

CHAPTER 4 . Summer

Introduction

In early summer, small groups of caribou move north and west through the foothills and along the coastal plain. Following calving in the first half of June, large aggregations of mixed age and sex usually form on the coastal plain of northeast Alaska or northwest Yukon Territory (Garner and Reynolds, 1986). It is generally thought that these aggregations form to reduce harassment by flies or predators (Bergerud 1974; Roby 1978; Calef & Heard 1980).

By mid July, large groups of caribou drift east or south. Caribou summering in northern Yukon Territory historically have used the mountainous region and coastal plain but avoided the Old Crow Flats (Russell *et al.* 1992b).

The activity of the herd during summer appears largely influenced by the activity of blood sucking and parasitic insects. The period of insect activity coincides with the time when caribou are restoring body reserves depleted during winter (White *et al.* 1975) and growing new hair and antlers, when cows are lactating, and when bulls are accumulating fat reserves in preparation for the fall rut. This period is important nutritionally, primarily because green vegetation, high in digestible nitrogen, is available for approximately 6 weeks before senescence reduces nutrient content and plant digestibility (Kuopat and Bryant 1983). This nitrogen source is essential to growth and maintenance in caribou (Russell and Martell 1984).

To optimize nutrient intake, caribou must employ strategies to minimize the detrimental effects of insect harassment. Observations of other herds suggest that the tactics include: moving to regions that have few insects and favourable food resources, are typically cool and windy, and employment of various behavioural responses (eg. formation of large dense aggregations).

In the following section, we review the historical information on summer movements of the Porcupine Caribou Herd. Caribou do not use the summer range randomly; certain regions appear to be preferred. We have attempted to rationalize these consistent patterns, focusing on the effects of insect harassment on foraging opportunities. We have provided an inventory of vegetation complexes within the region (Russell *et al.* 1992a). We also investigated the factors that influence insect activity, and identified those abiotic variables that can be used to predict insect activity. The regional weather patterns within the Yukon summer range can be predicted from the records of permanent weather stations and assessed in relation to potential insect abundance. We document activity budgets, habitat selection and food habits of the herd during harassed and unharassed time periods using this information to assess the strategies employed by caribou in minimizing the negative energetic effects of harassment in terms of group dynamics and behavior of individuals. In the concluding section we attempt to integrate all these factors to account for the movements, activity and behaviour of the herd during this critical time period.

Study area

The climate in the study area (Fig. 1.2) is characterized as «polar continental» in the extreme north and «subarctic continental» to the south (Wiken *et al.* 1981) with mean daily summer temperatures above 3°C and mean daily winter temperatures below -10°C. Precipitation is low at all times of the year.

Wiken *et al.* (1981) defined 3 broad ecoregions in this area: the Northern Coastal Plain, the Northern Mountains and the Old Crow Basin (Fig. 3.1). The Beaufort Sea and the northern limit of tree line define the northern and southern limits of the study area. The Northern Coastal Plain ecoregion stretches northward from the 150m elevation contour to the Beaufort Sea coast. Cold north winds often blow off the Beaufort ice pack resulting in cool summer temperatures. There are numerous lakes and ponds on the coastal plain, many associated with thermokarst features. More lakes occur east of the Firth River as this area was glaciated.

In the Northern Mountains ecoregion the British, Barn and Richardson Mountain ranges are separated by the large drainage basins of the Babbage and Blow Rivers. In each mountain range there are numerous valleys and occasional upland plateaus. Peaks in the British and Richardson Mountains reach an elevation of 1500m while the central Barn Mountains do not exceed 1100m. This region was unglaciated, so most mountain valleys tend to be narrow and V – shaped. Summer temperatures are slightly warmer than on the coastal plain to the north, although cooler temperatures are still found at high elevations. Broad valleys to the south of these mountains merge with the Old Crow pediments which surround the Old Crow Basin (Wiken *et al.* 1981).

The Old Crow Basin ecoregion has elements of both arctic tundra and boreal forest. The pediments in the northern sector of this region rise to 450m elevation and merge with the foothills of the Northern Mountains ecoregion. The southern sector consists of a huge wetland complex at an elevation of approximately 300m. The climate of this region is much warmer in summer than that of the mountainous and coastal regions to the north.

Russell *et al.* (1992a) has described the vegetation communities of the northern Yukon Territory. The range types of interest in this study are: tussock meadow, wet sedge meadow, dwarf shrub heath, and alluvial willow. We also refer to the alpine barren described in the spring section, as «sparsely vegetated» because it occurs at low elevation in the study area, and identify two additional habitat types: low shrub tundra and sedge heath.

Summer movements

Historical

The post-calving movements of the Porcupine Caribou Herd begin about 15 June, two weeks after the peak of the calving period (Calef 1974). Calving usually takes place on the Alaskan coastal plain during years of normal to early snowmelt. If snowmelt is delayed, pregnant cows may be dispersed south of the coastal plain throughout the hills north of the British and Brooks Mountains and in the intermountain basins. In the years when caribou calve in northern Yukon, they travel west to the Alaskan coastal plain after calving. Westerly movement continues as the caribou begin to coalesce into increasingly larger aggregations, usually on the uplands between the Jago and Hulahula Rivers (Garner and Reynolds 1986). The caribou move on to the coastal plain as the snowmelt progresses.

With the onset of insect harassment during the last week in June, the caribou often move to the coast, aggregating on the coastal plain from the Canning River delta to Beaufort Lagoon. In 1976 and 1981, severe inclement weather (fog, rain and cold) may have reduced insect activity as coastal aggregations did not form (Curatolo and Roseneau 1977; Whitten pers. comm.). Although insect harassment has often been postulated as the stimulus for formation of large dense groups, large groups have formed prior to insect activity in some years. Large groups have also formed in years of few insects, as in 1973 (Roseneau *et al.* 1974), though these aggregations were probably not as tightly spaced as those which form when weather conditions favour insect harassment.

During «normal» years, the caribou remain near the coastal plain in Alaska until the first week in July, when a concerted movement to the southeast begins. At this point, the cow calf component of the

Porcupine Herd is usually in several large groups of tens of thousands of animals, which may join into one or two huge groups totaling 70,000 – 80,000 animals as they progress towards the Yukon/Alaska border. These cow/calf groups usually encounter bull/juvenile groups in the vicinity of the Clarence River between 7 – 15 July, although some bulls may already have joined the cows on the coastal plain. These caribou usually move south into the foothills later in July. In 1972 and 1982, 10,000–15,000 caribou remained on the coastal plain for the summer, seeking relief from insects by wading in the Arctic Ocean or resting on ice pans along the shore (McCourt *et al.* 1974; Russell *et al.* 1992b).

After crossing the Yukon-Alaska border, the majority of caribou usually continue southeast through the foothills of the British Mountains in early July, crossing the Malcolm River and on into the valley of the Firth River. The lower Firth River cuts into a deep canyon which poses a major obstacle to the herd as they move up the Firth River valley searching for suitable crossing points. Many calves are separated from cows or drown during these crossings (Farnell pers. comm.). Upon reaching the southeastern end of the British Mountains, between the headwaters of the Babbage River and the Muskeg Creek, the caribou normally halt their concerted movement and stall at the northern edge of Muskeg Basin. As slower or later arriving caribou begin to gather over the next few days, the herds once again become more concentrated. Thus the south-eastern edge of the British Mountains (Muskeg Basin) appears to be consistently used as a «staging area» where caribou congregate before moving again around mid July.

From 1971 through 1975, the majority of post-calving caribou continued to travel southeastward crossing the southern flanks of the Barn Mountains and into the Richardson Mountains northeast of Bonnet Lake in the latter half of July (Roseneau and Curatolo 1976). In August, the caribou dispersed across the northern edge of Old Crow Flats and westward into Alaska. This pattern began to change in 1976 when the herd remained in the Richardson Mountains in August and did not return to Alaska (Curatolo and Roseneau 1977).

In 1977, the majority of the herd was last observed on 18 July – still on the coastal plain. One large group was south of Barter Island (60,000) and another group south of Herschel Island (30,000; Bente 1977). This was the first year, since studies began in 1971, in which the cow/calf aggregations did not travel to Alaska after calving. The large herd south of Herschel Island was seen to turn east rather than west after emerging from the Firth Valley onto the coastal plain. Unfortunately, their late movements were not observed.

The year 1978 marked another significant change in the post-calving movement pattern. Most of the herd did not move east across the Firth River, but travelled south within Alaska along the headwaters of the Firth and Malcolm Rivers (Russell *et al.* 1992b). This route to the west of the Firth retraced the spring migration route of that year, which had been abnormally far west, because an unusual snowmelt pattern resulted in easier travelling on the western side of the Old Crow migration route. As caribou tend to follow fresh trails, this unusual post-calving movement pattern may have been an artifact of the unusual spring migration route taken one month previously. As a result, in 1978, only 15,000 caribou reached the staging area at the south-eastern edge of the British Mountains. These caribou did continue along their «normal» route eastward and arrived in the Richardson Mountains later in July.

In 1979, it appeared that the majority of the herd again swung southwest into Alaska after the segregated cow/calf and bull /juvenile groups joined up on the coastal plain, but poor weather prevented full documentation of this movement. In that year 30,000 caribou reached the staging area on the southeast edge of the British Mountains. Then, instead of continuing to the Richardson Mountains, half of the herd split off and moved back into Alaska via the Firth River headwaters. This movement scenario seemed to be followed in subsequent years.

In conclusion, the post-calving movements of the Porcupine Caribou Herd followed a general pattern (Fig. 4.1) which persisted 1971–76, then changed abruptly in 1977-78. Since 1979, the majority of the herd has travelled to the staging area on the southeast side of the British Mountains, usually in the first half of July. From this point, a majority of the herd has moved back into Alaska, by-passing the

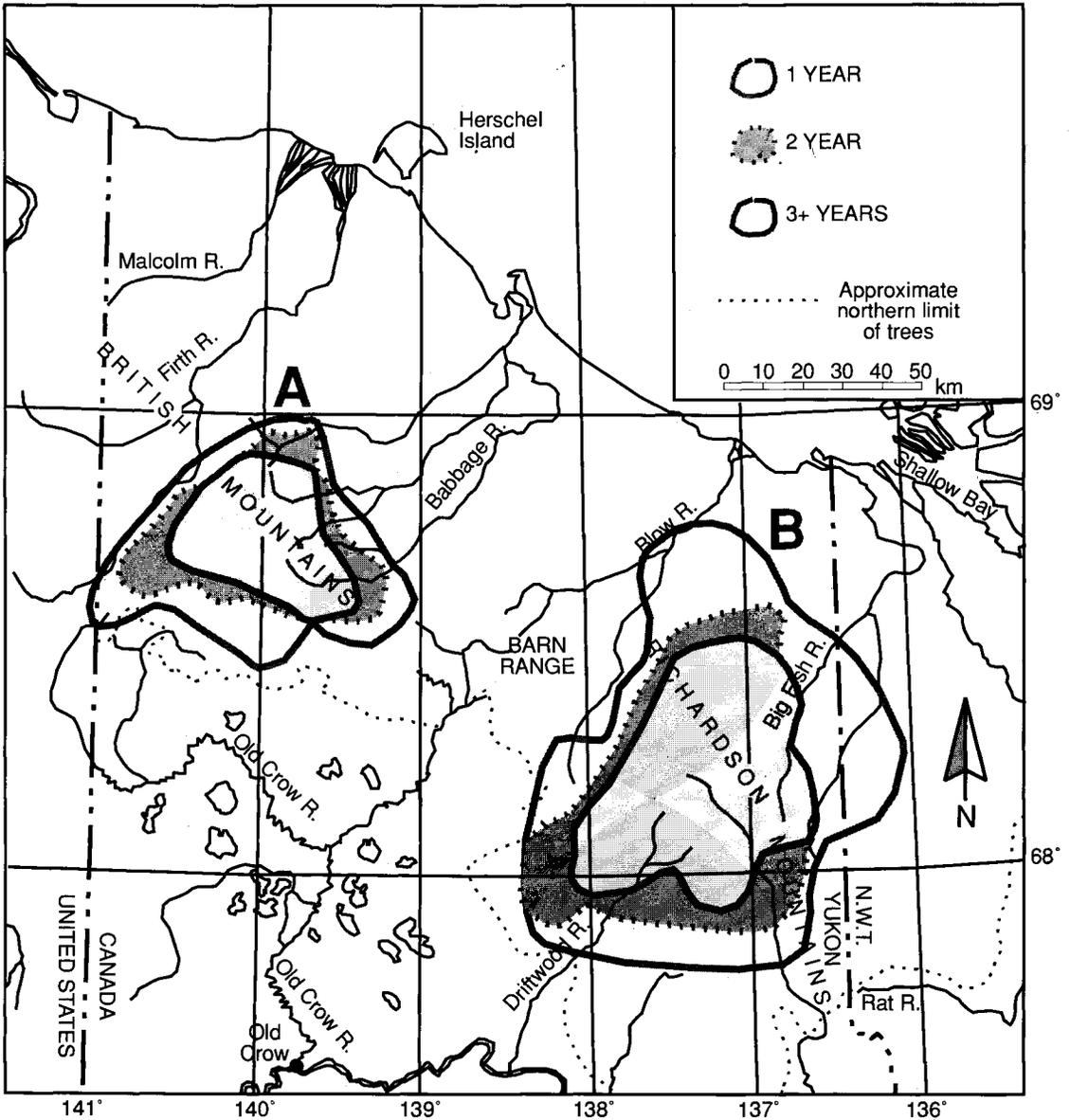


Figure 4.1. Mid summer insect relief habitat of the Porcupine Caribou Herd in Yukon.

Richardson Mountain insect relief areas traditionally used by the large post-calving aggregations. The Richardson Mountains still remain important to a smaller segment of the herd.

Herd movements - 1984, 1985

Methods

During our study period, intensive radio-telemetry flights and ground surveys provided a detailed account of group movements and distribution which could be related to known historical movements of the herd. We also wished to examine herd dynamics during periods of insect harassment, using radio-collared individuals as a means of keeping track of groups as they dispersed and coalesced.

