km ²) Movement		
	A	U	S	U	S	A	U	S	A	U	S	
Tussock meadow	51	60	0.47	82	0.71	88	97	0.11	76	80	0.05	
Wet sedge meadow	18	3	-0.69	1	-0.88	10	1	-0.87	19	17	-0.05	
Dwarf shrub Heath	21	18	-0.08	14	-0.20	-	-	-	4	2	-0.20	
Alpine barren	1	1	0.00	1	-0.05	-	-	-	1	<1	-0.83	
Alluvial willow	8	3	-0.36	1	-0.73	<1	1	0.54	<1	1	0.90	
Open white Spruce	1	-	-1.00	<1	-0.87	-	-	-	-	-	-	
Beach	-	-	-	-	-	1	<1	-0.75	-	-	-	
Late snowpatch	-	15	-	-	-	-	<1	-	-	<1	-	

1: selectivity measured as (U-A)/(U+A). Utilization values were adjusted by removing the snowpatches because their availability could not be measured.

Eriophorum are not; they appear high in relation to expected phenological stage, especially in late May. Duquette (1984) reported on diet of females of the Porcupine Caribou Herd based on fecal samples and found that in late (16-26) May samples were dominated by lichens (41%), *Salix* (22%) and evergreen shrubs (16%), with *Eriophorum* making up less than 1%. The high proportion of *Salix* is noticeably different either from that we observed (0%) or from that reported by Thompson and McCourt (1981) (0.1%). In late May, therefore, caribou of the Porcupine Herd apparently feed primarily on lichens but supplement the diet with whatever palatable green matter is available.

Summary and conclusions

In late May male caribou were distributed south of the mountains where snowmelt was more advanced than farther north. There they used tussock meadows, Dwarf Shrub Heaths and alpine barrens but avoided low-lying wet sedge meadows and alluvial willow thickets where snowmelt was slower. Diet consisted primarily of lichens and evergreen shrubs which were widely distributed in the habitat types utilized. By early June, as snowmelt progressed south of the mountains and on the eastern coastal plain, males moved northward to those areas. Intermountain basins, where snowmelt was retarded, were avoided. As the season progressed males continued to use, and avoid, essentially the same habitat types but made less use of Dwarf Shrub Heaths. They continued to feed on lichens but began to use *Eriophorum* as it came into flower. In mid June, males moved into intermountain basins as snowmelt there progressed. Caribou used tussock meadows and alluvial willow thickets as the diet shifted to *Eriophorum* and *Salix*. At the time, large aggregations of caribou formed in intermountain basins where they spent more time lying, less time walking, and had a lower rate of movement than in other periods. By late June, males began to use the western coastal plain where they used tussock meadows, wet sedge meadows and alluvial

Table 3.29. Average percentages of discerned plant fragments in fecal samples collected from male caribou in northern Yukon in 1983. Adjusted diet in parenthesis (see Table 3.14).

Food items	Pre-calving	Calving	Post-calving	Movement
Moss	8.6 (9)	4.3 (4)	2.6 (3)	0.1 (<1)
Lichens	33.9 (58)	34.9 (59)	3.0 (16)	0.3 (13)
<i>Cetraria</i> type	4.5	3.0	0.6	0.2
<i>Cladonia</i> -type	23.4	28.7	1.6	0.2
<i>Stereocaulon</i>	5.2	3.2	0.8	-
Horsetails <i>Equisetum</i>)	(0)	1.5 (2)	0.3 (<1)	0.1 (<1)
Graminoids	10.0 (10)	36.7 (37)	67.3 (67)	2.3 (2)
<i>Carex</i>	6.8	3.1	1.0	0.7
<i>Eriophorum</i>	3.2	33.6	65.8	1.5
Deciduous shrubs	(0)	2.0 (0)	16.5 (7)	95.8 (46)
(<i>Salix</i>)				
Evergreen shrubs	47.5 (18)	19.9 (9)	9.6 (5)	0.6 (2)
<i>Dryas</i>	1.5	0.7	5.0	0.3
<i>Ledum</i>	5.3	3.7	1.1	-
<i>Vaccinium</i>	40.8	14.7	3.6	0.1
Forbs	- (5)	0.6 (0)	- (2)	0.7 (37)

1: *Astragalus*, *Festuca*, fungi, *Lupinus*, *Peltigera*, *Picea*, *Poa*, *Saxifraga* and unidentified *Ericaceae* occurred at average frequencies of less than 1% in some sampling periods.

