Food Selection during Early Lactation by Caribou Calving on the Tundra in Quebec MICHEL CRÊTE,1 JEAN HUOT2 and LINE GAUTHIER3

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ABSTRACT. The ranges of two large caribou herds, the Rivière aux Feuilles and Rivière George herds, were sampled in June and July 1988 to compare vegetation composition. Lichens occupied more than 50% of the ground cover at Rivière aux Feuilles, whereas mosses, bare soil, and graminoids prevailed at Rivière George. Shrubs were more abundant on Rivière aux Feuilles, but the difference was not significant. Plant cover was similar whether sampling sites were selected at random or based on the presence of caribou. Within a season, diets of lactating caribou determined from analyses of rumen contents reflected the differences in vegetation cover. In June, lactating females from the Rivière George herd ate fewer lichens than those of the Rivière aux Feuilles, whereas in July their rumen contained fewer leaves of deciduous shrubs. In Rivière George caribou, graminoids compensated for the low lichen and leaf content in both collection periods; these animals exerted a high selection, particularly for lichens, which were 25 times less available but only 1.5-2 times less abundant in rumina. In July, fragments of Cladina sp. and leaves of Betula glandulosa were especially scarce in Rivière George samples. Protein contents of washed rumen samples were lower for both periods at Rivière George. This pattern of food selection by Rivière George caribou may be due both to long-term grazing of the summer range and to eco-climatic differences.

Key words: caribou, food, grazing, lactation, Quebec, Rangifer, tundra, vegetation

RÉSUMÉ. Les habitats utilisés à la mise bas et en été par deux grands troupeaux de caribous, ceux de la Rivière aux Feuilles et de la Rivière George, furent échantillonnés en juin et juillet 1988 afin de comparer leur composition. Les lichens couvraient plus de 50 pour cent du sol à la Rivière aux Feuilles alors que les mousses, le sol nu et les graminoïdes dominaient à la Rivière George. Les arbustes étaient plus abondants à la Rivière aux Feuilles, mais la différence n'était pas significative. Ces différences étaient apparentes que ce soit à des sites choisis au hasard ou d'après la présence de caribous au moment du relevé. Le régime alimentaire des femelles en lactation, tel que déterminé par l'analyse des contenus de rumen, réflétait ces différences du couvert végétal. En juin, les femelles du troupeau de la Rivière George consommèrent moins de lichens que celles de l'autre troupeau, alors qu'en juillet leur rumen contenait moins de feuilles d'arbustes décidus. Pour les deux périodes, les animaux de la Rivière George compensèrent avec des graminoïdes; ces caribous exercèrent une sélection élevée notamment pour les lichens qui étaient 25 fois moins disponibles, mais seulement 1.5-2 fois moins présents dans les rumens. En juillet, les fragments de Cladina sp. et les feuilles de Betula glandulosa étaient particulièrement rares dans les rumens à la Rivière George. La teneur en proteines des contenus de rumen lavés était plus faible à la Rivière George au cours des deux périodes. Nous suggérons que ce régime alimentaire des caribous de la Rivière George est attribuable à l'utilisation répétée de l'habitat estival et à des différences écoclimatiques.

Mots clés: allaitement, broutement, caribou, nourriture, Québec, Rangifer, toundra, végétation

INTRODUCTION

The Rivière George caribou herd in northern Quebec (Fig. 1) offers a unique situation to better understand the population dynamics of migrating caribou herds. After increasing at an annual rate exceeding 10% for many decades (Messier et al., 1988), it apparently stabilized at around 680 000 (SE=145000) individuals (Crête et al., 1989) by 1986-87 (Hearn et al., 1990). A reduction in calf production (Messier et al., 1988; unpubl. data), coupled with a slight increase in the mortality rate of adults, lowered the finite rate of increase to approximately 1.0 (Hearn et al., 1990). A deterioration in the physical condition of the females (Couturier et al., 1988) indicates that animals have suffered from inadequate nutrition in recent years; low fat reserves in fall indicate that summer range might be deficient (Huot, 1989).