Results

Caribou distribution April - August, 1984

The spring movement northward in 1984 was primarily west of the Richardson Mountains through the Barn Range, the Babbage River drainage, and the British Mountains. In May, other caribou (probably bulls and barren cows) were seen moving northward west of the Old Crow Flats.

By 5 July, large groups of post-calving cows joined with bulls and barren cows in the British Mountains by the Yukon/Alaska border to form a number of discrete groups. Our radio-telemetry flights indicated that about 100,000 caribou were in the Yukon in 13 groups. The largest of these groups was followed through the season. This group, located on the Spring River, contained close to 40,000 caribou including 32 with radio-collars. On 6 - 7 July strong winds blew from the southwest preventing us from monitoring the group. On 8 July winds had subsided enough to allow us to relocate it, greatly fragmented, approximately 50 km to the southwest at the head of the Trail River. For the next five days mosquitoes were

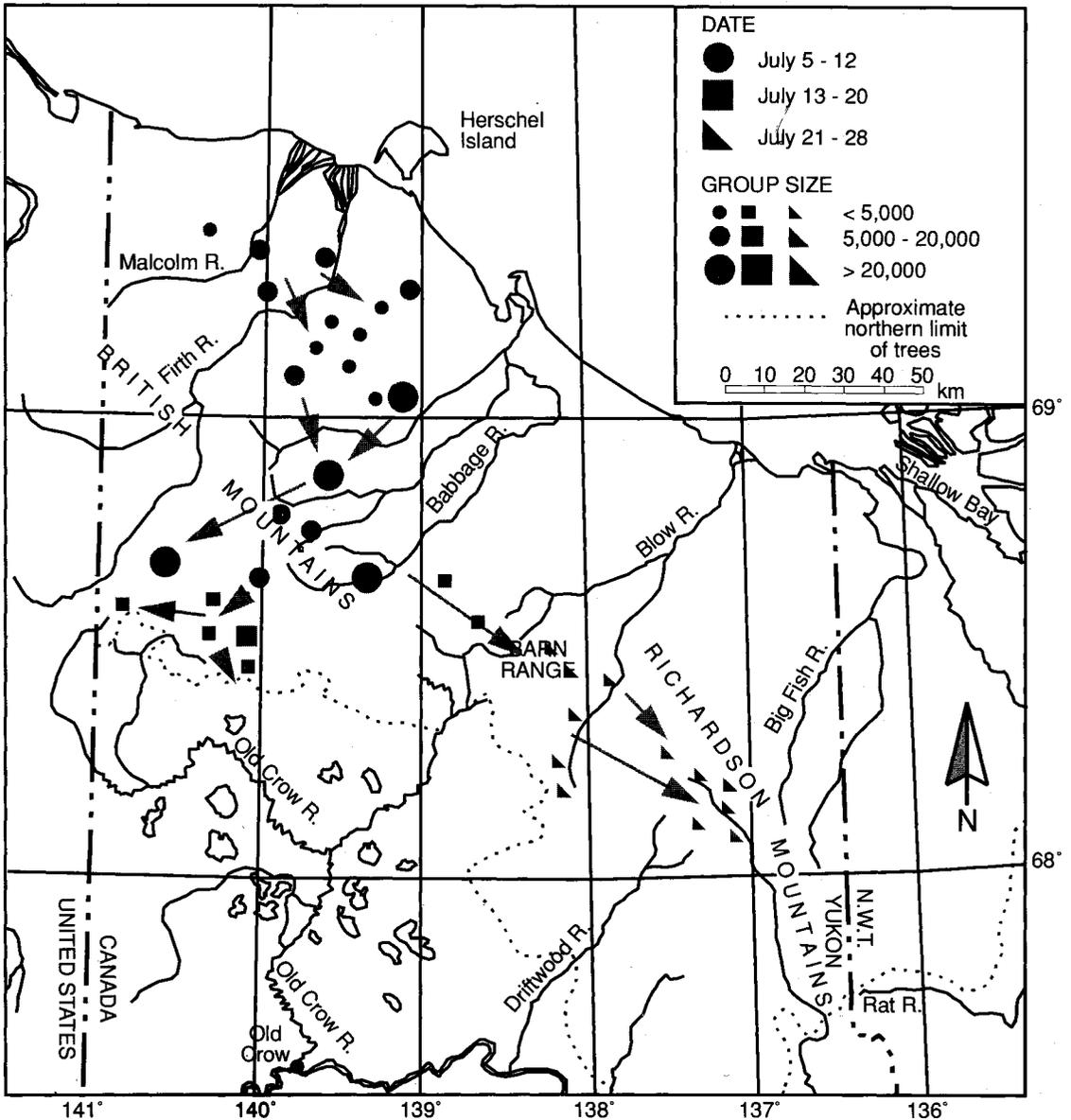


Figure 4.2. Movements of the Porcupine Caribou Herd in the summer of 1984.

bothersome and the caribou moved only short distances between lowland feeding areas and «insect relief habitat» on wind exposed ridges and uplands on the southeast edge of the British Mountains. The typical diurnal pattern for caribou was to forage at lower elevations at night, move up in elevation to wind exposed slopes by 0800, and remain in these areas until evening. As temperatures dropped and insect activity subsided, the caribou moved down into the basin of Muskeg Creek/Babbage River headwaters for another period of feeding.

On 12 July another storm began and continued until 15 July. The large group split into at least 6 smaller groups, all but two of which moved westward into Alaska along the northern edge of Old Crow Flats (Fig. 4.2).

By 19 July, only about 8,000 caribou remained in the Yukon. In groups of various sizes, they moved quickly eastward through the Barn Range, across the Blow valley, and remained in the northern Richardson Mountains until 1 August. In early August, the frequent storms and cool weather suppressed insect activity and served to disperse the larger groups. The maximum group size rarely exceeded 100 caribou in August.

Caribou distribution 22 June – 6 August, 1985

In 1985, approximately 40,000 caribou wintered in the Richardson Mountains north of the Dempster Highway. By late May, nearly half of them had moved west into Alaska along the coastal plain and north of the Old Crow Flats. Those remaining in northern Yukon in late May (approximately 22,000) were in the British Mountains and west of the Babbage River.

Fifty radio-collared caribou were located in a survey of the Yukon north slope on 22 June. These were primarily cows distributed in small bands (< 200 caribou) from west of the Babbage River to the Alaska border. Most of these bands were in the foothills and on the coastal plain between the Babbage and Malcolm Rivers. A brief survey flown on 23 June along the coastal plain and foothills indicated a steady westward movement of caribou. By 27 June, most were west of the Malcolm River and moving into Alaska.

Poor weather interfered with flying early in July. Relocation surveys on 5 and 6 July indicated an eastward movement of caribou from Alaska through the British Mountains, in groups ranging from 3,000 to 20,000 caribou. These animals made extensive use of the upland areas east of the Firth River, at the headwaters of the Crow and Trail Rivers. These groups periodically split up and reformed during the second week of July, varying in size from approximately 1,000 to 25,000. During this time, the caribou started moving south and east making extensive use of the Muskeg Creek drainage (Fig. 4.3).

By 11 July, several thousand caribou were moving eastward through the headwaters of the Babbage River. By mid July, approximately 20,000 caribou were found in the middle of the Barn Range. These caribou continued moving east and were found east of the Blow River 18 July in groups of 4,000 to 12,000 caribou.

Approximately 25,000 caribou used the Richardson Mountains in the last week of July and first week of August. Maximum group size varied from 1,000 to 9,000 depending on weather conditions and thus, insect activity. Movement was generally southward in the last week of July (as far as 68° 00'lat.) and then northward by 2 August to the Rapid Creek and Purkis Creek drainages. In the final survey on 6 August most caribou in northern Yukon were found in the hills north of the Richardson Mountains, on the edge of the coastal plain (Fig. 4.3).

Discussion

The Porcupine Caribou Herd and other barren-ground caribou herds move long distances to summer range and continue to move throughout the summer. These long range movements may be in response to predators, insects or food availability and quality.

The search for a combination of insect relief habitat and prime feeding areas may best explain caribou summer movements in northern Yukon. The large groups seen in early summer must move or they would quickly overgraze an area. Overgrazing by caribou has been documented recently on Rideout Island

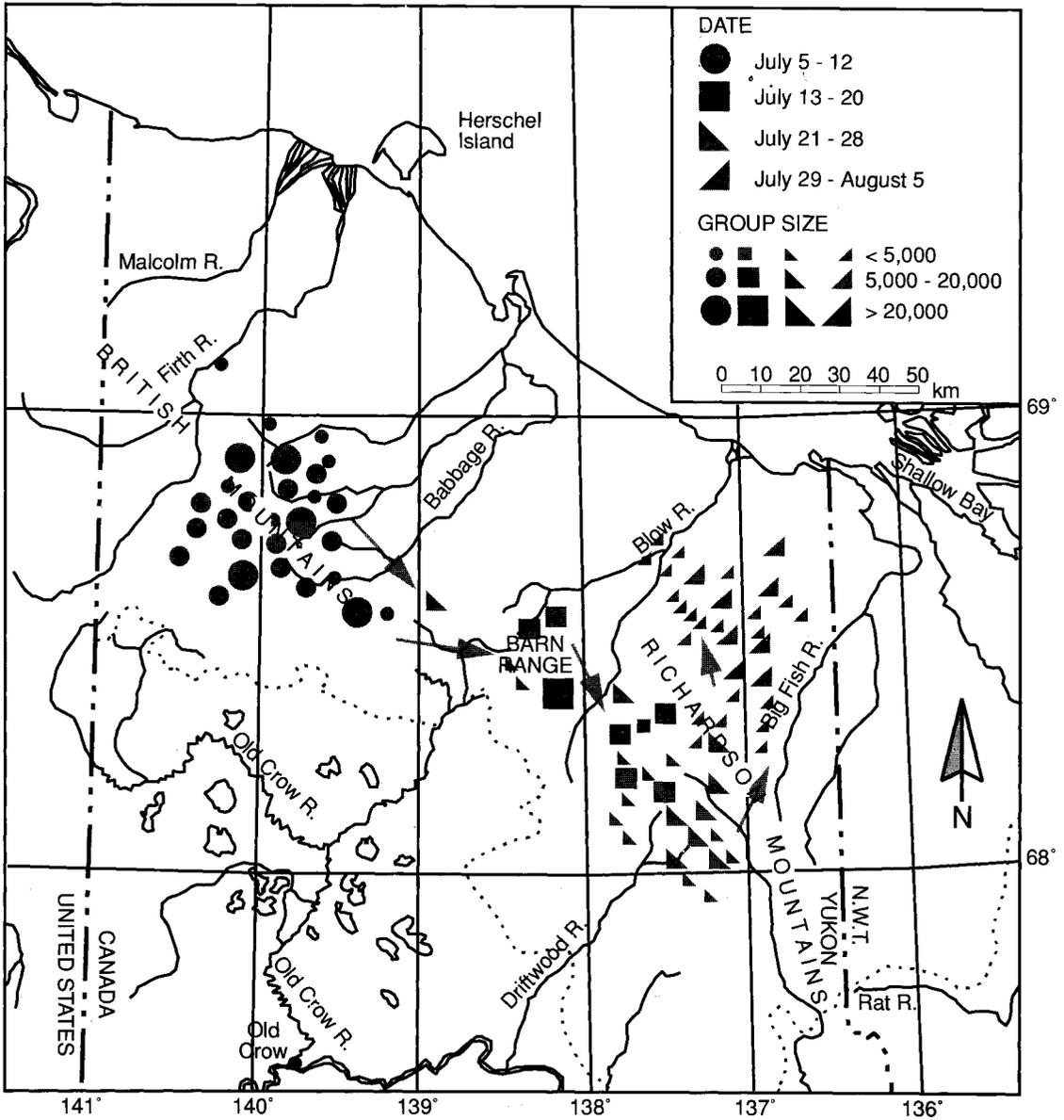


Figure 4.3. Summer movements of the Porcupine Caribou Herd in 1985.

N.W.T. (Heard 1988) and by reindeer on St. Matthew Island (Klein 1968). In addition to overgrazing, we have observed that trampling can destroy much of the vegetation in narrow valleys which several thousand caribou have passed through. Much of the western portion of northern Yukon is mountainous and therefore sparsely vegetated. These areas generally offer good wind exposure on uplands and are therefore good insect relief habitat. However, they are of limited use to caribou because they are not in proximity to extensive habitats with some shrub component.

The intensive monitoring of herd movements during this study confirmed the consistent patterns of distribution and use described historically. The shift from important staging areas on the southeast side of the British Mountains and the movement corridor to, and use of, the Richardson Mountains, must be considered as the «traditional» use pattern of the herd.

Activity of dipterans in relation to date and weather

Introduction

Approximately 12 species of mosquitoes (*Culicidae*) are found in northern Yukon Territory (Wood *et al.* 1979). Mosquitoes detect their prey by travelling in the direction of increasing CO₂ concentration (Wood *et al.* 1979) and they may travel several kilometers (Hocking 1953). At closer range, mosquitoes detect heat given off by the host and are also attracted visually to the target.

Adult nasal bot flies (*Cephenemyia trompe*) and warble flies (*Hypoderma tarandi*) mimic bees in appearance but do not feed and therefore have very reduced mouthparts. They emerge in early summer and mate. Mated females then search for caribou on which to deposit their larvae or eggs.

