BEHAVIOUR AND RANGE USE PATTERNS OF CARIBOU ON THE BEVERLY CALVING GROUND, N.W.T.

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ABSTRACT

The exploration for minerals on the tundra ranges of migratory barren-ground caribou (*Rangifer tarandus groenlandicus*) raised concerns about the potential effects of these activities on the well-being of caribou, especially on cows and calves. As a result, the Department of Indian Affairs and Northern Development implemented the Caribou Protection Measures in 1978. These measures limited the activities of mining companies exploring for minerals just before and during the calving and post-calving periods of the Beverly and Kaminuriak herds (15 May - 31 July). As an initial step to evaluating the Caribou Protection Measures and to develop appropriate methodology for measuring some behavioural responses to man-induced disturbance, we field-tested a sampling design for recording undisturbed behaviour of cow-calf pairs on the Beverly calving ground in 1981. Activity budgets and the frequency of events that reflect the strength of the cow-calf bond and that may be influenced by or indicative of disturbance, such as nursing and aggressive acts were recorded between 2-23 June. Patterns of range use in relation to snow melt and plant phenology were recorded. We emphasized rigorous definitions of behaviour categories and readily detectable classifications of range types under field conditions to reduce observer errors and to ensure repeatability. To be able to recognize behavioural responses to disturbance and to evaluate some of the short-term effects of human activities on cows and calves on the calving grounds, it is necessary to use the same study design during sampling periods involving exposure to foreign stimuli (helicopter landings and human activity on the ground). Findings and interpretations are preliminary and subject to change upon further analyses and evaluations.

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INTRODUCTION

Traditional calving grounds of migratory barren-ground caribou (*Rangifer tarandus groenlandicus*) are central to the social structure of each herd and, thus, are of paramount importance to caribou (Lent 1966, Klein 1970, Calef 1981). Every year the parturient cows return to their traditional calving grounds to give birth. There, during the first days of the newborn calf's life, the cow-calf pair forms a strong mother-young bond that is critical to the survival of the calf. Calving and post-calving are also the times when lactating cows face their highest energy output and nutrient intake demands, and when critical early growth of calves occurs, which will subsequently influence their chances of survival. Any disturbance that reduces foraging and disrupts the continuing formation and strengthening of the mother-young bond during the sensitive calving and post-calving periods is potentially detrimental to calf survival and to the long-term well-being of the caribou population. The definition of "disturbance" is a contentious and complex issue. In this report we are using disturbance in the sense of the introduction of man-induced, novel stimuli in the animal's environment.

Concerns have been raised about the consequences of human activities on cows and calves on their traditional calving grounds. In 1978, the Federal Department of Indian Affairs and Northern Development (DIAND), with the advice from the NWT Wildlife Service, developed and implemented the "Caribou Protection Measures" that were designed to restrict land-use operations in the areas used during calving and post-calving by the cows of the Beverly and Kaminuriak herds (Clement 1982). DIAND also recognized the need for research into the potential effects of human activities on caribou and, in 1980, funded the Northwest Territories Wildlife Service to "conduct disturbance studies".

The Caribou Protection Measures were based on the professional opinion and judgement of the biologists advising DIAND, but there were few relevant studies available to substantiate those opinions and judgements. Descriptions of the effects of human activities on caribou were anecdotal which is not to say that they were not true, but simply untestable and unrepeatable, and, therefore, could be easily disputed. The need to develop a scientific basis for the Protection Measures has prompted us to design a study that would allow us to start an evaluation of the Protection Measures in terms of documenting some effects of man's activities on caribou during the calving and early post-calving periods. This approach is necessary before we will be able to better review each individual aspect of the Protection Measures, such as whether the boundaries of the Caribou Protection Areas can be altered or the period during which the Caribou Protection Measures apply should be modified.

To better evaluate the Caribou Protection Measures it is necessary to document some effects of human activities on the calving grounds and, if possible, to assess their potential impacts on the well-being of the caribou population. We were limited to using behavioural responses, as means for documenting effects of disturbance, for three main reasons. Firstly, the state of the art for describing physiological responses is not yet advanced enough for general application (Anonymous 1980). Secondly, the strong local community feelings against handling caribou for the purposes of marking have to be acknowledged. The inability to monitor known individuals prevents us from looking at potential long-term effects of disturbance on such parameters as movements, productivity, etc. Our inability to measure effects does not, however, in any way detract from their significance. Even minute changes in population parameters may have accumulative impacts on a population. Thirdly, we have a professional responsibility to design and implement studies which do not include extreme levels of disturbance particularly during the calving period. It would be difficult to study responses if the caribou galloped out of sight but more importantly, less dramatic responses, such as changes in foraging patterns, may have just as an important effect on caribou biology as extreme responses. The first step is to document whether, indeed, there are behavioural changes after exposure to a controlled disturbance.

During the first year (1980) in this 3-year study, descriptions of environmental characteristics of the calving grounds of the Beverly, Bathurst and Kaminuriak herds were compiled from the literature and limited field work (Fleck and Gunn 1982). In 1981, we were interested in developing a sampling technique for describing certain behaviour and range use patterns of cow-calf pairs under "natural" or undisturbed conditions. Descriptions of how caribou use their calving grounds will assist our understanding of some of the reasons behind this traditional use. By developing a sampling technique that is repeatable under experimental conditions, we should be able to recognize changes in behaviour and some of the short-term effects of human activities. This recognition of behavioural responses to human activities has applications elsewhere in studies of man-induced disturbance and caribou, as well as in beginning to evaluate the basis for the Caribou Protection Measures.

STUDY AREA

Our study area was a segment of the northern portion of the Beverly calving grounds (Fig. 1). Based on 11 years of data between 1957-80, Fleck and Gunn (1982) showed considerable overlap between successive years in the use of this area for calving by Beverly cows. In comparison, use of the southern portion (south of the Thelon River) has been less regular and occurred primarily in years when the spring migration of pregnant cows was delayed by deep snow (Fleck and Gunn 1982). We used Fleck and Gunn's (1982:2) definition; where a "calving ground" is an area where parturient cows concentrate during calving in any one year, and "calving grounds" are all areas where parturient cows of a herd have been known to concentrate. Thus, the 1981 calving ground was located on the northern portion of the Beverly calving grounds.

The northern portion of the Beverly calving grounds lies on sedimentary deposits within the Canadian Shield. The flat-lying sandstones form a smooth surface that is overlain by various glacial landforms, such as eskers and drumlins. Drainage patterns are poorly developed in the rolling topography resulting in numerous lakes. Snow melt on the northern calving grounds is characteristically late and often over 70% of the area is still covered with snow at the initiation of calving in early June (Fleck and Gunn 1982).

The Thelon River, that divides the Beverly calving grounds into a southern and northern portion, also forms the continuation of a border between two phytogeographic subdivisions (Gubbe 1976)

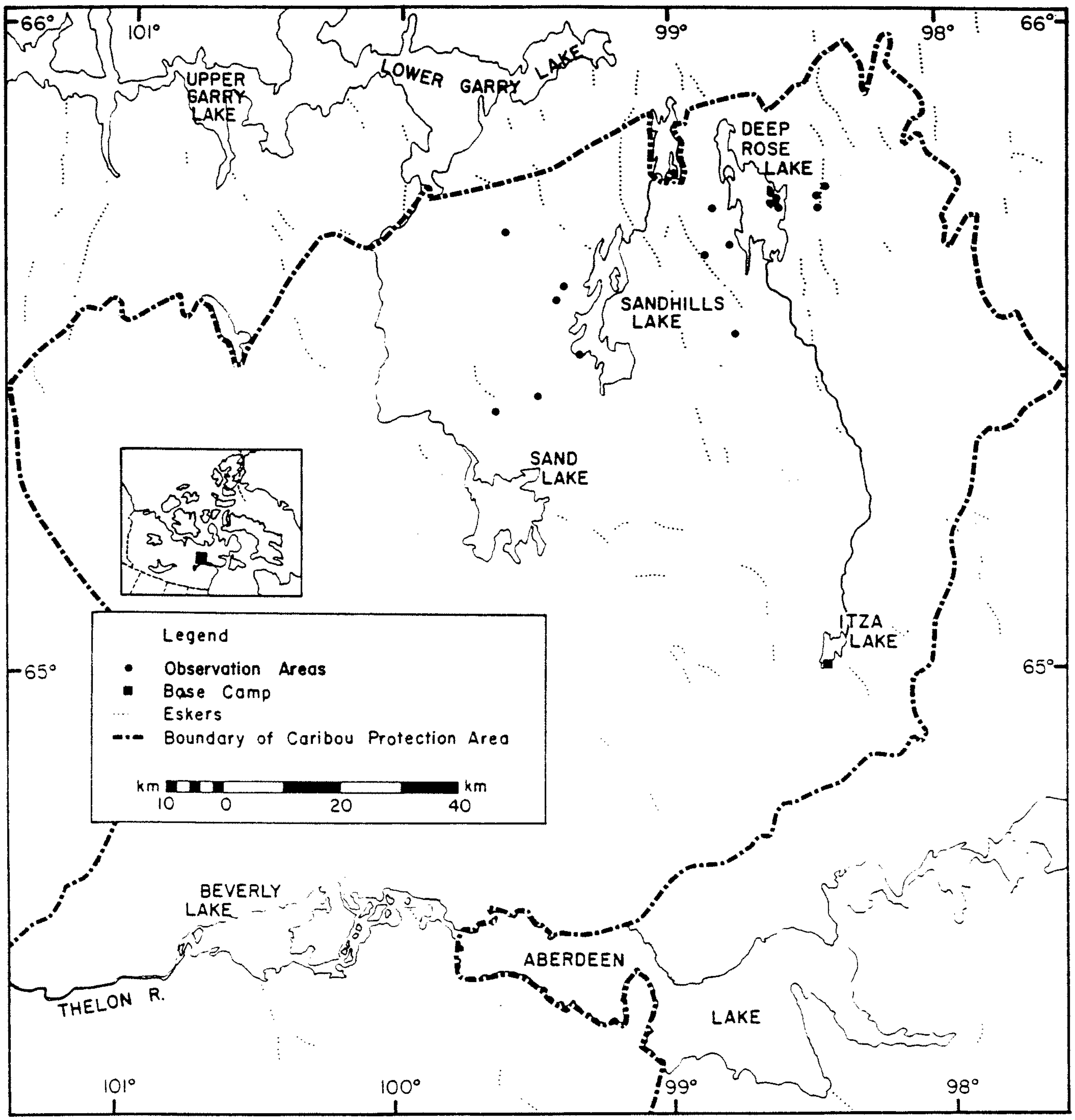

Figure 1. Locations of sampling areas for behavioural observations of caribou within the Protection Area of the Beverly caribou herd, 1981.

characterized by the presence or absence of phanerophytes (shrubs taller than 30 cm). On the northern portion of the calving grounds phanerophytes are absent. Lichen communities dominate the xeric and mesic ridge areas where prostrate shrubs, such as Vaccinium vitis-idaea and Ledum decumbens, are also found. Mosses and various graminoids (primarily Carex spp.) dominate the more hydric lowlands.

The parturient cows usually arrive on the Beverly calving grounds at the end of May (Darby 1978, 1980; Cooper 1981). Most cows give birth during a 5-7 day period; calving often extends from about 31 May to 15 June, with a peak between 4-10 June (Fleck and Gunn 1982). In 1980, Gunn and Decker (1982) estimated that about 47 000 caribou (1-yr and older) were within an area of 5 300 km^2 on the northern portion of the Beverly calving grounds. They observed no caribou on the southern portion of the calving grounds during reconnaissance surveys in 1980. The post-calving aggregations usually leave the northern portion of the calving grounds during July (Darby 1978, 1980; Cooper 1981).

METHODS

Study Design

Our intent was to develop a sampling technique for describing responses of caribou to some of man's activities on the calving grounds. A recognition of behavioural responses to man-induced disturbance requires a basic understanding of how caribou use their traditional calving grounds under "natural" or undisturbed conditions. An important criterion in developing a design for collecting baseline information on undisturbed behaviour was to make the design repeatable during a disturbance situation. This would enable comparisons between the observed results and those expected on the basis of information from undisturbed animals.

We focused on describing behavioural parameters of cow-calf pairs which could be uniformly recognized by all observers. We selected events that may indicate or be influenced by man-induced disturbance and that reflect characteristics of the mother-young bond (eg. nursings and aggressive acts). To document less obvious changes in behaviour, we recorded activity budgets (states) which reflect energy balance and may indicate the general well-being of cow-calf pairs. Both states and events represent relatively undramatic responses to man-induced disturbance and could be monitored by stationary ground observers during a controlled experiment that included a disturbance situation. To better understand how caribou use the calving grounds, we recorded patterns of range type use in relation to snow melt and plant phenology.

To make the design repeatable we provided rigorous definitions of the different behavioural categories. Descriptions of behaviour and range use patterns were quantified during predetermined, systematic sampling periods to avoid subjective interpretations and to facilitate data analysis. We emphasized collection of quantitative data that were necessary to allow analysis of variation between observer teams and to provide estimates of expected frequencies of behavioural events and activity budgets during undisturbed conditions.

We sampled caribou behaviour using two-person ground teams at stationary points of observation. We used this area sampling approach, having observers at fixed points rather than observers following caribou, to reduce the possible effects on caribou behaviour from the presence of the observers. As we were interested in describing undisturbed behaviour, it was imperative that the observers remained inconspicuous throughout the sampling period.

Activity Budgets

Activity budgets describe the proportion of time that animals spend in different maintenance activities or physical states that are usually behaviours of relatively long duration. We recognized and defined the following categories:

Bedded - a caribou was bedded when it was in a resting or ruminating position either upright on its brisket or lying on its side and showed no apparent signs of alertness to changes in its environment. Bedded caribou could and would exhibit alertness (head-high, head-low, or head-tracking alert positions) to undiscernible or observer-detected stimuli.

Foraging - a caribou was foraging when it was feeding while standing in place or walking with muzzle touching or nearly touching (head below knees) ground, and showing no apparent signs of alertness to changes in its environment. Foraging included nursing (suckling) and feeding-related activities such as visual or olfactory search for forage and cratering in snow for forage. A caribou was not considered as foraging if it assumed the head-high alert position; however, it was considered as foraging if it assumed a head-low or head-tracking alert position in the absence of observer-detected stimuli. A caribou was not considered as foraging if it assumed an alarm stance or exhibited alarm locomotor movements (walk, trot, or gallop).

Walking - a caribou was walking when it was moving in a relatively slow gait with head elevated above the knees and showed no apparent signs of alertness to changes in its environment. The "walk" is the slowest gait employed during feeding activities and unharrassed movements. The "walk", usually at a faster or more deliberate tempo, is also the slowest gait during periods of restrained flight behaviour.

Standing - a caribou was standing when it remained stationary with head elevated above the knees and showed no apparent signs of alertness to changes in its environment. A standing caribou could also exhibit alertness (head-high, head-low or head-tracking alert positions) to changes in its environment. A standing caribou could and would assume an alarm stance in the presence of undiscernible or observer-detected disturbing or harassing stimuli, but it could not perform alarm locomotor movements.

Trotting - a caribou was trotting when it employed a two-timed symetrical gait of medium speed. Trotting occurred during periods when no discernible alarm stimuli were present or during periods of apparently restrained flight behaviour to observer-detected stimuli.

Galloping - a caribou was galloping when it employed a rapid asymetrical gait during periods when no discernible alarm stimuli were present or during periods of unrestrained flight behaviour to observer-detected stimuli.

We used scan sampling (Altmann 1974) to record activity budgets. At regular time intervals, the observers scanned a group of caribou and recorded the activity and age/sex class of each individual animal. We also recorded various environmental parameters during each activity scan (see Field Observational Techniques).

Events

Events, or behavioural reactions, are typically of short duration. We recognized and defined the following events:

Nursing - an event lasting more than 5 s from the first observed bunting (striking at the udder) by the calf until the calf removed its head from the nursing position; if bunting was not observed, especially in the case of newborn calves, initiation was defined as the moment when the calf reached the nursing position. Repeated nursings were recorded as separate events if more than 30 s lapsed between the termination of the first nursing and the initiation of the second.

Attempted nursing - an unsuccessful nursing lasting less than 5 s from the initiation of the first bunting by the calf to the active rejection of the calf by the cow by stepping away; or by pushing the calf away with her hind foot; or by turning on, head swinging at, or kicking at the calf.

Head bobbing - at least two lowerings of the head in the vertical plane with a straight or slightly curved neck of the cow directed towards the calf to induce the calf to follow (see Pruitt 1960); repeated head bobbings by a cow were recorded as a single event after the calf responded to them, provided other behaviour patterns were not interposed.

Alarm stance - a deliberate placing of one hindleg set out from the body while the caribou with an elevated head faced the alarming stimulus (Pruitt 1960, Lent 1966) or, additionally, with head raised up and down; to avoid confusing an alarm stance with a caribou trying to change its footing, the stance had to persist for a 3-s count, to be recorded as an event.

Head swing - sudden movement of the head in the lateral plane by an antlered or unantlered caribou towards another caribou that overtly responded to the movement; this was a modification of the "antler threat" and "hooking" described by Lent (1966).

Kick - downward strike with either one or two (flail) forelegs directed at another caribou.

Rush - rapid advance (at a fast walk or trot) by a caribou with ears back, muzzle extended and antlers (if present) laid back along the neck; this was a modification of the "threat pose" (Pruitt 1960).

The head swing, kick and rush were aggressive acts. We used the all-occurrence sampling technique (Altmann 1974) when we observed one or several cow-calf pairs continually over a pre-determined time period to estimate the rate of occurrence of the behavioural events. This method of sampling was useful provided observational conditions were adequate; the behaviours had been carefully defined, so that they were easily recognized; and the behaviours did not occur more often (or more rapidly) than the observers could record them (Lehner 1979).

Range Delineation and Use

An important criterion in the delineation of plant communities in this study was to describe range types that could be easily recognized both on the ground (to determine caribou use) and from aerial photographs (to determine availability). The use of these different range types by caribou could then be related to the availability of the range types on the calving ground. Such comparisons supposedly are measures of "preference" or "selection" of a range type based on the assumption that the type is used in greater proportion than its availability (Petrides 1975).