In the past, the Rivière George herd used to spend the snow-free period in the vicinity of the calving area, migrate south and west to the forest-tundra and the boreal forest in autumn, and spend the winter south and west of Kuujjuaq. Since the early eighties, the herd has initiated its fall migration earlier than previously and has expanded its range west to Hudson Bay, occupying on an annual basis around 600 000 km² of range (Messier et al., 1988).

At the outset of the study, our knowledge of the Rivière aux Feuilles herd was limited: the herd exceeded 100 000 animals in 1986 and calved 7-10 days earlier than the Rivière George herd (Crête et al., 1987) in an area with earlier snow melt (Crête and Payette, 1989). The calving ground of the Rivière aux Feuilles herd was first located in 1975; preliminary observations of the spring and summer range, in 1987, suggested that the forage was more abundant and lightly used as compared to the Rivière George range. Limited telemetry data suggest that the Rivière aux Feuilles herd spends the summer north of the tree line and partly migrates south of it in winter, west of Kuujjuaq. Recently, its winter range has often overlapped with that of the Rivière George herd.

In this paper, we compare plant cover on the calving grounds of the Rivière George and the Rivière aux Feuilles herds. Moreover we report on the diet of lactating females immediately after the peak of parturition and one month later. We have restricted our study to lactating females to reduce intra-group variability and because this segment of the population is most likely to influence the population dynamics.

STUDY AREAS

The field work was centred on the calving grounds and on the summer range of lactating females of the two herds. Pregnant females from the Rivière George herd have consistently used the plateaus east of the Rivière George for calving during the last decade (Fig. 1). The area consists of a tundra habitat, at an altitude ranging between 500 and 700 m above sea level (ASL). The Rivière aux Feuilles herd calves in the middle of the Ungava peninsula, on a gently rolling tundra plateau, averaging 325 m ASL (Fig. 1).

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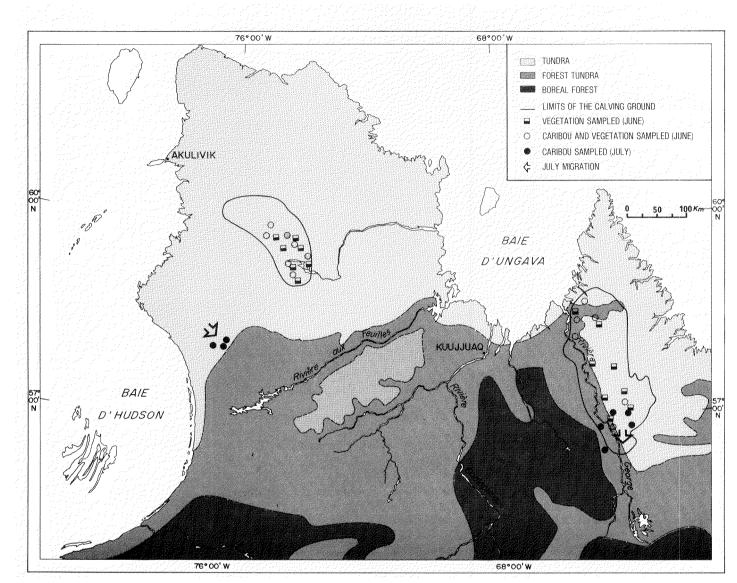


FIG. 1. Location of the 1988 Rivière George (east) and Rivière aux Feuilles (west) caribou calving ground in northern Quebec, and areas where ground cover and animals were sampled. Biome distribution was adapted from Payette (1983).

The Rivière George calving ground receives annually, on average, 500-600 mm of precipitation, with a snow fraction varying between 35 and 40%; the snow fraction is the same on the Rivière aux Feuilles calving area, but total precipitation reaches 400-500 mm (OPDQ, 1984). Mean annual temperature is apparently similar in both areas, colder than -7.5°C (OPDQ, 1984). Greater snowfall results in later snow melt in the Rivière George area than in the other calving ground (Crête and Payette, 1989).

METHODS

The Rivière George calving ground was mapped by a lowlevel reconnaissance flight carried out on 11 June 1988 as the first step of the herd census (Crête *et al.*, 1989). Location of radio-tagged caribou and helicopter flights helped to complete the mapping. The Rivière aux Feuilles calving area was delineated from radio location of 19 females at the beginning of June, during the peak of parturition. The location was very similar to that of 1986, as determined by a reconnaissance flight.

