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THE SNOWPATCH AS RELIEF HABITAT FOR WOODLAND CARIBOU (*Rangifer tarandus caribou* Gmelin) AT MACMILLAN PASS, N.W.T.

by

PETER GORDON ION

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled The Snowpatch as Relief Habitat for Woodland Caribou (*Rangifer tarandus caribou* Gmelin) at Macmillan Pass, N.W.T. submitted by Peter Gordon Ion in partial fulfilment of the requirements for the degree of Master of Science.

G.P. Kershaw

Supervisor

Keith D. Hage

Date 10 April 1986

ABSTRACT

Woodland caribou (*Rangifer tarandus caribou* Gmelin) have been observed to congregate on permanent snowpatches during the summer-fly season at Macmillan Pass. In this study it is proposed that the snowpatch is selected as 'relief habitat'. Reduced mosquito harassment and behavioural thermoregulation in response to heat stress have been identified as the two major hypotheses proposed to explain this behaviour. This study tests those hypotheses.

Air temperature and wind speed are identified as the most significant climatic parameters influencing caribou behaviour. Between mid-June and mid August 1984, directed movements of individuals and groups towards and away from permanent snowpatches above 2000 m a.s.l. were recorded. This was observed mostly under anticyclonic conditions typified by days with clear skies, mean air temperatures of over 13°C and mean wind speeds of less than 2.5 m s^{-1}. Snowpatch selection was less pronounced under cyclonic conditions.

General weather conditions also influenced the snowpatch microclimate. An air temperature difference of 3°C between stations located over snow and adjacent snow-free surfaces was recorded under anticyclonic conditions. Daytime wind speeds at exposed ridgetop sites were 39% higher than sheltered lowland sites and were selected as alternative relief habitat.

Mosquito activity increased with air temperature and decreased with wind speed. Quantified indices based on behavioural response to insect harassment were consistently higher on snow than off snow. Aggregation as a response to mosquito harassment was more frequently documented on snow than off snow. This contrasts with data collected from insect traps located over snowpatches and snow-free zones. This was thought to be due to limitations in trap design. No black flies or oestrid flies were trapped although behavioural responses to these insects were consistent with other caribou groups in the Yukon and Alaska. The ingestion of snow and meltwater was observed although positive correlations with ambient temperature were weak. The data support the hypothesis that snowpatch selection is primarily a response to insect harassment.

ACKNOWLEDGMENTS

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1. INTRODUCTION

1.1 Problem Statement

Permanent snowpatches occur during the summer months at high elevations in the Selwyn and Mackenzie Mountains of the Yukon and Northwest Territories. Woodland caribou (*Rangifer tarandus caribou* Gmelin) have been oberved to congregate on these in large numbers (Archibald 1973, Gill 1978, Kershaw and Kershaw 1983b). This type of behaviour appears common in other parts of the range of the sub-species (Edwards and Ritcey 1959, Bergerud 1978, Stelfox et al. 1978, Oosenbrug and Theberge 1980, Fuller and Keith 1981). Furthermore, most detailed studies of the ecology of North American caribou have noted a similar predeliction for snow at this time of year (Kelsall 1968, Skoog 1968, Elliot 1972, Jakimchuk and McCourt 1972, Curatolo 1975, Calef 1981). Although less widely reported, the observation ~~has~~ also been made in the alpine ranges of Eurasian reindeer (Formozov 1946).

Despite the frequency of observation and the recognized importance of the snowpatch zone to caribou during the summer-fly season no specific study has accounted for this behaviour. The solution to this problem must lie in a more detailed approach than the cursory treatment it has been afforded in the published literature. This study therefore attempts to quantitatively assess the degree of snowpatch use and to explain this aspect of habitat selection for Woodland caribou occupying the Mackenzie Mountains in summer. The findings from this analysis would facilitate more empirically-based notions of this behaviour in other populations of *Rangifer*.

1.2 Caribou/Snow Ecology

It is a truism of ecology that an animal cannot be considered apart from its environment. The various roles of ice and snow have been widely investigated in relation to ungulate ecology (Haugen 1971). In the Arctic and Subarctic, snow forms an integral part of the environment of caribou and reindeer for at least eight months of the year. The winter ecology of caribou is documented in detail for certain populations (e.g. Skogland 1978).

A combination of behavioural, physiological and morphological adaptations characterize the ability of caribou to thrive in the nival environment. Although Formozov (1946) originally classified caribou as *chioneuphores* - "a species that can withstand winters with considerable snow" - his own definition of a *chionophile* as a species "having characteristic adaptations which were undoubtedly perfected by snow cover taking part in selection" is more appropriate and has been adopted by subsequent workers (Pruitt 1959, Stardom 1975, Skogland 1978, Russell and Martell 1984). The distinction between the two classifications illustrates two different aspects of snow as an ecological factor. Snow may be considered as either a meteorological variable or a surface condition (the latter usually referred to as the snow cover or the snowpack). The following discussion describes how both have a significant impact upon the ecology of caribou.

In an historical perspective, zoogeographers have attributed great importance to ice and snow in caribou speciation. The advance of ice over the North American continent during the Pleistocene created glacial refugia from which the four major sub-species recognized in American texts were thought to have originated (Remmert 1980). By the same token, Banfield (1954) described a twofold role of ice in mammalian distribution. The seasonal freezing of water bodies acted as both an aid to the distribution of caribou and as a barrier to species [illegible]entiation. He cites the example of barren-ground caribou (*R. t. groenlandicus* L.) migrating between the Arctic Islands and the North American mainland.

Contemporary movements and patterns of seasonal distribution may also be ascribed to the influence of snow and ice. Many studies have hypothesized that the first snowstorms of autumn are thought to trigger the onset and influence the extent of the autumn migration (Kelsall 1968, Hemming 1971, Bergerud 1974). There is also strong evidence that unseasonal snow conditions can retard, disrupt, redirect or even halt the spring migration to the calving grounds (Skoog 1968, Kelsall 1968, Gavin 1975).

Nasimovich (1955) was one of the earliest workers to conclude that migrations and winter distribution were largely in response to the changing character of the snow cover. Pruitt (1959) went a stage further in claiming that "the timing, direction and speed of migration are intimately related to the characteristics of the snow cover" (p.171). Pruitt proposed that the movements of barren-ground caribou in relation to snow in northern Saskatchewan and the Northwest Territories were in response to thresholds of tolerance to particular snow depths, densities and hardnesses. His was the earliest study to quantify these relationships describing a threshold of hardness sensitivity of 50 g cm^{-2} for forest snow and 500 g cm^{-2} for lake snow. The density threshold was approximately 0.2 for forest snow and 0.3 for lake snow. A depth threshold of approximately 60 cm has been confirmed for other populations of barren-ground caribou (Henshaw 1968, LaPierre and Lent 1977, Thing 1977) with slightly greater thresholds of depth and density recorded for the larger Woodland subspecies (Bergerud 1974, Stardom 1975).

Winter movements of caribou appear to follow gradients in the snow from areas of relatively great depth, density and hardness, to areas of lesser values for all or one of these factors. Henshaw (1968) noted a general avoidance of deep snow and a preference for movement over hard-packed snow in Alaskan caribou. Stardom (1975) described how Woodland caribou in south-eastern Manitoba would prefer to enter areas of snow above their thickness threshold of 65 cm rather than be subjected to vesicular ice or snow crusts of hardness greater than 400 g cm^{-2}.

The hardness and thickness of various layers within the snowpack formed the basis of a "snow index" derived by Pruitt that attempted to model the winter activity (distribution and feeding) of feral reindeer in Finland (Pruitt 1979) and barren-ground caribou in northern Saskatchewan (Pruitt 1981). In concluding that the difference between New and Old World caribou-snow relations were real, the index was thought to have a high potential for determining nivally-suitable areas for caribou overwintering (Pruitt 1984). This index illustrates how caribou will avoid areas of unfavourable snow and select areas for feeding in snow (although some circularity exists in that the index is derived empirically to organise the observations). The selection of cratering sites within winter range may occur on a number of levels: Edwards (1956) described how caribou are found first on suitable foraging areas and then react to the various nival conditions within the range. Cratering by Alaskan caribou was similarly influenced by snow conditions at three levels (LaPierre and Lent 1977). The dietary shift from ground lichens to arboreal lichens is essentially dictated by snow conditions. The nival thresholds described previously by Stardom (1975) are those at which Woodland caribou switched from arboreal lichens in open bogs to jackpine-lichen rock ridges.

Survival through the Arctic and Subarctic winter is highly dependant upon the animal's ability to obtain forage through the snow. Deep snow can alter activity budgets by increasing the time required to obtain forage and thus reduce the time available for other activities. Firnification of snow been associated with major habitat changes in wild reindeer in late winter (Nasimovich 1955). Caribou may be prevented from digging for lichens by the formation of strong and long-lasting snow crusts or nasts. Nast persistence can lead to starvation and subsequent herd reduction in tundra areas and extirpation from isolated locations where alternative food supplies are scarce. Kelsall (1968) strongly suspected this as the reason for the disappearance of caribou from the Belcher Islands although overhunting is also suspected.

The reindeer herders of Eurasia and the Inuit of northern Canada and Alaska have long recognised the ecological significance of the changing snowpack in relation to feeding strategies. The glossary of specialized snow terminology used extensively by Pruitt (1984) illustrates the limitations of the English language in this respect. Of particular ecological significance to caribou is the basal layer of snow on the ground ("api") which is properly termed "pukak". Recrystallization and metamorphism of the snow cover leading to the formation of pukak dictates the availability of forage for overwintering caribou.

The ability of caribou, through their acute sense of smell to detect lichens through shallow snow cover has been widely observed and may be an evolutionary adaptation to survival in snow. The original definition of a chionophile was an animal adapted to survival in snow and in this respect no northern ungulate is comparable to the caribou. Not only does the caribou range further north than any other *Cervidae* but it most likely evolved in the Arctic and has since colonized a variety of Arctic and Subarctic environments (Remmert 1980). The ability to exploit this rigorous environment is undoubtedly attributable to a number of morphological, physiological and behavioural adaptations. The majority of morphological adaptations have evolved as a means of heat conservation during the long winter months when the gradient between deep body temperature and the environment may reach 100°C. The importance of a large nasal cavity for breathing cold air, the reduced size of extremities and a thick winter coat with extended guard hairs is well documented (Skoog 1968, Kelsall 1968). Most pertinent to survival in snow however, are the crescentic-shaped hooves with functional dew claws. The flexibility of the joints of the middle toes and the growth of the edges of the hoof in winter combine to provide a greater surface area. This aids traction and locomotion over hard-packed snow, reduces the sinking depth in soft snow and facilitates cratering. Foot-loading values recorded for caribou are a fraction of other ungulates (Kelsall and Telfer 1979).

The most significant physiological adaptation to snow and cold that caribou exhibit is the "counter-current heat exchange" system within the legs. The arrangement of blood vessels allows warm arterial blood to transfer much of its heat to the returning venous blood before reaching the environmental heat sink (Irving et al. 1955). This regional hypothermia reduces the thermal gradient across the surface of the skin. This in turn reduces heat loss from a part of the body in contact with ice and snow for much of the year.

Behaviourally, caribou are also well adapted for survival in snow. Kelsall and Telfer (1984) calculated (albeit subjectively) a behavioural index which rated caribou higher than any of seven other boreal ungulates in four out of six categories. Their locomotion techniques, migration patterns, cratering ability and trail-making behaviour were adjudged superior to all other ungulates and predators. Combining all morphological and behavioural adaptations caribou possessed a "mean snow-coping index" well above the second placed mammal - the moose.

As Kelsall (1968) noted, "of all meteorological variables, snow has the most profound influence on caribou " (p.236). And as Formozov (1946) first observed, "snow cover has become one of the most powerful of ecological factors which has dominated, by its influence, the seasonal rhythms of many biological phenomena and the morphological characteristics of some organisms" (p.1). The majority of published literature in the ensuing forty years has reinforced these conclusions. In spite of numerous adaptations, the movement and activities of caribou are heavily influenced by snow conditions. Snow impinges directly upon aspects of distribution, habitat selection, productivity, mortality and ultimately species survival.