We grouped the 12 or more plant communities based mainly on similarities of the dominant plant cover in the combined communities reported for the region that includes the Beverly calving grounds (Larsen 1972, Gubbe 1976, Fischer et al. 1977, Thompson et al. 1978, Thompson 1980, Fleck and Gunn 1982). We also used topography, moisture regimes, and landforms to combine the plant communities into four major range types: Rock/Sand Barrens, Lichen Upland, Dwarf Shrub and Meadow (Table 1, Appendix A).

Selection of feeding sites by caribou on the calving grounds is undoubtedly at a much finer level than at the community or range type level, and influenced by microtopography, phenology, etc. However, a simplified description of range types is justified, if we can obtain useful data and avoid observer biases. Caribou use of range types was recorded by the scan sampling technique described earlier for activity budgets. We related observed range use by caribou to the availability of the range types on the northern portion of the Beverly calving grounds.

Table 1. Range types and their characteristics on the Beverly calving ground, 1981.

Range type	Moisture regime	Key features	Dominant plant species
Rock/Sand Barrens	xeric	-low cover of vegetation; -dominant % cover of exposed bed-rock, coarse boulder, till or pure sand;	Pogonatum dentatum
Lichen Upland (I)[a]	xeric to dry-mesic	-dominant cover of fruticose lichens; -upland sites including slopes of eskers, drumlins and coarse well-drained till plateaus;	Cornicularia divergens Alectoria ochroleuca Cetraria nivalis C. cucullata
Dwarf Shrub (II, IV)	mesic	-dominant shrub plant cover; sites include the base of slopes, draws and some gently sloping uplands;	Betula glandulosa Salix arctophila S. planifolia
Meadow	wet-mesic to hydric	-often pure stands of sedges, -sites adjacent to permanent water bodies following local drainage patterns.	Carex aquatilis C. rostrata C. rariflora Eriophorum spp.

[a] The numerals refer to the closest physiognomic types described by Fleck and Gunn (1982, Table 11). Rock/Sand Barrens were not included in their description.

Availability was estimated from the proportional coverage of range types as determined from aerial photography. Ground sampling (truthing) throughout the field period aided in subsequent interpretation of the aerial photographs.

Phenology

To better understand why caribou may use or avoid particular range types, we recorded patterns of snow melt and plant phenology. We monitored the progression of snow melt along permanent transects and ground observers also noted it in the different sampling areas.

We used permanent plots in each of the four range types to monitor plant phenological development. We based the choice of plant species selected for phenological study upon the regular occurrence of a species within the range type and its potential importance to caribou. We also attempted to include a representative of each growth form, i.e., dwarf shrub, prostrate shrub, graminoid and forb. As a result, we monitored eight species for phenological development (Table 2). In the Rock/Sand Barrens range type we examined phenology on Sand Barrens rather than on Rock Barrens as the former was the most frequent expression of this range type and supported some plant species that did not frequently occur elsewhere. We also recorded temperature, precipitation, wind speed and direction once a day.

Table 2. Plant species selected for phenological study on the Beverly calving ground, 1981.

Range type	Plant species: Scientific name	Plant species: Common name
Rock/Sand Barrens	*Vaccinium uliginosum*	Blueberry
	Ledum decumbens	Labrador Tea
	Luzula confusa	Wood Rush
Lichen Upland	*L. decumbens*	Labrador Tea
	V. vitis-idaea	Lingonberry
	L. confusa	Wood Rush
	Hierochloe alpina	Holy Grass
Dwarf Shrub	*Betula glandulosa*	Shrub Birch
	L. decumbens	Labrador Tea
	Eriophorum vaginatum	Cotton Grass
Meadow	*E. vaginatum*	Cotton Grass
	Carex spp.[a]	sedge species

a Species of *Carex* were lumped into one category.

Field Observational Techniques

We were on the Beverly calving ground from 25 May to 27 June, 1981. A base camp was established at Itza Lake (65°02' N, 98°27' W) in the southeastern part of the study area (Fig. 1). We used a Bell 206B turbo-helicopter to move the observer teams between sampling areas and occasionally to map range types or to monitor phenology.

Each of the three two-person observer teams was equipped to remain at a sampling area for 4-5 days. We attempted to select areas that had clear natural boundaries and that provided good visibility. Sampling areas varied in size but were generally kept to about 1 km^2. Distances between observers and caribou varied depending on the topography of the sampling area; during most observations the observers were sitting concealed on high ground about 0.8-1.0 km from the caribou.

Each observer team had a SBX-11 radio to communicate with the base camp and the helicopter. If the caribou moved out of the sampling area and no other animals were in sight, the helicopter was called in to move the observer team to a different location. Depending on the movement of caribou, sampling areas could be widely scattered or confined to a relatively small tract (Fig. 1). Following relocation of observers, behavioural observations were not started until at least 30 min after the helicopter had left the area or until caribou had returned to ongoing maintenance activities and exhibited no overt signs of alertness. During behavioural observations the helicopter was not to operate in the vicinity of the sampling area.

Prior to field work we used films on caribou behaviour to illustrate to the observers the different behavioural patterns that we had defined. We familiarized ourselves with existing range types during the first days of the field season, prior to the collection of data. We also selected a sampling area with caribou where all observers as one group had an opportunity to practice the scan and all-occurrence sampling techniques before data collection started.

Activity Budgets

We recorded the number of caribou engaged in different activities at regular 20-min intervals. While one observer scanned a group of caribou in the sampling area with the aid of a zoom spotting scope (15-60x), the other observer recorded the information on data forms. The following information was recorded for every scan:

(1) Date.

(2) Observer team.

(3) Time - at beginning of scan.

(4) Wind speed - measured with a Dwyer anemometer hand-held at about 1.5 m above ground.

(5) Direction - wind direction was measured relative to caribou and observers as: (a) wind from caribou to observers, (b) from observers to caribou, (c) crosswind or, (d) calm.

(6) Temperature - measured in the shade.

(7) Cloud cover - recorded as overcast (100% cover), broken (50-99%), scattered (1-49%) or clear.

(8) Location - each sampling area was given an unique identification number.

(9) Activity - recorded as bedded, foraging, walking, standing, trotting or galloping.

(10) Age/sex class - recorded as cow, calf, yearling or "other". The latter included juvenile animals (2-yr-old and older) and bulls. We made no attempt to separate parous cows from barren cows.

We recorded data on range use on the scan sampling form (Appendix B) for each caribou during the scan, (see Range Delineation and Use).

We attempted to limit the time spent on each individual caribou at a scan to 3-4 s during which time activity, age class and range use were noted. To allow scan sampling at regular time intervals and to use the time in between scans for all-occurrence sampling of behavioural events, we limited the scans to include no more than 100 caribou per scan. If more caribou were present in a sampling area, we started each scan in the left end of the area to standardize scan sampling between observer teams and to reduce biases occurring as a result of the distribution of range types on a particular sampling area.

To document seasonal differences in activity budgets, we divided the field season into calving and post-calving periods.

The calving period roughly represented the time between the earliest and latest observed births and ended when we found no significant increases in calf:cow ratios. We also used the chronology of antler shedding among the parous cows to further separate the calving and post-calving periods.

Events

We recorded all occurrences of behavioural events during continuous 10-min observation periods that were scheduled in between scan samples. While one observer continuously watched a cow-calf pair with the aid of a spotting scope, the other observer recorded the following information for each sampling period:

(1) Date.

(2) Observer.

(3) Time - at beginning of sampling period; time was also noted when an event occurred and when an animal bedded or disappeared out of view.

(4) Number - the number of cows and calves under observation.

(5) Duration - the duration of time (min) cows and calves under observation were active (non-bedded) and in view; this represented the time base used for calculating rates (number of events/unit active time).

(6) Group size - the number of caribou within 10 body lengths (approximately 15 m) of observed cow or calf recorded as: (a) 0, (b) 1-5, (c) 6-10, (d) 11-15, (e) 16-20, or (f) 20+.

(7) Group composition - the age and sex category of caribou within 10 body lengths of observed cow or calf, recorded as: (a) cows, (b) calves, (c) yearlings, (d) juveniles, (e) 1+2, (f) 1+2+3, (g) 1+3, (h) 1+3+4, or (j) 3+4. Both group size and composition were recorded at the start of an observation period - if group characteristics changed during the 10-min period, the time of change was noted as were the new group characteristics.

(8) Wind direction - measured relative to observers and caribou as in the scan sampling procedure.

(9) Nursing - when a nursing occurred, the initiator and terminator were recorded -- if the observer missed the initiator of the nursing, only the terminator was recorded; complete nursings were timed and

the duration noted under "Remarks". Position of nursing was recorded as occurring from the left or right side (reverse parallel position), from the rear while standing between the cow's hindlegs or from the front with the calf standing underneath the cow's body.

(10) Nursing attempt - recorded occurrence of event.

(11) Head bobbing - recorded occurrence of event.

(12) Alarm stance - recorded occurrence of event.

(13) Aggressive acts - recorded occurrence of head swing, kick or rush; if the acts occurred together, the sequence was recorded. The initiator and recipient of the act(s) were noted as: (a) observed cow, (b) observed calf, (c) other cow, (d) other calf, (e) yearling, (f) barren cow, or (g) juvenile bulls, to separate between pairs under observation and others.

We used a separate data form for the all-occurrence sampling (Appendix B). The all-occurrence sampling technique requires observations under adequate conditions, so we selected focal pairs (cow-calf pairs under observation) that were the most readily visible to the observers. We always started with an active pair, but made no effort to repeat later observation periods with the same pair. If either pair member moved out of the field of view of the observers, we focused on the cow and terminated the calf's observational time. If both pair members moved out of view, we continued observations on another pair if they were present within 10 body lengths of the original focal pair and we noted the switch-over under "Remarks".

If several active cow-calf pairs were within the same field of view, we attempted to include them in our observations to increase sample size and thereby the "active time" base used when calculating the rates of occurrence of the different events. When observing more than one focal pair, we recorded group size and composition based on all pairs, eg. if two cow-calf pairs were under observation and no other caribou were present within 10 body lengths of either pair, group size was recored as "2" and composition as "cow-calf".

We did scan and all-occurrence sampling at regular pre-determined times; each hour starting with a 20-min interval scan sample, followed by a 10-min continual all-occurrence sample. We usually obtained three sets of data by each method during 1 h of observation. We made daily observations between 1000 and 1700 h, weather permitting.

Range Delineation and Use

We combined plant communities on the northern portion of the Beverly calving grounds into four major range types (Rock/Sand

Barrens, Lichen Upland, Dwarf Shrub and Meadow) prior to the field season. Once in the field, we attempted to further characterize the range types by recording their plant species composition and physical features such as moisture regimes. To permit collection of species composition data from a homogenous expression of each range type, we sampled vegetation at 10-m intervals along a 100-m transect and along two 50-m transects that ran perpendicular to the first at 25 and 75 m. At each sample point, we alternately placed a 10-point pin frame left or right of the transect and slowly dropped the individual pins through the vegetation; each plant species intercepted by the point of the pin was recorded. In each range type we calculated percentage cover and frequency of occurrence for each of the different species (Appendix C). These results are specific for the early part of the growing season and will likely vary as the season progresses.

To determine the relative proportion or availability of each range type on the northern portion of the Beverly calving grounds (approximately 15 000 km^2) we used black and white aerial photographs at a scale of 1:63 400. We sampled the central portion of one photograph in each stereo pair with a 10-point grid overlay on each aerial photograph. We identified the range type at each of the 10 sample points with the aid of a dissecting microscope (10x). We used 10 sample points per photograph to eliminate any errors incurred by the patterns of occurrence of the different range types. We examined reliability of the aerial photo analysis by recording all observations in a format which could be analyzed at successively smaller sample sizes. For instance, the relative proportion of range types could be calculated for a sample size one half the total by using every other sample point.

Interpretation of the aerial photographs was preceded by extensive ground sampling to permit the identification of range types from terrain features expressed as a shade, tone, texture or pattern on an aerial photograph. We drew vegetation maps for several of the sampling areas where caribou behaviour had been recorded as a further aid to aerial photo interpretation.

We recorded range use by caribou during the 20-min interval scans as the number of caribou (irrespective of age/sex class) bedded or foraging on the different range types (Appendix B). We characterized ground cover as either snow or bare. When caribou were bedded on snow or cratering through the snow cover, we did not attempt to record the underlying range type. In these cases we recorded only ground cover.

We did not attempt to record use of individual forage species by caribou. The long observation distances (0.8-1.0 km) that we used to minimize observer effects on caribou behaviour, made direct continued observations of forage use impossible. We examined some feeding areas after caribou had left the site and we collected fresh fecal samples for microscopic examinations of plant fragments as a further index of forage use. We obtained composite samples by collecting 10 pellets from 10 groups resulting in five replicates of 20 pellets each. The Composition Analysis Laboratory, Colorado State University, Fort Collins, analyzed the fecal samples for plant species composition.

Phenology

To describe the progression of snow melt, particularly with respect to topography, we used two 200-m transects 100 m apart, down a southwest facing slope located close to base camp. The transects included the entire slope and the valley bottom. We measured snow depth at 10-m intervals along the transect using an aluminum meter stick. Each observer team also visually estimated percentage snow cover in their sampling areas. Subsequent to the field season we examined snow melt patterns on the entire Beverly calving grounds using black and white LANDSAT imagery.

We examined plant phenology in seven permanent phenology plots (25x25 m) at sites close enough to base camp to be visited regularly. We located the plots in the same areas as the transects used for recording plant species composition. Four mature representatives of each selected species (Table 2) were tagged in each phenology plot. We used three Lichen Upland sites (ridge-top, southwest exposure and northeast exposure) to examine some of the variation within this extensive range type. Because of the unique nature of each small Carex-dominated draw (snow accumulation and ablation, drainage, aspect and surrounding vegetation), we also selected two plots to monitor phenological developments in an extensive lowland Meadow type. The measurements of phenological characteristics were unique for each species (Appendix D) and included visual assessment of the proportion of greening in tagged individuals, measurements of bud swell and bud break in both leaves and flowers, and the height of flowering culms, where present.

We recorded daily weather at our base camp. Air temperature was recorded at ground level using a shielded max-min thermometer. Precipitation was measured with a rain gauge (mm) or with a steel ruler (cm) for snow. Wind speed was recorded with the aid of a hand-held Dwyer anemometer. Weather data (temperature, wind speed and direction) were also collected during observations of caribou behaviour as previously described.

Data Analysis

We coded and transcribed behavioural observations directly on the data forms (Appendix B). This facilitated editing of the data to ensure that observers used the correct coding. We also edited the data files for any spurious values after the information was entered on the computer. We did data processing and analyses on a HP3000 using SPSS-Statistical Package for the Social Sciences (Nie et al. 1975).

Activity Budgets

We summed the number of caribou observed in each activity for each day and observer team. We weighed the sum for each activity over all other activities and expressed the sum as a proportion of time that caribou spent in that activity. Thus, we used proportions rather than absolute values as our basis for analysis and a sample consisted of the weighted proportions obtained by a particular team on a particular day.

Statistical analysis of scan samples, beyond simple frequency descriptions, is usually limited by the lack of independence between consecutive scans. This is particularly true for activity patterns of ruminant herbivores that are characterized by regular alternations between two main activities (bedding and foraging). By using different observer teams in different areas on different days to record caribou activity, we assumed independence between samples from each team and day of observations. If caribou activity was related to time of day, the independence assumption would be violated and we, therefore, tested for the presence of a diurnal activity pattern (see below). Prior to further data analysis, we tested the data for independence using runs tests for randomness (Sokal and Rohlf 1969); normality was tested using the Kolmogorov-Smirnov test (Sokal and Rohlf 1969).

We calculated the mean proportion of time (expressed as a percentage) spent in each activity based on differences between observations from each observer team. We tested seasonal differences in activity budgets between the calving and post-calving periods using standard t-tests. After testing for normality and independence and then using a F_{max}-test (Sokal and Rohlf 1969) to confirm equality of treatment variances, we examined differences between observer teams in an analysis of variance (ANOVA). We also used an ANOVA to test for the presence of a diurnal activity pattern. We used observation periods divided into 2-h intervals as independent variables and the proportion of time cows spent bedded or foraging over the different intervals was tested for significance. We chose 2-h intervals to reflect the duration of an average rest or active period during the calving and post-calving periods (Boertje 1981).

To test the assumption that we in fact were recording undisturbed caribou behaviour, we compared activity budgets during scans when the wind direction was from the observers to the caribou (i.e. caribou were downwind and potentially aware of the observers) with activity budgets recorded during other scans. We tested significance between the two conditions with standard t-tests.

Events

We calculated rates of behavioural events as the frequency of occurrence per unit active cow or calf time and selected 100 min as our basic time unit, eg., number of events per 100 cow-min. We initially computed rates for each 10-min observation period and tested for normality. If the data were not normally distributed, in the case of infrequently occurring events, we pooled samples on a per day, per observer, basis to avoid zero values.

We analyzed rates of nursing and attempted nursing on a seasonal basis where the calving and post-calving periods were further divided into 4-day phases. We used season rather than age as our independent variable because we could not accurately estimate the age of the calves. We examined seasonal differences as well as differences between observers in a 2-way ANOVA (Sokal and Rohlf 1969); significant effects were further analyzed by the Student-Newman-Keuls procedure (Sokal and Rohlf 1969). We analyzed the duration of nursing events on a seasonal basis using a 1-way ANOVA. We used SPSS cross tabulations (Nie et al. 1975) and the chi-square test statistic to examine the effects of season on the initiator and terminator of nursing events.

We only used acts initiated by the observed cow to calculate rates (i.e. number of aggressive acts per 100 active cow-min) although all aggressive acts involving the focal pair(s) were recorded. We analyzed the distribution of aggressive acts by group size, composition and observers using the non-parametric median test (Zar 1974) to calculate chi-square statistics. The procedure is to determine the median for all data in the different groups or categories of the independent parameter (group size, composition or observer). The distribution of events is analyzed in a 2xk contingency table where k is the number of categories and where the two rows correspond to the number of observations above or below the median. We did not include Yate's correction for continuity as it results in an unduly conservative test even with low sample sizes such as N=20 (Sokal and Rohlf 1969). We used the same test to examine the influence of wind direction on the occurrence of both aggressive acts and nursing.