Through two-stage sampling, we estimated the percentage of vegetation ground cover at each calving area. Sampling occurred on 17-18 and 21-22 June at the Rivière aux Feuilles and Rivière George areas respectively. Lichen, bryophyte, graminoid and shrub coverage was estimated on sampling plots systematically allocated over the calving ground and visited by helicopter. Ground cover was also measured at sites where caribou were collected. Fourteen sites (primary units) were sampled in each calving ground (Fig. 1); due to inaccessibility, only two-thirds of the Rivière aux Feuilles area could be covered. At each site, four 4 m transect lines (secondary units) were set at a 90° angle; the orientation of the first one was randomly selected, and each transect line was started 5 m away from the point centre of the site. The location of systematically allocated plots was first established on 1/ 250 000 topographic maps; once flying in the general area at low altitude, a stopwatch served to randomly set the exact sampling point. In the other cases, the sampling points were located where caribou were first observed. Along each transect line, we recorded the total number of cm (to the nearest 2 cm)

where each plant group dominated; we also included the categories: dead lichens, dead mosses, barren soil, stones and water. The dead lichen class refers to areas where only fragments of podetia were present on bare ground. As forbs never covered more than 5% of the ground in any transect, this class was not included.

Seven lactating females were harvested on 17-18 June at the Rivière aux Feuilles and 8 at the Rivière George area on 21-22 June. We tried to cover the whole calving grounds, although the distribution of animals at the time of sampling influenced the sampling allocation (Fig. 1). Moreover, 8 and 11 lactating females were sampled between 21-24 and 25-28 July from the Rivière aux Feuilles and Rivière George herds respectively. Radio-tagged animals helped to find groups of caribou during this sampling period (Fig. 1).

Approximately 2 L of rumen content were collected from each animal in the anterior and the posterior part of the organ. The sample was washed through a 2 mm sieve within 10 h of collection and preserved with 10% formaldehyde until analyzed. At the laboratory, each sample was washed again through a 2 mm sieve, and a fraction of the material was thinly spread in a tray. Its composition was estimated with point sampling (Chamrad and Box, 1964): 100 points were systematically allocated per sample. Fragments were assigned to the following categories: lichens, living or dead graminoids, living or dead leaves of shrubs, twigs of shrubs, bryophytes, unknown and blank (no specimen at this point). In addition, the species, the genus or the family of sampled specimens was determined whenever identification could be readily done. Another subsample was used to determine protein content. This fraction (approximately 100 g fresh) was washed under tap water and dried to a constant weight at 40-45°C. The dry material was ground in a Wiley Mill to pass through a 20 mesh sieve. Nitrogen content was determined with an auto-Kjeldahl analyzer (Kjell-Foss, Model 16210), following AOAC (1984:154) procedure. Values were corrected to 100% dry matter, and protein content was estimated to Nx6.25.

Ground cover at each calving area was compared using a nested analysis of variance. The location of calving grounds and the allocation of the sampling sites (random vs. presence of caribou) served as factors: the dependent variables tested were the number of cm occupied by each cover type. As there were four replications per sampling site, the error term used was "replication nested in location and allocation." Mean (and standard error) cover type length per category was estimated using a two-stage sampling procedure (Cochran, 1977:274). Means and standard errors were divided by 4 to express the results as percentage (number of cm • m⁻¹).

The botanical composition of rumen contents and protein concentration were also compared by means of an analysis of variance. Herd and month of collection served as factors; the number of observations per plant category or percent protein served as dependent variables. Composition of rumen contents was expressed as mean number of occurrences per caribou, which is equivalent to a percentage. The linear relationship between protein content and food items in the rumen was evaluated with regression analyses. In both analyses of variance, the model included an interaction term. The procedures GLM and REG of SAS (SAS Institute Inc., 1985) were used for the analyses.