1.3 Relief Habitat

Despite the recognized importance of snow and snow cover in the ecology of caribou it is largely ignored in discussions of summer range. Many groups come into contact with snow and ice in every month of the year yet it merits only a cursory treatment during the summer. The need to escape or find relief from the heat and biting insects is recognized as a factor of paramount importance in directing movement towards and within summer range. In this study it is hypothesized that permanent snowfields are selected as a form of 'relief habitat'.

In the North American literature the movements of the Porcupine, Bluenose and Bathurst caribou herds towards the Arctic Coast in early July are well documented (Surrendi and Debock 1976 , Banfield and Jakimchuk 1980). The cooler temperatures resulting from the vast expanse of sea ice and associated sea breeze provide relief to potentially heat-stressed or insect-harassed animals. On the central barrens, herds have been observed to congregate on the shores of large lakes which remain ice-covered well into July (Calef 1981). White et al. (1975) described a rapid, insect-evoked movement of the Central Arctic Herd towards and along the coast of northern Alaska around Prudhoe Bay and a slow dispersal south under conditions of no harassment. Caribou of the Porcupine Herd occupy the coastal tundra in late June moving eastward into the prevailing wind when insects are most virulent, and on occasion wading into the frigid water (although this has not been substantiated by actual measurement of numbers).

Standing in shoulder deep water was described as an apparent avoidance pattern in barren-ground caribou in central Baffin Island (Elliot 1972). River deltas and associated gravel bars and sand dunes are preferred areas of insect relief for barren-ground caribou because of the lack of vegetation and suitable mosquito breeding habitat (Calef 1981, Helle and Aspi 1984).

It has been concluded on the basis of studies of summer range in Alaska that a preference is exercised for slopes with a northern aspect during periods of mosquito harassment (Curatolo 1975, Roby 1978). The cooler, shaded north-facing slopes provide less than optimum conditions for mosquitos while providing sufficient forage to allow caribou to continue grazing. Curatolo (1975) found that relatively high mosquito levels were necessary to force animals onto exposed ridgetops, in part due to the changes in vegetation which accompany the shift. The location of preferred food species appeared to be of secondary importance to caribou congregating in large numbers on windswept ridges in northern Yukon (Surrendi and Debock 1976, Martell et al. 1984). On the relatively flat tundra any topographic rise may provide a little extra breeze. Kelsall (1968) noted that barren-ground caribou will use eskers as 'windswept refuges' from flies in summer. Kershaw (1981) thought that this was one factor which may explain why Woodland caribou at Macmillan Pass frequently altered their lines of travel to follow the Canol Road. Roby (1978) observed caribou adjacent to the Trans Alaska Oil Pipeline to utilize gravel pads and piles of road material apparently as relief habitat under severe harassment. Shade may also be a deterrent to insect pests due to the reduced radiation regime or lower air temperatures. Roby (1978) cites observations of bulls standing in the shade of buildings, machinery and even the elevated pipeline in Alaska. Similar reasoning may explain the observation of bull caribou close to buildings at the tungsten mine at Macmillan Pass (AMAX mining personnel pers. comm. 1984).

The degree to which specific relief habitat is utilized depends largely upon its availability. The use of relief habitat other than snow and ice may be due in part to the fact that certain populations do not have snowpatches to resort to in summer. Where they do occur, snowpatches and areas of overflow ice (*aufeis*) are widely used, both in mainland populations and on the Arctic islands where they constitute the usual refuge for the small summer groups (Calef 1981). The lower degree of insect harassment in the High Arctic (Parker and Ross 1976) suggests that there may be reasons other than insect harassment to explain the selection of snowpatches as relief habitat.

1.4 Hypotheses To Be Tested

A review of the literature that attempts to account for snowpatch selection in the summer reveals that the majority of explanations fall, singly or in combination, into one of two categories. For the purpose of this thesis, the two will be treated as separate hypotheses.

Caribou are well adapted to the cold ; less so for high summer temperatures. Under conditions of heat stress many mammals become easily fatigued. One of the characteristics of snow is its high albedo. Values of up to 0.95 for fresh snow and 0.4 for old snow are not unusual (Oke 1978). The rejection of such a large proportion of incoming radiation is of primary importance in the overall low energy status of snow. Furthermore, over a melting snowpatch at high altitude in summer, much of that energy is converted to latent heat and is not available for surface heating. The snowpatch zone therefore will possess a relatively cool microclimate. The first hypothesis thus proposes that caribou use snowpatches as a cool, resting area as a mechanism of thermoregulation (Figure 1.1). Formozov (1946) noted that "in summer, in the mountains the reindeer often lie down on zaboys (snowpatches)". Remmert (1980) attributes this to the coolness of these snowy areas. Kelsall (1968) and Calef (1981) also report snowpatches as a resting area for barren-ground caribou in the Northwest Territories. Gill (1978) noted that the Woodland caribou at Macmillan Pass on warm days would apparently attempt to remain cool "by lying on the snow or otherwise staying near the snowpatches". Aerial surveys flown over Macmillan Pass in August 1981 recorded 84% of all caribou observations on snow, although less than 1% of these were bedded (Kershaw and Kershaw 1983b).

Although snowpatch selection for a cool, resting area is a form of behavioural thermoregulation, caribou may attempt to thermoregulate in other ways. The ingestion of ice, snow or meltwater will cause the body to lose some heat in raising the water to body temperature. Gill (1978) recognized the snowfields at higher elevations in the Macmillan Pass area as an important source of water for the animals. Kelsall described "slurping" at ice and snow as a common practice performed by barren-ground caribou (pers. comm. 1984). Captive reindeer have been observed to consume two to three times their normal water intake at high temperatures (Yousef and Luick 1975). Caribou may thus use snowpatches to behaviourally thermoregulate by ingesting snow (Figure 1.1).

Pruitt doubts that the conventional explanation of coolness is correct (pers. comm. 1984). Indirectly though, this has a bearing upon the second hypothesis. The low air temperature immediately above the snow is known to inhibit the activities of blood-sucking insects that continually harass the caribou during the summer months (Skoog 1968, Calef 1981). Furthermore, the snowpatches, at least in alpine regions, occur in high and exposed locations where winds are stronger than at lower elevation. Stronger winds significantly reduce insect activity (White et al. 1975). These two axioms form the basis of the **reduced insect harassment** hypothesis (Figure 1.1). Formozov (1946), Pruitt (1960), Skoog (1968), Kelsall (1968), Bergerud (1978) and Calef (1981) have all made reference to this explanation.

In addition to the two major hypotheses, a number of other points are worthy of consideration. It has been noted that wolves in central Baffin Island tended to avoid high, rocky areas where deep snowpatches lingered in summer (Elliot 1972). Kelsall (pers. comm. 1984) also thought that caribou may favour extensive areas of ice and snow for resting because of the excellent visibility afforded to warn of the approach of any potential danger. It should be noted that it is just as valid to state that they themselves are more visible to predators on snow and so should avoid these areas. Finally, Pruitt (pers. comm. 1984) hypothesized that the contrasting properties of snow and rock surfaces initiate thermal gradients which cause winds to flow inwards - a beneficial situation for an animal with such an acute sense of smell.

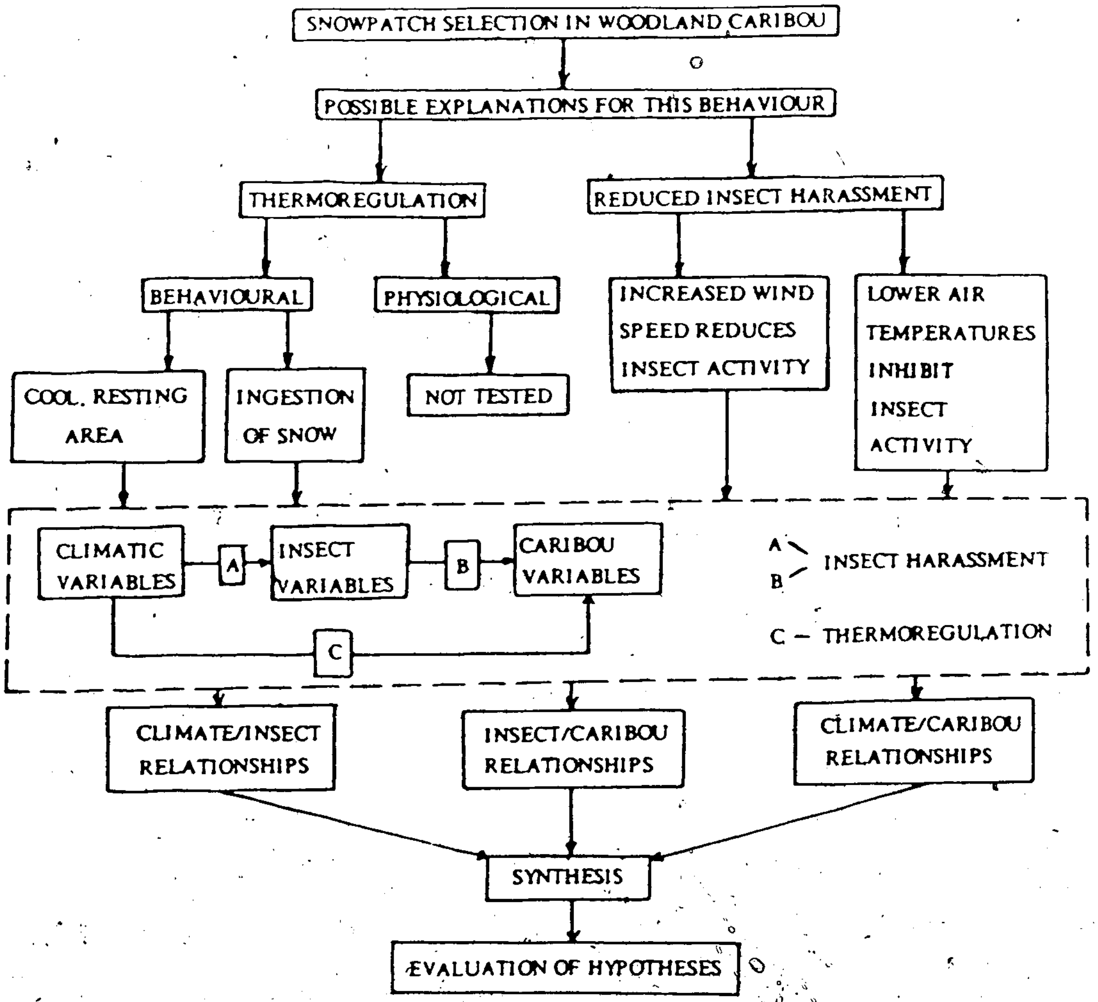


Figure 1.1 Summer selection of snowpatches by woodland caribou ; Hypotheses and research design

1.5 Objectives

In attempting to explain this aspect of summer habitat selection by Woodland caribou the thesis will aim to fulfil the following objectives:

1. Delimit the snowpatch zone, its areal extent and degree of change through the summer season.
2. Quantify the microclimate of one permanent, high elevation snowpatch in relation to adjacent and lower elevation snow-free zones.
3. Determine when the snowpatch habitat is selected within the daily activity cycle.
4. Assess the relative merits of the hypotheses through behavioural analyses of Woodland caribou on and off snowpatches under contrasting climatic conditions.

2. THE STUDY AREA

2.1 Location

Macmillan Pass, at an elevation of 1350 m. a.s.l. is located in the Selwyn Mountains at the Yukon/Northwest Territories border (63 15'N , 130 02'W) (Figure 2.1). The mountains along the Continental Divide reach elevations of up to 2430 m. a.s.l. To the east the Tsichu River drains into the Mackenzie Basin with the South Macmillan River draining into the Yukon River system to the west. The North Canol Road trends north-east to south-west through these two river valleys. The centre of the study area is located 11 kilometres east of the Territorial boundary and 8 kilometres south-west of the Tsichu River Airstrip at Camp 222 (Figure 2.1). Principles of site selection are discussed in Section 3.1.

2.2 Physiography

The south-western Mackenzie Mountains and Selwyn Mountains comprise beds of quartzite, argillite, slate, chert, limestone, sandstone and conglomerates arranged in closely folded strata. During the Quaternary, the area was glaciated at least once (Blusson 1971). Glaciation in this area was by local, cordilleran ice whereby major piedmont or valley glaciers in the Tsichu and Hess River valleys were fed by tributary glaciers emenating out of high elevation cirques (Kershaw and Kershaw 1983a). Glaciers are still present within the area around Keele Peak. Many cirques still contain glacierettes such as that at the head of the Main Valley in the south-western sector of the study area.