RESULTS

The first cows were observed on the calving ground on 24 May 1981 (Clement 1982). Due to poor weather in late May we were not able to make our first reconnaissance flight to locate concentrations of caribou until 31 May. At that time, we found many small groups (less than 20 animals) with several newborn calves around Deep Rose Lake about 80 km north of our base camp. Most of our subsequent observations of caribou behaviour were made in the Deep Rose Lake area (Fig. 1).

We separated the field season into a calving (2-9 June) and a post-calving (11-23 June) period. We made no attempts to delineate the area used for calving by Beverly cows. Our observations suggest that the peak of calving in the Deep Rose Lake area occurred between 2-5 June. Observations on 7 and 8 June by E. Broughton (pers. comm.) around Sand Lake, about 70 km to the southwest, of many newborn calves, calving cows and cows with afterbirth suggested a later peak of calving in that area. Our last observation of calving cows was on 10 June around Sandhills Lake, about 40 km north of Sand Lake. Between 2-9 June, 35.8% of cows observed during the all-occurrence sampling (n=173) were unantlered. During post-calving the proportion of unantlered cows had increased to 79.0% (n=447). While some newborn calves may have been born during the early part of what we defined as the post-calving period (eg. 11, 12 and 13 June) we only collected 6.4% of the all-occurrence samples (n=578) and observed 5.9% of all nursings (n=288) during that period (11-13 June). Hence, the presence of newborn calves during the "post-calving" period would not likely have affected our data analyses.

During the calving period, most caribou remained scattered in smaller groups. By 16 June, we observed aggregations of several thousand caribou, some apparently composed solely and some mainly of members of nursery bands. Most caribou had left the calving ground sometime after 27 June; by 13 July few caribou were observed on the 1981 Beverly calving ground (Clement 1982).

Activity Budgets

During 220 h of behavioural observations between 2-23 June, we obtained 658 scan samples that included 49 722 "point-in-time" observations of activities of individual caribou (Appendix E). We made the majority of those observations on cows (63.1%) and calves (35.6%) while yearlings and "others" represented 0.5 and 0.8% of all observations respectively. The following text is restricted to results from only observations of cows or calves.

For each observer team and day of observation we computed the weighted proportion (expressed as a percentage) of time caribou spent in each activity. The proportion of time spent bedded, foraging and walking was normally distributed for both cows and calves (Appendix F). Time spent trotting and galloping by cows and calves as well as standing by calves was not normally distributed. We found no reason to believe that data collected on consecutive days by each observer team were not independent (Appendix F). We did not statistically test the activities trotting and galloping as they did not appear to be normally distributed, presumably due to the low proportion of time caribou devoted to these activities resulting in many zero values.

When we combined activity budgets over the calving and post-calving periods (Table 3), calves spent proportionately more time bedded than did cows (62.7% versus 36.9%, t=7.7, 44 df, P<0.05). Also, cows spent more time foraging than did calves (48.1% versus 16.1%; t=13.3, 44 df, P<0.05). Both cows and calves spent 2% or less of their time trotting and galloping. The only significant difference in activity budgets between the calving and post-calving periods was the reduced proportion of time cows spent walking during post-calving (Table 3). While not statistically significant, cows spent more time bedded during post-calving (32.8% versus 40.2%); we noted a similar trend among calves (58.5 versus 66.0%).

We examined the variability of activity budgets between the three observer teams in a 1-way ANOVA (Table 3). Only activities that were found to be normally distributed, independent and had equal variances were analyzed; hence, we did not include trotting or galloping. Differences between observer teams were not significant (P>0.05) during calving or for the combined season. There was a difference (P=0.05) between observer teams in the proportion of time cows were observed bedded during post-calving.

A diurnal pattern of activity during our periods of observation was not apparent. When we computed the proportion of time spent bedded or foraging over 2-h intervals (between 0900 and 1700), no differences in time budgets were found between the intervals (F values = 0.149 and 0.296, 3 df, P>0.05).

When testing the influence of wind direction on activity budgets, we included the activities trotting and galloping as

Table 3. Seasonal activity budgets of caribou expressed as the mean proportion of time spent in each activity, Beverly calving ground, 1981.

Season	Age	Activity	Proportion of time (%) $\bar{x}$	SD	n[a]	t statistic[b]	F ratio
Calving (2-9 June)	Cow	Bedded	32.8	12.1	20	-	0.226
		Foraging	49.4	11.9	20	-	0.610
		Walking	12.4	6.8	20	-	1.987
		Standing	4.8	2.6	20	-	1.289
		Trotting/ Galloping	0.6	-	20	-	-
	Calf	Bedded	58.5	21.0	20	-	1.770
		Foraging	16.2	13.1	20	-	0.619
		Walking	11.0	7.7	20	-	0.471
		Standing	13.5	21.1	20	-	1.806
		Trotting/ Galloping	0.9	-	20	-	-
Post-calving (11-23 June)	Cow	Bedded	40.2	15.8	25	-	3.504*
		Foraging	47.0	13.7	25	-	2.991
		Walking	7.9	4.7	25	-	1.024
		Standing	4.1	1.9	25	-	0.992
		Trotting/ Galloping	0.8	-	25	-	-
	Calf	Bedded	66.0	11.9	25	-	0.328
		Foraging	15.9	6.1	25	-	0.197
		Walking	10.6	5.8	25	-	0.676
		Standing	4.8	2.9	25	-	2.781
		Trotting/ Galloping	2.6	1.6	25	-	-
Combined (2-23 June)	Cow	Bedded	36.9	14.6	45	-1.61	2.892
		Foraging	48.1	12.9	45	0.51	2.704
		Walking	9.9	6.1	45	2.73*	1.477
		Standing	4.4	2.3	45	0.76	1.205
		Trotting/ Galloping	0.7	-	45	-	-
	Calf	Bedded	62.7	16.8	45	-1.44	1.536
		Foraging	16.1	9.7	45	0.09	0.837
		Walking	10.7	6.7	45	0.30	1.135
		Standing	8.7	14.7	45	1.74	2.712
		Trotting/ Galloping	1.9	1.3	45	-	-

a Number of days summed over each observer team.

b H_o: There is no difference between seasonal means, (1 df).

c H_o: There are no differences between observer teams, (2 df).

* Significant at 5%.

their incidences were likely to be affected if the animals were disturbed by the presence of the observers. The t-test is sufficiently robust to use, without affecting the validity of the test, even when assumptions of normality or equality of variances may not be met (Lehner 1979). The proportion of time cows and calves spent in the different activities did not vary between observations when caribou were downwind of the observers and when they were not (Table 4). While not significant, cows and calves did spend proportionately more time walking when they were downwind of the observers. In summary, the presence of stationary ground observers, at distances of 0.8-1.0 km from the caribou, did not appear to have a marked affect on activity budgets.

Events

We observed 744 cows for a total of 6464 active cow-min and 692 calves for 4329 active calf-min. Out of 578 continual 10-min observation periods, single cow-calf pairs were observed during 79.3% (452) of the sampling periods. When single pairs were observed, 19.0% (86) of the observation periods were incomplete (<10 min) as the pair bedded or moved out of sight. We switched to an alternate focal pair in 53.8% (46) of these cases. We observed more than one cow-calf pair, but never more than four pairs at any one time during 20.7% of the sampling periods. Observations of more than one pair at a time was more common during post-calving when caribou were aggregated in larger groups.

Table 4. Influence of wind direction on caribou activity budgets, Beverly calving ground, 1981.

		Wind direction						
		From observers to caribou			Other[a]			
Age	Activity	$\bar{x}$[b]	SD	n[c]	$\bar{x}$	SD	n	t statistic
Cow	Bedded	33.0	25.7	9	36.6	9.8	19	0.40
	Foraging	45.3	14.8	9	48.8	9.2	19	0.37
	Walking	15.9	16.9	9	9.5	5.0	19	-1.11
	Standing	5.0	2.5	9	4.2	2.1	19	-0.82
	Trotting	0.8	1.9	9	0.6	0.6	19	-0.21
	Galloping	0.0	-	9	0.3	1.0	19	0.84
Calf	Bedded	58.0	22.1	9	65.0	9.7	19	0.90
	Foraging	16.2	12.5	9	16.0	7.9	19	-0.04
	Walking	15.8	16.9	9	10.8	5.2	19	-0.86
	Standing	7.9	7.5	9	6.1	3.8	19	-0.69
	Trotting	1.9	1.1	9	1.3	1.0	19	-0.51
	Galloping	0.2	0.1	9	0.8	1.5	19	1.67

a Includes observations when wind was recorded as calm, crosswind or from caribou to observers.

b Mean proportion of time (expressed as a percentage) spent in each activity.

c Number of days when wind direction was recorded as indicated.

Nursing Behaviour

We pooled observations of nursings and attempted nursings on a per day, per observer basis; i.e. the number of events and active calf-min were summed by day and observer. But we analyzed observations by all six observers (two per team) separately. Both the rate of nursings and nursing attempts (number of events per 100 calf-min) were normally distributed when analyzed on a per day, per observer basis (K-S Z=0.921 and 1.157 respectively; P>0.05).

The effect of season (divided into 4-day periods) on rates of nursing was significant (P<0.05), suggesting that the mean rate for at least one 4-day period was markedly different from the overall mean (Table 5A). When adjusted for observer effects, the variation between time periods explained 29% of the observed deviation in rates of nursing. Differences between observers were not significant; only 6% of the observed deviation was explained by observer differences. In comparison, the rate of attempted nursings were not significantly affected by either season or observer (Table 5B).

The rate of nursings decreased as the calving season progressed (Table 6). The mean nursing rate during early calving (2-5 June; 12.4 nursings/100 calf-min) was higher (P<0.05) than during other periods. Nursings also occurred more frequently between 2-14 June than between 15-23 June (P<0.05). The overall mean rate of nursing between 2 and 25 June was 7.3 nursings/100 calf-min. While not significant, the rate of attempted nursings also decreased during June, as the calves grew older. However,

Table 5. Effects of season and observer on the rates of nursing (A) and attempted nursing (B) by caribou calves, Beverly calving ground, 1981.

A. Nursing rate

Source of variation	SS	df	MS	F ratio
Main effects	1003.8	10	100.4	3.706*
Season	825.0	4	206.3	7.614*
Observer	240.4	6	40.1	1.479
2-way interactions	464.0	18	25.8	0.952
Explained	1467.8	28	52.4	1.935*
Residual	1381.6	51	27.1	-
Total	2849.4	79	36.1	-

B. Attempted nursing rate

Source of variation	SS	df	MS	F ratio
Main effects	261.6	10	26.2	1.363
Season	138.3	4	34.6	1.802
Observer	141.8	6	23.6	1.231
2-way interactions	233.9	18	13.0	0.677
Explained	495.5	28	17.7	0.922
Residual	978.7	51	19.2	-
Total	1474.2	79	18.7	-

* Significant at 5%.

Table 6. Seasonal variation in the rates of nursing and attempted nursing by caribou calves, Beverly calving ground, 1981.

Period	n[a]	Nursing rate (Events/100 calf-min) $\bar{x}$	SD	Attempted nursing rate (Events/100 calf-min) $\bar{x}$	SD
2-5 June	18	12.4AC[b]	7.5	6.3E[b]	5.0
6-9 June	15	7.9BC	4.7	5.8E	4.1
11-14 June	11	7.7BC	5.4	4.7E	4.9
15-18 June	18	4.7BD	3.8	3.1E	3.2
19-23 June	18	4.2BD	3.9	3.9E	3.9
Combined	80	7.3	6.0	4.7	4.3

a Number of days summed over each observer.

b Means followed by the same letter are not different (P>0.05) and represent a homogenous subset. There are four homogenous subsets for nursing rate and one for attempted nursing rate.

the success rate appeared to decline as there were relatively more nursing attempts per successful nursing during post-calving. The overall mean rate of attempted nursings was 4.7/100 calf-min.

The distribution of nursings and attempted nursings did not seem to vary under different wind conditions (Table 7) suggesting that the occurrence of these events were not affected by the presence of the observers.

We timed the duration of 271 nursing events. The distribution of observations was normalized by a logarithmic transformation. We found no apparent differences in the duration of nursing events between periods of observation ($F=0.415$, 4 df, $P>0.05$) using the 4-day intervals. Within each time interval, the duration of nursing events varied considerably (Table 8). While the mean duration did not appear to change, at least between 2-18 June, the duration of the longest nursings decreased as the season progressed.

Most nursings occurred from the left side of the cow (52.8%, n=271); 39.1% took place from the right side. We observed 21 nursings (7.7%) from the rear and one from the front, with the calf standing underneath the cow's body. The selection of side was independent of season ($X^2=9.24$, 12 df, $P>0.05$).

Calves initiated 91.5% (248) of all nursings. Most of the nursings initiated by the cow occurred during the early part of the calving period (2-5 June) when 16.0% of all nursings (n=50) were cow-initiated. In contrast, cows terminated 76.1% (206) of all nursing observed. A larger proportion of calf-terminated nursings occurred during calving than post-calving (29.0% versus

Table 7. Distribution of bouts of nursing and nursing attempts by cow-calf pairs of caribou by wind direction, Beverly calving ground, 1981.

	Wind direction		
Event	From observer to caribou	Other	X^2
Nursing			
Above median [a]	31	170	
Below median	63	308	0.131(NS)
Attempted nursing			
Above median [a]	25	111	
Below median	69	367	0.569(NS)

a Median = 0; i.e., values "above median" represent the number of times an event occurred.

NS = not significant.

Table 8. Durations of nursing events by caribou calves during calving and post-calving, Beverly calving ground, 1981.

	Durations of nursing events (s)			
Period	n	$\bar{x}$	SD	Range
2-5 June	49	55.2	53.6	5-280
6-9 June	101	50.5	44.9	5-182
11-14 June	34	52.0	40.3	10-179
15-18 June	45	50.1	33.4	7-162
19-23 June	42	42.2	22.6	7-116
Combined	271	50.2	41.6	5-280

17.4%; X^2=4.64, 1 df, P<0.05). There was not enough evidence to suggest that the age class of the initiator or terminator of nursings was dependent on the season (P>0.05).

Aggressive Acts

The infrequent occurrence of head swings, kicks and rushes prompted us to lump these events into one category, "aggressive acts". When summed on a daily basis, the mean rate of aggressive acts was 2.0/100 cow-min (SD=1.6; n=19). There was no difference in the rate of aggressive acts between calving and post-calving (t = 0.47, 17 df, P>0.05).

The rate of aggressive acts was dependent upon both group size and composition (P>0.05). Since group characteristics were recorded during each 10-min observation period and aggressive acts occurred only infrequently, the resulting median was zero. Thus the distribution of observation periods when aggressive acts did occur (above median) was compared over the different categories of each parameter. Lower than expected rates of aggressive acts were recorded when no other caribou were within 10 body lengths of the observed cow (Table 9A). Rates were proportionately higher than expected at a "medium" group size (6-15) as indicated by the chi-square contributions. The relationship was not linear as the frequency of aggressive acts in large group sizes did not appear to deviate from the expected values; however, sample sizes were low. Due to several categories with expected values close to zero, group composition was lumped into four groups (Table 9B). Again, the largest chi-square contribution resulted from the

Table 9. Distribution of aggressive acts by caribou cows by group size (A) and composition (B), Beverly calving ground, 1981.

A. Group size

	Group size						
Rate of aggressive acts	0	1-5	6-10	11-15	16-20	20+	Total
Above median	5	39	18	16	3	1	82[a]
Below median	146	185	82	44	19	20	496
Chi-square contribution	14.7	1.9	1.2	7.7	0.0	1.5	27.0*

B. Group composition

	Group composition				
Rate of aggressive acts	0[b]	Cows	Cows and calves	Other[c]	Total
Above median	5	8	65	4	82
Below median	146	41	292	17	496
Chi-square contribution	14.7	0.2	4.8	0.3	20.0*

a Represents the number of observation periods when aggressive acts occurred; i.e., when the rate was above 0 (median = 0).

b Indicates that no other animals were within 10 body lengths of observed cow(s).

c Includes groups with only calves or yearlings, or groups with both cows and yearlings.

* Chi-square statistic significant at 5%.

relatively low rates of aggressive acts when no other caribou except the calf was close to the observed cow. When other cows and calves were present within 10 body lengths of the observed pair, aggressive acts occurred more frequently than expected.

During observation periods when a change occurred in group size and composition, aggressive acts were observed more frequently than expected ($P<0.05$) (Table 10A). A similar increase in the rate of aggressive acts was evident during periods when caribou were downwind of the observers (Table 10B). We also found differences between observers ($X^2=19.2$, 5 df, $P<0.05$) with the largest chi-square contribution coming from one observer who recorded a proportionately higher rate of aggressive acts than the others.

While rates of aggressive acts could only be calculated for cows under observation (for which we had a time base), we recorded all interactions that included the observed cow or calf, i.e. aggressive acts directed towards the observed cow or calf by other caribou were included. We recorded 264 aggressive acts, 67.8% (179) were head swings, 25.4% (67) were rushes and 6.8% (18) were kicks. Forty-two antler threats (23.5%) were followed by rushes and 2 (1.1%) followed by kicks. Most aggressive acts initiated by cows were directed towards calves (74.6% during calving and 77.5% during post-calving -- Table 11). Aggressive acts during calving were directed almost equally towards the observed cows' own calves and other calves (Table 11). The observed cows directed a larger proportion of aggressive acts during post-calving (72.7%) towards other calves than towards their own (2.6%). What appeared to be

Table 11. Seasonal variation in the initiator and recipient of aggressive acts among caribou, Beverly calving ground, 1981.