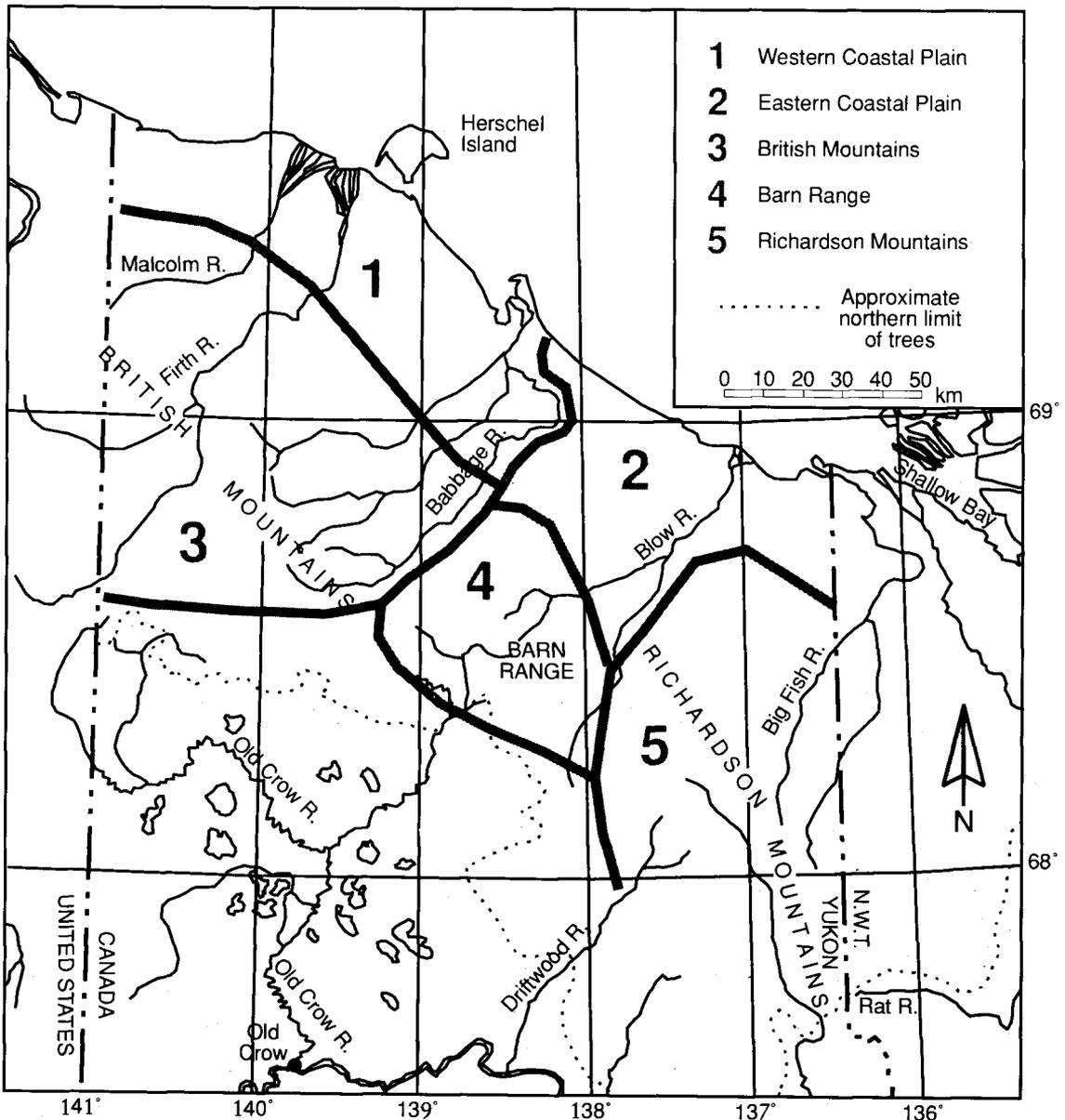


Figure 4.4. Sampling regions for mosquito sweep samples on the summer range of the Porcupine Caribou Herd, 1986.

The objective of this part of the study was to determine the abiotic factors, particularly weather conditions and season, that influence activity of mosquitoes. We predicted a negative relationship between wind speed and mosquito activity, and a positive relationship between temperature and mosquito activity. We were not able to determine how weather and season influenced activity of Oestrid flies, but we did infer from the literature how weather conditions influence the activity of these flies.

Methods

Weather

We recorded weather conditions concurrently with each mosquito sample. Wind speed (m/s) was measured at a height of about 1.5 m with a hand held Sims (TM) anemometer. Wind direction was determined by compass and recorded as north, northeast, east, southeast, south, southwest, west, or northwest. Cloud cover was estimated to the nearest 5%. Ambient temperature was determined from a mercury thermometer (°C) suspended 30-40 cm above the ground and shaded. In 1985 and 1986, we determined relative humidity with a hand-held sling psychrometer.

Mosquito sampling

Mosquitoes are relatively easy to capture because they are poor fliers and most northern species are attracted to any warm-blooded animal. Mosquitoes were sampled using a sweep net 40 cm in diameter on a 1.6 m dowel. With each sample we recorded weather conditions, habitat type, date, time and location.

The most complete sampling of mosquitoes was made in 1986, when sweep samples were collected systematically between 1 July and 5 August. Therefore, analyses to determine the effect of weather, date and time on mosquito activity were conducted only on the 1986 data.

Sampling sites were assigned to one of five geographic regions (Fig. 4.4), plus the Bonnet Lake base camp (where most of the samples were collected). Three of these regions fall within the Northern Mountains ecoregion (Fig. 3.1), but do not extend to its northern limits. The two coastal regions (Fig. 4.4) extend as far south as the 350 m contour.

Only female mosquitoes were used in the analyses. In addition to actual and mean numbers of mosquitoes caught, we used the proportion of total sweep samples having one or more female mosquitoes for each degree of temperature or each m/s of wind speed. To consider interactions between temperature and wind speed, a functional response index was developed using the following equations;

$$\begin{aligned} &\text{If temperature } > 18^{\circ}\text{C then } TI=1 \\ &\text{If temperature } < 6^{\circ}\text{C then } TI=0 \quad TI=1-((18-\text{temp})/13) \\ &\text{where temp}=\text{temperature } (^{\circ}\text{C}) \\ &\text{If wind } > 6 \text{ m/s then } WI=0 \\ &WI=(6-\text{wind})/6 \\ &\text{where wind}=\text{wind speed (m/s)} \\ &INDEX=TI \times WI \end{aligned}$$

This INDEX is based on the following sampling results:

- a. no mosquitoes were caught at temperatures $< 6^{\circ}\text{C}$ in any year.
- b. the proportion of samples with mosquitoes did not increase much above 18°C .
- c. no mosquitoes were caught at wind speeds $> 6\text{m/s}$.

Oestrid flies

These flies are difficult to study without specialized traps because they are not usually attracted to humans and are strong, fast fliers compared to mosquitoes. Limits to flight for oestrid flies therefore were

taken from the literature. Kelsall (1975) cited studies on reindeer that set a minimum temperature of 13 to 15°C and an optimum of 15 to 27°C for oestrid flight. Kelsall (1975) also observed that warble flies were inactive at winds greater than 8 to 9 m/s even if other conditions were favorable. Based on these limits, a functional response index was developed for oestrid flies using the following equation;

If temperature > 18°C then TI=1
If temperature < 13°C then TI=0 $TI=1-((18-\text{temp})/10)$
where temp=temperature (°C)
If wind > 9 m/s then WI=0
 $WI=(9-\text{wind})/9$
where wind=wind speed (m/s)
INDEX=TIxWI

Thus as INDEX values approach 1.0, weather conditions were considered more favorable to mosquitoes and oestrid flies.

Results

Mosquito sweeps

Seasonal effects

The number of female mosquitoes caught in sweep samples ranged from 0 to 141 with a mean of 3.2 (n=399, SE=0.46). In 1986, mosquitoes were caught throughout the sampling period and the maximum catch was greatest in the second week of July.

The overall mean mosquito catch was compared for the first and second half of the study period. The difference in means between 1 – 18 July and 19 July – 5 August (3.8 vs 2.0) was significant (Mann-Whitney, U=-3.95, p<0.01). The proportion of samples with mosquitoes was also lower in the second half (0.66 vs 0.46).

Diurnal variation

Mean mosquito catch was generally higher after 1900 hours. A quadratic regression of mean mosquito catch on time was significant ($r^2=0.47$, $p=0.001$). A quadratic regression of time on mean temperature was significant ($r^2=0.63$, $p=0.014$), indicating that the relationship between temperature and time of day was non-linear. The apparent relationship between time and number of mosquitoes caught is probably due to the increase in ambient temperature throughout the day. No collections were made between 2400 hrs and 0700 hrs, so a complete evaluation of diel pattern in mosquito catch was not possible.

Relative humidity

Mosquito catch was not significantly correlated with relative humidity (Spearman's correlation coefficient= -0.098, $p>0.05$).

Temperature

In 1986, no mosquitoes were caught below 7°C, and the catch remained low up to 10°C. The highest mean catches were at 18°C and 19°C. Mean catch of mosquitoes was regressed on temperature. The quadratic regression was significant. The regression curve indicates that the highest mean catch of mosquitoes was at approximately 18°C (Fig.4.5).

A quadratic regression of proportion of samples with mosquitoes on temperature was highly significant ($p<0.01$) at $r^2=0.82$.

Wind speed

The number of mosquitoes caught in sweep samples dropped off above wind speeds of 4 m/s, and no mosquitoes were captured above 6 m/s. The highest mean catch was at 1 m/s wind speed. A regression of the mean mosquito catch on wind speed was negatively related to wind speed (Fig. 4.6; note the regression line appears to increase above 11 m/s. This is simply an artifact of fitting a quadratic equation to the data.) The quadratic regression had a much higher r^2 than was found with temperature; therefore, wind speed appears to be the best single predictor of mosquito activity.

The proportion of samples with mosquitoes also was significantly related to wind speed; a quadratic regression had an $r^2=0.95$.

Wind/temperature index

The mean number of mosquitoes caught was higher above the 0.5 wind/temperature INDEX level though a quadratic regression of mean mosquito catch on INDEX was not significant. A quadratic regression of the proportion of samples with mosquitoes on wind/temperature INDEX was significant at $r^2=0.91$.

A quadratic regression of the proportion of samples with mosquitoes on wind/temperature INDEX was significant at $r^2=0.91$.

Region

It was difficult to compare differences in mosquito activity among regions because weather conditions often varied among sample sites. However, a Kruskal-Wallis test on mean mosquito catch indicated that there were locational differences in number of mosquitoes caught (X^2 approximation=16.33, $p=0.01$).

Among the regions sampled, the highest mean number of mosquitoes caught in sweep samples was in the area west of the Babbage River (including Trout Lake), and the second highest mean was in the Blow River Valley (Table 4.1.). There was a significant difference in mean mosquito catch between the Blow River Valley vs. the British, Barn, and Richardson Mountains ($p < 0.05$).

Wind speeds recorded with each mosquito sample were compared among regions and no significant difference was found ($p < 0.05$). It appears that difference in wind speeds alone do not account for the variation in mosquito catch in the different regions. Temperatures recorded with each mosquito sample were significantly different among regions (Kruskal-Wallis, X^2 approximation=10.80, $p=0.002$). In the Richardson Mountains, samples were taken at significantly lower temperatures than in each of the other regions ($p < 0.05$).

Discussion

Influence of season and weather on Dipterans

The initial increase and subsequent decline in the mean number of mosquitoes caught suggest a seasonal

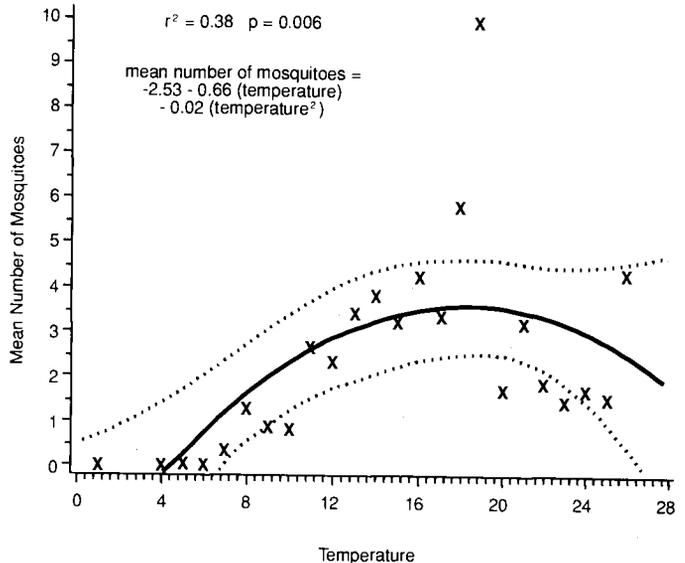


Figure 4.5. Quadratic regression (with 95% confidence intervals) of mean number of mosquitoes on temperature ($^{\circ}\text{C}$).

change in the mosquito population. The lower mean catch of mosquitoes caught in the second half of the study period was not a result of inclement weather at the time of sampling. The same proportion of samples (87%) were taken within the limits for flight for both the first and second half of the study period. Thus, the changes that we observed in the number of mosquitoes caught in relation to date probably reflect changes in the population size.

Time of day did not appear to influence the level of mosquito activity, and no midday lull in activity was observed, unlike in southern latitudes (Taylor 1963; Downes 1965). Downes (1965) observed that the diel pattern of insects at northern latitudes is a function of weather rather than a response to light intensity, and reported that blood-seeking flies may have periods of very intense activity within their short life span as adults.

The strongest relationship between actual number of mosquitoes caught over the entire sample period and weather/temporal variables was with wind speed, which appears to be the best predictor of mosquito activity.

With regard to presence/absence of mosquitoes, the proportion of samples with mosquitoes had high r^2 values for quadratic regressions with wind speed, wind/temperature INDEX and temperature. These results suggest that it may be more realistic to predict presence/absence of mosquitoes rather than actual level of activity based on known weather conditions.

The difference in mean mosquito catch between the Richardson Mountains and other regions was attributable, at least in part, to differences in temperature. Regional differences in the population of emergent mosquitoes were not measured, but may have contributed to the differences in mosquito catch between regions.