The surficial geomorphology of the Macmillan Pass area has been extensively mapped by Kershaw and Kershaw (1983a). Localized, descriptive studies centred around the tungsten mine at the Continental Divide have also been completed (AMAX 1976, Kershaw 1976). The study area is classified as lying within the discontinuous permafrost zone (AMAX 1976) although Kershaw and Kershaw (1983a) proposed that low mean annual temperatures and high elevation would ensure that the area is underlain by continuous permafrost except where

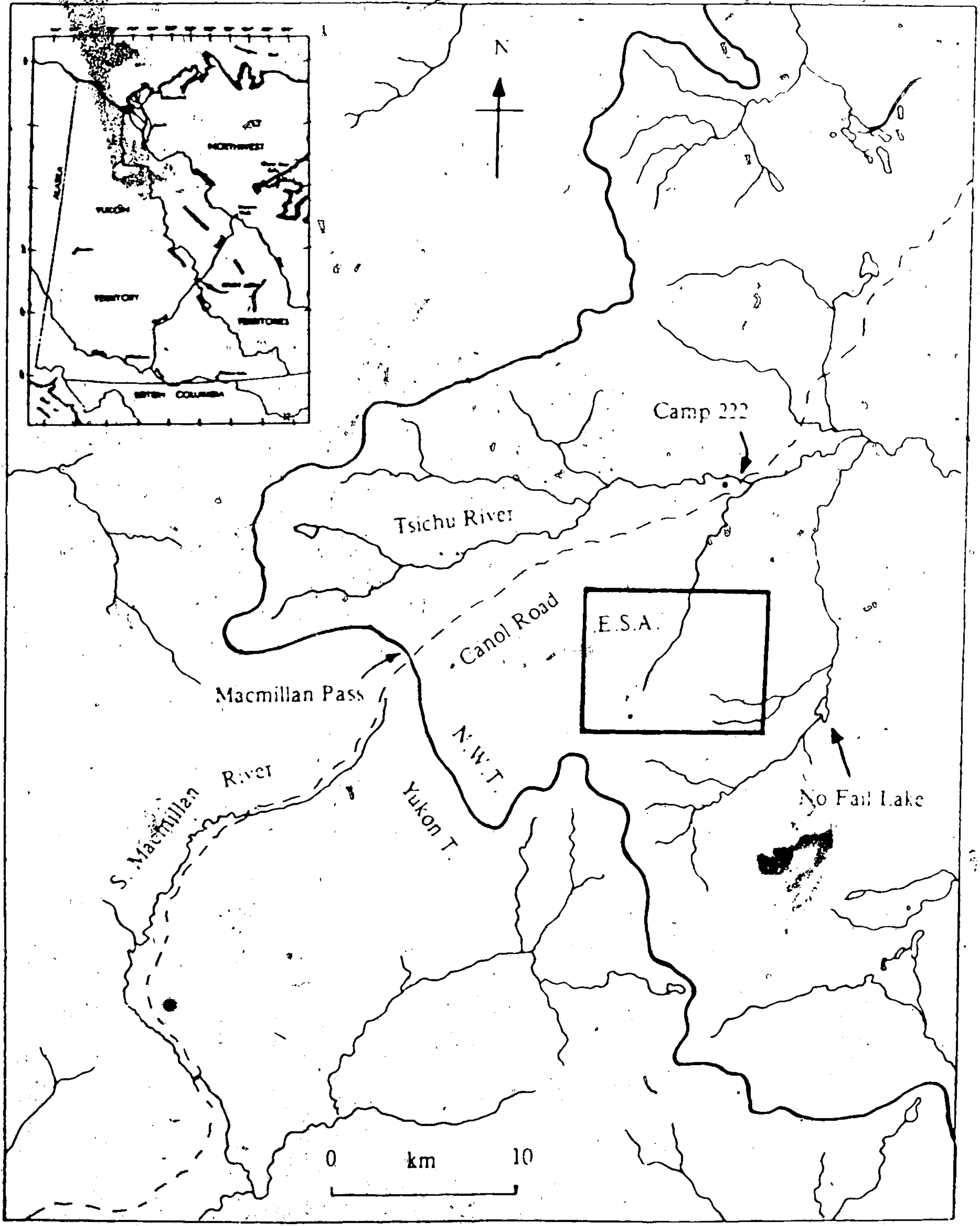


Figure 2.1 Location of the Extensive Study Area (E.S.A.).

permanent wetlands and lakes occur. Several glacial, periglacial, fluvial, masswasting and organic landforms are evident at Macmillan Pass. Within the study area blockslopes and patterned ground occur at high elevation. Solifluction lobes were observed on gently sloping surfaces in the centre of the study area. To the north, eskers, palsas and peat plateaus have been identified on and around the floor of the Tsichu River valley. (Kershaw and Gill 1979)

2.3 Mesoclimate

Macmillan Pass experiences a Continental climatic regime modified by the alpine environment. Summers are short and warm with long, cold winters. Between October 1974 and August 1982 the Tsichu River Meteorological Station was operated by AMAX Northwest Mining Company Ltd. to provide surface data on a potential airstrip location. This station was located 2 kilometres north of the study area. The Tsichu River Station recorded a mean annual temperature of -7.7°C, a mean annual precipitation of 490 mm and a mean annual snowfall of 294 cm. The mean temperature of the warmest month (July) is 10°C with a mean of -25°C for the coldest month in December. Freezing temperatures have been recorded in every month with precipitation concentrated between July and October.

No comparable data exist for the mountains above the Tsichu River Station. Comparisons with the limited data collected in 1984 are not valid due to the small data base. It is likely that mean summer air temperatures within the study area in the mountains above Macmillan Pass would be lower than the Tsichu River Station due to adiabatic cooling of air with increasing elevation. However, during periods of clear, calm weather, strong temperature inversions form over the valleys, paticularly in winter. Cold air drainage onto the broad, flat terrain of the Tsichu River valley under anticyclonic conditions has been documented (Stobbe 1975).

2.4 Vegetation

Macmillan Pass lies mostly above timberline. At increasing distance to the east of the Continental Divide the tundra gives way to subarctic forest (Porsild 1951). These treed areas are generally dominated by subalpine fir (*Abies lasiocarpa*) and mature stands of white spruce (*Picea glauca*). The study area lies entirely above timberline. Analysis of aerial photography summarized in Kershaw and Kershaw (1983a) was supplemented by ground surveys for the study area in 1984. The terminology used to describe plant communities follows that of Kershaw and Kershaw.

Within the study area vegetation graded from lichen-encrusted felsenmeer above 1900 m to willow- and birch-dominated communities below 1600 m. At exposed, high elevation sites, a total lichen cover of over 90% was frequently observed. Below 1900 m Alpine Lichen Grass communities were common at well-drained sites. Kershaw and Kershaw (1983a) described similar sites dominated by graminoids such as *Deschampsia caespitosa*, *Festuca altaica*, *Poa arctica* and *Carex atrofusca* . Lichens including *Cetraria cucullata*, *C. nivalis* and *Cladonia mitis* were also an important component of this plant community. Lichen Heath tundra dominated by *Cassiope tetragona* and *Cladonia mitis* (Plate 3 - Appendix 1) occurred on flat or gently sloping sites at elevations generally below 1700 m. Relatively moist sites below 1700 m. supported Alpine Meadow communities with a high cover of vascular plant species. One such meadow dominated by *Eriophorum angustifolium* is visible in Plate 8. Below 1600 m. Birch-Lichen communities dominated by *Betula glandulosa* were common. At poorly-drained sites and along water courses a variety of willow species were present including *Salix lanata*, *S. glauca* and *S. planifolia*.

3. RESEARCH METHODS

3.1 Principles of Site Selection

The selection of a study area occurred at three levels : a regional selection, the choice of a site, and the delimitation of extensive and intensive study areas. The Macmillan Pass area was selected because of the existing data base (Archibald 1973, Gill 1978, Collin 1983, Kershaw and Kershaw 1983b) and ease of access. The Pass is accessible via the North Canol Road in summer and support equipment may be transported into the surrounding mountains from a helicopter base 11 kilometres west of the territorial boundary.

The summer surveys of Kershaw and Kershaw (1983b) recorded large concentrations of caribou on and around the slopes of an unnamed mountain 9 km southwest of the Tsichu River airstrip at Camp 222 (Figure 2.1). The snowpatch on which Kershaw and Kershaw (1983b) photographed a large herd of 68 animals was easily recognizable from aerial photographs taken seven years previously. The aerial photographs also showed the location of several other snowpatches thought to be permanent in this area. As field reconnaissance prior to arrival was not possible, these data and interviews with those familiar with the Macmillan Pass area (Kershaw pers. comm. 1983) formed the basis of site selection. Other than the basic requirements of a relatively dry and sheltered site with access to a continuous water supply, a permanent basecamp was erected in a location which would afford an unobstructed view of the largest snowpatch but with a minimal impact on caribou. The principles for the delimitation of the extensive and intensive study areas are discussed in Section 3.3. Between June 17 and August 17 1984 a two-man camp was maintained with a total of 104 man-days in the study area.

3.2 Abiotic Components

In the last ten years significant advances have been made in the development of instrumentation and measurement for environmental sciences. Automatic Data Acquisition Systems (ADAS) have rendered conventional, mechanical means of measurement almost obsolete. The application of microchip technology to environmental monitoring has proven advantageous in several respects. Not least of these are the compactness, portability, reliability and storage capability of multi-channel dataloggers similar to those used in this study.

Two automatic weather stations were erected within the study area. Their purpose was twofold:

1. To provide comparative data between the snowpatch and snow-free areas.
2. To provide comparative data between exposed, upland sites and relatively sheltered, lowland sites.

The first station was operational for the duration of the field study between June 21 and August 16. The station was located in Lichen-Heath tundra at 1676 m a.s.l. (Figure 3.1). It was relocated in a Willow-Forb community at 1601 m a.s.l. on August 6. This was because it became apparent that it was into these communities below 1600 m a.s.l. that most caribou moved at night. The microclimatic variation between night-time and daytime habitat selection could thus be more appropriately assessed. It is referred to as the Willow-Forb or Lichen-Heath station throughout the thesis.

The depth of snow in the high ground throughout June and July meant that the second station could not be established until July 10. Once in place, it too was operational until August 16. This station was situated over lichen-encrusted felsenmeer and snowpatch sites at an elevation of 1981 m a.s.l. (Figure 3.1). This station is referred to as the Snowpatch or Blockfield station depending upon the location of the sensors. Although the two stations were simultaneously gathering data for a relatively short period (38 days) this was thought sufficient to assess any microclimatic gradients (see points 1 and 2 above) under contrasting general weather conditions.