Initiator	Recipient								Total
	Calving				Post-calving				
	Observed cow	Observed calf	Other cow	Other calf	Observed cow	Observed calf	Other cow	Other calf	
Observed cow	-	22	17	23	-	2	19	56	139
Observed calf	0	-	0	0	0	-	0	5	5
Other cow	12	40	-	-	12	49	-	-	113
Other calf	0	0	-	-	0	7	-	-	7
Total	12	62	17	23	12	58	19	61	264

Table 11. Seasonal variation in the initiator and recipient of aggressive acts among caribou, Beverly calving ground, 1981.

	Recipient								
	Calving				Post-calving				
Initiator	Observed cow	Observed calf	Other cow	Other calf	Observed cow	Observed calf	Other cow	Other calf	Total
Observed cow	-	22	17	23	-	2	19	56	139
Observed calf	0	-	0	0	0	-	0	5	5
Other cow	12	40	-	-	12	49	-	-	113
Other calf	0	0	-	-	0	7	-	-	7
Total	12	62	17	23	12	58	19	61	264

aggressive acts initiated by calves were observed only during post-calving and were always directed towards other calves.

Other Events

We only observed 10 head-bobbings and 12 alarm stances during 6464 active cow-min. The overall rates were 0.15 and 0.19/100 cow-min, respectively. The low frequency of occurrence precluded any further analysis.

Range Delineation and Use

We needed 380 aerial photographs to cover the northern portion of the Beverly calving grounds. At maximum sampling intensity (n=1900; 10 sample points on 190 photographs), Lichen Upland represented 38.8% of the total area; Dwarf Shrub, 24.1%; Meadow, 12.3%; Rock/Sand Barrens, 4.0% (Table 12). Lakes and other water bodies covered 20.8% of the calving ground. Proportional coverage varied little with sample sizes over n=500.

During 658 scans we recorded 40 197 "point-in-time" observations of caribou range use (Appendix G). We computed weighted proportions (expressed as percentages) for the number of caribou observed bedded or foraging on different range types by observer team and day of observation. The proportions of caribou observed bedded or foraging on Lichen Upland and Meadow were normally distributed and independent between days of observation (Appendix H). Observations of caribou on Rock/Sand Barrens and Dwarf Shrub were not normally distributed except during post-calving when the

Table 12. Proportional coverage (%) of range types at different sampling intensities, Beverly calving ground, 1981.

Range type	Sample size					
	1900[a]	1500	500	200	100	50
Rock/Sand Barrens	4.0	3.9	3.6	4.0	5.0	6.0
Lichen Upland	38.8	38.9	39.2	36.0	31.0	36.0
Dwarf Shrub	24.1	23.4	24.6	27.0	24.0	34.0
Meadow	12.3	12.1	12.4	9.5	11.0	12.0
Water	20.8	21.7	20.2	23.5	29.0	12.0

[a] n = 10 points per aerial photograph; eg. 1900 = 10 points from 190 photographs.

occurrence of caribou on Dwarf Shrub met the assumptions of normality and independence. Less than 1% of all caribou observed used Rock/Sand Barrens, so we did not include this range type in further analysis.

Fecal samples from primarily adult female caribou contained mostly fragments of graminoids and deciduous shrubs (Table 13). Lichens and mosses occurred less frequently. We took two subsamples from each collection date to examine differences within a composite sample. Variation in percentage relative densities between subsamples and within seasons (4 and 8 June versus 20 and 25 June) made comparisons between seasons difficult.

Most caribou observed were bedded or foraging on Lichen Upland, particularly during the calving period (Table 14). During post-calving we observed a larger proportion of caribou foraging on Dwarf Shrub and Meadow than during calving but still less than on Lichen Upland. There was a significant increase ($P<0.05$) in the proportion of caribou bedded on Dwarf Shrub during post-calving. We used a Mann-Whitney U-test (Sokal and Rohlf 1969) that does not require normality or randomness to test for seasonal differences in use of the Dwarf Shrub range type (results from a t-test were similar). A subsequent decrease in the use of Lichen Upland during post-calving, particularly for foraging, was evident. There were no differences ($P>0.05$) between observer teams suggesting that range use was similar in the different sampling areas.

During calving, 94.1% (SD=12.1%) of all caribou observed were bedded and 90.5% (SD=8.6%) were foraging on snowfree ground.

Table 13. Paired comparisons of identified plant fragments from composite caribou fecal samples, Beverly calving ground, 1981. Based on 100 fields per sample.

	Percent relative densities									
Species	4 June[a]		8 June		20 June		25 June		$\bar{x}$	SD
Graminoids										
Carex spp.	12	13	16	18	38	51	16	16		
Eriophorum spp.	4	1	2	0	14	4	4	15		
Poa spp.	8	4	3	5	2	3	4	1		
Unknown grass	0	1	2	0	0	0	0	0		
	24	19	23	23	54	58	24	32	32	15.3
Forbs										
Astragalus spp.	7	0	2	4	3	2	0	0		
Saxifraga spp.	0	0	0	0	0	0	1	0		
Stellaria spp.	4	0	0	0	0	0	0	0		
	11	0	2	4	3	2	1	0	3	3.6
Deciduous shrubs										
Salix spp.	6	6	8	16	18	17	13	17		
Vaccinium spp.	19	12	34	17	15	14	17	21		
	25	18	42	33	33	31	30	38	31	7.4
Evergreen shrubs										
Dryas spp.	2	3	0	3	1	0	1	2		
Ledum spp.	4	0	2	2	3	1	2	1		
	6	3	2	5	4	1	3	3	4	1.6
Nonvasculars										
Lichen I[b]	3	0	0	2	0	1	3	1		
Lichen II[c]	10	0	12	12	4	3	24	14		
Stereocaolon spp.	0	2	1	3	0	0	0	1		
	13	2	13	17	4	4	27	16	12	8.4
Mosses	10	15	13	16	2	6	16	13	11	5.1
Mushrooms	10	8	5	3	0	0	3	1	4	3.7

a Two subsamples were compared within each composite sample.

b "Lichen I" is represented by the genera *Cetraria*, *Alectoria* and *Dactylina*.

c "Lichen II" is represented by the genera *Cladonia* and *Thamnolia*.

Table 14. Seasonal range use by caribou expressed as the mean proportion of caribou observed bedded or foraging on each range type, Beverly calving ground, 1981.

			Proportion of caribou (%)				
Season	Range type	Activity	$\bar{x}$	SD	n[a]	t statistic[b]	F ratio[c]
Calving	Rock/Sand Barrens	Bedded	< 1.0	-	20	-	-
		Foraging	< 1.0	-	20	-	-
	Lichen Upland	Bedded	50.4	29.4	20	-	0.263
		Foraging	52.5	27.8	20	-	1.758
	Dwarf Shrub	Bedded	17.3	26.9	20	-	-
		Foraging	16.8	23.7	20	-	-
	Meadow	Bedded	27.3	18.3	20	-	0.676
		Foraging	30.7	20.1	20	-	0.068
Post-calving	Rock/Sand Barrens	Bedded	< 1.0	-	25	-	-
		Foraging	< 1.0	-	25	-	-
	Lichen Upland	Bedded	48.3	34.2	25	-	2.805
		Foraging	37.7	31.5	25	-	2.013
	Dwarf Shrub	Bedded	33.7	29.8	25	-	0.950
		Foraging	26.9	22.8	25	-	1.313
	Meadow	Bedded	18.0	17.2	25	-	2.401
		Foraging	35.3	21.9	25	-	1.800

Table 14. (continued)

Season	Range type	Activity	Proportion of caribou (%) $\bar{x}$	SD	n[a]	t statistic[b]	F ratio[c]
Combined	Rock/Sand Barrens	Bedded	< 1.0	-	45	-	-
		Foraging	< 1.0	-	45	-	-
	Lichen Upland	Bedded	49.2	31.8	45	0.41	1.337
		Foraging	44.3	30.5	45	1.80	2.071
	Dwarf Shrub	Bedded	26.4	29.4	45	-2.50[d*]	0.359
		Foraging	22.4	23.5	45	-1.67[d*]	0.577
	Meadow	Bedded	22.1	18.1	45	1.90	2.372
		Foraging	33.3	21.0	45	-0.77	1.567

a Number of days summed over each observer team.

b H_o: There is no difference between seasonal means.

c H_o: There are no differences between observer teams.

d The Mann-Whitney U-test was used to calculate a Z statistic.

* Significant at 5%.

During post-calving, the proportion of caribou observed bedded or foraging on snowfree ground increased to 99.5% (SD=1.1%) and 99.3% (SD=1.3%) respectively. Most areas were snowfree during early post-calving (see Phenology).

We compared caribou use of the different range types to their availability or proportional coverage (Table 15). Observed use deviated significantly (P<0.05) from what would be expected based on a random distribution of caribou. During calving and post-calving foraging caribou used the Meadow range type most intensively (selectivity index of 0.3 and 0.4 respectively). Meadow received relatively less use by bedded animals during post-calving. Dwarf Shrub was used relatively little during calving and in approximate proportion to its availability during post-calving. During both seasons, most caribou were observed on Lichen Upland; however, this type was also the most common on the calving ground and therefore received a low selectivity index. The use of range types was more restrictive by foraging caribou than by bedded caribou.

Phenology

Upon arrival in the field (23 May) we estimated that 80-85% of the area around base camp was snow covered. Most ridge tops on the prevalent NW-SE oriented glacial landforms were clear of snow while slopes and lowlands were still covered. Measurements of snow depth along slope transects in the vicinity of base camp indicated a rapid progression of melt between 8-11 June (Fig. 2). Melt progressed from the upper slope (Lichen Upland) down towards

Table 15. Seasonal range use by caribou in relation to availability of range types, Beverly calving ground, 1981.

Season	Activity	Number of caribou observations in range type[a]: Lichen Upland (0.49)[b]	Dwarf Shrub (0.31)	Meadow (0.16)	Total	X^{2*}
Calving	Bedded					
	Observed	5351 (+0.2)[c]	588 (-0.6)	1755 (+0.2)	7694	2246.1
	Expected	3770	2347	1193		
	Foraging					
	Observed	3532 (0.0)	607 (-0.5)	1851 (+0.3)	5990	1854.1
	Expected	2935	1827	928		
Post calving	Bedded					
	Observed	8691 (+0.1)	4777 (0.0)	2504 (0.0)	15972	97.7
	Expected	7826	4871	2476		
	Foraging					
	Observed	3638 (-0.2)	3013 (0.0)	3862 (+0.4)	10513	3500.7
	Expected	5151	3206	1630		
Combined	Bedded					
	Observed	14042 (+0.1)	5365 (-0.2)	4259 (+0.1)	23666	1086.9
	Expected	11596	7218	3668		

Table 15. (continued)

Season	Activity	Number of caribou observations in range type[a]				
		Lichen Upland (0.49)[b]	Dwarf Shrub (0.31)	Meadow (0.16)	Total	X^{2*}
	Foraging					
	Observed	7170 (-0.1)	3620 (-0.2)	5713 (+0.4)	16503	4385.1
	Expected	8086	5033	2558		

a Rock/Sand Barrens were not included due to the low observed use (< 1%) and availability (< 5%).

b Availability (expected value) expressed as the proportion of calving area covered by this range type. Proportional coverage was recalculated from Table 12 after excluding water.

c Selectivity index = $\frac{U - A}{U + A}$ where U = use, and A = availability. From Ivlev (1961). Proportional use is given in Table 14.

* Significant at 5%.

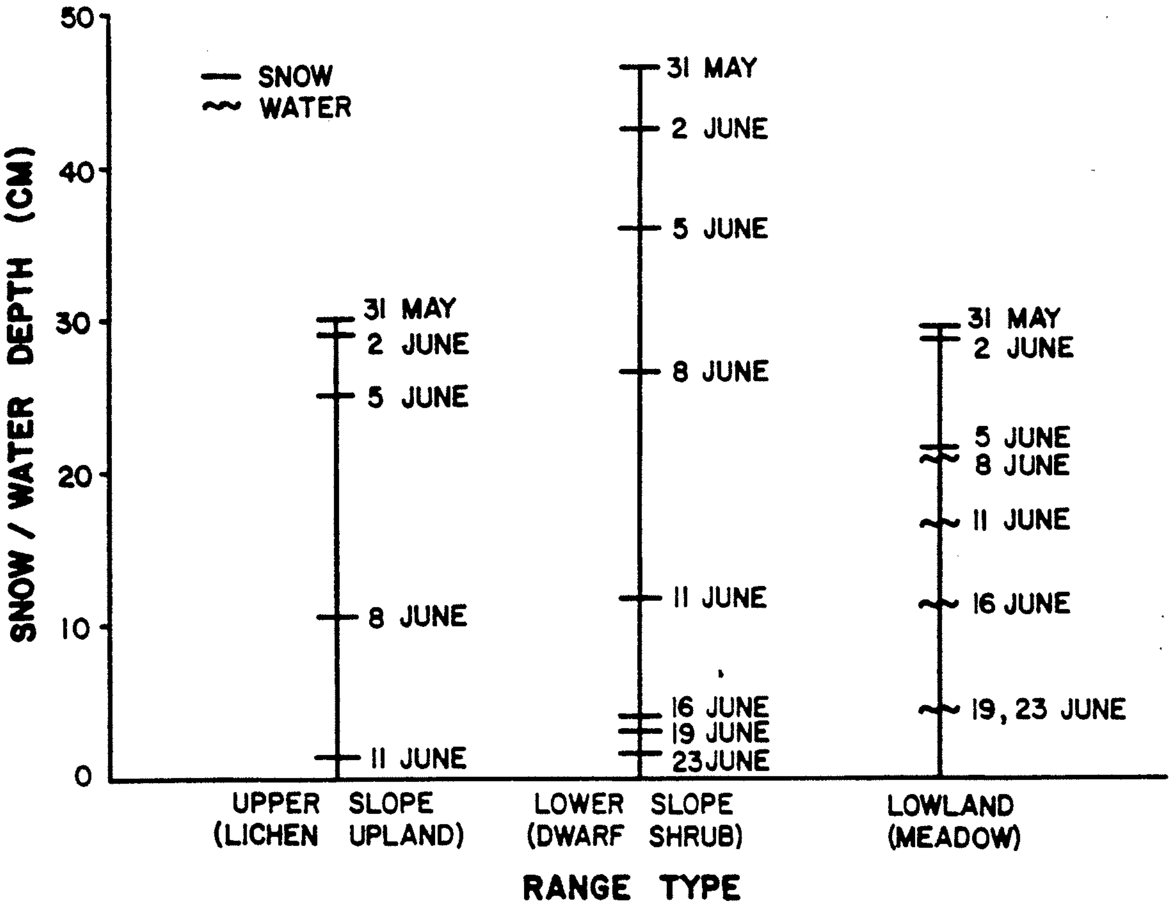

Figure 2. Snow depth in different range types on the Beverly calving ground, 1981. Some sites were snowfree in each range type before the latest dates shown.

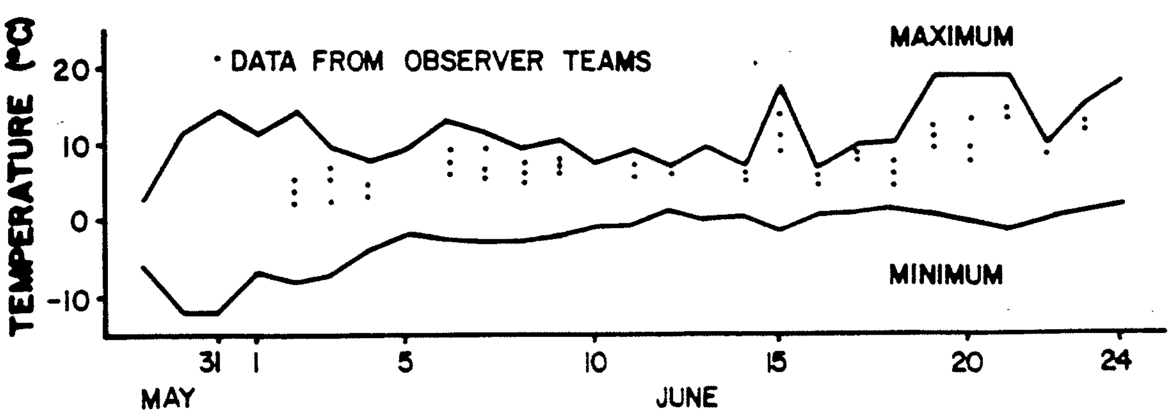

Figure 3. Temperature recordings (max-min) from the base camp, Itza Lake, compared with recordings from the observation areas, Beverly calving ground, 1981.

the lowland (Meadow). Standing meltwater was evident on the meadow lowlands from 8 June onwards. Visual estimates of percentage snow cover in the different observation areas ranged from 60-70% during early calving (2-5 June) to 30-40% during late calving (6-9 June). Following 11 June, which we characterized as the start of the post-calving period, most areas were snowfree except for late-lying snowbeds along shorelines and on northeast exposures.

Examination of LANDSAT imagery from 24 May to 2 July was complicated by the high degree of cloud cover during that period. Of 21 images available, 16 had more than 75% cloud cover which made any interpretations of snow melt patterns difficult. The patterns we observed from the ground appeared to be generally consistent with what we could discern from the remaining images. On 24 May, snow cover on the 1981 study area was close to 100% and any bare ground was restricted to ridge tops. On 2 July, land areas were virtually free of snow; small lakes were open while larger water bodies, such as Deep Rose Lake and Sand Lake (Fig. 1) were still mostly ice covered with shore leads of open water. In comparison, Beverly Lake, which is located 80 km south of Sand Lake, was largely open.

Temperatures recorded by the observer teams in the different sampling areas fell within the max-min range measured from base camp (Fig. 3). Mean daily minimum during June was $-2.7^{o}C$ and mean daily maximum was $11.1^{o}C$. Mean daily wind speed during June was 13 km/h.

The outcrops, ridge tops or steep slopes of Rock/Sand Barrens were snowfree earlier than other areas. Crustose lichens and isolated pockets of other vegetation (primarily prostrate shrubs, such as Vaccinium uliginosum and Ledum decumbens) were thus available early in the growing season. While some signs of greening were evident in early June (Fig. 4), phenological development was comparatively slow in this range type.