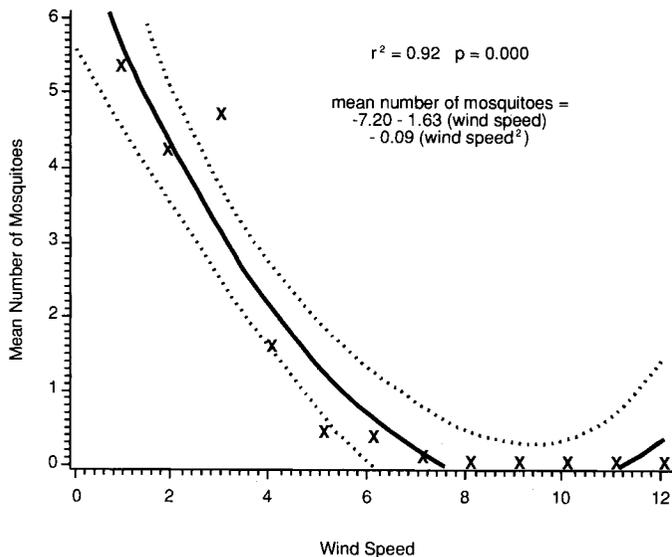


Figure 4.6. Quadratic regression (with 95% confidence intervals) of mean number of mosquitoes on wind speed (m/s).

Table 4.1. Mean number of mosquitoes and proportion of samples with mosquitoes in each location.

Location	Number of mosquitoes			Proportion of samples with mosquitoes
	Mean	Standard deviation	Sample size	
Trout Lake and west of Lower				
Babbage River	14.3	38.3	13	.91
British Mountains	1.6	4.9	30	.66
Barn Range	1.6	2.5	34	.60
Bonnet Lake	3.1	6.8	238	.53
Richardson Mountains	2.9	5.6	32	.47
Blow River Valley and east of				
Lower Babbage River	3.7	4.4	30	.73

Though we did not quantify the wind and temperature thresholds for oestrid flight, incidental observations in this and previous studies suggest that oestrid flies are active at higher wind speeds than mosquitoes, but require a higher temperature to initiate flight. Because of the problems in sampling for oestrids, and the fact that the best relationships between weather conditions and mosquito activity were for presence/absence of mosquitoes, weather conditions were not used to predict dipteran activity beyond presence/absence. Thus, caribou group dynamics and behavior were related to weather conditions which either favoured both mosquitoes and oestrid flies (wind speed less than 6 m/s and temperature greater than 13°C) or limited their activity (wind speed greater than 6 m/s or temperature less than 13°C). Other subsets of weather conditions were used where indicated.

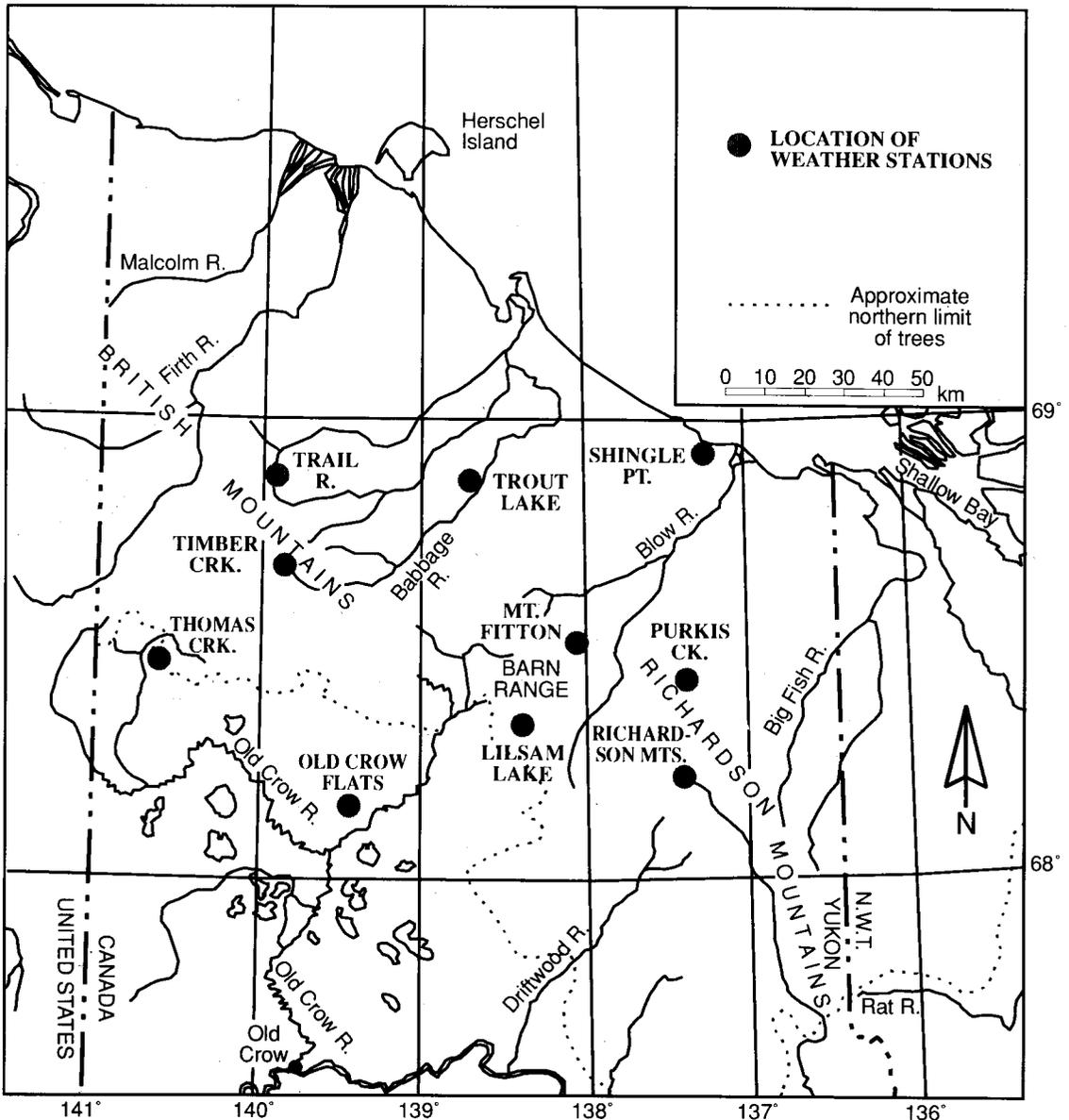


Figure 4.7. Location of weather stations.

Climate and weather patterns

Introduction

As the Porcupine Caribou Herd exhibits rather consistent movement patterns over the years during the insect season and the local activity of insects is strongly influenced by weather variables, it is important to explore the detailed regional weather patterns within the study area in an effort to understand the regional distribution of the herd.

The study area is influenced by two interacting regional climates; the subarctic continental climate and the arctic coastal climate (Ritchie 1984). These types are generally delineated by a line roughly paralleling the coast along the first set of foothills south of the coastal plain region. The line that delineates the two climates corresponds to a 30% isoline, areas south of the line being influenced by Pacific air for over 30% of July, areas to the north for less than 30%. The line shifts annually, dependent on the strengths of the interactions between the polar air mass and the warm, moist Pacific westerlies. The continental climate to the south is distinguished by a rapid transition from winter to spring and by warm, moist summers. Spring is greatly retarded in the arctic coastal climates (Ritchie 1984).

In the process of monitoring and predicting storms surges for Beaufort Sea drilling operations, Atmospheric and Environment Service determined that 8 storm patterns generally influence the study area (Atmospheric Environment Service 1985). In July and early August, the most prevalent patterns result in northeasterly/southwesterly air flows.

Methods

At the end of June, 1986, we deployed 10 remote weather stations throughout the study area (Fig. 4.7) intended to encompass the expected variation in weather patterns in northern Yukon. One station (Roland Creek) was destroyed by a grizzly bear. The remaining 9 provided data until the first week of August. Stations were deployed in similar sites, i.e. within tussock tundra vegetation communities, on flat relatively unobstructed terrain. Each station included CR-21 or CR-21x (Campbell Scientific) data recorders which were programmed to record hourly a range of information including: shaded air and ground temperature, relative humidity, wind direction, wind speed and solar radiation. In addition, weather information collected every 6 hours was obtained from the three permanent weather stations bordering the study area, Old Crow, Shingle Point and Komakuk.

No recordings were available from Old Crow at night.

Results and discussion

Data summaries

There were several problems with the raw data from the automatic stations. Equipment malfunctions required us to disregard a portion of the data sets for Timber Creek and Trail River. Some air temperature values at Timber Creek, Purkis Creek, Thomas Creek and Old Crow Flats were well beyond the range of possibility. Where unrealistic values were evident, air temperature was calculated by multiple regres-

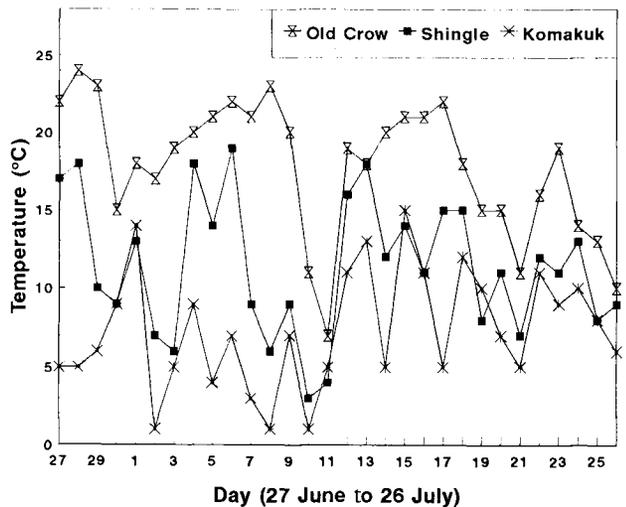


Figure 4.8. Average daily air temperatures at three sites on the summer range of the Porcupine Caribou Herd, 1986.

sion, using ground temperature, solar radiation and time of day as the independent variables. During the morning hours of 10 July, a strong low pressure system passed through the region, causing strong winds and a significant drop in temperatures. Due to the small size of some of the data sets, this phenomenon may affect all conclusions that are based solely on statistical analyses.

Average daytime air temperatures

At the permanent stations the mean daily temperature was calculated from the 1300 and 1900 hour temperatures. The daytime period was chosen because no nighttime temperatures were available from the Old Crow permanent station. The hours chosen reflect the hottest time of the day since solar noon at this latitude at this time of year is roughly 14:15 PM. Average daytime temperatures for the remote stations were calculated as the mean of recorded temperatures every two hours from 1100 to 2100.

Old Crow enjoys the warmest temperatures among the permanent stations while Komakuk is typically the coldest (Fig. 4.8). Mean daily temperatures at the temporary stations indicate that two groups emerge, those with warmer temperatures (Old Crow Flats, Timber Creek and Thomas Creek; overall mean 17.9°C), and those with cooler temperatures (Purkis Creek, Trout Lake, Trail River, Lilsam Lake, Mount Fitton and Richardson Mountains; overall mean 13.0°C). The Old Crow Flats was the warmest site (mean 19.2°C) and the Richardson Mountains the coolest (mean 10.7°C).

Average hourly air temperatures

The daily curve of the mean hourly air temperatures was of typical sinusoidal shape at five of the temporary stations (Mount Fitton, Purkis Creek, Lilsam Lake, Trail River, Trout Lake; Fig. 4.9A), with an obvious peak around 1600 - 1800 hours. At three of the

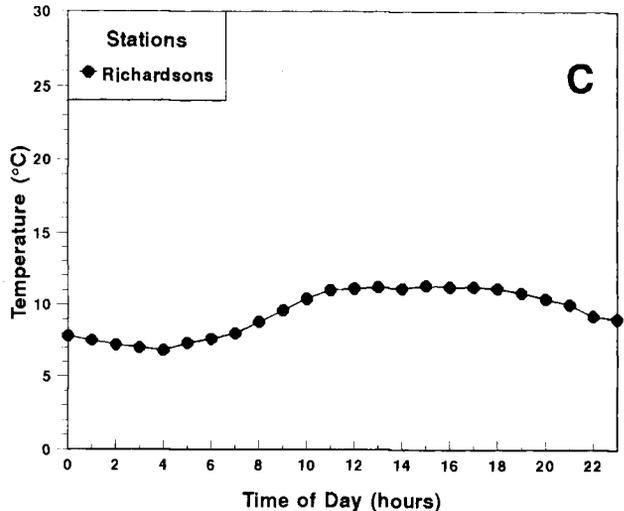
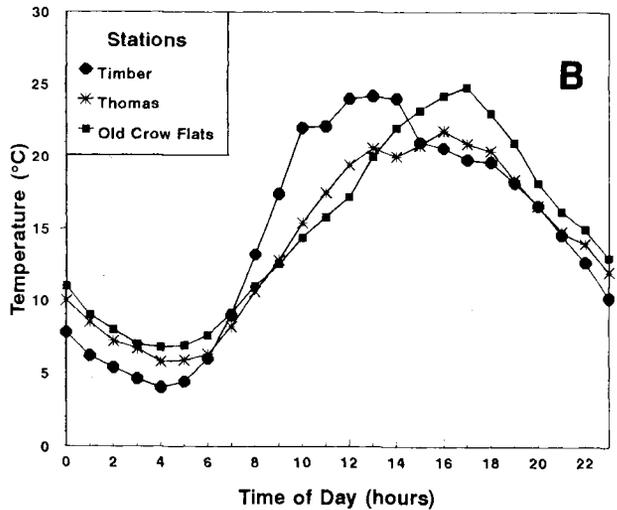
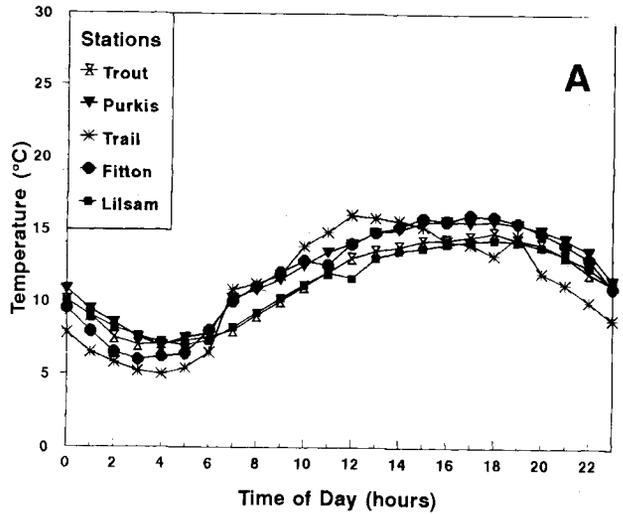


Figure 4.9. Average hourly air temperatures at nine sites on the summer range of the Porcupine Caribou Herd, 1986.

stations (Old Crow Flats, Timber Creek, Thomas Creek; Fig. 4.9B) a much more pronounced daily peak occurred (at 1400 hours at Timber Creek). At Richardson Mountains the daily peak was much dampened (Fig. 4.9C).