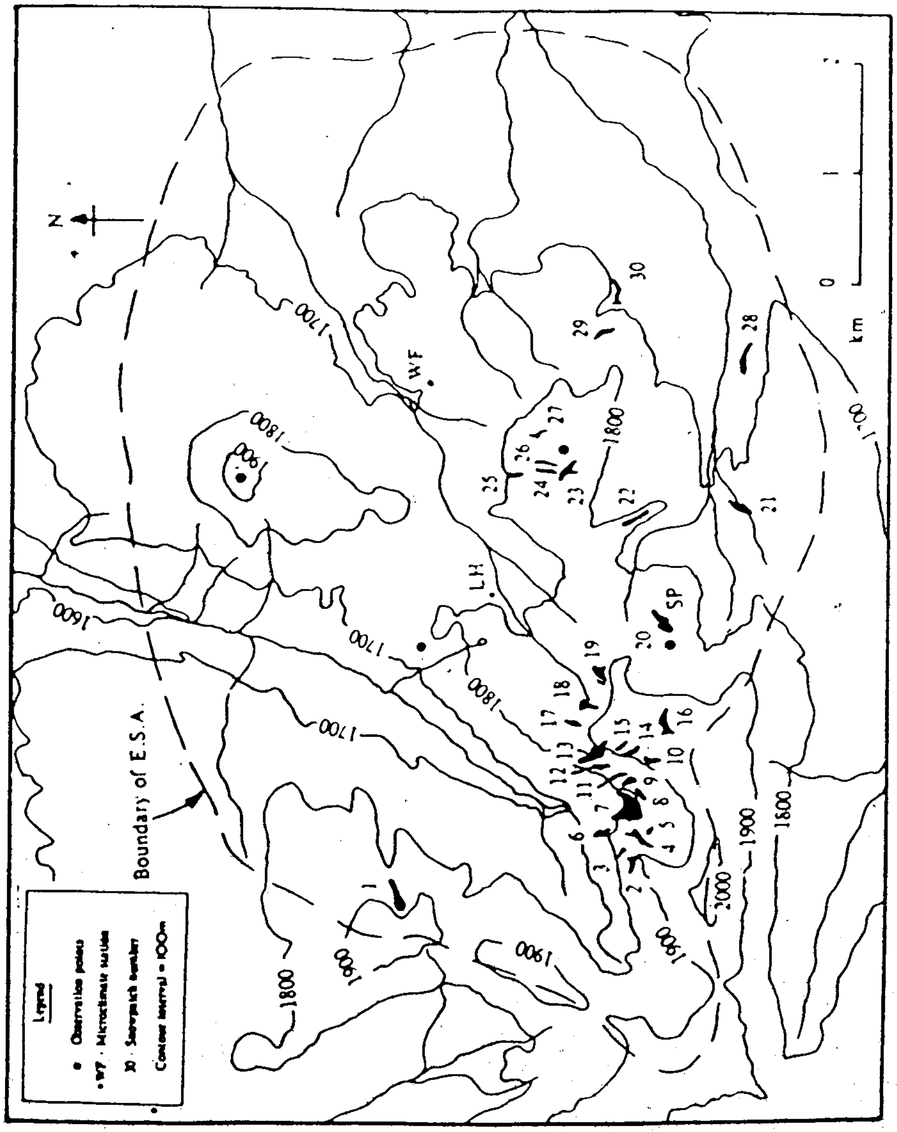


Figure 3.1 Location of permanent snowpatches within the Extensive Study Area. WF = Willow-Forb Station, LH = Lichen-Heath Station, SP = Snowpatch Station.

At the low station (i.e. at the Lichen-Heath or Willow-Forb Stations) a shielded thermistor recorded air temperature at 0.5 m. An electro-humidity sensor automatically compensated for an inbuilt temperature sensor (Rosenberg et al. 1983) measured relative humidity and air temperature at a height of 1.5 m. This sensor was mounted horizontally within a louvred screen enclosure. These sensors were naturally ventilated.

A silicon pyranometer, mounted and levelled on the station measured global (diffuse and direct beam) radiation at a height of 2 m. Wind speed at a height of 2 m was also recorded. A tipping bucket raingauge monitored precipitation.

Air temperature, relative humidity and wind speed measurements were comparable between the two sites at the high station. Additional pyranometers and rain gauges were not thought to be necessary. A heavy duty wind direction sensor was mounted at 2 m. Shielded thermistors recorded air temperature at heights of 0.5 and 1.5 m over a permanent snowpatch. These sensors were located 12 m from the station. Although this distance was limited by the length of the sensor cable, the centre of the snowpatch could be monitored. This would minimize any "edge effect" and maximize the snow/snow-free gradient. The temperature sensors were positioned at 0.5 and 1.5 m as these heights closely approximated to the "head lowered" and "head raised" posture of caribou quantified in the behavioural analysis (Plate 1). Simple temperature profiles above the various surfaces could also be drawn. All sensors were calibrated in the laboratory before and after their use in the field. The thermistors were calibrated against each other in the field. All sensors operated within their specified accuracy range (Campbell Scientific 1983) and no correction factors were applied.

The data from all sensors were processed and stored in the internal memory of a Campbell Scientific CR21 micrologger. At the low station the signals were transferred to magnetic tape. At the high station (the more extreme environment) a solid state storage module was used with a cassette recorder as a backup. At each station the micrologger and storage devices were placed in weatherproof plastic cases packed with desiccant gel. These were secured inside converted tool boxes for further protection (Plate 2).

The microloggers were programmed to scan each sensor every 15 minutes. This provided climatic data at a resolution comparable to the observation data. Twenty-four hour summary tables were also generated to record totals, means, extremes and times of extremes. The low station was visited on a daily basis and the high station every second or third day.

Prior to the installation of the high station one micrologger was used to conduct two temporary experiments. In the first of these, the temperature profile within the snowpack was recorded with a vertical array of thermistors. This would be used to explain the supra-nivean microclimate (Chapter 5.2). The second experiment involved sampling wind speed and direction along transects at various locations within the study area. An appreciation of how topography generates or modifies surface winds would be of value in explaining animal behaviour (Chapter 7.4) and patterns of snow accumulation (Chapter 5.1). A portable radiometer was used in conjunction with the pyranometer to calculate the albedo of various surfaces within the study area. Patterns of snow ablation were documented through the repeated photography of panoramas from selected viewpoints.

3.3 Biotic Components

The third stage of site selection (see Section 3.1) was the delimitation of the study areas. These limits were determined by the animal observation techniques employed. As all fieldwork was undertaken on foot, the most efficient means of data collection was one in which travelling distance and time were minimized and observing time was maximized.

Four observation points were selected which provided extensive vistas of each of the cardinal points of the compass (Figure 3.1). The east, west and north observation points were situated on ridges or topographic rises. The southern observation point coincided with the high station. A traverse beginning and ending at basecamp, encompassing each observation point would take four hours. The high elevation of these observation points and their overlapping angles of view were such that a spotting scope fitted with a 20x eyepiece could survey a total area of 50.7 km^{-2} This is referred to throughout the text as the "extensive study area". The area bounded by these four vantage points (9.8 km^2) was constantly within view. With the exception of some local obstructions it could be surveyed at any time. This was the "intensive study area".

Of all wild species of *Cervidae*, mountain caribou may be the most difficult to study. Their irregular distribution and continuous movement can hinder the location and tracking of local populations. Moreover, the rugged terrain of the Mackenzie and Selwyn Mountains is, in many respects less conducive to viewing than the tundra of the Canadian Shield inhabited by barren-ground caribou. As Edwards and Ritcey (1959) state :

"Studying caribou in mountainous terrain is strenuous work with small returns in knowledge from long hours afield in all kinds of weather...A biologist afoot could easily devote most of his time to searching" (p.21).

It soon became apparent that a more effective means of collecting observation data was to randomly select one observation point and to reject other observation points as soon as a sighting was made. The group or individual was then tracked until out of view. A constant effort was made to avoid harassing the caribou as this may have altered their normal movements. All caribou sightings were recorded. Movements initiated or influenced by human encroachment were excluded from later analysis. The time and location of the beginning and end of each sighting were noted on 1:50,000 topographic maps. Intermediate movements were also documented. Records of group size and composition in terms of age and sex were kept.

Caribou are notoriously difficult to classify accurately as to sex and age. The presence of antlers on both sexes hinders positive identification at certain times of the year. This problem is limited mostly to aerial surveys. Ground surveys are generally superior for the analysis of discrete herds (Stelfox and McGillis 1977). A combination of identifying characteristics were considered to classify caribou in this study. During the summer months, body size, antler development, pelage tone and external genitalia are sufficient to classify caribou into one of four groups : calf, yearling, adult cow and adult bull. Any animals which could not be identified using these criteria were left unclassified.

Observational study of animal behaviour has been perfected mostly through the analysis of captive animals in an artificial environment. The study of laboratory-housed animals benefits from an increased internal validity (statements about the sample) at the expense of decreased external validity - the interpretation or generalization from the sample to other situations or populations in the wild (Altmann 1974). Observational field studies tend to show the converse imbalance. Field situations are essentially "observation selective" as opposed to the "manipulative" environment of the controlled laboratory experiment. The selection of sampling variables and methods in such a non-manipulative environment as the Mackenzie Mountains was aimed at maximizing the internal validity of the data. In the following discussion the sampling method terminology follows that of Altmann (1974).

Many of the early observation data were of an informal and non-systemmatic nature. Such *ad libitum* sampling was of some heuristic value in searching for ideas and in planning more systematic sampling. The choice of the most appropriate sampling method was influenced by both the conditions of observation and the number and behaviour of the animals under study. Under these constraints a combination of focal animal sampling and scan sampling were selected. Focal animal sampling concentrates on a single animal and records behaviour during a predetermined sample period. This is a technique adopted widely in the study of primates although it has also been applied to ungulates (Struhsaker 1967). Scan sampling (or instantaneous sampling of groups) is used to obtain data from a large number of group members by observing each in turn.

The selection of a focal individual may be either random, stratified random, regular or irregular (Altmann 1974). All but the first of these categories were used, with selection determined by one or more of the following criteria :

1. Herd size
2. Nearest neighbour distance
3. Degree of movement
4. Viewing conditions

The principal objective of the behavioural analysis (other than to test the hypotheses) was to assess any variation in snowpatch use with reference to age and sex. Therefore, whenever a large (i.e. over 5) herd of mixed age and sex could be observed at length, focal individuals were randomly chosen within each of the four age/sex classes. Larger aggregations were often closely spaced and sampling was inevitably biased towards individuals nearer the observer. Herds of less than five animals that were relatively well spaced were sampled regularly. This involved the rotation through a fixed schedule of each animal.

In addition to the sampling of focal animals, scan sampling of the larger groups was attempted. This was done by recording an individual animal's current activity at preselected intervals. This was thought to be of value in describing patterns of group behaviour and provided comparative data to the focal animal sampling. A technique was perfected whereby a scan sample would be taken at regular intervals after a fixed number of focal animal samples. All time budgeting analyses of focal animal samples were undertaken on a ten minute basis. This interval was chosen as it was the longest time that an individual animal could be continuously monitored through a spotting scope before movement obstructed or interrupted vision and observer fatigue became influential. This interval also made the data comparable with similar studies on other populations (e.g. Fischer and Duncan 1976). A cumulative stopwatch was used to record the time budgeting of various activities on a two point scale (standing/bedded, head raised/head lowered etc). The scan samples also provided data on groups for which focal animal samples could not be attempted (e.g. short observations). In some cases the frequency of specific behaviour was sampled, for example in assessing response to insect harassment. In this form of sampling the onset and termination of the sample period was dependant upon the behaviour under study. Otherwise, the interval between regular sample periods was usually five minutes.

In addition to recording behavioural response to harassment, insect traps were placed at ground level at different elevations and in specific habitats. Each trap took the form of a dark green rectangular box with dimensions 40 x 25 x 25 cm (Plate 3). A 225 cm^{-2} square section on each side was lightly smeared with a strong, weatherproof adhesive ('Tanglefoot'). (Successive experiments using traps of various tones provided no evidence that insects cue to specific colours). Any insect alighting on this surface was entrained. Each of the four sections were divided into a grid pattern to facilitate totalling. One trap was placed adjacent to each weather station. Counts were made whenever the weather station was visited (see Section 3.2 for frequency of visitation).

3.4 Major Problems and Limitations

Automatic weather stations are naturally exposed to the elements which they are to measure (Van Cauwenberghe 1981). Battery drain in the tape recorder accounted for a 4.1% data loss from all sensors at the exposed high station. A broken anemometer cable resulted in a further 8.3% loss of wind speed data at this station. At the low station the same problem caused a 1.4% loss of wind speed data. The accumulation of 0.5 centimetres of snow on the pyranometer was sufficient to lead to the rejection of 0.6% of the radiation data.

Several factors combined to hinder the collection of observational data. Viewing times and distances were frequently reduced by low cloud cover and poor light. Tripod vibration in strong winds made any accurate study of distant animals almost impossible. Conversely, on the warmest afternoons vision through the spotting scope was blurred by thermal disturbances of the air. Many of the focal animal samples were abandoned because of these problems and the irregular movements of individuals which obscured the animal under study.

4. SEASONAL DISTRIBUTIONS

4.1 Introduction

This chapter contains a brief discussion of the various factors which influence caribou movements on a seasonal time frame. Numerous environmental and physiological variables combine to direct migrations in Woodland caribou. Snow and snow cover are emphasized. These are discussed with reference to the literature on populations in western Canada and Alaska. This is followed by a review of the literature documenting the movements of the "herd" under study. The distribution of caribou within their summer range in and around Macmillan Pass is discussed in the conclusion.