RESULTS

The composition of ground cover measured at sites systematically allocated on calving areas and at places where caribou were observed did not differ significantly (P>0.05), although the caribou tended to avoid stoney areas (P=0.056). Ground cover data were then pooled by calving area (Table 1). Striking differences were observed between the two places: lichens covered more than half of the ground in the Rivière aux Feuilles area, while they were almost absent on the Rivière George calving ground. On the other hand, graminoids, mosses, dead lichens and bare soil were significantly (P<0.05) more abundant at the Rivière George calving area than at the other location. Abundance of erect (mostly Betula glandulosa and Salix sp.) and creeping (mainly Vaccinium sp; Salix sp.) shrubs was not systematically recorded, but the former were almost absent on the Rivière George calving ground. Forage plants as a whole (shrubs, lichens, graminoids) covered 78% of the ground at the Rivière aux Feuilles calving area, as compared to 31% for the Rivière George area.

TABLE 1. Percentage of ground cover measured in 1988 in the calving areas used by the two large caribou herds of northern Quebec

	Line intercept (%)			
	Rivière George herd ^a	Rivière aux Feuilles herd		
Lichens ^b	2 ± 1 ^c	55 ± 7		
Graminoids ^b	19 ± 6	5 ± 1		
Mosses ^b	22 ± 4	6 ± 2		
Shrubs	10 ± 3	18 ± 4		
Dead lichens ^b	9 ± 4	0		
Dead mosses	3±3	0		
Bare soil ^b	22 ± 5	3±1		
Stones	11 ± 3	12 ± 4		
Water	3 ± 2	1±1		

^a 8 and 7 sampling sites were systematically allocated on the Rivière George and the Rivière aux Feuilles calving area respectively; 6 and 7 were selected based on the presence of caribou respectively.

^b Significant difference between the two calving grounds for this item (P<0.05). ^c SE.

By 20 June, most females with calves observed in the Rivière George herd were converging toward the northwest limit of the calving ground, which influenced the distribution of the sampling (Fig. 1). At the same period, many females had probably already left the southern half of the Rivière aux Feuilles calving area, judging by the moderate density of animals observed at the time of collection. At the end of July 1988, most caribou had left the northern portion of the Rivière George calving ground and were migrating southward at an approximate rate of 30 km per day (Fig. 1). The herd was following the same migration pattern as in July 1987, but one week later. In general, mature males were rare in the groups sampled at Rivière George. In contrast, all age and sex categories were well represented in the groups of caribou observed in the Rivière aux Feuilles area. The herd had completely left the calving ground and was migrating southeast (Fig. 1). Due to fuel shortage, we could sample only the most accessible groups, although we could locate about one-third of the radio-tagged animals. The rest of the herd appeared to be to the northwest of the first groups.

Plant material found in rumina differed significantly according to herd and to month of collection (Table 2). Lichens and leaves of shrubs were more abundant in rumen samples from the Rivière aux Feuilles animals than in specimens

TABLE 2. Percentage of	plant material identified in the rumen contents and overall	percent protein

	June		July		Analysis of Variance (P=)		
	RG ^a (n=7)	RAF ^b (n=7)	RG (n=11)	RAF (n=8)	Herd	Month	Interaction
Lichens	11 ± 2 ^c	25 ±4	8 ± 3	11 ± 2	< 0.01	<0.01	0.06
Graminoids							
living	18 ± 5	10 ± 2	27 ± 4	10 ± 2	< 0.01	0.23	0.27
dead	43 ± 2	49 ± 4	7±1	3 ± 1	0.64	< 0.01	0.03
Leaves of shrubs							
living	\mathbf{T}^{d}	Т	37 ± 3	54 ± 2	0.02	< 0.01	< 0.01
dead	7 ± 2	5±1	3 ± 0.5	1 ± 1	0.10	< 0.01	0.80
Twigs	3 ± 1	2±1	8 ± 1	12 ± 1	0.12	< 0.01	0.03
Bryophytes ^e	8 ± 2	2±1	2 ± 0.3	Т	< 0.01	< 0.01	0.01
Unknown	3 ± 1	4 ± 1	5±1	5 ± 0.5	0.44	0.20	0.61
Blank	7 ± 0.4	5 ± 1	4±1	5 ± 1	0.24	0.05	0.07
Protein content	8.2 ± 0.5	9.4 ± 0.5	15.1 ± 0.8	17.3 ± 0.7	0.03	< 0.01	0.49

^a Rivière George. ^b Rivière aux Feuilles.