Average hourly wind speeds

There is a much less consistent relationship between windspeed and time, using hourly recordings, for the three temperature regions identified in Figure 4.9. This is not surprising as wind speed is more variable than temperature. In spite of the variability, all but one of the stations identified in Figure 4.9A had similar patterns of mean wind speed (Fig. 4.10A). The winds at the Lilsam site were significantly higher than elsewhere. Lilsam appeared to be on the boundary of two systems, as it was common to see winds coming from opposite directions on adjacent small lakes in the area. Most sites experienced a wind lull from 0600 to 0800 hours and a daily peak around 1800 hours (Figs. 4.10A and 4.10B). The Richardson Mountain region exhibited the least variation in daily wind speed, with moderate winds all day (Fig. 4.10C). Mean average daily wind speed was highest at Lilsam and lowest at the Trail River site.

Correlations between permanent and temporary sites

Correlation tables were calculated for the period 27 June - 26 July for readings at 0700, 1300 and 1900 hours. These tables include;

1. temperature and wind correlations between permanent and temporary stations (Table 4.2).

2. temperature and wind speed correlations between temporary stations (Table 4.3).

We were able to determine strong air temperature correlations for most stations. Komakuk was invariably the poorest predictor of temperature for all of the temporary sta-

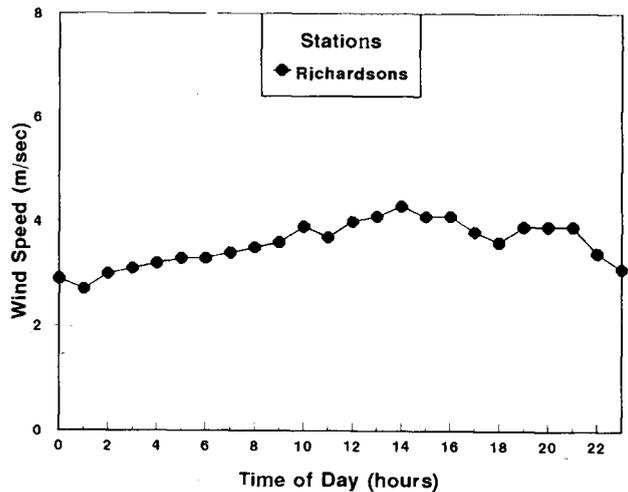
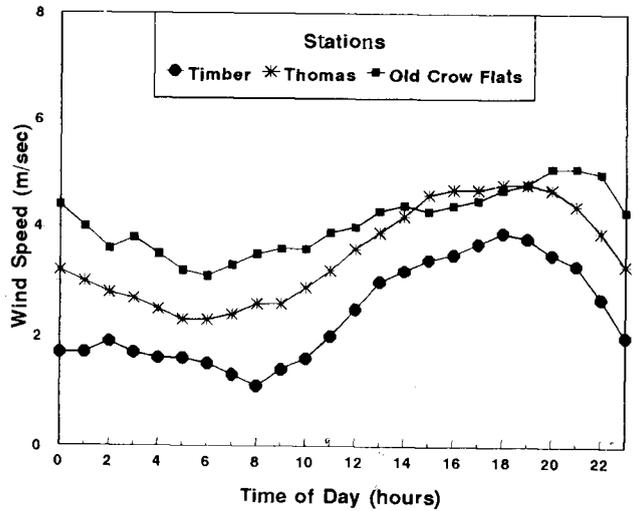
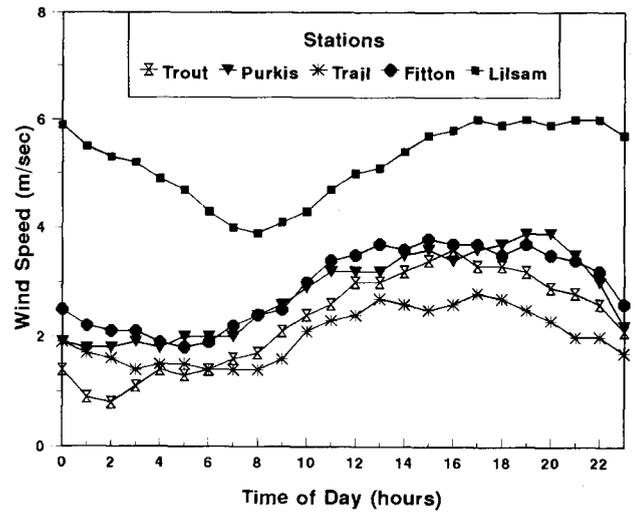


Figure 4.10. Average hourly windspeeds at nine sites on the summer range of the Porcupine Caribou Herd, 1986.

Table 4.2. Temperature and wind correlations between temporary and permanent weather stations on the summer range of the Porcupine Caribou Herd, July 1986.

Temporary weather station	Permanent weather station								
	Komakuk			Shingle			Old Crow		
	Wind	Temp	n	Wind	Temp	n	Wind	Temp	n
Trout22	.61	85	.46	.86	83	.24	.79	83
Purkis40	.60	79	.49	.88	77	.37	.78	77
Trail32	.32	48	.41	.56	49	.28	.64	48
Fitton14	.59	83	.55	.83	81	.58	.79	82
Timber15	.26	85	.44	.54	83	.43	.80	83
Lilsam02	.49	86	.35	.80	84	.54	.85	84
Richardson01	.34	86	.09	.65	84	.40	.83	84
Thomas24	.29	82	.43	.55	80	.40	.88	81
Old Crow Flats04	.38	82	.38	.63	80	.63	.91	81

tions. Shingle Point was a good predictor of temperatures for Trout Lake, Purkis Creek and Mount Fitton while Old Crow proved the best predictor of temperature at all the remaining temporary stations. Using this combination the lowest correlation coefficient we would have to employ is 0.80 with the single exception of Trail River (0.64). Among the temporary stations Lilsam Lake provided the highest mean correlation to all other stations (mean 0.86, range 0.72 - 0.96). For wind speed, the correlation coefficients were not as good as for temperature. Using the highest correlation coefficients between permanent and temporary sites, the mean correlation would be 0.49 (range 0.40 - 0.63). Although all of the correlations were significant, the resulting accuracy was less than we had hoped. Among the temporary stations, correlations were only marginally better. Mount Fitton provided the highest overall predictability among stations with a mean correlation coefficient of 0.57 (range 0.48 - 0.68). If only one remote station was to be established in the study area, the Mount Fitton site would be the most valuable, due to the highest correlation with wind and a very good correlation with temperature (0.83, range 0.66 - 0.96).

Regional weather versus insects

From the tabular summaries of average hourly temperatures, and using our algorithm for INDEX of mosquito and oestrid fly activity, we were able to rank the weather stations in terms of potential insect harassment (Table 4.4). One of the major factors that we were not able to consider was habitat type. We assumed that with equal weather parameters, wetland areas would produce more mosquitoes than drier terrain types. From our analysis, the Richardson Mountains and Lilsam Lake stations appeared to be significantly more favourable in terms of insect relief than all the other sites. Cool temperatures and moderate winds at the Richardson station indicated that it was the most favourable site for oestrid fly relief and the second most favourable site for mosquito relief. The Lilsam Lake site provided the best conditions to avoid mosquitoes, and the second best for avoiding oestrid flies. At the other end of the scale, Timber Creek, Trail River and Purkis Creek were the least favourable for mosquito relief, while Timber Creek, Old Crow Flats and Thomas Creek were the least favourable for oestrid fly relief.

Table 4.3. Temperature and wind Spearman correlation matrix among temporary weather stations on the summer range of the Porcupine Caribou Herd, July 1986.

	Temperature correlation									
	Trout	Purkis	Trail	Fitton	Timber	Lilsam	Richardson	Thomas	Old Crow Flats	
W	-	.96	.68	.94	.77	.92	.81	.80	.82	
I										
N	.59	-	.67	.96	.76	.94	.85	.77	.80	
D										
C	.60	.53	-	.66	.81	.72	.72	.70	.64	
O	.68	.55	.52	-	.73	.96	.87	.76	.79	
R										
R	.57	.36	.58	.65	-	.77	.75	.93	.86	
E										
L	.31	ns	ns	.56	.64	-	.92	.81	.84	
A										
T	ns	.30	ns	.47	ns	ns	-	.77	.77	
I										
O	.55	.41	.58	.54	.69	.55	ns	-	.95	
N										
Old Crow Flats	.38	.29	.41	.57	.68	.65	.39	.57	-	

ns=not significant

Table 4.4. Mean daily oestrid fly and mosquito harassment indices for the temporary weather stations on the summer range of the Porcupine Caribou Herd, July 1986.

Station	Oestrid index	Mosquito index
Old Crow Flats.....	0.28	0.22
Timber Creek	0.36	0.31
Richardson	0.03	0.12
Trail River	0.21	0.29
Trout Lake	0.16	0.25
Mount Fitton	0.21	0.24
Purkis Creek	0.24	0.28
Lilsam Lake	0.09	0.04
Thomas Creek	0.26	0.20

Response of groups and individual caribou to insect harassment

Introduction

A few studies have attempted to quantify the relationship between caribou behavior and activity and the presence of insects on summer range. Roby (1978) found group size was positively correlated with his subjective measure of mosquito activity. White *et al.* (1975) showed that caribou in the Central Arctic Herd segregated and formed small groups on days with little or no insect activity, and formed larger mixed groups on days when mosquitoes and oestrid flies were active. Helle and Aspi (1983) attempted to quantify how group formation might serve to reduce attack of insects on reindeer in the middle of a group vs. reindeer on the periphery of a group or on solitary individuals outside the group. They conducted an experiment with insect traps that simulated the size and shape of reindeer and found that significantly fewer insects were caught in the middle of a group of traps. However, their results have limited application as the trials were run in the absence of wind on small groups of traps. The effectiveness of group formation in reducing contact between caribou and insects is unclear from these studies, although the occurrence of large groups during periods of insect harassment has been consistently reported.

The first objective of this part of the study was to relate caribou group response to different weather conditions which either favored or limited insect activity. We predicted that when insects are active and winds are calm or low, caribou will form larger, tighter groups.

The second objective was to relate the display of annoyance responses to weather conditions that favored or inhibited insect activity, while considering possible sources of individual variation among caribou. Annoyance responses were used as an index of the level of harassment experienced by individual caribou. We predicted that when weather conditions favor insect activity, caribou will exhibit more frequent annoyance responses (head shaking, foot stamping, ear flicking, etc.).

The third objective was to determine the advantage or disadvantage of occupying certain positions in a group. We predicted that when insects are active and winds are low or calm, caribou in the core of a group will display fewer annoyance responses than those on the periphery. When insects are active and winds are moderate, caribou on the windward side of a group will display fewer annoyance responses than those in the core or leeward side of a group. We also predicted that caribou on the leeward side of the group will attempt to move to the centre or windward side of the group.

Methods

In past years, several caribou in the Porcupine Herd have been fitted with radio-collars (Garner and Reynolds 1986). During our study period, groups of caribou were located daily (when weather permitted)

using radio-telemetry. Daily straight-line movement rates of individuals were determined from successive relocations of radio-collared caribou.

In 1984 and 1985, estimates of group size and group composition were recorded for each group of caribou located during radio-telemetry flights. From the air, a group was defined as three or more caribou within 100 m of each other. Group size was estimated to the nearest 1000 for groups larger than 1000, and to the nearest 100 for groups smaller than 1000. Group composition was recorded as: mixed age and sex, predominately bulls or predominately cows. Weather conditions were not consistently recorded in conjunction with these observations of group size. The data were combined with ground observations on group size to determine the relationship between group size versus date and weather conditions.

The average spacing between the majority of caribou in the group was recorded. Inter-animal spacing was gauged by estimating the number of adult caribou lengths between individuals, using 1.5 m as the approximate length of an adult caribou. The categories used for spacing were: less than 1m, 1 to 4.9m, 5 to 9.9m, 10 to 14.9m, 15 to 24.9m, 25 to 49.9m and 50 to 99.9m.

In 1985, detailed observations of caribou activity patterns and behavioural response to insects were made between 3 July and 6 August. Mosquitoes and oestrid flies were active during this period, though the timing and duration of insect activity varied with date and weather. When a group of caribou was located, two to four observers were placed within walking distance of a vantage point near the caribou. Observations were made by one observer with a 20–40 x variable power spotting scope, while a second person timed the behaviours using hand-held stop watches or recorded data directly into an Epson HX20 (TM) field computer.

On the ground, group size was estimated to the nearest thousand for groups larger than about 1000, and the nearest 100 for groups between about 500 and 1000. A total count was made of groups smaller than 500. For the focal animal observations, an individual was chosen from each of the windward, core or leeward positions. Although most groups observed were of mixed age and sex, the majority of animals (and observations) were of cows with calves. Spacing in the immediate area of the focal animal was recorded. Caribou annoyance responses were recorded as individual events because their short duration made accurate timing impossible. Annoyance responses included head shaking, shaking of back and rump, tail flicking, ear flicking, stomping of foot and leg, and head dropping to the ground.