4.2 Seasonal Migration in Woodland Caribou

Woodland caribou inhabiting mountainous regions of the Yukon and Northwest Territories undertake vertical seasonal migrations between forested winter range and alpine and subalpine tundra zones in summer. The causal mechanisms behind migration have been widely discussed and involve a complexity of physiological (endogenous) and environmental (exogenous) considerations. There are several suggested reasons to explain why caribou migrate. Banfield (1974) includes amongst the most important factors, a change in diet as a result of seasonal growth in vegetation, rutting and calving requirements, changing snow conditions, loss of range to forest fires, weather conditions and the prevalence of biting flies and mosquitoes. Photoperiodism, terrain features and predation could also be added to this list.

The importance of snow (and snow cover) as an exogenous factor was discussed in Chapter 1. The role of snow varies significantly on an annual basis. Throughout May the receding snowpack and the stimulus of advanced pregnancy in the adult female initiates a movement out of the trees into the subalpine region (Kelsall 1968). This is reinforced by the emergence of new, nutrient-rich plant growth. During the spring migration the calving grounds are the focal point for the movements of individuals and groups. These are situated mostly in gently rolling tundra although evidence of calving in more mountainous terrain is not uncommon (Archibald 1973, Bergerud 1978).

In terms of physiology, the months between June and September are a time of major growth and replenishment of energy reserves depleted during the winter. The major environmental determinant in summer is the need to escape or find relief from the heat and biting insects. The summer distribution and movements of barren-ground caribou are well documented. Repeated aerial surveys have lead to a better understanding of the distribution and timing of migration between winter and summer range in northern Canada and Alaska (Banfield and Jakimchuk 1980). Post calving movements towards the Arctic Coast in search of cooler temperatures and stronger winds typify the attempts of heat-stressed or insect-harassed animals to find relief habitat (although this has not been empirically tested.) Similar environmental controls may dictate the movements of Woodland caribou throughout their summer range. Whereas major latitudinal and longitudinal migrations are undertaken by barren-ground caribou, this is replaced by an altitudinal seasonal shift of Woodland caribou in the mountains of western Canada. Late-lying snowpatches and windswept ridges at high elevations provide the greatest potential for relief from heat and insects within the Woodland caribou's summer range.

During the late September/early October rut, the rapid accumulation of snow forces caribou to lower elevations below timberline. Although caribou will tolerate a wide spectrum of snow conditions, the softer and lighter snow of the treed wintering grounds is favoured for foraging on ground and arboreal lichens. The forest also affords a much higher degree of shelter during the long winter months until the spring migration recommences. This pattern of vertical migration is documented for mountain caribou in British Columbia (Edwards 1958, Edwards and Ritcey 1959, Bergerud 1978, Freddy 1979) Yukon (Oosenbrug and Theberge 1980) and Alberta/British Columbia (Stelfox 1974, Stelfox et al. 1978).

4.3 Seasonal Distribution of the "Redstone Herd"

The exact home range limits of Woodland caribou occupying the Macmillan Pass area during the summer months are not known. No detailed work encompassing an entire year has been attempted and those surveys replicated on a seasonal basis are limited in space and time (Simmons 1969 and 1970, Kershaw and Kershaw 1983b). Winter surveys in the central Mackenzie Mountains undertaken by Lortie (1982) found evidence of wintering caribou to be more or less continuous from the head of the Thundercloud River to the upper tributaries of the Mountain River (Figure 4.1). From this evidence it was still speculative whether this distribution represented one wintering "herd" or was composed of several discrete smaller herds. In spite of these limitations it is possible to define approximate limits to winter and summer range and migration routes of caribou summering at Macmillan Pass.

Despite the transient and nomadic nature of Woodland caribou in the Mackenzie and Selwyn Mountains there appears to be an annual migration to primary winter range centred on the Wrigley Lake area 160 kilometres to the north-east of Macmillan Pass. The spring and autumn migrations are characterised by topographic funnelling through the valleys of the Keele River and its tributaries and the North Redstone River (Archibald 1973). Hence, throughout the thesis, this herd is referred to as the Redstone Herd (Farnell and Nette 1981).

Simmons (1969) noted concentrations along the North Redstone River moving upstream in mid-March 1969 which complements observations he made at the same time in the two previous years. In 1970 movement up the North Redstone River valley was rapid and caribou were sighted only 8 kilometres to the east of the Keele River by mid-February. Sightings were also made in the drainage valleys north of the Twitya River as early as January in 1970 (Simmons 1970). In February 1982, over 100 caribou were observed in the lower reaches of the Tsichu River only 30 kilometres from the Continental Divide (Kershaw and Kershaw 1983b). Similar observations of up to 500 caribou along the Tsichu River were made the following month by Lortie (1982).

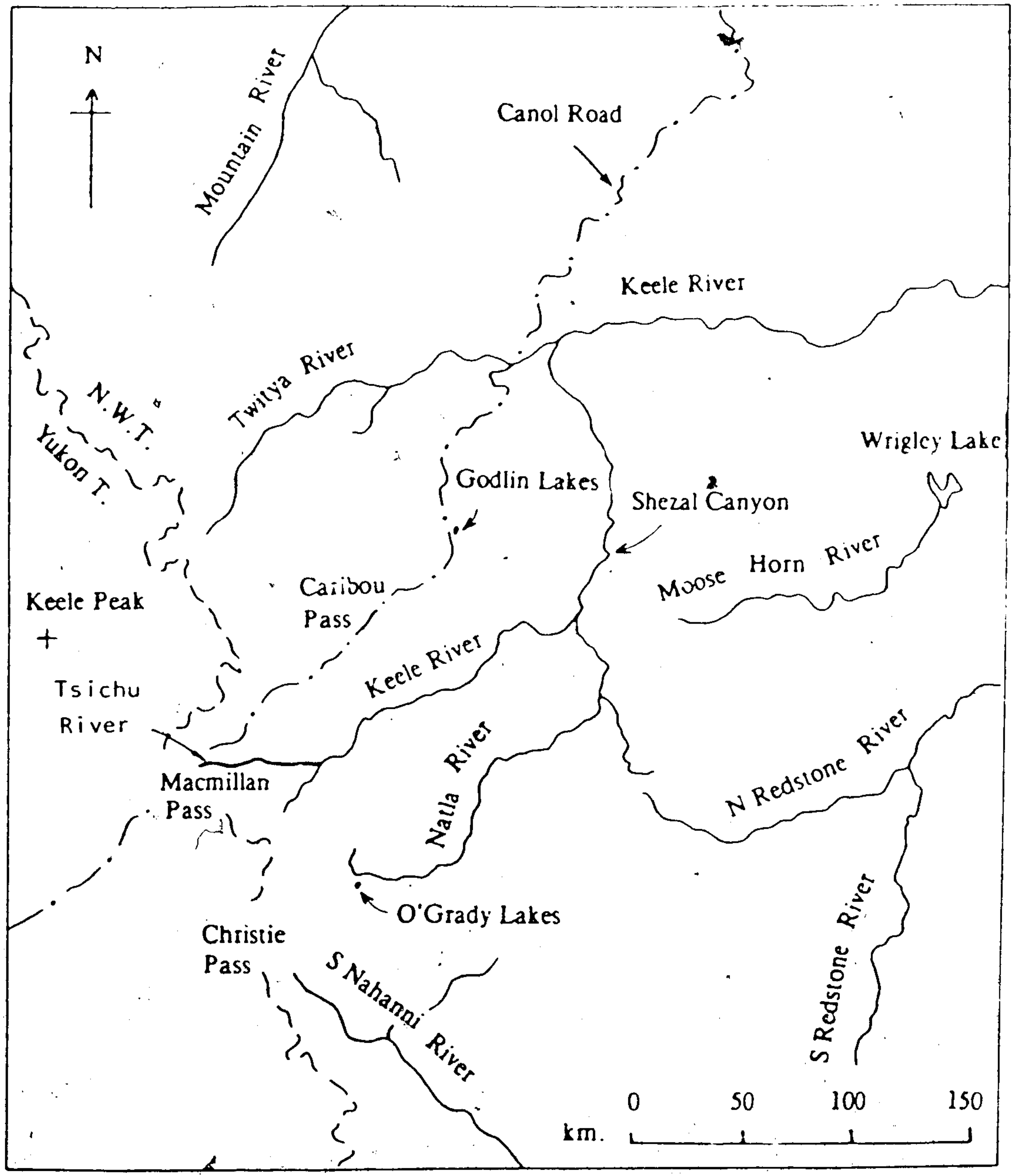


Figure 4.1 The general region used by Woodland caribou associated with the "Redstone Herd".

Most calving occurs in the headwaters of the Keele, Twitya and Natla Rivers. Aerial surveys flown in the first week of June in 1982 and 1983 identified large concentrations above the Tsichu River to the east of the Canol Road (Kershaw and Kershaw 1983b) The same spring surveys also revealed a small number along the continental divide and into the Yukon. Some calving occurs here. Numerous observations were also made along the Divide between Christie Pass and Keele Peak in late May and early June of 1981 (Farnell and Nette 1981). It is possible that these animals were part of the Redstone herd but more likely to be part of a herd wintering in the Yukon. The highest concentrations of caribou in the Mackenzie and Selwyn Mountains occur at O'Grady Lakes (Collin 1983) although most of the alpine regions to the east and west of Macmillan Pass are inhabited during the summer months.

The autumn migration may begin as early as August with a return to winter range in the Northwest Territories although some may cross to winter in the Yukon. In August 1976 there was a pronounced eastward movement through the Selwyn Valley to the North of Keele Peak (AMAX 1976). Similar directed drifting through the upper Tsichu River valley has been observed in August and September (Miller 1976). As the rut approaches in late September and early October very few caribou remain in the Tsichu River area with the majority moving down below timberline to the east. Caribou sign have been observed as late as November 26 in the Tsichu River valley (Gill 1978). Stelfox (1976) counted many caribou at Shezal Canyon at the confluence of the Keele and Natla Rivers and at Caribou Flats to the east of the Keele river in late September 1967. Some of the caribou occupying Macmillan Pass during the summer may congregate in the upper reaches of the South Nahanni River where large winter concentrations have been known to occur (Farnell and Nette 1981). The same authors confirmed the eastward migration in autumn by relocating post-rut caribou in the Northwest Territories over 200 km. from their original location at Keele Peak in July.

Between November and April, caribou of the Redstone Herd are widespread throughout their winter range along the Keele, Natla, Ekwi, Twitya and Redstone River valleys and their tributaries. Contrary to the early opinion of Rand (1945) that caribou are "present the year round" at Macmillan Pass, more recent winter wildlife surveys in the area described by Gill (1978) and Kershaw and Kershaw (1983b) provide no evidence of caribou activity at this time.

4.4 Distribution within Summer Range

There is strong evidence for the overlap of summer range with calving grounds centred on an area approximately 15 kilometres to the east of the Continental Divide. Aerial surveys flown over a 500 km^2 study area centred on the upper Tsichu River in the first week of June in 1982 and 1983 located concentrations of caribou in mountainous terrain south of the Tsichu River (Kershaw and Kershaw 1983b). This evidence is reinforced by an abundance of dropped female antlers in this area and to the west in the mountains due south of Camp 222 (Figure 2.1).

During calving, the caribou at Macmillan Pass are concentrated around the lower reaches of the Tsichu River but the summer distribution is much more widespread within and above Macmillan Pass. The aerial surveys flown by Kershaw and Kershaw (1983b) in August 1981 and 1982 located concentrations in the mountains to the south of the Tsichu River but also a wide dispersal within the mountains north of the river. The elevational distribution of Woodland caribou at Macmillan Pass during the summer is higher than at any other time of the year (Table 4.1). Archibald (1973) described a similar change in distribution with elevation through time for caribou in the Mackenzie Mountains. Between May 11 and 21 1973 (the pre-calving period) over 96% of animals observed were below 1530 m a.s.l. Between June 3 and 30 over 83% were observed above this elevation. During the fly season (July 1 to Sept 3) 93% were located above 1530 m a.s.l. and 56% above 1830 m a.s.l. No comparative data were available for autumn or late winter.