Lichen Uplands were also free of snow early because of their exposed location. In early June, exposed vegetation was dominated by dense mats of fruticose lichens, such as Cornicularia divergens and Alectoria ochroleuca. While snowfree early, phenological development appeared even slower than on Rock/Sand Barrens. Greening in Luzula confusa occurred later on Lichen Upland (Figs. 4 and 5) and flower bud break in Ledum decumbens, about 50% in Rock/Sand Barrens by 23 June (Fig. 4), was never seen on Lichen Upland (Fig. 6). Aspect appeared to have little effect on the rate of phenological development on the area sampled. While the start of greening in Hierochloe alpina was about 1 wk behind on the ridge top location, similar rates of development were evident for the remainder of the season (Fig. 5). Luzula confusa showed signs of greening earlier along the southwest exposure; by 23 June, phenological development was similar along the northeast exposure but slightly delayed on the ridge top (Fig. 5). Late greening on the ridge top location was also apparent in Vaccinium vitis-idaea (Fig. 6).

Although snow melt in Dwarf Shrub communities was slower than in both Rock/Sand Barrens and Lichen Upland, phenological

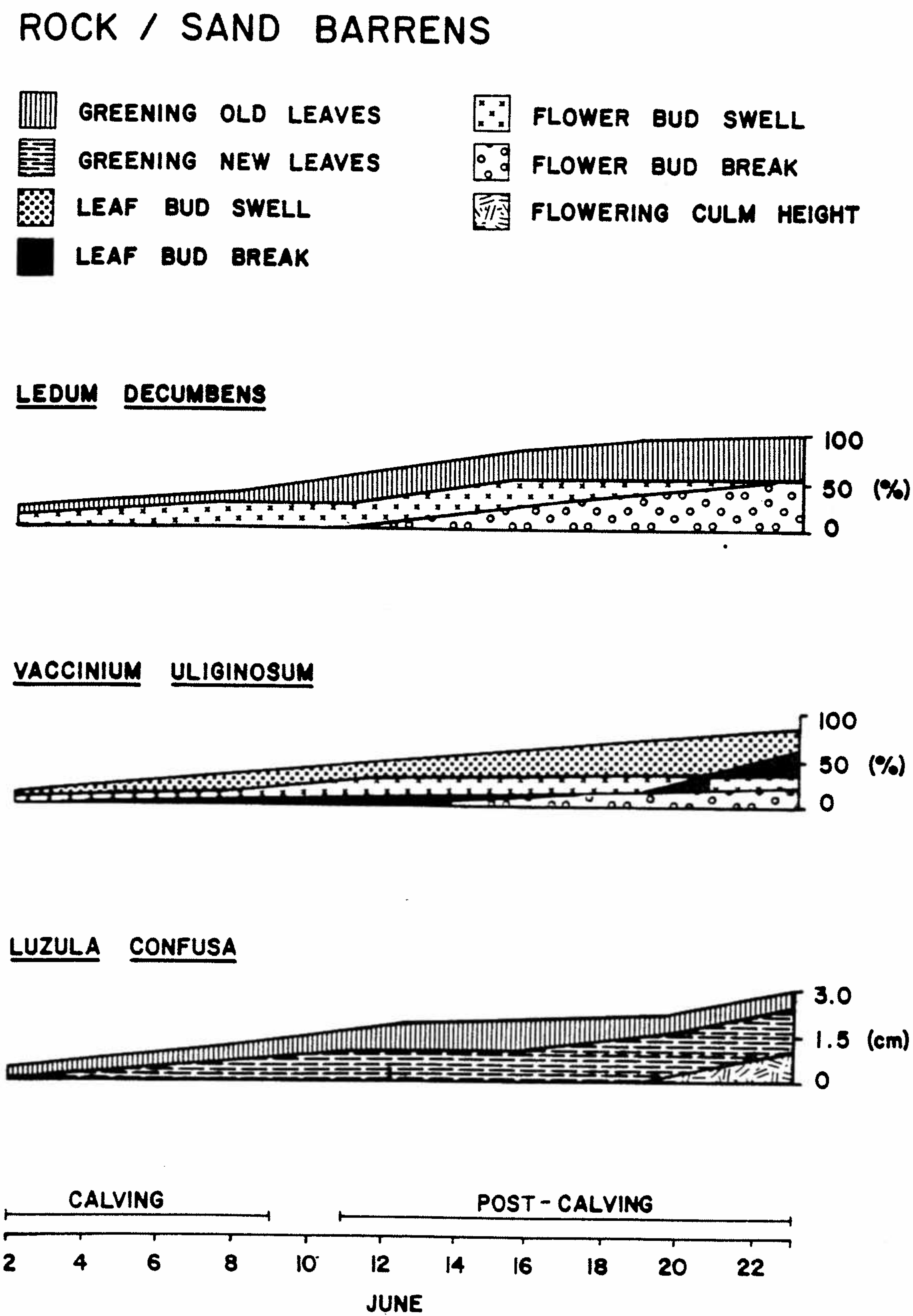

Figure 4. Phenological development in the Rock/Sand Barrens range type, Beverly calving ground, 1981.

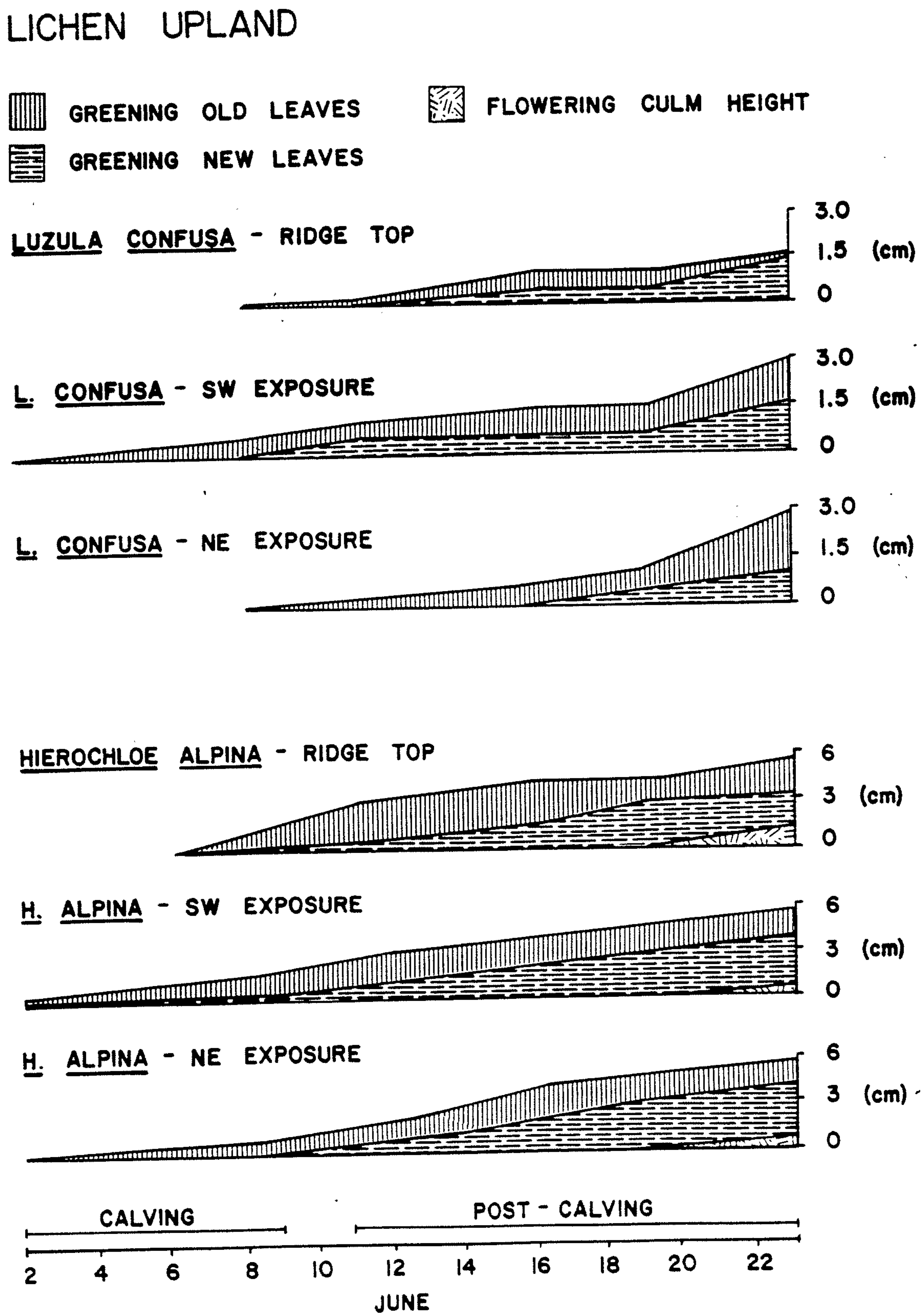

Figure 5. Phenological development of *Luzula confusa* and *Hierochloe alpina* on different aspects of Lichen Upland, Beverly calving ground, 1981.

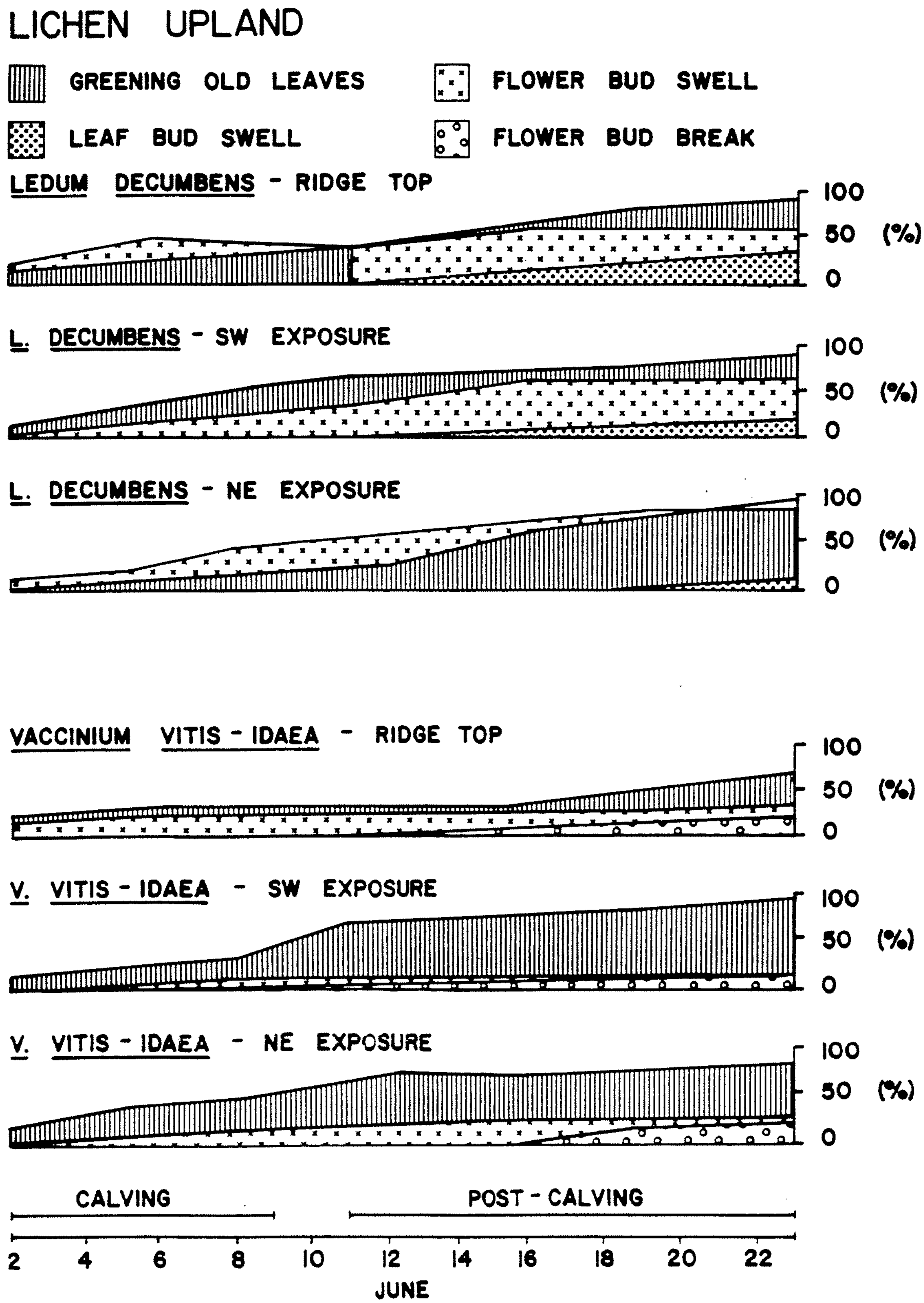

Figure 6. Phenological development of *Ledum decumbens* and *Vaccinium vitis-idaea* on different aspects of Lichen Upland, Beverly calving ground, 1981.

development in species such as Eriophorum vaginatum and Ledum decumbens was more advanced (Fig. 5, 6 and 7). E. vaginatum, just exposed from underneath the snow cover, had floral heads and some were even at anthesis as early as 2 June. In comparison, the first sign of budbreak in the deciduous shrub Betula glandulosa was not evident until 12 June; by 23 June, only half of the marked individuals had leafed-out.

Once clear of snow or standing water, phenology in the Meadow communities also progressed rapidly. Greening in Carex spp. was similar in both phenological plots on 23 June (Fig. 8) although snow melt occurred 2 wk later in the Meadow II than in the Meadow I community. Considerable greening was observed while roots and lower plant parts of graminoids were still frozen in the ground. On 23 June most meadows were no longer saturated with standing water, and forbs such as Pedicularis spp. started appearing.

We compared phenological development in the permanent plots with that in the different observation areas on six occassions between 3-22 June. We found no marked differences in the progression of plant phenology among the same range types within different areas of the 1981 calving ground.

We used two phases with a third beginning just before departure to summarize phenological development on the calving ground:

Early June Phase (2-10 June): Rock/Sand Barrens and Lichen Upland (ridge tops) were clear of snow and both crustose and fruticose lichens were readily available. Eriophorum tussocks in Dwarf Shrub and some in Meadow, were exposed and

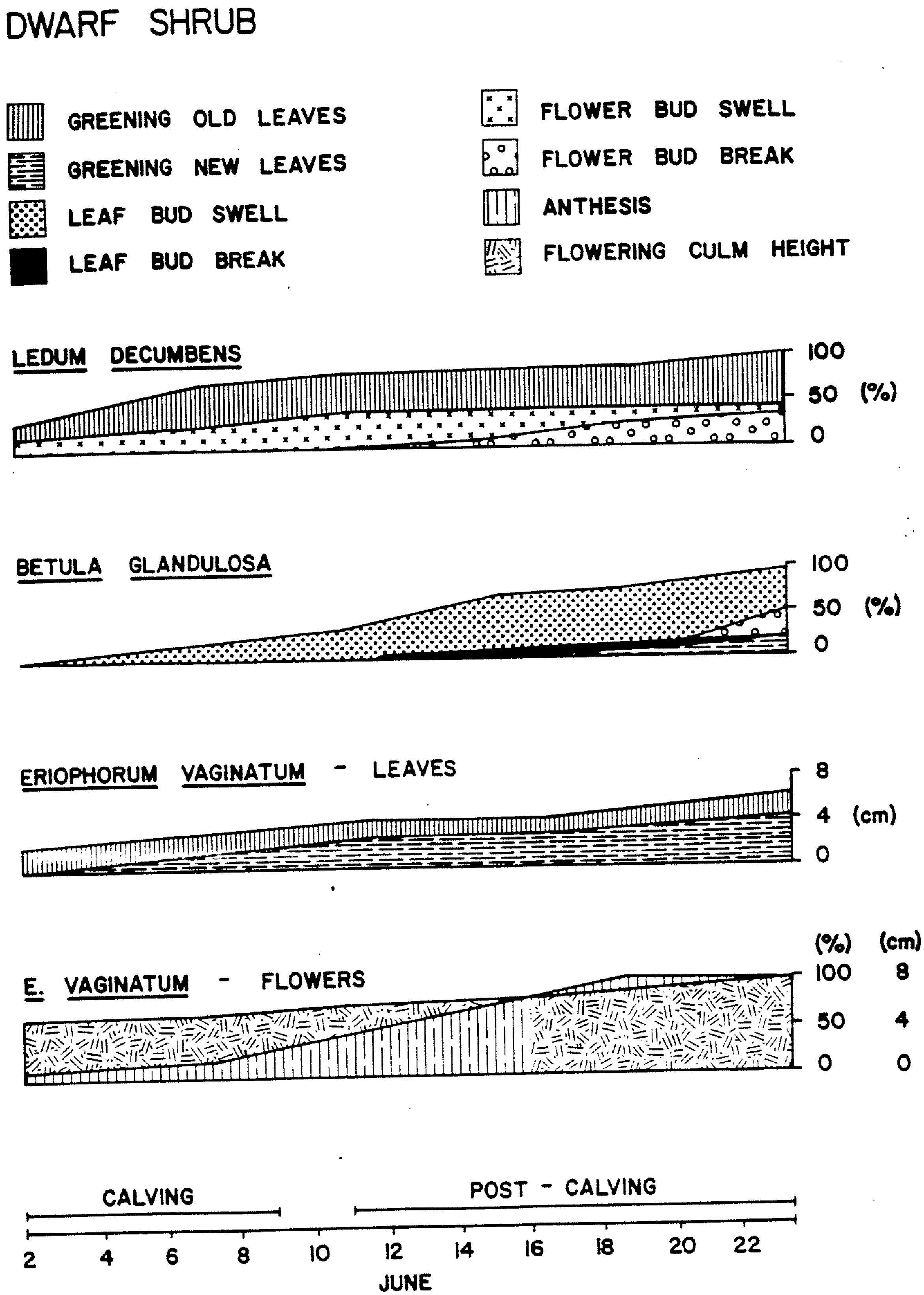

Figure 7. Phenological development in the Dwarf Shrub range type, Beverly calving ground, 1981.