Two quantitative methods were used to determine the degree of harassment experienced by individual caribou occupying different positions within a group. The first method measured frequency of annoyance responses and activity patterns on a focal animal for a five-minute period. The second method recorded the time interval between the start of an observation on a focal animal and the first annoyance response displayed by that animal.

In the first method, a caribou was observed continuously for five minutes while age/sex, proportion (%) of hair shed, activity, annoyance responses, habitat occupied, and local weather conditions were recorded. Individuals were classified as cow with a calf, cow without a calf, yearling, mature or immature bull. The amount of hair shed was estimated to the nearest 5% on each caribou.

For analysing the advantage or disadvantage of being in a certain position in a group, only groups with inter-animal distance of less than 10 m were used. Caribou that were 10 or more meters apart were assumed to have equal exposure to wind regardless of the configuration of the group and were defined as being in loose groups. A group had to have at least 7 animals in diameter in any direction so that the central caribou was at least three caribou bodies inside from any peripheral animal. This generally was not a problem as most groups observed were composed of several thousand caribou. Position in a group was categorized as windward, core or leeward. The windward and leeward positions were combined as «peripheral» position for some of the analyses. The core was defined as the centrally located 20% of individuals in a group.

Few caribou remained in the same position within a group for the entire five minute period, so position was recorded both at the start and end of an observation period. For analysing the advantage or disadvantage of occupying a certain position, only the start position was used, so long as the individual remained

in a tightly spaced group for the entire period. The distance an individual moved in five minutes was categorized as 0, >0 and <10m, >10 and <100m or >100m.

The second method used to determine harassment experienced by individual caribou was designed to collect a large sample from different age/sex classes of caribou in different positions within a group. Individuals were chosen from each position and the time from the beginning of each observation to the time of the first annoyance response was recorded. This measure of time falls anywhere along the interval between two annoyance responses, so the mean of this measurement should be equal to half of the «real» interval time. A longer mean recorded time should reflect a longer mean interval between annoyance responses, indicating a lower frequency of annoyance responses. This measure of time is referred to as the «response interval» with the understanding that it does not represent the true interval. The type of annoyance response, age/sex of the caribou, proportion (%) hair shed, habitat occupied, activity and local weather conditions were recorded concurrently with these observations. Response frequency and response interval provided independent measures of harassment experienced by the caribou.

The level of harassment experienced by individual caribou in one position relative to another position in a group was tested by comparing the response frequency and the response intervals of individuals in different position categories.

Linear regression was used to test the relationship between group size and date. Kruskal-Wallis test, Mann-Whitney and Friedman's two-way analysis of variance on ranks of group size, spacing and movement rates were used to determine the relationships between each of these variables and categories of weather conditions and date. In many cases, date was treated as either the first half (1 July 1 - 18 July) or second half (19 July - 5 August) of the study period.

To analyse changes in group size, spacing and movement rate, the first record of these characteristics for each group on each day was used. If there was a significant change in weather (i.e. from weather conditions unfavorable for insects, to weather conditions favorable for insects or vice versa), a second observation of group size, spacing and movement rate was included in the data set.

Spearman's rank correlation coefficients were produced to determine the relationship between annoyance responses and all weather variables. Kruskal-Wallis tests, and Friedman's tests (two-way and three-way analysis of variance on ranked values of the dependent variables response frequency and response interval) used to determine their relationship with the independent variables: percent of hair shed, sex, date, location, habitat type, position in group, and weather conditions which either favored or limited insect activity. Few observations were made on yearlings and calves, so these were not included in the analyses done with the independent variables. Because of small sample sizes in the response frequency data, some of the categories of certain variables were grouped for analysis (e.g. habitat).

Results

Group dynamics

Based on radio-tracking surveys in 1984 and 1985, the maximum estimated group size observed was higher in early and mid July than in the last week of July. However the absolute number of animals in the study area also declined by the latter half of July.

In 1985, more detailed weather data were collected concurrent with observations of group size. There was no significant relationships between group size and weather conditions.

When all recorded observations of spacing were combined, we found no significant difference in spacing between the first and second half of the study period (Analysis of variance, $F=0.93$, $p=0.33$). We did find significantly tighter spacing (1-4.9 m) when weather was favorable for insects, compared to spacing of 5 to 9.9 m when it was unfavorable (Analysis of variance, $F=38.55$, $p < 0.001$).

Annoyance responses of individual caribou

Early in July, all cows had shed less than half their hair, while several bulls were already in an advanced stage of shedding. Later in July, about 85% of the cows observed had shed less than half their hair,

while 86% of the bulls observed had shed more than half their hair. There was a significant relationship between sex and % shed over the entire study period (Kruskal-Wallis, X^2 approximation=682, $p < 0.001$, $n=1352$).

The most commonly observed annoyance responses were head shakes; head drops were the least common. Cows displayed a higher frequency of back shakes and head shakes, while bulls displayed more frequent head drops and foot stamps. There was no significant difference in mean response frequency or mean response interval between the sexes or between caribou less than 50% shed versus 50% or more shed.

Caribou annoyance responses in relation to date and weather

Linear regression analysis of mean response frequency vs. weather variables indicated that both wind speed ($r^2=0.31$, $p=0.03$) and temperature ($r^2=0.41$, $p=0.001$) were significant, although the r^2 values were low. A quadratic regression with wind/temperature INDEX ($r^2=0.049$, $p=0.02$) gave a higher r^2 than wind speed or temperature. Regression analysis with mean response interval was only significant for temperature ($r^2=0.35$, $p=0.02$). Regressions with date were not significant for response frequency or response interval.

Mean values of annoyance responses indicated a higher frequency earlier in later July (14.5/min vs. 7.5/min). and a lower response interval (27.5 s vs. 41.1s). The mean response frequency recorded for caribou increased when weather was favorable for insects, and the mean response interval declined. In the two-way analysis of variance on ranks of response frequency and response interval, the date - weather effects were not significant, so there was no interaction between the dependent variables.

Relationship between position in group and insect harassment

We examined position in a group to determine if any advantage in occupying the core position was gained at low wind speed (≤ 3.5 m/s) vs. moderate wind speed (> 3.5 to 9 m/s). For the response frequency and response interval measurements, position was significant for both categories of wind speed (Friedman's $F=12.5$, $n=54$ for low wind speed; $F=17.8$, $n=68$ for moderate wind speed). At low wind speed, the mean response frequency was lowest in the core position (8.2/min - core vs. 16.3/min - peripheral), suggesting that caribou occupying that position were less harassed. The mean response interval was longer in the core at low wind speed (56.7 s - core vs. 36.5 s - peripheral), also suggesting that caribou occupying the core were less harassed.

When wind speed was moderate, the mean response frequency was lower in the peripheral positions (5.2/min) than in the core (14.1/min). Mean response interval was slightly longer in the peripheral positions (35 s) and shorter in the core (33 s). Thus, at moderate windspeed, caribou in peripheral positions were less harassed.

Discussion

Caribou group dynamics

Contrary to our hypothesis, weather conditions that favored or limited insect activity did not account for variations in group size. Groups size was strongly related to date. Assuming that formation of large groups is an adaptive response to insect harassment, it is possible that most groups observed were already large enough, and that further grouping would not increase the advantage of occupying a group. Baskin (1970) reported «little change in defensive capacity» against insects for groups larger than 3000 caribou. The mean group size we observed over the 1985 study period was approximately 4900.

The decline in group size after mid July probably coincided with a decline in the mosquito population, though mosquitoes were not sampled systematically in 1984 and 1985. In 1986, the mean number of

mosquitoes caught did decline significantly after mid July. The reduction in mean group size could be explained by the reduction in the number of caribou in the study area in the latter half of July in both years.

An increase in genetic fitness, derived from forming large dense groups when insects are active, can be hypothesized. The ultimate cause of such behaviour may be «selfish avoidance» as suggested by Hamilton (1971). As a member of a group, the probability of attack (by a predator or parasitic insects) is reduced for individuals, providing that the group is not more easily detected by predators. If caribou in large groups have reduced contact with insects they would experience less irritation and blood loss from mosquitoes and have a smaller parasite load than caribou in small groups.

The decline in group size later in July may be related in part to forage quality. After first leaf-out, the quality of forage (especially shrubs) declines (Skogland 1980, Kuropat and Bryant 1983, this study). Caribou in smaller groups may have an advantage in selecting microsites where vegetation is in an earlier phenological stage. A combination of mosquito and oestrid fly harassment, forage quality, and/or presence of predators may influence group size, but it is difficult to sort out the ultimate causal factors.

The results of our study supported the hypothesis that tighter groups would form when weather favoured insect activity. Our observations agree with other studies on barren-ground caribou that report greater spacing in groups of caribou when weather conditions preclude insect activity (Curatolo 1975, Roby 1978, Dau 1986).

Behavioral responses of individual caribou

The lack of difference in mean response frequency or mean response interval between caribou of different sex or different degree of hair shedding suggests that warble flies were not cueing in on caribou with most hair shed. If warble flies are attacking both sexes equally, larvae that hatch out of eggs laid on female caribou may still be less successful in reaching the epidermis due to greater difficulty in traversing thick, dense winter pelage. We found a difference in the types of annoyance responses displayed by bulls and cows, but this would not necessarily explain the documented difference in warble larvae infestation (Kellsall 1975).

Our results supported the hypothesis that caribou display more frequent annoyance responses when weather conditions favored insect activity. The decline in annoyance responses later in the study period may reflect the phenology of the mosquito population. We have no data to relate this decline to phenology of oestrid flies.

The most common response observed among caribou – head shaking – may have indicated either oestrid fly or mosquito harassment. The types of annoyance responses attributed to mosquito harassment and oestrid fly harassment probably overlap considerably, apart from the «head drop» which is a characteristic response to nasal bot flies (Espmark 1967).

Position in a group

Our results regarding the advantage or disadvantage of occupying a certain position in a group suggest that, at the lower range of wind speed, caribou in the core experience less harassment. Such caribou did display responses to insect attack, so they were not evading insects entirely. At the higher range of wind speeds there was an apparent advantage in occupying one of the peripheral positions.

Activity budgets, food and habitat selection

Introduction

In addition to forming aggregations, caribou and reindeer change their activity pattern at moderate or high levels of insect harassment, and spend less time feeding and more time moving or standing (Curatolo 1975, White *et al.* 1975, Thomson 1977, Boertje 1981, Fancy 1983, Thing 1984). Several studies have

reported that, during periods of harassment, caribou and reindeer spend more time in habitats with typically fewer insects such as windswept ridges (Surrendi and DeBock 1976, Skoog 1968), gravel or sandy areas (White *et al.* 1975, Helle and Aspi 1984), or snowbeds (Thomson 1977).

The summer months are critical for the Porcupine Caribou Herd. In winter, caribou cows will draw heavily on their energy and nutrient reserves (Adamczewski *et al.* 1986). During the short season that green vegetation is available, they must replenish these reserves or their reproductive capability will be limited (Thomas 1982).

Disrupting the normal activity budgets of caribou can have important energetic implications. Modeling studies have demonstrated that the decrease in time spent feeding, with a corresponding increase in time spent running, has a surprising multiplier effect on the daily energy balance of an individual (S. Fancy and R. White pers. comm.). This consideration is even more dramatic when the caribou are close to, or in, a negative energy budget under normal conditions.

The first objective in this aspect of our study was to document the normal activity budgets of the Porcupine Herd on their summer range, paying particular attention to the role of insect harassment on the determination of activity budget. With such dynamic relationships in hand, we can then begin assessing the implications of additional man-caused disruptions during this critical period. We predicted caribou would alter their activity pattern, and reduce their feeding intensity when dipterans were active.

The second objective was to relate movement rate of individual caribou to weather conditions which favored or limited insect activity. We predicted that as insect activity increases, caribou increase their rate of movement, they move into the wind, and they spend more time moving.

Methods

Data were obtained during the summers of 1984-85 from early July until the first week of August, as described in the preceding section. Both 15 minute scans and 5 minute continuous observations were used to determine the relationship between insect harassment, activity, food and habitat selection. Activities included feeding, feeding intensity (eating time/total active time), walking, standing, lying, and trotting/running. Observations on caribou activity were analysed using presence or absence of mosquitoes and oestrid flies as categories.

Nine composite fecal samples were collected during the summer of 1984. Our objective was to compare the composition of feces from caribou that were severely harassed by insects, and thus spent extended periods in sub-optimal forage areas (eg. barren ridges, scree slopes) with that from caribou which were relatively unharassed and thus able to forage freely. We assumed a 12 hour rumen turnover rate during the summer months (White and Trudell 1980) and therefore collected samples from groups of animals that had been under observation over a 24 hour period. For example if we observed caribou confined to ridge tops from 0800-1600 hours we collected the fecal samples from the same group around midnight of the same day. A collection consisted of 10 pellets from each of 20 fecal groups, thus 10 replicate samples could be analysed.

As in other phases of the study, fecal composition analysis was carried out at the Plant Composition Lab, Fort Collins, Colorado and correction factors were applied in order to correct for differential digestibility of the different plant groups, (Duquette 1984).

Results

Movement rates of caribou

A total of 667 locations of radio-collared caribou were plotted during the 1985 field season. Based on minimum straight line distances between successive locations, the mean movement rate was 10.9 km/day (range 1.5 - 21.2 km/day). Movement rates decreased significantly later in the study period ($r^2=0.21$, $p=0.01$). We could not record wind speed and temperature in the proximity of each radio-collared caribou

Table 4.5. Summary of proportion of time in summer the Porcupine Caribou Herd spent in various activities when insects were present or absent.