Similar seasonal shifts in distribution on an elevational basis have been noted in other Woodland caribou populations in the mountains of Western Canada (Edwards and Ritcey 1959, Freddy 1979, Stelfox 1978, Bergerud 1978, Oosenbrug and Theberge 1980). Each of these studies describe a seasonal shift of distribution with elevation and the highest values were

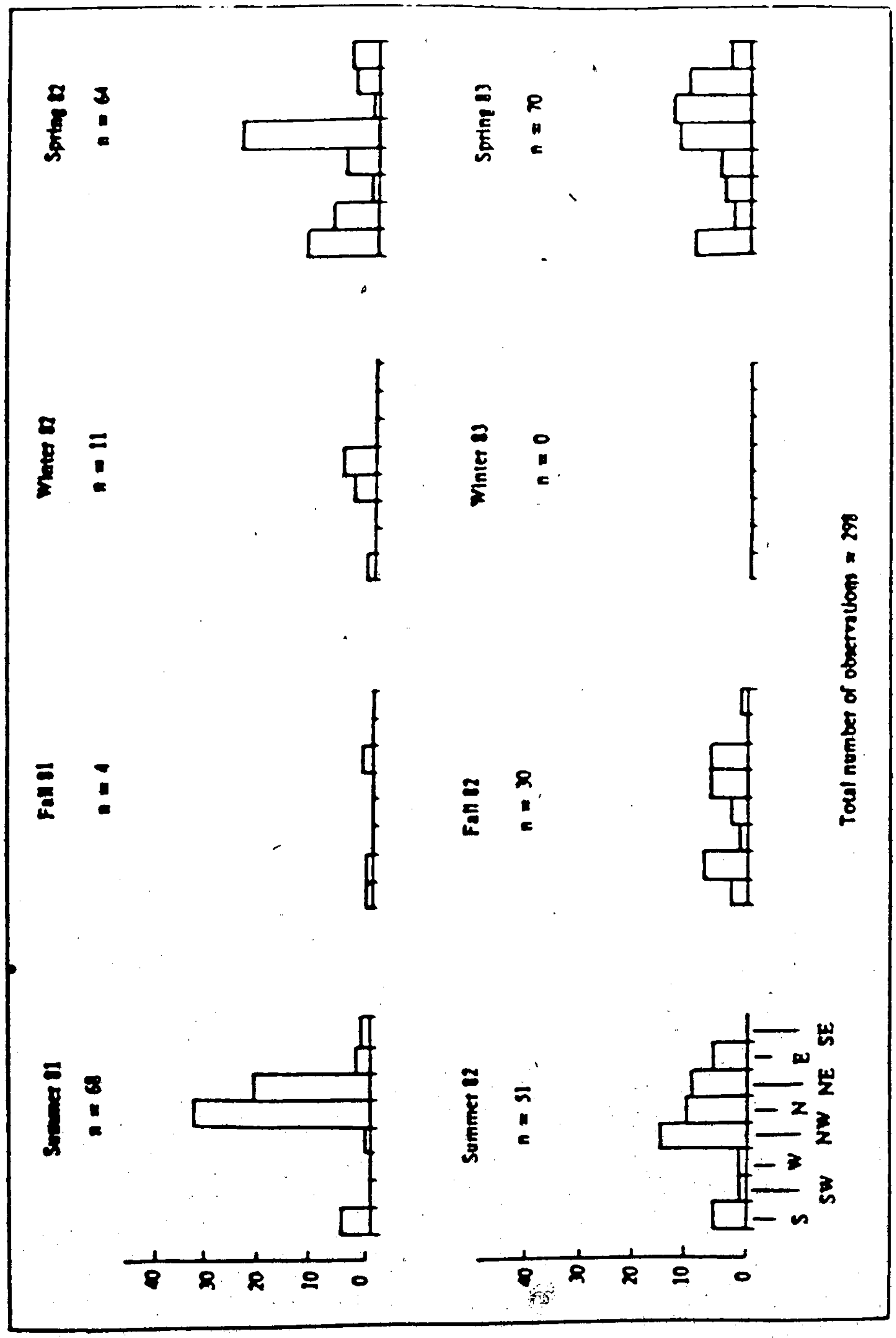
Table 4.1 Seasonal distribution of caribou at Macmillan Pass with respect to elevation.

Season	Number observed	Mean elevation (m)	Range (m)
Summer 81	466	1848	1280 - 2120
Fall 81	32	1535	1460 - 1640
Winter 82	27	1158	1160 - 1180
Spring 82	452	1481	1220 - 2000
Summer 82	174	1628	1250 - 2000
Fall 82	117	1532	1250 - 1820
Winter 83	0		
Spring 83	597	1491	1220 - 1880
Total	1865		
Mean		1524	1160 - 2120

(Adapted from Kershaw and Kershaw 1983)

achieved in July and August. With the exception of the work of Freddy, these studies also describe a second shift to higher elevation in mid-winter. There are two possible explanations for this reascent. The first is that snow accumulation and compaction allows caribou to move to higher elevations to forage on arboreal lichens from the platform provided by the snowpack. The second is that stronger wind speeds on exposed high land reduces snow depth and facilitates access to ground lichens. Although no data on feeding preferences are available the former explanation is more feasible in accounting for the location of a band of caribou on the Tsichu River in February 1982, well west of the traditional winter range (Kershaw and Kershaw 1983b).

Within their summer range at Macmillan Pass, Woodland caribou strongly select slopes with a northerly aspect. From the surveys flown by Kershaw and Kershaw (1983b) in August 1981, 82.3% of observations were made on slopes facing either to the north or north-east. The following summer 72.5% of observations were made on slopes oriented towards the north, north-west or north-east (Figure 4.2). A similar predilection was described by Gill (1978). This he attributes to the cooler and more humid environment of the north-facing slopes and the resultant retarded phenologic state of vegetation found here. The more obvious explanation is the distribution of snowpatches on slopes facing north and east due to the lower level of irradiance and the prevailing wind direction. Preferences for north- and east-facing slopes were also described by Bergerud (1978) for caribou in British Columbia. These observations are completely at variance with those of Stelfox (1974) for mountain caribou in Jasper National Park. Between June and September 1973 these caribou selected slopes with a variety of exposures but predominantly those facing south and west. The north and east exposures selected by caribou at Macmillan Pass were used mostly in winter at Jasper.



Adapted from Kershaw and Kershaw 1983b

Figure 4.2 Seasonal distribution of Woodland caribou at Macmillan Pass by aspect.

5. ABIOTIC COMPONENTS : SNOWPATCHES AND MICROCLIMATE

5.1 Snowpatch Mapping

5.1.1 Snowfall at Macmillan Pass

Between October 1974 and August 1982 Amax Northwest Mining Company Limited maintained a meteorological station at Camp 222 on the North Canol Road. At an elevation of 1265 m a.s.l., the Tsichu River meteorological station was located 1.8 km north of the northern boundary of the extensive study area. In conjunction with data from the Yukon weather office, data for this period were synthesized by Kershaw and Kershaw (1983b) . The 8 year data base was thought sufficient to provide an accurate description of snowfall at Macmillan Pass.

With a mean annual precipitation of 490 millimetres and sub-zero temperatures recorded in the warmest month (July), snowfall has been documented in every month of the year. The first major snowfalls occur in September when mean monthly temperature falls below 0°C. October, November and December, when combined, account for over 49% of the mean annual snowfall. Snowfall between January and April is comparatively light with settling and compaction of the snowpack. Some precipitation will occur as snow in May when the mean monthly temperature exceeds 0°C for the first time and the spring melt begins. In June, July and August less than 1% of precipitation occurs as snow with a gradual retreat of the snowpack to higher elevations.

5.1.2 Snow Cover on June 17

By the end of the second week of June 1984 little snow remained on the floor of the Tsichu River valley at Macmillan Pass (Plate 4). Adjacent to the North Canol Road snow remained in isolated depressions where wind drifting had created deep accumulations. River icings remained on the South Macmillan and Tsichu Rivers. The mountain peaks at The Pass still retained a relatively continuous snow cover at this time. In the extensive study area snow blanketed most of the terrain above 1700 m a.s.l. Exposed ridges and south-facing slopes were largely free of snow (Plate 5). Within the extensive study area snow still covered 53% of the surface.

Although no data were available on patterns of snow accumulation in the area, something may be inferred from the nature of the snow cover in mid June. From a random sampling of snow depths within the intensive study area, it appeared that the deepest accumulations of snow formed along water courses, in small valleys and in any topographic depressions deep enough to hold snow. Depths of over 2 m were recorded along north- and north-east-facing river banks and lee slopes. A similar distribution of snow though with a stronger southerly component was observed by Kerby (1979) in the Richardson Mountains.

The central section of the intensive study area was a gentle, north-facing slope and still retained a relatively continuous snow cover with the deepest accumulations in gullies and former water courses to the south of the basecamp. The gently rolling ridges and hummocks between these depressions were free of snow. Meltwater which flowed off the tundra slopes into hollows and gullies cleared channels to the north and east of the intensive study area. To the west, snow still covered the entire surface of the glacierette and filled avalanche chutes in the cirque headwall. Similar features on the south-facing wall of the mountain also retained snow. Linear snowpatches remained in the lee of debris slides on the eastern wall of the main valley. Below 1500 m a.s.l., snow cover was more discontinuous as the extensive snowfields gave way to individual and widely-spaced sinuous patches following water courses and hollows as far as No Fail Lake (Plate 6).

5.1.3 Snow Cover on August 17

By mid-August no snow remained in the main Tsichu River valley floor and all land below 1750 m a.s.l. in the extensive study area was free of snow. Most of the larger snowpatches occurred on favourable slopes above 2000 m a.s.l. (Figure 5.1). This increase in snowpatch frequency with elevation is probably a result of adiabatic cooling with increasing

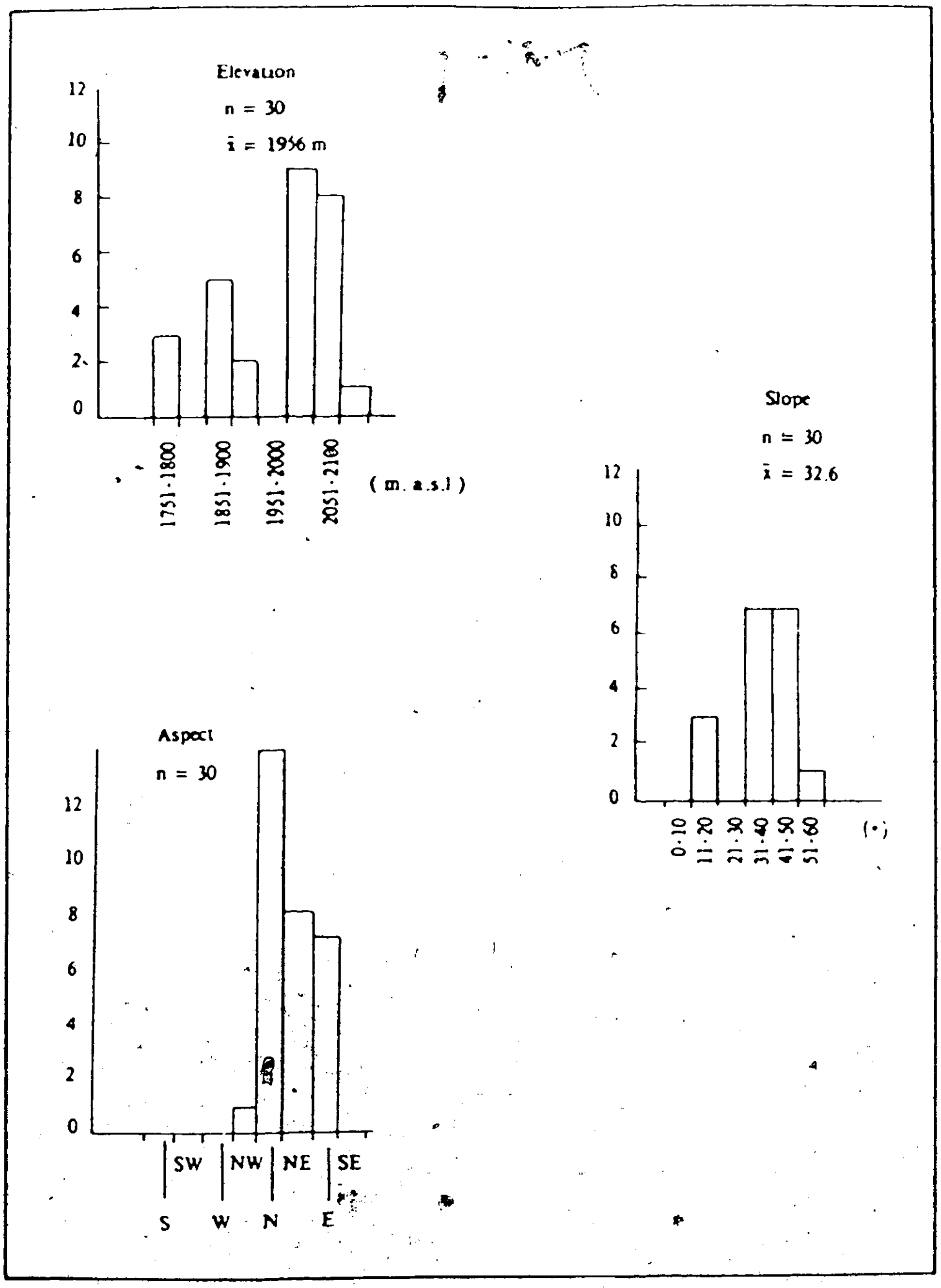


Figure 5.1 Permanent snowpatch distribution with respect to elevation, slope and aspect.