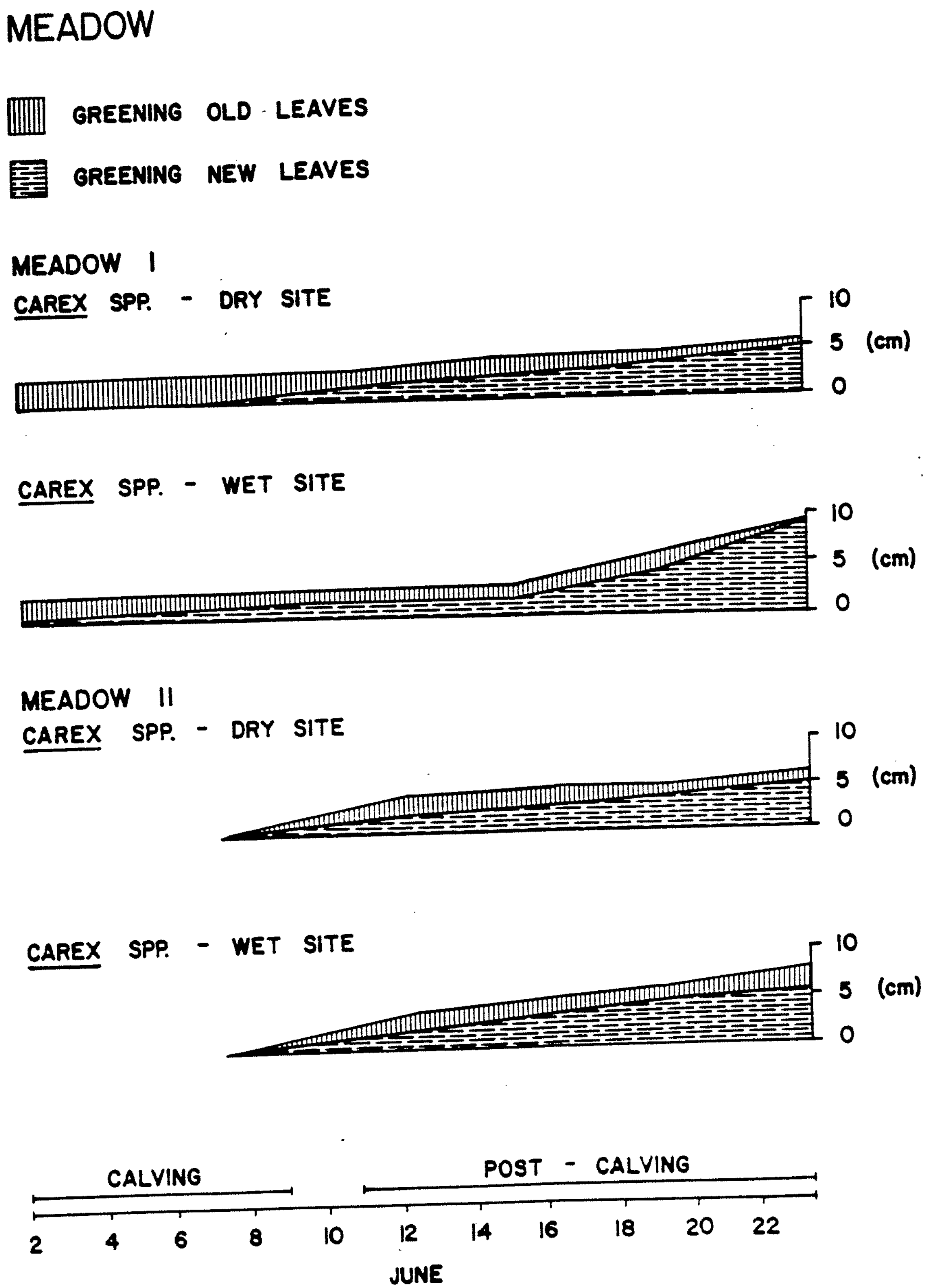

Figure 8. Phenological development in the Meadow range type, Beverly calving ground, 1981.

provided some new green growth of both floral heads and leaves. The rate of development in shrubs and graminoids, other than *Eriophorum*, was slow.

Mid-June Phase (11-23 June): Meadow communities became free of snow and a rapid phenological development in both Dwarf Shrub and Meadow surpassed that of Rock/Sand Barrens and Lichen Upland.

Late-June Phase (20 June +): Most areas were snowfree, and major developments occurred among the prostrate shrubs (leafing-out, flower bud break). Forbs appeared and so did flowering culms of most graminoids.

DISCUSSION

Relationship of the Study to the Caribou Protection Measures

Consideration of the relationship between this study and the Caribou Protection Measures comes to rest on four salient points. Those points are: (1) our empirical understanding of caribou biology; (2) the basis for the enactment of the Caribou Protection Measures; (3) the rationale for the use of behavioural responses to describe disturbance; and, (4) the wider issue of human activity, in this case industrial activities, and caribou land management.

With respect to timing and location, the arrival of the parturient cows on their calving ground every year is the most predictable characteristic of the migratory barren-ground caribou's annual movements. During the first year of our study we compiled data to describe some of the reasons that favour returning cows to a specific calving ground (Fleck and Gunn 1982). Apparent reasons for the importance of calving above treeline do not explain the use of a specific area from year to year and Fleck and Gunn (1982) concluded that, in the presence of alternatives, traditional behaviour most likely dictated the choice. The implication of that conclusion for land and caribou managers is the need to respect the caribou's choice of what has proven most successful to the caribou over many generations. That is, we cannot answer, in the light of our current knowledge, where else the caribou could calve or what the consequences of displacement from the traditional calving grounds would be. To predict the consequences of displacement would require a detailed understanding of the effects that various characteristics of the calving ground have on the successful birth and early development of calves. The potential impact of enforced displacement on the well-being and calf-rearing ability of cows cannot be dismissed as inconsequential. However, the consequences of such displacement are not readily measureable.

The need to develop a scientific basis for the Caribou Protection Measures has already been identified (see Introduction). We cannot afford to lose sight of the axiom, that "one cannot credibly infer causes if an effect has not been reliably demonstrated" (Caughley in Connolly and Wallmo 1981). To document some effects (if any) of man's activities on the calving grounds we were limited to using behavioural responses. We designed our study with emphasis on techniques in recognition of the state of our knowledge about calving grounds and that many questions, such as the effect of displacement, are beyond short-term research.

There is a growing awareness of the short-comings of the environmental impact assessment processes that parallel industrial developments. One of the most recurrent themes is the failure to tackle an understanding of the basic relationships within biological systems. The main cause has been the reliance on short-term inventory studies rather than attempting an understanding of the whys and hows. In our attempt to "conduct disturbance studies" on the calving grounds, we have tried to mesh the inventory approach (i.e. the physical and biological characteristics) with understanding some of the whys and hows of the traditional use of calving grounds. Our observations of range type use, foraging strategies and careful documentation of behaviour will help us evaluate the importance of the calving grounds to the caribou. We have added another aspect to the study by developing the methods for describing some behavioural responses to human activities. Nevertheless, the results of our study should be measured against its relatively short duration and limited scope. The answers to the contentious issues of caribou and industrial activities are not yet readily at hand.

Study Design

Our approach has been to describe some behavioural and range use patterns of caribou cows and calves under "natural" or undisturbed conditions. An inherent assumption in the study design has been that certain visible or overt reactions are responses to disturbance. While we realize that physiological changes as a result of disturbance may occur even without visible reactions, descriptions of overt behaviours are currently the most feasible method for studying disturbance responses of free-ranging ungulates. We assumed that our presence did not affect caribou behaviour and we used wind direction to test this assumption. Our results indicate that activity budgets and the occurrence of most events were not influenced by the presence of the stationary ground observers. Whether the observed increase in aggressive acts was caused by the presence of the observers is unclear, particularly as we found no similar increase in the occurrence of alarm stances, head bobbings, or changes in nursing behaviour.

The results only provided a basic understanding of certain caribou behaviours. However, the measurements of behavioural patterns must be repeatable and refined enough to enable comparison of small scale changes in disturbance-induced behaviour. This prompted us to take a systematic and quantitative approach to describing behaviour. We classified activities (states) and events into mutually exclusive categories that could be uniformly recognized by all observers to reduce subjective interpretations and biases resulting from the lack of reliability between observers. Inter-observer reliability can only be measured under rigorously controlled conditions when the same behaviours are observed at the same time. We found a general agreement between observers suggesting that the behaviours were adequately defined and the results were largely representative of caribou in different areas of the calving ground.

Observation conditions were not always adequate. Fog, strong winds, precipitation and heat waves reduced visibility and occasionally hampered continous observations of caribou from a distance. Bedded calves were easily missed during some scan sampling probably resulting in an underestimate of the proportion of time they spent bedded. Composition counts of nursery bands in the Deep Rose Lake area, where most activity observations were made, suggested calf:cow ratios of about 0.75 (n=754 cows) during the calving period and 0.90 (n=1353 cows) during post-calving. In comparison, scan samples during calving included only an overall mean of 0.47 calves per observed cow and 0.62 during post-calving. This suggests that our samples were from, at most, 63-69% of the calves present.

We used systematic sampling procedures to reduce biases resulting from observers being attracted by and thus more conscious of certain types of behaviour. We predetermined the scheduling of sampling sessions, so that they would be independent of the behaviours under study. We set a conservative upper time limit (10 min) on the continual all-occurrence sampling to avoid observer fatigue. As rates rather than durations of behavioural events were of primary interest, the length of each sampling session was theoretically immaterial (Altmann 1974). However, the time base for samples to be pooled must be long enough to represent even the least frequently occurring behaviours. We believed that three 10-min periods per hour were adequate to obtain representative estimates for the rates of the behavioural events. We sampled throughout the day (from 1000 to 1700) because we could not assume, *a priori*, the absence of diurnal variability in activities or behaviours.

As a result of the mobility of caribou on the calving ground and our inability to recognize individuals, we needed a study design that could be applied to all caribou on several areas of the calving ground. To maximize data collection during the short calving period, we used three observer teams working in different areas, each providing a replicate sample. Through replicate sampling, we avoided sampling bias incurred from observing areas where only certain behaviours may have occurred. Replication also provided a means for calculating estimates of activity budgets and range use with associated variances. While each observer team had several potential observation areas in any one location, the choice was not pre-determined since we always started with an area that had caribou on it. This probably resulted in a slight observational bias with a tendency to over-record stationary activities during scan sampling. However, the alternative was to observe an area that initially or during the remainder of the day may not have had any caribou on it and thus, sacrifice sample size. During all-occurrence sampling this same observational bias was eliminated as frequencies of events were recorded per unit active time.

The recording of the range type being used was often difficult, particularly early in the field season when the ground was partly snow covered and the observers had little experience in distinguishing the characteristics of each range type. Although we lumped plant communities into four range types to facilitate accurate recording by the ground observers, we sometimes had difficulty in separating Dwarf Shrub from Meadow. As a result of the patchy distribution of plant communities on the calving ground, homogenous expressions of the different range types were not always found. In some Dwarf Shrub areas of rolling topography, Carex spp. co-dominated with the shrubs giving an area the impression of a Meadow type. Only closer examination revealed these sedges to be upland varieties (C. misandra and C. Bigelowii) preferring drier than Meadow habitats. When the ground observers were recording caribou range use, a closer examination of the range types was impossible without disturbing the animals. Thus subjective decisions were sometimes made. As the plant communities became snowfree and observers became more experienced, the identification of range types became more accurate.

Activity Budgets

As a ruminant herbivore, the pattern of *Rangifer* activity is characterized by regular alterations between activity and resting periods. Thomson (1973) described the activity pattern of wild reindeer (*Rangifer tarandus tarandus*) as consisting of two rhythms: a short-term polycyclic rhythm of activity/resting periods and a long-term 24-h rhythm controlled by photoperiod which set the activity to the time of day. The pattern of activity has been related to seasonal changes in physiological condition of the animal (eg. lactation), food quality and quantity, abiotic factors such as photoperiod and the modifying influence of weather and harassment by insects, predators and man (White et al. 1981). Comparisons of activity budgets or the proportion of time devoted to different activities, have recently been used in *Rangifer* research to evaluate animal condition and range quality (Gaare et al. 1975; Roby 1978 and 1980; Reimers 1980; White et al. 1981; Boertje 1981).

The scan sampling method has been used exclusively for recording activity budgets of caribou. Unfortunately no studies describe in complete detail how their activity data were collected and what methods of analyses were used. It seems most sampling sessions were not predetermined but that observations were made for as long as caribou were in view. In most cases, it is not apparent whether the presence of the observers influenced the activity of the animal. Activity budgets are usually obtained by summing the number of animals observed in each activity and expressing the proportions as percentages. Proportions have been weighted for entire seasons resulting in an estimate for each season without an associated variance (Gaare et al. 1975), for individual days (White et al. 1975), for individual active/rest cycles (Boertje 1981) or for individual scans (Roby 1978). While the assumption of independence between observations appears reasonable when comparisons are made between days or active/rest cycles, there is no indication whether independence or normality was tested prior to analyzing differences between seasons or cohorts. Differences in the methods of obtaining and analyzing data, as well as differences in environmental conditions, limit useful comparisons between different studies.

Biases inherent in the scan sampling technique include the differential visibility of bedded calves. The results likely underestimate the proportion of time that calves were bedded, especially during the calving period. An underestimate of feeding time by young calves may result from the short but frequent feeding bouts. Scan sampling is designed for behavioural states, i.e. behaviours of relatively long duration. Scan sampling by stationary observers tends to underestimate non-stationary activities, such as walking, trotting and galloping which move the caribou out of sight. These activities become more important later in the summer, however, during periods of moderate to severe insect harassment (Thomson 1973, Gaare et al. 1975, White et al. 1975, Roby 1978, Wright 1979, Boertje 1981).

Activity budgets of cows on the Beverly calving ground (Table 16) most closely resembled those reported for wild reindeer on Hardangervidda, Norway (Gaare et al. 1975) and caribou at Prudhoe Bay, Alaska (White et al. 1975). Beverly cows spent proportion-

Table 16. Summary of activity budgets of reindeer (R) and caribou (C) during and following the calving period. Activity budgets are expressed as the percentage of time cows and calves spent in each activity.

		Proportion of time (%)										
		Cow					Calf					Age of calf
Reference/location	Animal	B[a]	F	W	S	T/G	B	F	W	S	T/G	(Wk)
1. Norway												
Hardangervidda	R	37	54	4	4	<0.1	66	11[b]	12	9	2	1-2
Ottadalen	R	42	36	10	10	2	63	11[b]	10	13	3	1-2
USA												
2. Prudhoe Bay, AK.	C	33	53	11	1	2	55	24	11	5	6	3-7
3. Pipeline corridor, AK.[c]	C	52	33	12	3	1	-	-	-	-	-	-
4. Denali Nat'l Park, AK.	C	52	37	7	3	1	70	12	10	6	2	1-5
5. Canada												
Beverly calving ground, N.W.T.	C	37	48	10	4	1	63	16	11	9	2	1-4

a Activities are bedded, foraging, walking, standing and trotting/galloping.

b Includes 4% of the time spent nursing.

c Refers to cow dominated groups during spring migration and calving (14 May - 21 June).

(1) Gaare et al. (1975); (2) White et al. (1975); (3) Roby (1978); (4) Boertje (1981);

(5) this study.

ately less time feeding than animals on Hardangervidda and Prudhoe Bay. Gaare et al. (1975) suggested that differences between activity budgets of reindeer on Hardangervidda and in Ottadalen were partly due to differences in nutritional status and animal condition between the populations. The nutritionally stressed population on Hardangervidda spent considerably more time foraging (54%) and less time in activities other than bedded and foraging (8%) than the "healthy" population in Ottadalen (36% and 22%, respectively). On the basis of this comparison, Boertje (1981) suggested a moderate to good nutritional status among cows of the Denali herd. If this comparison is extended to the cows of the Beverly herd (48% foraging, Table 3), activity budgets would indicate a poor to moderate nutritional status that might cause low calf production and survival. However, composition counts on the Beverly calving ground showed 80-90 calves/100 cows by mid-June and about 50 calves/100 cows in November (NWT Wildlife Service files) which indicates a high calf survival of about 70% to November. We have little quantitative data to compare range quality and quantity on the Beverly calving ground with other areas but the activity budgets of the undisturbed cows were probably not indicative of a nutritionally stressed population. However, the availability of new green growth was limited spatially during the calving and early post-calving period (see Phenology) which may have influenced the observed activity budgets.

Activity budgets for calves were more similar to those reported from other areas (Table 16). The higher incidence of foraging at Prudhoe Bay (24% versus 16% observed among Beverly calves) is probably because older calves (3-6 wk old), that would be foraging more and nursing less, were observed at Prudhoe Bay.

Events

Nursing Behaviour

The gradual decrease in the frequency of nursing bouts with age, observed among calves in the Beverly herd is usual among caribou (Lent 1966, 1974; White et al. 1975) and reindeer (Espmark 1971). In caribou less than 2 days old, Lent (1966) observed 40 nursings during 720 min of observations, or 1 every 18 min. Assuming observations were only made on active calves, this corresponds to 5.6 nursings /100 calf-min which is less than half the frequency of nursings we observed between 2-5 June (12.4 nursings/100 calf-min), when most calves were less than 1 wk old. The frequency of nursings in the Beverly herd was also higher than reported by Espmark (1971) who noted a mean time interval of 20 min between successful nursings (or 5.0 nursings/100 calf-min) among calves less than 1 wk old. Espmark (1971) defined a successful nursing as one that "doubtless led to sucking, regardless of duration". Rather than making a subjective decision as to what constitutes a successful nursing, we used a 5-s minimum before recording the event as a nursing bout. While not quantified, many nursings appeared to occur when the calf rose from a bedded position. Our choice of "active calves" as the time basis for recording nursing rates, will tend to bias our sample in favour of calves which have been active over a period of time and may already have nursed. Hence, our results are probably conservative estimates of the average nursing rate.

We noted a mean of 6.3 nursing attempts/100 calf-min between 2-5 June which is agreement with Espmark's (1971) observations of about 3 attempts/h (or 5.0/100 calf-min) during the first week following parturition. He also noted an increase in the proportion of unsuccessful nursings (nursing attempts) out of the total number of attempts (including successful nursings) as the calves grew older.