°SE.

^d Trace, <0.5%. e Mostly mosses.

collected in the other herd. On the other hand, living graminoids and bryophytes were observed more often in samples from the Rivière George herd than in those from the other herd. Lichens, dead graminoids, dead leaves and bryophytes were more common in June than in July samples, whereas the contrary was true for living leaves and twigs.

Difference in food composition resulted in higher protein concentration in rumen contents of animals from the Rivière aux Feuilles herds (Table 2). On the other hand, differences in protein content between areas in July were almost twice those of June. Protein content was positively related to abundance of living leaves and twigs, but not to graminoids in the rumen (leaves: R²=0.82, P<0.001; twigs: R²=0.41, P<0.001; graminoids: R²=0.01; P=0.45; N=33).

Many lichen and shrub fragments could be identified to the genus in the rumen contents (Table 3). Because of the nature of the data (many empty cells, possible bias and reduced sample size), we did not carry out statistical tests to compare herds. Nevertheless, the genus Cladina was dominant among lichens in both herds in June; in July, it continued to dominate in the rumen content of the Rivière aux Feuilles animals, while cf Cornicularia was second in importance. During the same period, caribou from the Rivière George herd could apparently find mostly Cetraria sp. lichens. In July, leaves of Betula glandulosa completely dominated rumen contents of the Rivière aux Feuilles caribou, while leaves of Vaccinium uliginosum were almost as abundant as those of Betula glandulosa for the Rivière George herd.

DISCUSSION

These results indicate that major differences exist in the quality of the calving and summer ranges occupied by the Rivière George and Rivière aux Feuilles caribou. On the Rivière George range forage plants covered only 31% of the ground, as compared to 78% for the Rivière aux Feuilles range. On the former range, patches of dead lichens were also frequently encountered. This is probably sufficient to explain the poor quality of the lactating females reported for the Rivière George caribou in fall (Huot, 1989). However, with our limited data, it is not possible to determine if this situation

TABLE 3. Percentage of lichen and shrub fragments identified in the
rumen contents

	Ju	ine	July		
	RG ^a (7 ^b)	RAF ^c (7)	RG (11)	RAF (8)	
Lichens	(n=44 ^d)	(n=165)	(n=52)	(n=64)	
Alectoria ochroleuca	0	3	27	16	
Cetraria (brown) sp.	16	1	38	0	
Cetraria nivalis	5	2	6	11	
Cladina sp.	59	61	13	45	
Cladonia sp.	5	0	4	0	
cf Cornicularia sp.	2	Te	2	28	
Nephroma arcticum	0	0	2	0	
Sphaerophorus globosus	7	0	0	0	
Stereocaulon sp.	0	33	6	0	
Umbilicariaceae	7	0	2	0	
Shrubs	(n=1)	(n=1)	(n=75)	(n=120)	
Arctostaphylos alpina		_	1	0	
Betula glandulosa			48	83	
Larix laricina	_	_	1	0	
Ledum decumbens		_	1	0	
Salix herbacea	_		1	2	
Salix sp.	-	_	0	13	
Vaccinium uliginosum	_	_	43	0	
Vaccinium vitis-idaea		_	4	3	

^a Rivière George.

^bNumber of animals sampled.

^c Rivière aux Feuilles.

^dNumber of specimens identified.

^eTrace, <0.5%.

has existed for a long time and what role caribou grazing has played in bringing about the differences. We believe that in the Rivière George area the presence of dead lichens probably results from past grazing by caribou. Some patches of bare soil may also be due to grazing, but some of the mineral soils on exposed sites may never have been colonized by vegetation. The abundance of mosses in the Rivière George area is probably not the result of caribou, although Klein (1987) reported that grazing by caribou favoured mosses on St. Mathew Island, Alaska. Most of the mosses were observed on seepage sites, which are usually favourable for their developement (Hedderson and Brassard, 1986; Brassard, pers. comm. 1989). The effects of caribou grazing on graminoids is also difficult to assess. In Greenland, Thing (1984) observed that heavy grazing pressure stimulated vegetative expansion of graminoids, which replaced shrubs. Similar conclusions were reached in Alaska based on simulated grazing (Chapin, 1980). On the Rivière George calving area, graminoids appeared to resist to grazing and trampling, but detailed studies are necessary to determine if caribou is significant in the dynamics of graminoid communities.