Year	Insects	Scans	Feed	Lie	Stand	Walk	Trot/run
<i>1984</i>							
All data		286	.32 ± .09	.16 ± .05	.24 ± .08	.19 ± .04	.09 ± .04
Mosquitoes	present ¹	175	.25 ± .03	.14 ± .03	.30 ± .05	.20 ± .03	.11 ± .03
	absent ²	111	.44 ± .05	.20 ± .04	.14 ± .04	.16 ± .03	.05 ± .02
Oestrids	present ³	165	.27 ± .04	.10 ± .02	.34 ± .05	.18 ± .03	.11 ± .03
	absent ⁴	121	.40 ± .04	.25 ± .05	.10 ± .03	.19 ± .04	.06 ± .03
<i>1985</i>							
All data		873	.38 ± .04	.13 ± .05	.24 ± .08	.18 ± .02	.06 ± .02
Mosquitoes	present	646	.36 ± .02	.11 ± .01	.28 ± .03	.19 ± .02	.06 ± .01
	absent	227	.46 ± .04	.20 ± .03	.12 ± .03	.17 ± .02	.06 ± .02
Oestrids	present	530	.38 ± .02	.09 ± .01	.30 ± .03	.16 ± .02	.06 ± .01
	absent	343	.39 ± .03	.20 ± .03	.14 ± .03	.21 ± .02	.06 ± .02
<i>All years</i>							
All data		1159	.37 ± .04	.14 ± .04	.24 ± .06	.18 ± .02	.07 ± .02
Mosquitoes	present	821	.33 ± .02	.12 ± .01	.28 ± .02	.19 ± .01	.07 ± .01
	absent	338	.45 ± .03	.20 ± .03	.12 ± .02	.17 ± .02	.06 ± .02
Oestrids	present	695	.36 ± .02	.09 ± .01	.31 ± .02	.17 ± .01	.07 ± .01
	absent	464	.39 ± .02	.21 ± .02	.13 ± .02	.21 ± .02	.06 ± .02
Both	present ⁵	589	.33 ± .02	.09 ± .01	.33 ± .03	.17 ± .01	.07 ± .01
	absent ⁶	155	.45 ± .04	.25 ± .04	.10 ± .03	.16 ± .03	.04 ± .01

1: if wind speed less than or equal to 6 mps or temperature greater than or equal to 7°C

2: if wind speed greater than 6 mps or temperature less than 7°C

3: if wind speed less than or equal to 9 mps or temperature greater than or equal to 13°C

4: if wind speed greater than 9 mps or temperature less than 13°C

5: if wind speed less than or equal to 6 mps or temperature greater than or equal to 13°C

6: if wind speed greater than 9 mps or temperature less than 6°C

in order to test movement rates in relation to weather. After 18 July, when the majority of caribou were in a region that was subsequently found to have fewer mosquitoes (Richardson Mountains), they still moved an average of 8.9 km/day.

Movement rates determined from the instantaneous scan observations were tested in relation to weather and date. We predicted that movement rates would be significantly faster when weather favored insect activity. In 1984 and 1985, there were no significant differences in movement rates based on weather that favored or inhibited dipteran activity (1.6 km/h vs. 0.6 km/h). In 1984, movement rates declined significantly later in the season while in 1985 movement rates did not change significantly with date.

Direction of movement in relation to wind direction was also determined from the instantaneous scans. Chi-square analysis showed a significant relationship between direction of movement and wind direction in 1984 ($X^2=0.64$, $p=0.01$, $n=219$), but not in 1985 ($X^2<0.01$, $p=0.98$, $n=645$). In 1984, when weather conditions favored insect activity, more caribou moved into the wind than would be expected by chance.

Activity budgets and feeding intensity

A total of 1159 scans (286 - 1984; 873 - 1985) were recorded during July and August under a variety of weather conditions. There was no significant difference in activity budgets between the two years, except for proportion of time spent walking, which was higher in 1985, primarily in late summer. In 1984 there was no significant difference in activity budgets between early and late summer. In 1985, time spent feeding was significantly higher, while time spent standing and lying was significantly lower in early than in late summer.

The 15 minute scans showed a significant shift in activity budget when insects were active in both 1984 and 1985 (Table 4.5). Once weather conditions became favorable for mosquitoes and oestrid flies, there was a decrease in time spent feeding and lying, and an increase in time spent standing.

The 5 minute continuous observations also showed an increase in proportion of time spent standing (from 11% to 20%) when weather was favorable for insect activity (Mann-Whitney, $U=2.11$, $p=0.03$). Feeding intensity was 14% lower when insects were active (Mann-Whitney $U=-3.6$, $p<0.01$). However, there is a link between the different feeding intensities observed for caribou in different habitat types and under different weather conditions. When insects were active, more observations were made of caribou feeding in barren and sparsely vegetated *Dryas* habitat types than was expected by chance (Table 4.6). In these habitats we would expect to observe lower feeding intensities among caribou.

The 15 minute scans showed that the proportion of time caribou spent walking and running was not significantly affected by insect harassment (Table 4.5). However, the five minute continuous observations indicated that the proportion of time spent moving increased significantly (from 18% to 25%) when insects were active (Mann-Whitney, $U=-2.2$, $p=0.03$).

Diurnal activity

Using the weather data obtained during our observations, we calculated the mean mosquito and oestrid fly harassment levels throughout the day. The two values generally tracked each other with a strong increase from 0900 to 1100 followed by a gradual decline from 1700 to 2200. Our observations from 2300 to 0800 were too few to determine a total 24 hour pattern. However, from recordings at automatic weather stations, we know that mosquito harassment does occur most evenings (lesser amounts at cool temperatures) while oestrid fly harassment is essentially non-existent from roughly 1100 to 1900.

We combined all observations on caribou for July and August, to determine if any diurnal activity patterns existed during the study period. Based on a combination of feeding, walking and running, caribou appeared most active prior to 1000 and after 1700. The patterns were not very distinct, possibly due to the variation in insect activity from day to day (Fig. 4.11). Feeding appeared sporadic throughout the day, with an indistinct lull at midday. Standing and lying appear to be almost

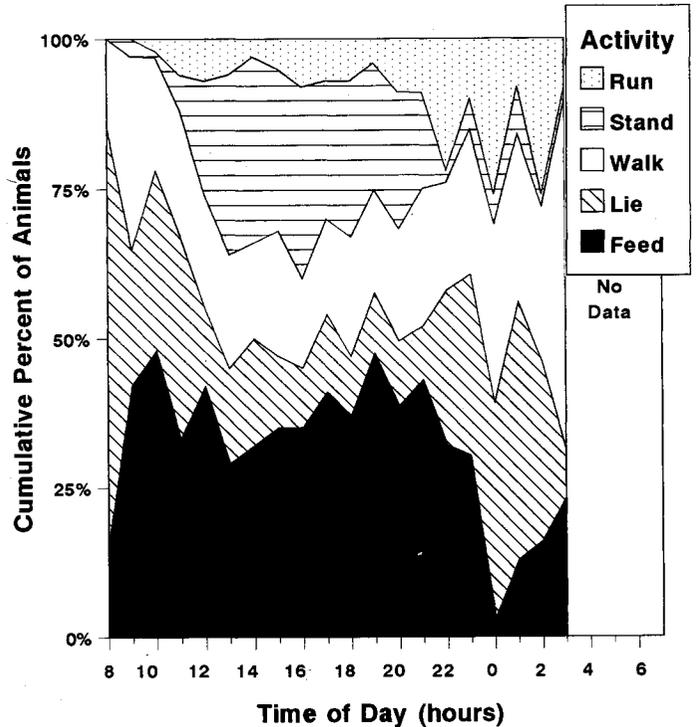


Figure 4.11. Diurnal pattern of various activities recorded for the Porcupine Caribou Herd in summer of 1984 and 1985.

Table 4.6. Vegetation types and position selected by the Porcupine Caribou Herd in relation to insect activity, n (%)¹.

Insect activity	Position	Tussock tundra	Sedge meadow	Sedge heath/ beath	Dryas barren	Forb heath	Alluvial gravel & rock	Dense willow	Lichen barren	Open spruce	Low shrub tundra	Total
Present	Crest	0 (0) ¹	0 (0)	8 (5)	21 (10)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	10 (25)	39 (7)
	Upper slope	0 (0)	0 (0)	50 (31)	91 (42)	1 (20)	15 (71)	1 (3)	0 (0)	0 (0)	21 (52)	179 (31)
	Mid slope	4 (21)	21 (32)	52 (32)	79 (37)	0 (0)	4 (19)	1 (3)	11 (92)	0 (0)	3 (8)	175 (30)
	Lower slope	0 (0)	0 (0)	8 (5)	7 (3)	4 (80)	0 (0)	26 (87)	1 (8)	7 (100)	1 (2)	54 (9)
	Valley floor	14 (73)	34 (52)	25 (15)	17 (8)	0 (0)	2 (9)	0 (0)	0 (0)	0 (0)	5 (13)	98 (17)
	Plain	1 (5)	10 (15)	18 (11)	0 (0)	0 (0)	0 (0)	2 (7)	0 (0)	0 (0)	0 (0)	51 (6)
	Total	19 (3) ²	65 (11)	161 (28)	215 (37)	5 (1)	21 (4)	30 (5)	12 (2)	7 (1)	40 (7)	576
Absent	Crest	0 (0)	0 (0)	5 (1)	5 (2)	0 (0)	0 (0)	0 (0)	2 (33)	0 (0)	10 (1)	10 (1)
	Upper slope	0 (0)	0 (0)	58 (21)	82 (38)	0 (0)	2 (40)	2 (2)	2 (33)	0 (0)	146 (20)	146 (20)
	Mid slope	6 (11)	4 (13)	101 (37)	62 (29)	0 (0)	3 (60)	32 (35)	2 (33)	0 (0)	215 (29)	215 (29)
	Lower slope	8 (14)	13 (43)	74 (27)	32 (15)	1 (100)	0 (0)	25 (26)	0 (0)	0 (0)	159 (22)	159 (22)
	Valley floor	12 (21)	13 (43)	35 (13)	32 (15)	0 (0)	0 (0)	18 (19)	0 (0)	0 (0)	152 (21)	152 (21)
	Plain	31 (54)	0 (0)	18 (11)	0 (0)	0 (0)	0 (0)	19 (20)	0 (0)	0 (0)	50 (7)	50 (7)
	Total	56 (8)	30 (4)	271 (37)	213 (29)	1 (0)	5 (1)	96 (13)	6 (1)	0 (0)	54 (7)	732
Subjective insect risk level		High	High	High/ Medium	Low	Medium	Low	High	Low	High	High	

1: % of animals observed in vegetation type within a position and insect activity category.

2: % of animals in vegetation type within an insect activity category.

Table 4.7. Percent cover of land cover types found in each sub-region of mapped area.

	British Mountains	Barn Mountains	Richardson Mountains	Coastal plain west	Coastal plain east
Dense shrub slope	2.1	5.7	12.8	0.0	1.7
Low shrub tundra	0.4	2.2	13.5	0.0	1.4
Tussock tundra with 26–35 % shrubs	12.4	12.6	6.7	3.4	10.6
Tussock tundra with 16–25 % shrubs	20.9	26.9	21.1	16.7	23.9
Tussock tundra with 0–15 % shrubs	7.2	17.0	17.0	0.9	9.5
Heath	13.8	9.1	3.8	24.9	13.6
Dryas/sedge	4.5	2.1	1.2	15.9	1.1
Lichen/alluvial	29.3	18.9	17.6	20.6	19.3
Barren rock	9.5	5.6	6.3	9.0	13.3
Wet alluvial	0.0	0.0	0.0	8.6	5.4

inverse (Fig. 4.11). There was a strong peak in proportion of caribou standing between 1000 and 2000, while the proportion lying peaked at 0900 and 2200. We have shown that standing increased primarily at the expense of lying when insects were active. Therefore, standing appears to track the mean harassment levels during the day. Caribou movement (walking and running), although low throughout the study, is most prevalent during the evening hours. We can speculate that this movement corresponds to a decline in mosquito and oestrid fly activity, with caribou moving from insect relief areas toward preferred feeding areas.

Habitat use

Our measure of habitat use was based on the observed location of groups of caribou during the 15 minute scan observations. The 15 minute scans gave a better picture of habitat use than the 5 minute spells of continuous observation. If the groups were dispersed so that they occupied more than one habitat type, they were assigned to two or more habitat types with equal weight for each type. The range type used can be subjectively rated as high, moderate and low »risk« categories in terms of their potential for insect harassment. This subjective rating is based on vegetative characteristics (taller, denser – higher risk), moisture (wetter – higher risk), and physical location (valley bottoms – higher risk; Table 4.6). We hypothesized that caribou would respond to increased insect harassment by choosing lower risk habitats.

Throughout the study period, over one half of the observations on caribou were in heath/sedge heath or *Dryas* barren vegetation types (Table 4.6). When weather was favorable for insect activity, a higher proportion of observations were in *Dryas* barrens and at higher elevations (i.e. upper slopes). When weather was not favorable for insect activity, a higher proportion of observations were in heath/sedge heath and on mid-slope.

As weather became more favourable for insect activity, fewer observations of caribou were made in dense willow and tussock tundra. Both of these communities have a higher risk of potential insect harassment (Table 4.6). Low shrub tundra was a high risk vegetation type which remained unchanged in percent use with increasing insect activity. However, when insects were active, more observations were made at higher elevations within this community.

From satellite mapping (Russel *et al* 1992a) we determined the relative availability of vegetation types in the British, Barn and Richardson Mountain subregions (Table 4.7). Combining habitat use (Table 4.6) with habitat availability (Table 4.7) we can determine habitat selection for the herd in the summer when insects are present and when they are absent (Fig. 4.12). Dense shrub slopes appear to be avoided when insects are present and selected when they are absent. There also appears to be a stronger selection for *Dryas* communities when insects are present.