Pruitt (1960) described most nursing bouts to last between 10-20 s among newborn caribou calves, which is lower than reported from other studies (Lent 1966; Espmark 1971, 1980; White et al. 1975; this study). We recorded a mean duration of 55 s between 2-5 June (calves less than 1 wk old), while the mean duration had decreased to 42 s during the third week following the birth of most calves; differences between time periods were not significant. Lent (1966) found no differences in the mean duration of nursing during the first 3 wk and reported a mean duration of 32 s (n=143). White et al. (1975) recorded a similar value (36 s) for calves 3-4 wk old. Following 3 wk of age, the duration of nursing bouts declined. Espmark (1971) noted longer durations among reindeer calves 1-2 wk old (mean of 60 and 73 s respectively), he documented shorter bouts during the third week of life. The duration of nursings is sometimes difficult to determine for the newborn calf as it seldom bunts the udder vigorously when a nursing is initiated.

Most of the nursings we observed occurred from the side (92%, n=271); only 7.7% took place from the rear. Similar results were obtained by Espmark (1971). Lent (1966) noted a much higher proportion to occur from the rear (36%, n=128). Nursings from the side have been found to be more successful and of longer duration than those from the rear (Lent 1966, Espmark 1971).

We observed that 8.6% of all observed nursings (n=256) were initiated by the cow; between 2-5 June, 16% of the nursings (n=50) were cow-initiated. This is higher than the 3% (n=137) observed by Lent (1966). The higher proportion of calf-terminated nursings that we observed among young calves (29% between 2-9 June compared with 17% between 11-23 June) agrees with observations by Espmark (1971).

The calves on the Beverly calving ground apparently nursed more intensively (higher frequency and longer duration) than reported from most other areas in Alaska and Norway. Most nursings occurred from the normal side position and the cows often allowed nursings to continue until the newborn calves were satisfied or sufficiently nourished and terminated the nursings. The intensive nursings, the positioning and the calf-terminations are characteristics similar to those described for calves in the healthy reindeer population in Ottadalen, Norway (Thomson 1973, in Gaare et al. 1975) as compared with the nutritionally stressed population at Hardangervidda.

Aggressive Acts and Other Events

We are not aware of any comparable studies of *Rangifer* where all-occurrence sampling has been used to calculate rates of different short-duration behaviours (events). Observations of aggressive acts, alarm stances and head bobbings have been descriptive with no quantification of frequencies (Pruitt 1960, Lent 1966, Espmark 1971).

We found no change in the rate of aggressive acts initiated by the maternal cow between calving and post-calving. Espmark (1971) observed most aggressive acts during the first days following parturition; a sharp decrease was noted after the second week. A significant decrease during post-calving has also been noted in the proportion of aggressive acts directed towards calves (Lent 1966). Lent attributed this to an increased ability of the calves to recognize their own mothers and to avoid other classes of individuals. Lent (1966) also suggested that cows accompanied by calves showed a greater tolerance towards other calves after the end of the calving period when the nursery bands formed large aggregations. In our study, cows directed aggressive acts equally towards their own calves and other calves during calving, while only 2.5% were directed towards their own calves during post-calving. The results suggest a greater tolerance by cows towards their own calves during post-calving which may be related to better recognition of each other by the cow-calf pair or to the lower rates of nursing attempts at that time. We often observed aggressive acts (particularly head swings) directed towards calves that made persistent attempts at nursing. During post-calving, group sizes were also larger with more calves close to the observed cow and a higher probability of aggressive acts directed towards other calves. Espmark (1971, 1980), in his studies of mother-infant behaviour in reindeer, never observed cows direct aggressive acts towards their own calves. On a few occasions, when group sizes were large and observer teams observed several cow-calf pairs, it was sometimes difficult to ascertain whether the recipient of an aggressive act was an "observed calf" or "other calf". At most times, however, when only one cow-calf pair was being watched, it was clear that maternal cows directed aggressive acts towards their own calves.

While group size and compostion will influence the rate of aggressive acts, their effects on infrequently occurring events are difficult to analyze. When a sudden influx of new animals came within close proximity of the observed cow during the 10-min observation period, the rate of aggressive acts increased. A higher probability of aggressive acts in such a situation seems self-evident by chance alone.

If we assume that we were not disturbing the animals, a low rate of alarm stances and head bobbings would be expected. Head bobbings are likely to occur among cows with newly born calves in situations when individuals are presented with a conflict of "drives" (Lent 1966). These conflicts may occur when the urge to escape potential danger (eg. predators or man) or to follow or join a group is opposed by the urge to remain with the calf that is too young or has difficulty in following the cow. Lent (1966) observed head bobbings by both cows and calves. We only noted the event for cows, as the behaviour is less conspicuous among calves and often confused with other behaviours such as exploratory or play behaviour. Head bobbings were more commonly observed during calving and early post-calving periods in the Kaminuriak herd (F.L. Miller pers. obs.). In reindeer, it is seldom observed (Espmark 1971, Thomson 1980) and it was rarely observed in Peary caribou (*Rangifer tarandus pearyi*) on Prince of Wales Island, N.W.T. (A.Gunn and F.L. Miller pers. obs.).

Reactions to Human Disturbance

Observations of activity budgets and the rate of events were primarily done on undisturbed caribou. In two instances (3 and 8 June), caribou downwind of the observers moved out of the sampling area and observations were discontinued. Hence, responses to disturbance such as an increase in the incidence of walking were therefore not recorded. In most cases, however, the presence of stationary ground observers did not appear to disturb the caribou possibly because caribou did not perceive the observers. Observations were made of caribou passing within 25 m of the observers without any overt responses (2 and 9 June). On 2 June, caribou were upwind of the observers and on 9 June, a crosswind was recorded. Stronger reactions were evident towards observers that were moving on foot, i.e. on their way to or from a sampling area. Responses varied, but usually included alarm stances, head-high alerts and movement away from the source of disturbance. On 7 June, three cow-calf pairs and one yearling were disturbed by observers walking to their sampling area. The group of caribou trotted about 500 m away from the observers. On 9 June, in a crosswind, a group of six caribou became aware of the two observers walking along a shoreline. The group trotted towards a larger group of about 300 caribou and this movement appeared to trigger a minor stampede among caribou in the large group. For 20 min the group milled back and forth on the ice of a lake before returning to land and resuming ongoing maintenance activities.

While the helicopter did not operate in the immediate vicinity of the sampling areas during observation periods, we noted three incidences when caribou apparently reacted to the sound of the turbo- machine. On 6 June, the helicopter was observed flying on the west side of Deep Rose Lake about 8 km from one of the observation areas. We noted several alarm stances by caribou apparently directed towards the sound of the helicopter, at the time, there was a 10 km/h crosswind between the helicopter and the caribou. There were erratic movements (milling) within the same group of 500 animals for 5-10 min following the disturbance. On 22 June, a helicopter landed 2-3 km from one observation area which resulted in a movement of caribou out of the area with cow-calf pairs trotting and occasionally galloping.

Range Use and Phenology

Foraging caribou were not randomly distributed on the calving ground. Large areas of Lichen Upland were the first to become free of snow and that range type was used by caribou primarily during the calving period in 1981. The relative availability and abundance of fruticose lichens, which provides a readily available source of digestible energy (White et al. 1975), also contributed to the use of this range type. Lichen Upland received a low selectivity index because of its relative availability on the calving ground, (Table 15). We agree with White et al. (1981), that the proportionally large use of a forage species or range type independent of "selectivity" is important. During post-calving in 1981, the use of Lichen Upland was primarily by bedded caribou probably because they preferred a dry substrate for resting; for foraging, succulent green growth was relatively more available on Meadow and Dwarf Shrub at that time. The exposed location of Lichen Upland also provides good visibility which may be important for the detection of predators.

Plant phenology was comparatively slow on Lichen Upland. The dense lichen mat insulates the underlying frozen soil from warming air temperatures and radiation, thus the slow heating of the soil delays plant development (Tegler 1980). Luzula confusa (Figs. 4 and 5) was slower greening in Lichen Upland than on Rock/Sand Barrens where the soil warmed up more quickly in the absence of a dense lichen mat. We noted little effect of aspect on plant phenology, probably because the terrain was rolling rather than steep and also because of the wide arc of the sun during the month of June.

Although, snow melt occurred later on Dwarf Shrub and Meadow, early phenological development of Eriophorum vaginatum provided new green growth and caribou selected this early growth in the few areas where available. The tussock growth form of this graminoid allows rapid nutrient absorption and, consequently, rapid growth at the time of snow ablation (Chapin et al. 1979). The apparent choice of the Meadow range type compared to Dwarf Shrub during the calving period, may partly reflect our difficulties in separating these range types under a broken snow cover. *Eriophorum* tussocks, although by no means abundant (Appendix C), were also relatively more common in the Meadow range type. As larger areas became free of snow or standing water, plant phenology in both Dwarf Shrub and Meadow progressed rapidly. However, leafing-out among shrubs and the appearance of forbs did not occur until late June. The most marked changes in snow melt and plant phenology occurred between the end of calving and the beginning of post-calving.

Results from the fecal analysis were not consistent with our observations of caribou range use. For example, the observed switch from Lichen-dominated areas (Lichen Upland) to wetter areas of shrubs and graminoids (Dwarf Shrub and Meadow) was not apparent from the fecal analysis. Differences between subsamples from the same collection date (composite sample) suggest an inherent variability in the analysis of fecal samples. Boertje (1981) discussed biases of fecal analysis in estimation of actual dietary composition, including differential digestibility between species and within a species as influenced by phenological stage and plant part used. For instance, mosses tend to be overrepresented in fecal analysis due to their extremely low digestibility, their high degree of fermentation and the ease with which minute moss fragments can be identified. Despite these shortcomings, Boertje (1981) suggested that fecal analyses were useful in assessing seasonal trends of major food items (graminoids, shrubs, etc.). During calving (samples from 4 and 8 June), the large proportion of *Carex*, *Salix* and *Vaccinium* in our samples probably reflect the relatively low digestibility of these genera prior to greening.

The low proportion of lichens, particularly _Alectoria_ and _Cornicularia_, detected in the feces cannot be readily explained; however, the proportion of unidentified plant fragments in our samples was quite large, 60-70% (T. Foppe pers. comm. 1982). The occurrence of mushrooms in samples from the calving period agrees with our observations of caribou seeking out frozen mushrooms (mainly _Russula_ spp.) from underneath the snow cover. Later, as the mushrooms became exposed, they started to decompose and seemed to be eaten less by caribou. Decomposition of mushrooms can lead to the production of toxins (Alexopoulus and Mims 1979) which may explain the reduced use by caribou.

Fleck and Gunn (1982) described the calving grounds of the Beverly, Bathurst and Kaminuriak herds as the last portions of each herds' range to become snowfree and that snow cover often exceed 75% at the beginning of calving. Our observations suggest that the timing of snow melt on the Beverly calving ground in 1981 was similar to that reported for the northern portion of the Beverly calving grounds during the last 4 yr (Fleck and Gunn 1982). The relatively late snow melt on the calving ground used in 1981 was evident compared to the area of Ursus Islands ($64^{o}15'$ N, $101^{o}45'$ W) on the Thelon River through which the pregnant cows usually pass on their way to the calving ground. On 31 May, the Thelon River was open and adjacent areas virtually free of snow while on the 1981 calving ground about 175 km to the NE, snow cover was still about 80%.

The use of plant communities following snow ablation is largely related to the selection of certain plant species and parts in early growth stages to optimize nutrient intake (Klein 1970, Skogland 1975) or the ratio of nutrients to secondary metabolites (toxins and digestion inhibitors) in the forage (Kuropat and Bryant 1980). We did not examine forage use *per se* and any conclusions regarding feeding strategies could only be speculation restricted to observations in 1981. The late snow ablation on the Beverly calving ground and the delayed development of most potential forage species likely restricts the phenological options available for cows to optimize their nutrient intake during calving. Therefore, the abundant fruticose lichens may be of significant importance as the primary source of energy until new growth of other forage species is available.

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APPENDIX A. Description of Range Types on the Northern Portion of the Beverly Calving Grounds.

Rock/Sand Barrens - This range type is characterized by a low percentage plant cover with the moss *Pogonatum dentatum* being the most prominant species. Bare ground is the dominant surface cover. The restriction of plant development stems from the poor moisture supply on Barrens sites.

The rocky portions of Rock/Sand Barrens are typified by outcrops of bedrock or coarse bouldery substrates along ridge tops offering little moisture retention capabilities and leading to the establishment of crustose lichens. Fruticose lichens may attain high frequencies within these communities; however, they are small, open branching forms of low biomass.

The sandy portions of Rock/Sand Barrens are areas of regular occurrence of pure glaciofluvial sand deposits with little cover of vegetation. These areas include: (1) beaches up to several kilometers long and 50-100 m wide with blowouts extending 0.5 km inland; (2) sandy upland plateaus where loose sand and high winds prevent community establishment; (3) inland blowouts which remove the stabilizing vegetation; and (4) sides of sandy esker ridges where a combination of steep slopes and exposure to wind prevents the establishment of vegetation.

Lichen Upland - This range type occurs on abundant xeric, glacial till deposits (drumlins and ground moraines) and on glaciofluvial deposits (eskers and outwash plains). The continuous, dense mat of fruticose lichens up to 15 cm thick is unique to this range type and represents a substantial amount of plant biomass. The dominant lichens and their preferred habitats are *Cornicularia divergens* on xeric ridge tops, the black thallus of this lichen distinguishes the community; and *Alectoria ochroleuca* on less xeric, protected slopes, often integrating with *C. divergens* dominated communities along frost cracks. The green thallus of *A. ochroleuca* is a key to the identification of this expression of Lichen Upland. *Cetraria nivalis* and *Cetraria cucullata* dominate in dry-mesic habitats, occurring at the base of slopes and might be referred to as lichen lowlands. The bright yellow thallus color of those *Cetraria* spp., again, assists in the identification of Lichen Upland.

Besides the dominant lichens there are other regularly occurring plant species which characterize Lichen Upland. *Ledum decumbens*, a low shrub, may attain 12% cover in Lichen Upland communities. *Empetrum nigrum* and *Vaccinium vitis-idaea*, two inconspicuous prostrate shrubs, may attain percentage covers of 5% and 8% respectively. At low percentage cover, but highly visible, are tufts of the grass *Hierochloe alpina* and the rush *Luzula confusa*.

Dwarf Shrub - In sites where a good silty-organic soil has developed and mesic moisture conditions prevail, a more robust vegetation type is prevalent. Leafy shrubs *Betula glandulosa*, *Salix arctophila*, *S. planifolia* and *S. reticulata* characterize the Dwarf Shrub range type and are seldom found elsewhere. Sedges may co-dominate with the shrubs and this, physionomically gives the impression of a meadow community. When the sedge species are more closely examined, however, they are found to be upland varieties preferring drier than meadow haitats; Carex Bigelowii, C. glacialis, C. misandra. Also, by definition, within the Meadow range type sedges dominate with a high percentage cover and few other plant species are present. Other species, frequently occurring but of low percentage cover in the Dwarf Shrub range type, include the shrubs Cassiope tetragon, Vaccinium uliginosum, V. vitis-idaea, Ledum decumbens and the forbs Oxytropis maydelliana, Pedicularis spp. and Polygonum viviparum.

Meadow - With a suitable combination of organic substrate and wet moisture regime sedges proliferate forming near pure stands. These sites include wet lowlands with standing water where Carex aquatilis monodominates, or seasonally very wet areas where C. rostrata monodominates. Tussock meadows where Eriophorum spp. and C. rariflora dominate run uphill following local drainage into moist mesic sites. The variable microtopography of hummocks provides various microhabitats where the woody species Andromeda polifolia, Salix herbacea, Vaccinium spp. and forbs such as Cardamine hyperborea, Pedicularis lapponica, Rubus chamaeomorus become established.

APPENDIX B. Recording Forms for Scan and All-Occurrence Sampling, Beverly Calving Ground, 1981.

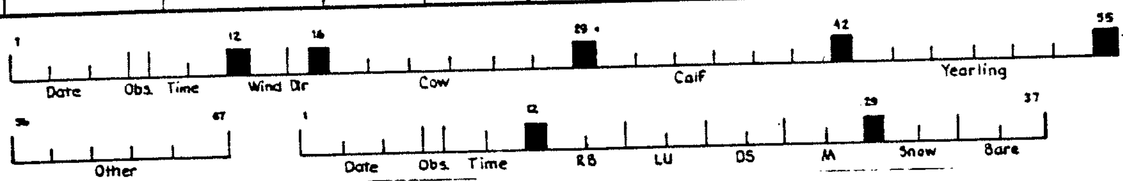
Northwest Territories Canada

Behavioural Study Record

SCAN SAMPLE FORM

Wind Speed	Direction	Temp.	Location	Cloud Cover	Time	Date	Obs. Team

	COW	CALF	YLG	OTHER	RB	LU	DS	M	SNOW	BARE
B										
F										
W					Remarks					
S										
T										
G										



Legend

Activity

B - bedded
F - foraging
W - walking
S - standing
T - trotting
G - galloping

Range Use

RB - Rock/Sand Barrens
LU - Lichen Upland
DS - Dwarf Shrub
M - Meadow

ALL-OCCURRENCE

START TIME 8-11 TIME	NOs 13 C	14 Ca	GROUP START 19 Size	20 Comp	22 Wind	NURSE INIT 23 C	24 Ca	TERM 25 C	26 Ca	27 AFP Nurse	28 Head BoB	29 Allure	AGGRESSIVE ACTS 30 ANT	31 Kick	32 Rush	33 INIT	34 REC	35	36	37	7 OBSERV REMARKS	DATE 1-6
TOTALS																						

1 6 7 8 11 12 13 14 15 16 17 18 19 22 23 26 27 29 30 32 33 34 35 36

TOTALS																						

1 6 7 8 11 12 13 14 15 16 17 18 19 22 23 26 27 29 30 32 33 34 35 36

DATE Obs TIME C Ca Dur C. Dur Ca Size Comp Chng Wind C Ca C Ca A/N BOB ALA ANT Kick Rush INIT REC

APPENDIX C. Plant Species Composition of Different Range Types, Beverly Calving Ground, 1981.