altitude. Assuming a dry adiabatic lapse rate of 1°C 100 m^{-1} the temperature difference between the Tsichu River at Camp 222 and the mountain peak in the south-western corner of the study area may exceed 10°C. The frequency and duration of sub-zero temperatures reducing snowpatch ablation should thus be longer at higher altitude. Furthermore, the lichen-dominated communities at the higher ground give way to denser vegetation below 1650 m a.s.l. Unequal heating around vegetation protruding through snow would enhance melting at lower elevations.

The location of snowpatches remaining at the end of the study period is given in Figure 3.1. These snowpatches covered 0.9% of the extensive study area for a total surface area of 0.46km^2. This area comprised 30 discrete snowpatches distributed throughout the study area but concentrated in the higher ground to the south-west. Despite sub-zero temperatures and snowfall in the second week of August it was thought that ablation was still occurring at the end of the study period. This would probably have melted out most of the smaller snowpatches which were too small to be accurately mapped. These thirty patches were thus thought to be the only permanent areas of snow in the extensive study area.

All but one of the 30 permanent snowpatches occurred on slopes with a north, north-east or eastern aspect (Figure 5.1). This is due to the lower irradiance on slopes with a northern aspect and the prevailing westerly winds in winter (Stobbe 1975) which cause drifting in the lee of mountain ridges on east-facing slopes. Slope angle is less influential upon snowpatch formation as permanent patches occurred on angles of [illegible]1° to 51°. Solar receipt decreases with increasing slope angle on north-facing slopes. All snowpatches occurred on plant-free surfaces or lichen-encrusted felsenmeer.

The largest snowpatch in the study area (number 7) with a surface area of approximately 1900 m^2 covered the upper slopes of the glacierette in the south-eastern corner of the extensive study area. This arcuate patch extended up the headwall of the cirque along steep avalanche chutes. The gradient of the headwall was too steep to allow any direct solar radiation to reach the snowpatch at any time. Air temperature within the cirque below the moraine was recorded at 7.3°C cooler than that at the lower elevation station on July 28 at 14:00 h. This drainage of cold air onto the cirque floor and the low irradiance ensured that the rate of snow ablation within the cirque would probably be slower than at any other location in the study area. Several smaller snowpatches occupied hollows in the cirque headwall (numbers 2 to 6 and 8 to 11).

Seven snowpatches (numbers 12 to 18) were located in the south-western corner of the intensive study area centred on two steep-sided hills. The largest of these (# 13) extended for 140 m along a steeply sloping rockface bordering the cirque wall. The south-eastern edge of the snowpatch dipped over an arete 15 m into the adjoining valley (Plate 8). This snowpatch possessed similar dimensions to the one appearing in an aerial photograph taken in the summer of 1974. The same patch was also easily identifiable from oblique angle aerial photographs taken in early August 1982 (Kershaw and Kershaw 1983b). This provides strong evidence for the recurrence of certain snowpatches in the same location in successive years. Two snowpatches (numbers 16 and 17) occupied a small col between the two peaks. This topographic constriction produced wind speeds up to 55% stronger than the exposed high station. This would cause deep drifting below the col and a small cornice had developed on snowpatch number 17.

Snow occupied four deep troughs thought to be structural faults in the west-facing slope of a mountain in the east of the intensive study area (numbers 23 to 25). Snowpatch 21 was located in the upper slope of a depression left by a debris slide with snowpatch 22 similarly located in the lee of an east-west trending ridge. Large drifts will form in the lee of major obstacles or steep drops in elevation where wind speeds are reduced. Snowpatches 27 and 28 exemplify this. Both were located in the lee of ridges trending north-east to south-west. At the site of snowpatch 28 south-easterly winds encounter a change in gradient of 5° to 35° over 4 metres of elevation. This produced a 77% drop in wind speed during a 10 minute sampling period and this acts as an effective snow trap. Snowpatches 26, 29 and 30 also occurred on steep scree slopes with a north or north-eastern aspect. Some impression of the change in snow cover during the study period is illustrated in Plates 7 and 8.

5.2 Snowpatch Microclimate

5.2.1 Introduction

As Geiger (1965) states, "the essential characteristics of similar microclimates are repeated everywhere. It suffices for many purposes to measure these characteristics at a few experimental areas and relate them to other sites within the same macroclimate". The following discussion of microclimatic variation within the study area is based on this assumption. Analyses of climatic conditions across the snowpatch boundary and at high and low elevation sites are intended to fulfil the two major objectives of work attempting to quantify relationships between 'macroclimate' and microclimate identified by Holmes and Dingle (1965). These are first: to establish general relationships between microclimate and 'macroclimate' (e.g. the snowpatch microclimate) and second: to illustrate the highly variable nature of microclimate (e.g. 'local' mountain climates).

5.2.2 Radiation Budget

Snow (and ice) surfaces possess unique properties in terms of their radiation budget. Snow is almost a perfect black body in the long-wave portion of the spectrum but also has a very high short-wave albedo. The surface (and sub-surface) reflection of a high proportion of insolation and the strong re-radiation of terrestrial energy are the reasons for a snow-covered surface being classified as a radiative "sink". as a radiative "sink". In addition, the low thermal conductivity of snow ensures that surface radiative heat losses are not quickly replaced by heat fluxes from below (Munn 1966).

Unlike many other natural surfaces, snow will allow the transmission of incident short-wave radiation, thus ensuring that radiation absorption occurs within a volume rather than at a plane. Solar radiation not lost by reflection at the surface may penetrate to a depth of

1 m in snow (Geiger 1965) and up to 10 m in ice (Munn 1966). The distance decay of the flux within the snowpack follows an exponential curve which is influenced by the properties of the snow and the wavelength of radiation (Oke 1978). The significance of radiative exchange within snow becomes apparent in explaining the sub-nivean and supra-nivean microclimate.

5.2.3 Energy Balance

The rejection of such a large portion of incoming short-wave radiation is of paramount importance in explaining the overall low energy status of snow surfaces. In attempting to formulate the energy balance over snow, Oke (1978) draws the distinction between "cold" and "wet" snowpacks. The former case is more typical of high latitude snow surfaces in winter with very little or no solar input. The high aridity under these conditions ensures that latent heat flux is likely to be a negligable component in its energy balance. An ablating snowpatch in a mid-latitude alpine environment such as those under study more closely corresponds to Oke's "wet" snowpack. During the summer months at Macmillan Pass when temperatures exceed freezing, precipitation as rain becomes a significant energy balance component in enhancing snowmelt. Rain percolating through the snowpack represents an additional heat source for the pack. This, together with phase changes of water involving the release and uptake of energy are the primary means of heat transfer within the snowpack. Sublimation also contributes to snowpack removal during the summer.

During the summer when ablation exceeds accumulation, both radiation and convection act as energy sources to support melting. The temperature of the snow changes very little in this process therefore the large change of energy storage is due to latent rather than sensible heat uptake. The energy balance of a melting snowpatch high in the Selwyn Mountains in summer can thus be best approximated by:

$$Q^* + QR = QH + QE + \Delta Qs \qquad (5.1)$$

where Q^* is net all wave radiation flux density, QR is the rate of heat supplied by rainfall, QH is turbulent sensible heat flux density, QE is turbulent latent heat flux density and ΔQs is net energy storage.

5.2.4 Thermal Climate

The radiation balance and energy budget of snow together with its physical properties (specifically its low thermal conductivity and thermal diffusivity - see Table 5.1) are a key to understanding its sub-surface thermal climate. This in turn helps to explain conditions above the snow surface, in particular the first 1.5 to 2.0 m - the zone of critical importance in this study. Emphasis in the following discussion of the snowpatch microclimate is placed upon the *general* pattern evident from snow profile and snowpatch margin analyses. This is supported by specific examples such as 24 h analyses.

Unlike bare soil and vegetated areas, sub-surface temperature profiles through snow exhibit a maximum just beneath the surface (Figure 5.2). This is because, by day, radiative heat transfer dominates over heat conduction in the upper 50 cm (Schwerdtfeger and Weller 1967) and also because the transmission of short-wave radiation is much greater than the long-wave component in this medium (Oke 1978). Radiative losses comprise short-wave reflection and long-wave emission to the atmosphere. The strong absorptivity of snow to long-wave radiation permits this loss to occur from a thin surface layer - measured at around 3 cm in light, loosely-packed snow (Takahashi 1960). The relative attenuations of short- and long-wave radiation and this balance between gains and losses is such that net radiation had maximum absorption just below the snow surface during the day. Consequently, this is the site of maximum heating and has the highest temperature. This phenomenon has been observed in "dry" snowpacks at high latitude (Holmgren 1971) and to a lesser degree in isothermal packs such as those under study (Figure 5.2).

The reflection and transmimssion of short-wave radiation below the snow surface and the conversion of a large portion of the energy budget to latent rather than sensible heat results in a relatively cool microclimate over snow. Surface temperatures remained close to 0°C (as is expected at the site of maximum evaporation and sublimation) illustrating the strong thermal

Table 5.1 Thermal properties of natural materials.