Food habits

Deciduous shrubs were by far the most frequent plant group observed in the fecal sample slides, among all samples collected (Table 4.8). However, once correction fac-

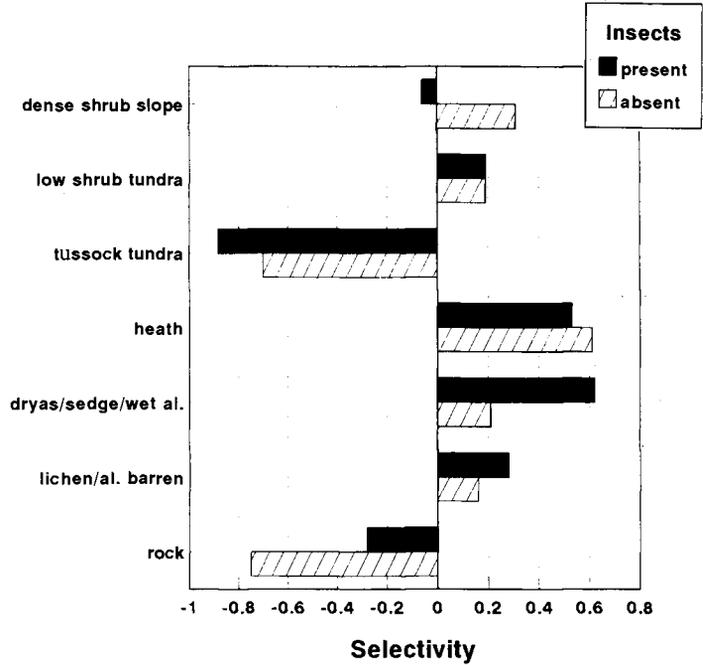


Figure 4.12. Selection of major range types on summer range by the Porcupine Caribou Herd during insect harassment and in the absence of insects.

Table 4.8. Proportion (%) of fragments from different types of plants in the feces of caribou from the Porcupine Caribou Herd in July 1984. The numbers in parenthesis represent an estimate of the composition of the diet of standard correction factors to the data from fecal analysis. (See Methods).

July Date	Insects present	Mosses	Lichens	Deciduous shrubs	Evergreen shrubs	Forbs
8	no	0 (0)	0 (0)	97.6 (47)	1.5 (3)	0.3 (49)
10	yes	0 (0)	0 (0)	95.9 (46)	1.6 (3)	2.1 (50)
15	no	0 (0)	0.7 (3)	96.0 (46)	0.3 (1)	2.7 (50)
20	no	0 (0)	0.3 (1)	96.5 (46)	2.5 (4)	1.1 (48)
22	yes	0.5 (1)	1.1 (4)	90.2 (43)	2.3 (4)	4.6 (45)
24	yes	0.6 (1)	3.2 (12)	80.5 (39)	1.8 (3)	12.3 (44)
25	yes	0 (0)	0 (0)	94.7 (45)	0.5 (1)	4.9 (54)
26	no	0.8 (1)	0.3 (1)	89.2 (43)	6.4 (10)	2.4 (42)
29	no	2.6 (3)	6.2 (23)	85.5 (41)	3.5 (6)	2.9 (24)
Mean		0.5 (1)	1.3 (5)	91.8 (44)	2.3 (4)	3.8 (45)

Correction factors:

Mosses	1.0	Graminoid	1.6
Lichens	3.8	Evergreen shrubs	2.03
Deciduous	0.48	Forbs	100 (total of others)

tors were applied, the contribution of deciduous shrubs was not significantly different from that of forbs (Table 4.8). This illustrates the importance of dietary correction factors.

From the samples collected we were not able to establish any differences between the diet of caribou harassed by insects and those not harassed (Table 4.8). More careful collection of samples would be required to detect actual dietary differences. An important illustration of this point is the composition of the 26 July sample. The group of animals from which the sample was taken was observed standing on a scree slope eating very little, if any, vegetation from 0800 to 2200, making only one brief foray into the valley below to feed. Collection of fresh fecal samples were obtained from where the animals were observed at midnight that night. The sample does not illustrate any difference in dietary composition from the other samples (Table 4.8). During the collection of fresh samples, however, field crews found it extremely difficult to find 10 pellets in any pellet group and those that were found were unusually small. This confirms that when little food is taken, fecal output is reduced, rumen turnover time is increased and the fecal composition reflects the diet of the individuals over much longer than 12 hours.

By contrast, the sample of feces collected on July 24 does reflect an apparent decline in deciduous shrub and forb intake and an apparent increase in lichen intake. During our observations, this group of caribou was confined to drier ridge habitats during insect harassment, however they were observed feeding at irregular intervals in this and adjacent habitats. In this case, total food intake may not have declined significantly, the only effect of the harassment being a shift in species intake from their preferred summer forage.

Our observations cover the transition period from a typically graminoid/shrub diet in late May/June to a lichen diet by early September. The high lichen value documented in the latest sample (24%, 29 July), may be the beginning of a shift toward the lichen dominated fall and winter diet. This shift corresponds with a shift in quality of *Salix* as the season advances. Graminoids were not a significant component of the July diet.

Discussion

Movement of groups and individuals

Our observations did not support the hypothesis that caribou increase their movement rate when weather conditions favored insect activity. However, the proportion of time spent moving did increase significantly. Roby (1978) and Downes (1985) found that the proportion of time spent moving (i.e. running and walking) increased significantly during periods of mosquito harassment. Curatolo (1975), Fancy (1983) and Dau (1986) found that caribou increased their rate of movement, particularly during periods of mosquito harassment. Dau (1986) found more stationary caribou when oestrus were present.

The successful evasion of insects by mobile caribou would depend on the exact rate of movement, the wind speed and the direction of movement in relation to wind direction. Our observations in 1984 support the hypothesis that caribou orient their movement into the wind, but in 1985 there was no relationship between wind direction and direction of movement. Other factors may influence direction of movement, such as orientation toward sparsely vegetated areas or other habitat types that have characteristically fewer insects.

Activity

The relationship between insect harassment and activity of caribou was more clearly defined than the relationship between insect harassment and habitat used by caribou. This may be due in part to the fact that most observations were made during the day, and insects were active most days, although some days had only low levels of harassment. Observations were therefore weighted toward habitats that caribou occupied during the day when insects were bothersome. The few observations that were made on days with few or no insects probably show caribou using lower elevation sites and lush vegetation communities. Another reason that change in activity is the more clearly defined variable is the fact that it is an immediate response while change in habitat is a latent response.

We found the predominant use of *Dryas* communities throughout the study period surprising, considering that this community type is sparsely vegetated compared to others. It seems possible that one important effect of sporadic, perhaps unpredictable bouts, of insect harassment is that caribou are faced with a trade-off between occupying good forage sites and places where there are few insects. The ideal conditions would then be when good forage sites coincide with good foraging conditions. This combination is found in coastal vegetation communities early in the season when graminoid vegetation provides most of the diet. As willows and forbs increase in importance, the caribou move inland.

The increase in use of the wet sedge communities is significant because they often contain lush willow species in close proximity to windswept ridgetops. Tussock tundra, the most abundant community type at lower elevations, was seldom used even when insects were absent. We conclude that tussock tundra was not utilized primarily because there were few convenient opportunities to reach these communities from the high elevation/ low risk *Dryas* communities. *Dryas* barren communities may provide the optimal trade-off.

Feeding intensity and activity

The decline in feeding intensity with increase in insect harassment was related in part to the habitat occupied by the caribou when weather conditions favoured insect activity. Some sparsely vegetated habitat types were almost devoid of vegetation, so that the caribou could do little feeding. Other studies have also reported a decrease in time spent feeding when insects were active (Baskin 1970, Curatolo 1975, White *et al.* 1975, Dau 1986, Murphy 1988). Thing (1984) reported a five to six fold decline in feeding intensity between periods of no harassment and severe harassment. This has important implications with regard to the energy budget. Fancy (1986) found that reduced ingestion time (ie. energy intake) was more important in overall energy balance than increased walking/running time. Helle and Tarvainen (1984) found that the level of insect harassment in summer affected the yearly variation in calf weights recorded in the fall. The significance of reduced energy intake is important at both the individual and population level, because body condition affects reproductive success (Couturier *et al.* 1988) and adult cows that have not replenished their energy and nutrient reserves by the time of autumn rut are less capable of reproducing successfully (Thomas 1982).

We found that caribou spent proportionally less time feeding and more time standing and running/walking when weather was favorable for insect activity. Other studies have also reported an increase in time spent standing (Baskin 1970, Curatolo 1975, White *et al.* 1975, Dau 1986, Murphy 1988). Stationary *Rangifer* are often vigilant for insects (primarily oestrid flies). Certain annoyance responses are only exhibited when they are standing as opposed to lying (Espmark 1968, Thomson 1977). More time spent standing may better enable caribou to detect oestrid flies and make the appropriate annoyance responses.

Conclusions

Caribou in the Porcupine Herd consistently form large aggregations in early July, a time of year when they are at an energetic low and face a horde of summer insects. We found a significant relationship between insect activity and the density of these groups. By remaining in large, dense groups, the harassment of individuals is reduced. Local insect populations could be swamped by several thousand caribou. However, by opting to remain in large aggregations, an individual caribou severely limits its choice of insect relief habitat. The areas that caribou travel to at this time of year must provide both insect relief and sufficient forage to sustain up to 50,000 caribou for several weeks. Furthermore, the region chosen must be the one that in the long term has the most stable, thus most predictable, environmental conditions. Once in the region, the caribou maximize their energy balance by exploiting habitats and subregions as the conditions of that particular year permit.

Our intention in this study was to determine the relationship between caribou and insects and to assess how the caribou respond to insect harassment while they concurrently maximize their opportunity to feed. We believe that the key to regional, subregional and localized habitat selection by caribou at this time of year is a continuous evaluation of these two factors. The herd has many regional options to avoid insects and there are numerous locations where caribou could obtain optimal forage. Only a few locations offer both in close proximity and sufficient abundance to sustain 50,000 or more caribou for several weeks.

The only criterion for good insect relief is a lack of insects. Using this criterion, obvious choices are sites generally devoid of vegetation and/or exposed to wind such as strips of land along the Beaufort Sea coast and in the water itself, late snowbeds, gravel bars and high windswept ridges. We have documented the use of all of these habitats. Gravel bars and late snowbeds are too few and too small to accommodate large aggregations of caribou. Coastal strips are indeed an important habitat early in the summer (late June - early July). In the northern Yukon the foothills become free of snow first, then melting proceeds northward to the coast. The intermountain regions are last to be snowfree. In late June, coastal habitat provides new vegetation that is high in nitrogen and weather conditions that generally limit mosquito activity.

Once willow leaves emerge in late June, caribou quickly shift their diet. Willows are not very abundant on the coastal plain, so the shift in diet also involves movement inland to the intermountain regions. However, when weather is warm and calm, caribou would encounter mosquitoes in these vegetated areas. Thus groups of caribou must seek relief on mountain slopes and ridges, areas where high convective winds limit insect activity and sparse vegetation offers insects little protection from the wind.

Ideal regions for occupation in early July, when mosquitoes are the major consideration, should provide windy, sparsely vegetated habitat in close proximity to valleys with lush willows and forbs. The region used in late July should contain optimum foraging conditions, as the first part of August marks a decline in insect harassment and a fragmenting of large groups into smaller scattered bands of caribou.

The herd must constantly be evaluating options. In years of inclement weather, with few insects, the herd can shift into regions with more favorable forage. However, even in those years there appears to be a tendency for herds to remain relatively close to insect relief areas, so that they would not be vulnerable should conditions become more favorable for insects.

One of our tasks was to identify critical insect relief habitats to be protected or avoided should development occur. As an outcome of our work we have attempted to differentiate «primary» insect relief habitat from «secondary» insect relief habitat. By primary relief habitat we mean those areas that are consistently used and provide relief and forage for the herd. These are «destination» areas, the areas caribou remain in for an extended period of time during the brief summer. Secondary relief areas are used opportunistically by the herd while moving to a destination area. While primary areas tend to provide the ideal combination of conditions for that particular year, secondary sites lack certain attributes and cover a smaller area. Because the relief areas may be required by 50,000 or more caribou at one time primary areas tend to be regions rather than isolated sites. Our movement data indicated that even within a primary relief region, caribou still move four to five kilometres per day.

The northern Yukon is comprised of an extremely diverse complex of environments, from wet coastal plains in the north to rocky, windswept ridges in the mountains to the warm pediments in the south. The northern region is influenced primarily by weather systems coming off the Beaufort Sea, the southern region by the warmer northeasterly flows from central Alaska and the intermountain region appears to be influenced by both. If we were asked to predict the weather within the three regions we would say the northern region would be cold, the southern region warm and the intermountain region windy. The upslope wind conditions of the intermountain region provide the relief from insects that the caribou seek. Within this intermountain region three areas have a higher density of shrubby vegetation that form the staple summer diet of caribou; the southeast edge of the British Mountains, the north flank of the Barn Mountains and the entire Richardson Mountains. All three areas could provide adequate forage for the large aggregations of summering caribou, however, they are not used equally.

The southeast edge of the British Mountains appears to be an important region in early to mid July. Caribou use the windswept slopes for insect relief during the days, venturing into the more densely vegetated valleys to the south and southeast when conditions permit. The large aggregations tend to linger in this region in mid July before «deciding» to move east or west. In most years the aggregations split up – some returning west through the upper Firth River into Alaska, the remainder turning east toward the Richardson Mountains which appear to provide the required relief from insect harassment for the remainder of the summer. This area was documented to have the coolest temperatures within the study area. Once in the Richardson Mountains, caribou use the higher elevations of the upper Bell River, and the ridges and valleys to the north. These areas have extensive slopes of lush willow in close proximity to wind exposed ridges, if relief from insects is required. The north flank of the Barn Mountains is used only when insect levels are low, either due to inclement weather or the advance of the season. This region is too far inland to benefit from the coastal breezes and it is too low to produce upslope wind conditions or significantly cool temperatures.

Any land based development in northern Yukon should not proceed without due consideration to protection of the primary insect relief areas we have identified and equally important, unobstructed access to those areas. Finally, any disturbance that could cause large aggregations of caribou to fragment during periods of insect activity, or alter activity patterns such that energy intake is reduced and energy expenditure increased, should not be permitted.