Rock/Sand Barrens

24 June 1981 n = 40

Species	Cover (%) x̄	Cover (%) SD	Frequency (%)	P.V.[a]
Pogonatum dentatum	13.0	14.0	58	99
Cornicularia divergens	3.8	9.5	18	16
Empetrum nigrum	2.3	8.9	8	7
Ledum decumbens	1.5	9.5	3	3
Vaccinium uliginosum	1.3	4.6	8	4
Vaccinium vitis-idaea	1.0	3.8	8	3
Luzula confusa	Tr[b]	-	Tr	-
Cetraria nivalis	Tr	-	Tr	-
Alectoria ochroleuca	Tr	-	Tr	-
Xanthoparmelia centrifuga	Tr	-	Tr	-
Crustose lichens	Tr	-	Tr	-
Bare ground	75.5	23.8	100	755

Lichen Upland - Ridge top

13 June 1981 n = 25

Species	Cover (%) $\bar{x}$	Cover (%) SD	Frequency (%)	P.V.[a]
Cornicularia divergens	43.6	26.8	88	409
Alectoria ochroleuca	42.8	27.5	84	392
Cetraria nivalis	16.9	7.9	64	135
Ledum decumbens	12.0	18.7	44	80
Moss spp.	5.2	10.0	28	28
Cladina rangiferina	5.2	10.9	24	25
Cladina mitis	2.4	5.2	20	11
Vaccinium vitis-idaea	2.0	4.1	20	9
Empetrum nigrum	Tr[b]	-	Tr	-
Hierochloe alpina	Tr	-	Tr	-
Luzula confusa	Tr	-	Tr	-
Lycopodium selago	Tr	-	Tr	-
Cassiope tetragona	Tr	-	Tr	-
Spherophorus globosis	Tr	-	Tr	-
Cetraria laevigata	Tr	-	Tr	-
Cetraria andrejevii	Tr	-	Tr	-
Stereocaulon sp.	Tr	-	Tr	-
Cladonia spp.	Tr	-	Tr	-
Crustose lichens	Tr	-	Tr	-
Bare ground	5.2	10.5	28	28

Lichen Upland - NE Exposure

18 June 1981 n = 25

Species	Cover (%) $\bar{x}$	Cover (%) SD	Frequency (%)	P.V.[a]
Alectoria ochroleuca	49.6	25.2	100	496
Cornicularia divergens	34.4	20.6	96	337
Moss spp.	16.4	29.0	40	104
Cetraria nivalis	11.6	13.8	64	93
Vaccinium vitis-idaea	8.4	11.1	48	58
Cladina mitis	7.6	9.7	48	53
Cetraria cucullata	6.4	10.8	32	36
Ledum decumbens	6.0	10.8	28	32
Hierochloe alpina	3.6	8.6	20	16
Clandonia spp.	2.0	4.1	20	9
Luzula confusa	Tr[b]	-	Tr	-
Cassiope tetragona	Tr	-	Tr	-
Empetrum nigrum	Tr	-	Tr	-
Xanthoparmelia centrifuga	Tr	-	Tr	-
Dactylina arctica	Tr	-	Tr	-
Cladina rangiferina	Tr	-	Tr	-
Cladina stellaris	Tr	-	Tr	-
Rhizocarpon geographicum	Tr	-	Tr	-
Spherophorus globosis	Tr	-	Tr	-
Thamnolia subuliformis	Tr	-	Tr	-
Cetraria laevigata	Tr	-	Tr	-
Umbilicaria sp.	Tr	-	Tr	-
Bare ground	3.6	9.9	16	14

Lichen Upland - SW Exposure

18 June 1981 n = 25

Species	Cover (%) $\bar{x}$	Cover (%) SD	Frequency (%)	P.V.[a]
Alectoria ochroleuca	60.8	28.6	96	596
Cornicularia divergens	26.4	22.3	88	248
Cetraria nivalis	16.4	14.1	76	143
Ledum decumbens	11.6	19.5	40	73
Cetraria cucullata	5.6	10.0	32	32
Cladina stellaris	4.8	9.2	28	25
Cladonia spp.	4.4	7.7	32	25
Hierochloe alpina	2.8	10.2	12	10
Moss spp.	2.4	8.3	12	8
Cladina mitis	2.0	5.0	16	8
Vaccinium vitis-idaea	1.6	3.7	16	6
Luzula confusa	Tr[b]	-	Tr	-
Empetrum nigrum	Tr	-	Tr	-
Cetraria laevigata	Tr	-	Tr	-
Cetraria andrejevii	Tr	-	Tr	-
Dactylina arctica	Tr	-	Tr	-
Thamnolia subuliformis	Tr	-	Tr	-
Stereocaulon sp.	Tr	-	Tr	-
Xanthoparmelia centrifuga	Tr	-	Tr	-
Bare ground	11.6	16.0	48	80

Dwarf Shrub

24 June 1981 n = 25

Species	Cover (%) $\bar{x}$	Cover (%) SD	Frequency (%)	P.V.[a]
Ledum decumbens	20.0	21.8	64	160
Cornicularia divergens	18.4	23.2	60	143
Moss spp.	18.0	28.4	44	119
Cetraria nivalis	17.6	18.8	68	145
Betula glandulosa	16.8	25.9	48	116
Alectoria ochroleuca	16.0	21.6	56	120
Carex spp.	12.0	19.4	48	83
Vaccinium uliginosum	10.0	13.5	40	63
Cetraria cucullata	6.8	9.0	44	45
Vaccinium vitis-idaea	6.4	9.1	40	41
Spherophorus globosis	5.2	9.2	32	29
Dactylina arctica	4.0	6.5	32	23
Empetrum nigrum	Tr[b]	-	Tr	-
Andromeda polifolia	Tr	-	Tr	-
Eriophorum vaginatum	Tr	-	Tr	-
Luzula confusa	Tr	-	Tr	-
Cassiope tetragona	Tr	-	Tr	-
Salix spp.	Tr	-	Tr	-
Cetraria delisei	Tr	-	Tr	-
Cetraria laevigata	Tr	-	Tr	-
Cetraria andrejevii	Tr	-	Tr	-
Cladina mitis	Tr	-	Tr	-

Continued...

Dwarf Shrub cont'd

Species	Cover (%) $\bar{x}$	Cover (%) SD	Frequency (%)	P.V.[a]
Cladonia spp.	Tr	-	Tr	-
Crustose lichens	Tr	-	Tr	-
Thamnolia subuliformis	Tr	-	Tr	-
Bare ground	4.8	9.2	28	25

Meadow I

24 June 1981 n = 25

Species	Cover (%) $\bar{x}$	Cover (%) SD	Frequency (%)	P.V.[a]
Carex spp.	86.0	10.8	100	860
Moss spp.	78.4	36.0	88	470
Salix spp.	3.6	-	20	16
Cetraria delisei	3.6	-	20	16
Cetraria andrejevii	Tr[b]	-	Tr	-
Ledum decumbens	Tr	-	Tr	-
Betula glandulosa	Tr	-	Tr	-
Pedicularis sp.	Tr	-	Tr	-
Carex aquatilis	Tr	-	Tr	-
Carex rariflora	Tr	-	Tr	-
Carex rostrata	Tr	-	Tr	-
Eriophorum vaginatum	Tr	-	Tr	-
Salix arctica	Tr	-	Tr	-
Luzula parviflora	Tr	-	Tr	-
Vaccinium uliginosum	Tr	-	Tr	-
Andromeda polifolia	Tr	-	Tr	-
Bare ground	2.4	-	16	10

Meadow II

24 June 1981 n = 25

Species	Cover (%) $\bar{x}$	Cover (%) SD	Frequency (%)	P.V.[a]
Carex spp.	85.2	13.9	100	852
Moss spp.	52.8	37.6	84	484
Cetraria delisei	10.4	20.1	28	55
Ledum decumbens	2.8	7.4	16	11
Andromeda polifolia	2.4	6.0	16	10
Vaccinium uliginosum	Tr[b]	-	Tr	-
Luzula parviflora	Tr	-	Tr	-
Cladonia spp.	Tr	-	Tr	-
Salix spp.	Tr	-	Tr	-
Eriophorum vaginatum	Tr	-	Tr	-
Bare ground	4.8	7.1	36	29

[a] Prominence value:

$$P.V. = \bar{x} \cdot \sqrt{F}$$

$\bar{x}$ = mean percentage cover, and

F = frequency of occurrence of that species

P.V. max = 1000

[b] Trace (<1.0%)

APPENDIX D. Description of Phenological Characteristics Measured for Different Plant Species, Beverly Calving Ground, 1981.

Ledum decumbens - This plant overwinters in full leaf, the leaves appearing reddish-brown in spring as chlorophyll degenerates during the winter. With the onset of suitable weather, metabolism resumes, chlorophyll is manufactured and the greening of leaves is a general indication of plant development. On each day that phenology measurements were taken, the overall greening of each plant was visually assessed and given a percentage value. This value was recorded in increments of 25% to provide a more general and less subjective representation of phenological development.

Swelling of leaf and flower buds is a phenological key indicating rehydration and growth of previously formed plant parts. In order to differentiate swollen and unswollen buds, phenology observations began while the buds were still winter-hardened and, thus, in an unswollen state. The data were subjectively expressed as a percentage where 100% was equal to one swollen bud on each stem of the plant; a 50% value indicated half of the total plant stems had swollen buds. Leaf buds, recognized by their much smaller size than flower buds, will always reach 100% as each stem produces new leaves. Maximum flower bud swell may be substantially less than 100% as each stem does not necessarily produce flowers each year.

Bud break, the next phenological phase, was also expressed as a percentage of the total number of stems on the plant. The definition of bud break was that point at which the inner, expanded parts (leaves or flowers) became visible to the *Vaccinium vitis-idaea* - This small prostrate shrub is also an evergreen species belonging to the same family, Ericaceae, as *L. decumbens*. Phenological observations of percentage greening, flower bud swell and flower bud break followed the same criteria as that outlined for *L. decumbens*.

Hierochloe alpina - This grass species occurs as solitary tufts throughout a community; mature leaf lengths are 10-15 cm and flowering culms reach 10-30 cm. In spring, the dry, brown, apparently dead leaves are viable. Greening in the old leaves proceeds from the base towards the tip, but seldom does the entire old leaf become functional. New leaves, green from the tip, appear following old leaf greening and soon surpass the leaf growth of the previous year. Greening of both old and new leaves was measured from ground level to the maximum height observed. As *H. alpina* is an early flowering species the height of the flowering culm was also recorded. Anthesis, the maturity of a flower including functional male and female parts, was not measured, beacuse it did not occur during the field study.

Luzula confusa - This member of the rush family also occurs as solitary tufts throughout a community; mature leaves are 5-10 cm long and flowering culms are 10-30 cm. The greening of old leaves, development of new leaves and flowering follows a similar pattern to *H. alpina*; consequently, phenology measurements are the same as for *H. alpina*.

Betula glandulosa - This deciduous shrub appears in early spring as dry twigs with small leaf buds and catkins preformed during the last season. To aid in the determination of the initiation of leaf bud and catkin swell it was useful to slice open the buds; moist green tissue was revealed inside when swelling had begun. Bud break was defined as that point in time when the small young leaves could be seen between the opening bud scales or when the catkins split up exposing the numerous male or female bracts. Percentages of these phenological events were calculated as previously described where one event per stem equals 100%. Greening was recorded as the percentage of the plant which shows clearly discernible, but small, unfolded leaves.

Eriophorum vaginatum - This is a member of the Cyperaceae that develops old and new leaves like H. alpina and L. confusa. Mature leaves lengths are 15-25 cm; maximum observed leaf lengths were recorded in centimeters as for Hierochloe alpina. In addition, E. vaginatum is an early flowering species, therefore, the phenology of flower height (measured in cm) and the percentage of functional flowers (anthesis) were also recorded. Anthesis was discerned by noting anthers protruding from the flower and producing pollen.

Vaccinium uliginosum - Leaf and flower bud swell and bud break phenology were recorded in the Ericaceous shrub species as for L. decumbens and V. vitis-idaea. Pink swollen flower buds appeared first. They are fat and barrel-shaped on short stalks; leaf buds, also pink, are thin rocket shaped appendages directly attached to the stem. Flower bud break is easy to distinguish as the inner flower parts are revealed. Leaf bud break is somewhat difficult to distinguish, the leaves themselves forming the bud. Leaf bud break was defined by that point in time when the small, rosy leaf blades could be distinguished from the tightly wrapped buds.

Carex spp. - Because of the difficulty in distinguishing the individual species in the dry remaining leaves of last year's sedges, it was necessary to examine all species as one unit in Meadow communities. The height of greening of old and new leaves follows the same format as for *H. alpina*, *L. confusa* and *E. vaginatum*. Any single measurement recorded for phenology was the average of 10 separate measurements. For instance, the recording of one height for old leaf greening is the result of measuring the maximum height of old leaf greening in 10 separate plants.

APPENDIX E. Distribution of "Point-in-Time" Observations of Caribou Activity by Season and Observer Team, Beverly Calving Ground, 1981.

Age	Activity	Calving			Post-calving		
		Team 1 (93)[a]	Team 2 (114)	Team 3 (111)	Team 1 (61)	Team 2 (97)	Team 3 (171)
Cow	Bedded	1664	1972	857	1469	2893	3617
	Foraging	2201	2108	1198	1853	2247	4774
	Walking	614	474	229	251	393	774
	Standing	251	353	102	101	278	407
	Trotting	31	45	4	16	7	86
	Galloping	9	0	0	7	0	30
Calf	Bedded	1499	1677	425	1535	2466	4252
	Foraging	432	561	86	355	555	853
	Walking	199	278	62	186	373	642
	Standing	178	133	69	120	116	318
	Trotting	34	19	3	42	31	107
	Galloping	3	23	0	17	19	49

[a] Number of 20-min interval scans; an additional 11 scans were made by a fourth observer team during post-calving.

APPENDIX F. Tests for Normality and Independence of Caribou Activity Data, Beverly Calving Ground, 1981.

		Test for normality	Test for independence								
			Team 1			Team 2			Team 3		
Age	Activity	K-S Z[a]	R[b]	n[c]	t_s[d]	R	n	t_s	R	n	t_s
Cow	Bedded	0.750	8	10	1.38	9	15	0.44	12	17	0.61
	Foraging	0.512	8	10	1.38	10	15	0.22	10	17	0.61
	Walking	0.895	6	10	0.28	11	15	0.87	13	17	1.31
	Standing	0.919	7	10	0.55	10	15	0.22	10	17	0.61
	Trotting	1.908*	-	-	-	-	-	-	-	-	-
	Galloping	3.245*	-	-	-	-	-	-	-	-	-
Calf	Bedded	0.644	8	10	1.38	9	15	0.44	14	17	1.83
	Foraging	0.902	5	10	0.87	12	15	1.52	11	17	0.00
	Walking	0.936	8	10	1.38	9	15	0.44	12	17	0.61
	Standing	1.912*	6	10	0.28	9	15	0.44	14	17	1.83
	Trotting	1.397*	-	-	-	-	-	-	-	-	-
	Galloping	1.913*	-	-	-	-	-	-	-	-	-

a Kolmogorov - Smirnov Z statistic (Sokal and Rohlf 1969:573); n=46

b Number of runs or sets of elements with similar signs (plus or minus) preceded or followed by unlike signs. The sign of the difference from the previous value is recorded; if the data were monotonically increasing or decreasing, these signs would be all alike. Cyclical data would show more than the number of runs expected in a random sequence of values (Sokal and Rohlf 1969:626).

c Number of observation days minus one. Represents the number of elements from which runs were calculated.

d Test statistic (t_s) is compared with the standard normal deviate (t_e = 1.96); the normal approximation is satisfactory for N as low as 10 (Sokal and Rohlf 1969:628).

* Significant at 5%.

APPENDIX G. Distribution of "Point-in-Time" Observations of Caribou Range Use by Season and Observer Team, Beverly Calving Ground, 1981.

Range type	Activity	Calving			Post-Calving		
		Team 1 (93)[a]	Team 2 (114)	Team 3 (111)	Team 1 (61)	Team 2 (97)	Team 3 (171)
Rock/Sand Barrens	Bedded	0	0	0	7	0	0
	Foraging	1	0	0	15	0	1
Lichen Upland	Bedded	2319	2593	439	722	3829	4140
	Foraging	1665	1390	477	675	1393	1568
Dwarf Shrub	Bedded	0	258	330	1695	1059	1990
	Foraging	2	307	298	854	547	1603
Meadow	Bedded	584	690	480	589	416	1499
	Foraging	819	660	372	695	811	2337

[a] Number of 20-min interval scans; an additional 11 scans were made by a fourth observer team during post-calving.

APPENDIX H. Test for Normality and Independence of Caribou Range Use Data, Beverly Calving Ground, 1981.

		Test for normality	Test for independence								
			Team 1			Team 2			Team 3		
Range type	Activity	K-S Z[a]	R[b]	n[c]	t_s[d]	R	n	t_s	R	n	t_s
Rock/Sand Barrens	Bedded	3.641*	-	-	-	-	-	-	-	-	-
	Foraging	3.300*	-	-	-	-	-	-	-	-	-
Lichen Upland	Bedded	0.588	6	10	0.28	10	15	0.22	12	17	0.61
	Foraging	0.862	7	10	0.55	10	15	0.22	10	17	0.61
Dwarf Shrub	Bedded	1.560*	5	10	0.87	6	15	2.39	11	17	0.00
	Foraging	1.434*	5	10	0.87	8	15	1.09	7	17	2.43*
Meadow	Bedded	0.983	8	10	1.38	9	15	0.44	10	17	0.61
	Foraging	0.888	8	10	1.38	9	15	0.44	9	17	1.22

a Kolmogorov - Smirnov Z statistic (Sokal and Rohlf 1969:573); n=46.

b-d See Appendix E.

* Significant at 5%.