Note: There is a problem with correction factors when high graminoids and lichens and low deciduous shrubs are found in fecal fragments (see corrected calving diet).

willow thickets. *Salix*, which was common in all three habitat types, predominated in the diet. At that time, *Salix* on the coast was at a similar phenological stage to that at inland sites two weeks earlier, when it had not been used as heavily as *Eriophorum*. By late June *Eriophorum* was in seed and therefore not as desirable as a food for caribou. In late June average band size increased significantly and the rate of movement was greatest as males moved westward towards Alaska. The mean length of active/resting cycle decreased by about 35%. This sharp decrease may reflect both the high availability and high digestibility of young willow leaves.

In general, the distribution of male caribou followed the pattern of snowmelt and plant phenology and their diet reflected both preference and phenological stage of different species of plants. Activity and movements, however, were not related to snowmelt, plant phenology or diet. Rather, they appeared to follow a seasonal pattern.

Comparison of bulls and cows

Bulls are better able than cows to follow closely the progression of phenology (Whitten and Cameron 1980). In the Porcupine Caribou Herd the bulls tend to delay spring migration by at least two weeks, remaining on the winter range into May before migrating north. In the Central Arctic Herd, Whitten and Cameron (1980) reported that bulls wintering with the cows on the Arctic Coastal Plain actually move south in the spring to take advantage of earlier phenological stages available on south-facing slopes in the Brooks Range and the southern foothills.

Early to mid May is undoubtedly an important time in comparing the activities of bulls and cows. However our field investigations were made only from late May to the end of June. Fecal samples we collected in 1987, from animals wintering north of treeline, indicated that lichens drastically decline in the diet with an associated increase in evergreen shrubs and moss. This suggests that animals moving north of treeline early would face a poorer quality range (prior to snowmelt).

In the pre-calving period bulls were found in the Old Crow Pediments, a region of early snowmelt in the northern Yukon. They foraged in smaller groups and with a lower rate of movement than cows, many of which were already north of the British Mountains. These bulls are switching from a lichen dominated winter diet, substituting evergreen shrubs, deciduous shrubs and graminoids as they become available. Meanwhile the diet of cows has a characteristically high component of moss.

While cows break into smaller groups and move slowly during the calving period, bull movement increases, oriented northward to the newly open areas towards the coast. Bulls maintain their intake of lichen but rapidly replace evergreen shrubs with newly exposed *Eriophorum* flowers. The cows are still feeding on moss, graminoids and evergreen shrubs. In 1983 a good production of *Eriophorum* was recorded (Shaver *et al.* 1986). We would expect *Eriophorum* intake that year to follow the pattern documented for cows in 1981, another good *Eriophorum* year. In 1983 cows did indeed consume more *Eriophorum* than did the bulls in the pre-calving period and equal amounts in the calving period, while the bulls consumed more *Eriophorum* in the post-calving period. The major difference in their diets still remains the high amount of moss eaten by cows and of lichens by bulls. Bulls may indeed be located in areas of better lichen stands than cows or have the ability during the calving period to travel to more favourable sites.

By the post-calving period both components of the herd reduce the proportion of time spent walking, although rate of movement of the cows tends to be higher, indicating that they may be moving more while feeding. By this time the cows have switched to a diet of deciduous shrubs whereas bulls have increased their intake of *Eriophorum* at the expense of lichens. This difference in diet was not due to the late flushing of shrubs in 1983, when shrub leaf unfolding occurred as early or earlier during our study of cows.

By the movement period, the diets and activity of both bulls and cows are similar, both having switched to a predominantly shrub and forb diet, increased group size and movement rate. We would assume that neither group would be at an energetic advantage during this period because advanced phenological development is so widespread and the females are no longer limited by the movement of their calves.

By moving from the Old Crow Pediments in late May to the coastal plain and intermountain basins east of the Firth River in late June, bulls are moving from the zone of earliest snowmelt in the Northern Yukon to the area of latest snowmelt. Their high intake of *Eriophorum* heads as late as the post-calving period indicates that they must be obtaining flowers prior to anthesis. Lent (1980) noted that the coastal plain loses snow later east of the Firth River than to the west. Bulls therefore can take advantage of early phenology and their mobility and inter-regional movement allows them to track the early phenological stages for longer than the cows.

Our data indicate similar trends in the length of active and rest cycles over the four periods observed, although those cycles were significantly longer for bulls which have proportionally larger rumen volumes (White and Trudell 1980) but not proportionally larger intake rates (g per min eating), so that they have to eat for longer to fill their rumens.