Caribou apparently attempted to maintain a high-quality diet in the Rivière George area by increasing selection for some rare food items. Lichens were roughly 25 times less abundant there than on the Rivière aux Feuilles calving ground, but they were only 1.5-2 times less frequent in the diet. However some lichens could have been consumed before the caribou reached the calving ground in June, since Cladina sp. lichens were almost absent in the Rivière George area. Increased selection also probably occurred for deciduous leaves, but the difference between availability and consumption was less obvious, possibly due to the use of vegetation cover as an index of available biomass. On the Rivière George sites, most deciduous shrubs were prostrate Vaccimium uliginosum, offering less biomass per unit of cover than erect shrubs such as Betula glandulosa or Salix sp. Graminoid consumption was higher in the Rivière George area, where lichens and erect shrubs were rare. As a consequence, the protein level of washed rumen content was 1-2% higher in samples collected in the Rivière aux Feuilles area. This difference may appear biologically meaningless; however, because of the relatively low protein content of lichens and the fact that the Rivière aux Feuilles rumens included larger percentages of lichens in both June and July, the relative quality of the vascular plants consumed by the Rivière aux Feuilles caribou must have been considerably greater than those consumed by the Rivière George animals.

The Rivière George herd recently changed the timing and pattern of its migrations. Since the beginning of the eighties, most animals have left the tundra plateaus east of the Rivière George, in late July or August, as compared to September and October in the seventies. A decline in hunting success along the Rivière George reflected this shift. Moreover, adult males no longer join the females on the plateaus in July and, apparently, spend the summer in the forest-tundra, west of the calving ground. Finally, females did not leave their winter range in the boreal forest before late May in 1988, and they quickly migrated to the calving area within a few weeks. We think that all these shifts result from the deterioration of the summer range.

As compared to the Rivière aux Feuilles herd, caribou from the Rivière George herd can utilize a limited amount of tundra habitat close to the calving ground (Fig. 1). To the south and west the forest-tundra dominates, while the alpine tundra of the Torngat Mountains to the north may offer limited forage. The drive for female caribou to give birth on the tundra and to spend the first 5-6 weeks of lactation in this biome must be very high, considering that better foraging conditions probably prevail in the adjacent forest-tundra. Migration to the tundra appears to be a selected strategy in caribou for the protection of newborn calves from predators (Fryxell *et al.*, 1988). The use of the forest-tundra by many males and barren females during the same period supports this explanation.

If the forage availability on and around the calving ground is responsible for the recent leveling off of the Rivière George herd (Crête et al., 1989; Hearn et al., 1990), the future of the herd should be different whether the limiting factor was lichens early during the growing season or leaves a little later on. Because of their slow recovery (Klein, 1987), lichens could favour demographic cycles (Messier et al., 1988). Fluctuations around KCC (MacNab, 1985) may be of less amplitude if deciduous leaves are the main regulating factor, since response to grazing relief should be faster for shrubs than lichens, if tundra shrubs behave as do those of the boreal forest (e.g., Bédard et al., 1978). We think that leaf rarity in July possesses the greatest potential as a regulating factor. Ungulate birth is synchronized with the spring green-up in northern latitudes, because the emergent forage is rich in protein and digestible energy (Thing et al., 1987; Klein, 1989; Renecker and Hudson, 1988). Adequate protein content of the forage is necessary for the calf to grow normally during early lactation (Smith et al., 1975; Sadleir, 1980) and for females to restore their musculature. In our samples, protein content of the forage was mostly related to leaf consumption. The Rivière George caribou herd has suffered from negative protein balance during winter (Huot, 1989), as lichens make up the bulk of the diet during this season (Gauthier et al., 1989). This negative balance may last through the first month of lactation. Lichens are poor in protein (Luick, 1977) and certainly cannot replace green vegetation during lactation. Detailed studies on the interactions between caribou and its forage on the Rivière George area are necessary to better predict the future of the herd.

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