Material	Remarks	Density	Specific Heat	Heat Capacity	Thermal Conductivity	Thermal Diffusivity
		kg $m^{-3}.10^3$	J kg^{-1} K^{-1} $.10^3$	J m^{-3} K^{-1} $.10^6$	W m^{-1} K^{-1}	m^2 s^{-1} $.10^{-6}$
Peat Soil	Dry	0.30	1.92	0.58	0.06	0.10
	Saturated	1.10	3.65	4.02	0.50	0.12
Snow	Fresh	0.10	2.09	0.21	0.08	0.10
	Old	0.48	2.09	0.84	0.42	0.40
Ice	0 C,pure	0.92	2.10	1.93	2.24	1.16
Water	4 C,still	1.00	4.18	4.18	0.57	0.14
Air	10 C,still	0.0012	1.01	0.0012	0.025	20.5
	Turbulent	0.0012	1.01	0.0012	125	10 10^6

Adapted from
: Oke (1978)

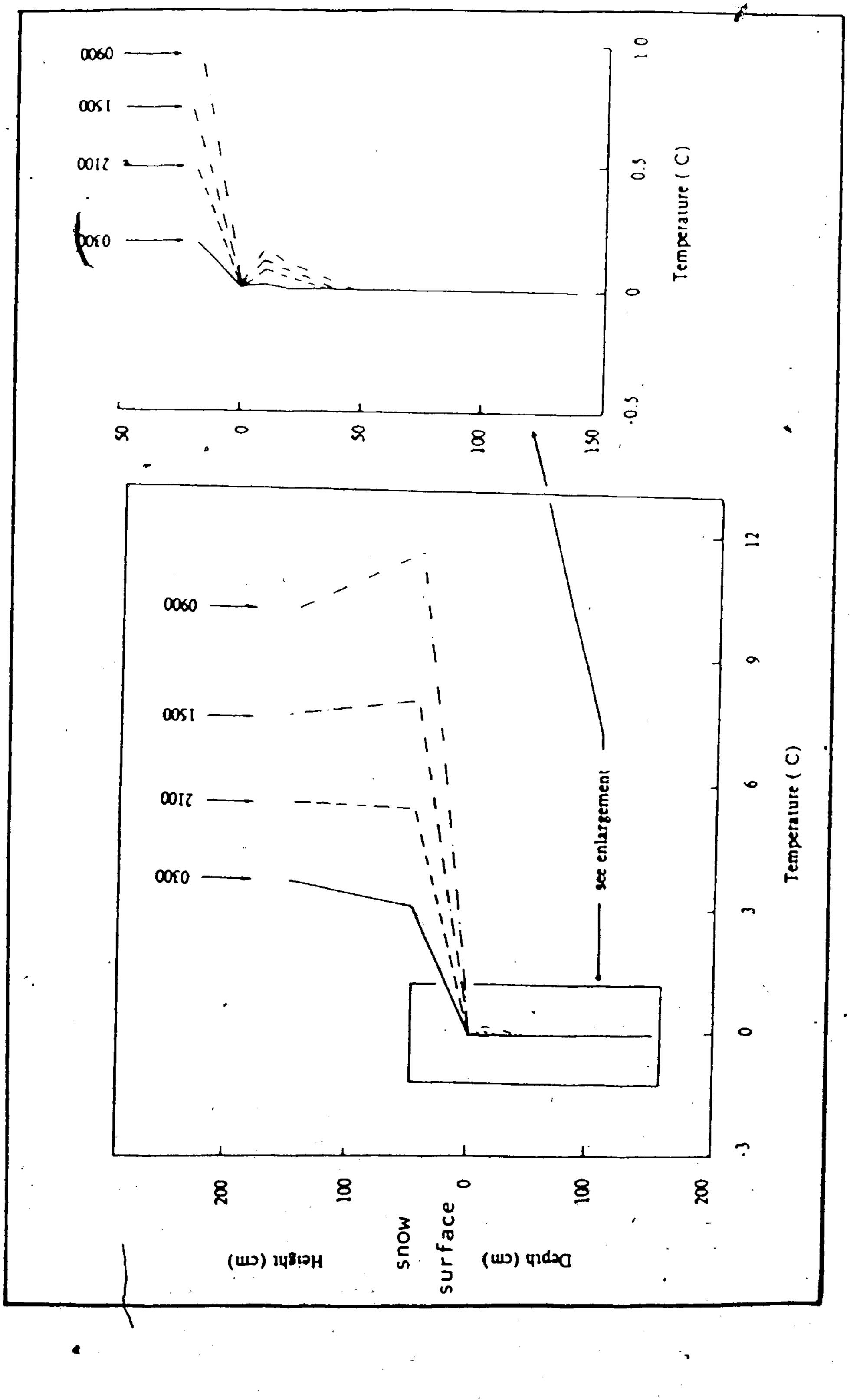


Figure 5.2 Temperature profiles within and above the snowpack — June 25.

inertia of snow with lapse profiles commonly observed during the daytime. At night the poor thermal diffusivity of snow (Table 5.1) causes fast and intense surface cooling and the development of inversion profiles over snow (Figures 5.2 and 5.3). These profiles are best developed under calm conditions at night; Daytime convective heating generated at the tundra surface sets up strong winds which enhance mechanical mixing and destroy or diminish vertical temperature differences. This may explain the temporary reversal of gradients at 02:00 h in Figure 5.12. This condition was recorded for 7.6% of the hourly values. Strong daytime winds also enhance snowpatch ablation by increasing turbulence and the transfer of sensible heat from the overlying air to the snow surface.

Horizontal temperature differences are also influenced by wind speeds. In Figure 5.4 the temperature difference between comparative heights over the snowpatch and adjacent blockfield is approximately constant at 3°C. This pattern is supported by reference to the summarized data for this temperature difference (Figure 5.9). Again, the air temperature at 0.5 metres over the snow was around 3°C cooler than the corresponding position over the blockfield. This difference was slightly reduced and more variable on average in the afternoon whilst higher and less variable at night. Night-time winds were generally weaker and the temperature difference more constant. (Hourly values for 00:00 h to 06:00 h were 48.4% of those for 12:00 h to 18:00 h).

Heat flow is greater under warm, anticyclonic conditions (when radiation flux density is high) than cyclonic conditions. The contrasting radiative and physical properties of snow and rock set up stronger horizontal differences under clear skies when the direct beam comprises a large portion of insolation. Under unstable, cyclonic conditions the convective process of heat exchange is suppressed and the horizontal differences reduced (Geiger 1965). This is exemplified with reference to Figure 5.5.

The snowpatch margin represents a sharp surface discontinuity. It has been suggested by Pruitt (pers. comm. 1984), that differential warming and cooling under cloudless skies and weak large scale motion gives rise to horizontal temperature and pressure differences which may

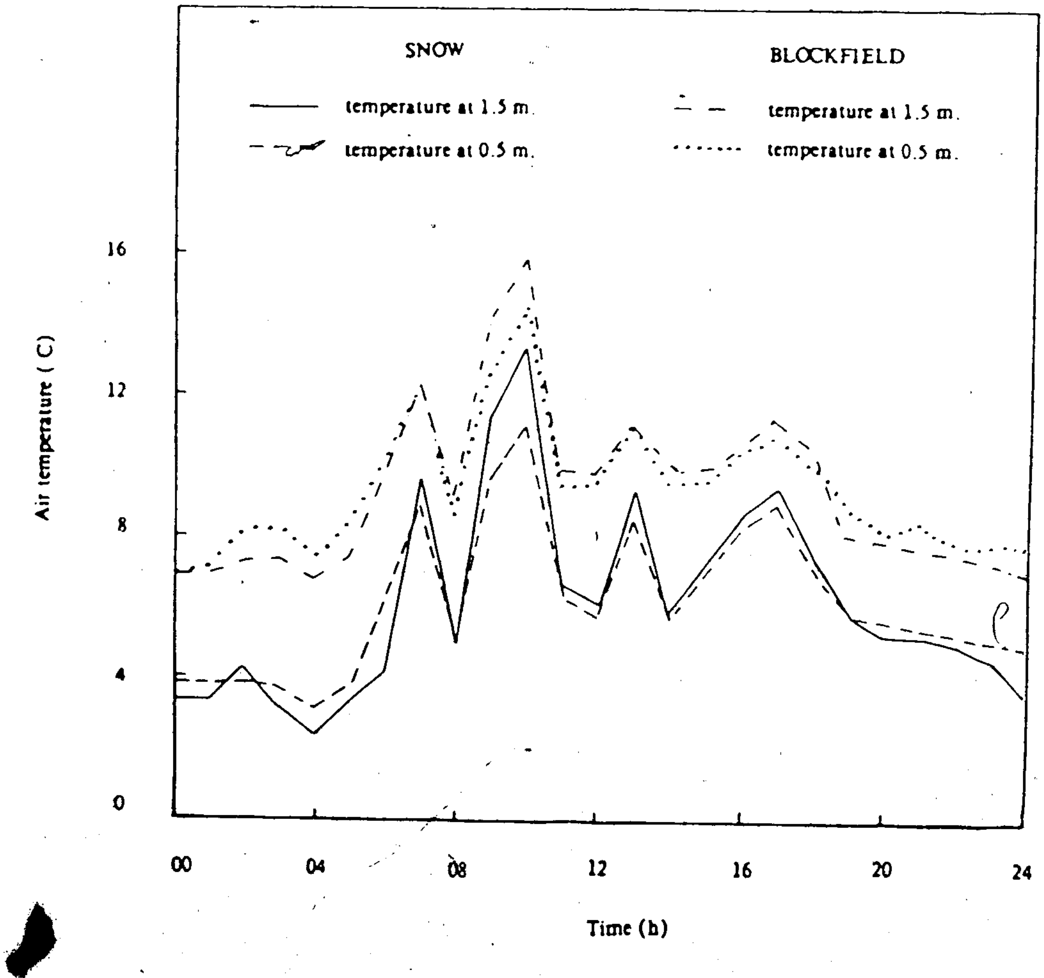


Figure 5.3 Air temperature over the Snow and Blockfield stations — July 23.

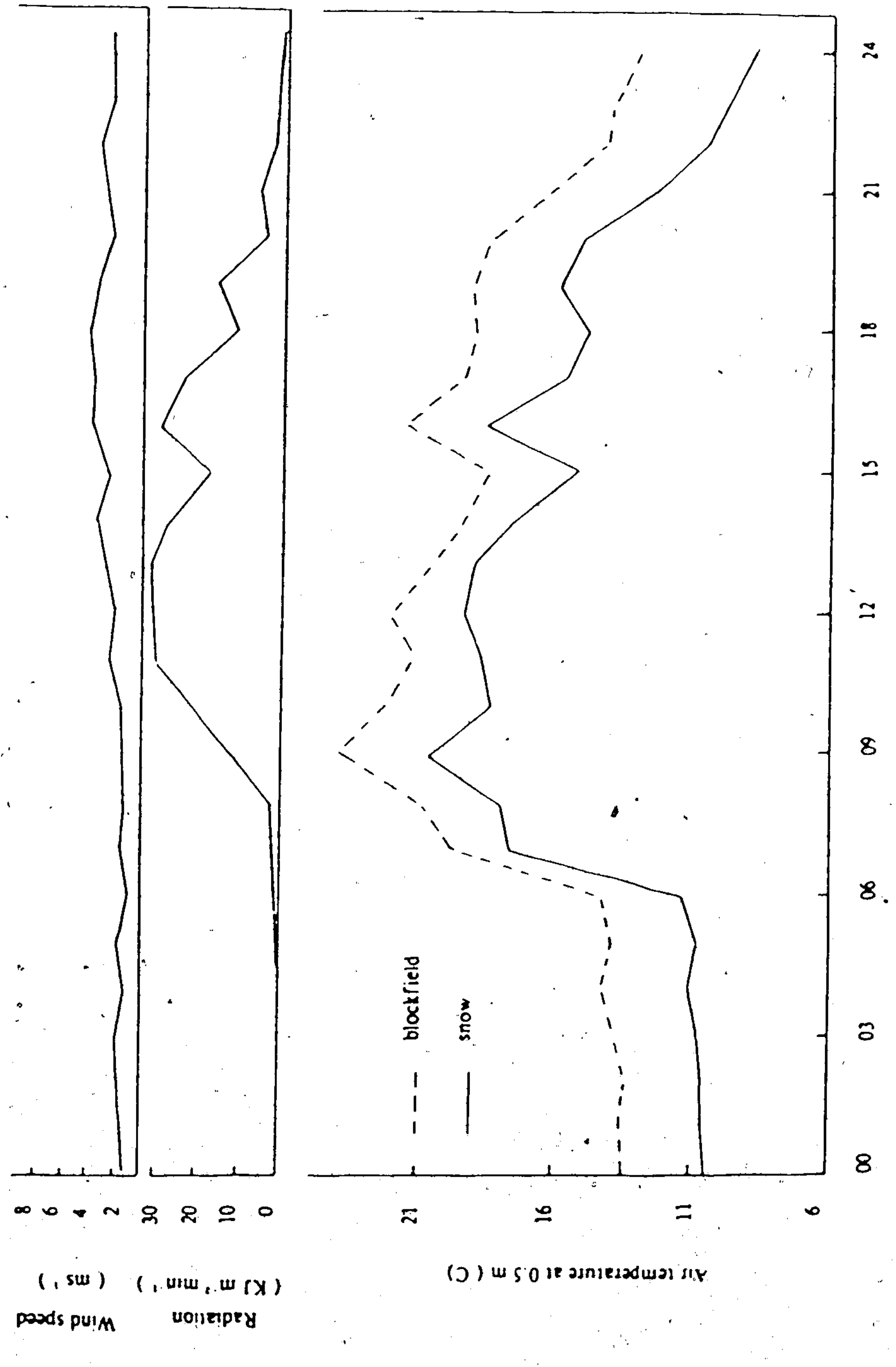


Figure 5.4 Diurnal fluctuation in the Snow/Blockfield air temperature difference under anticyclonic conditions. July 26.

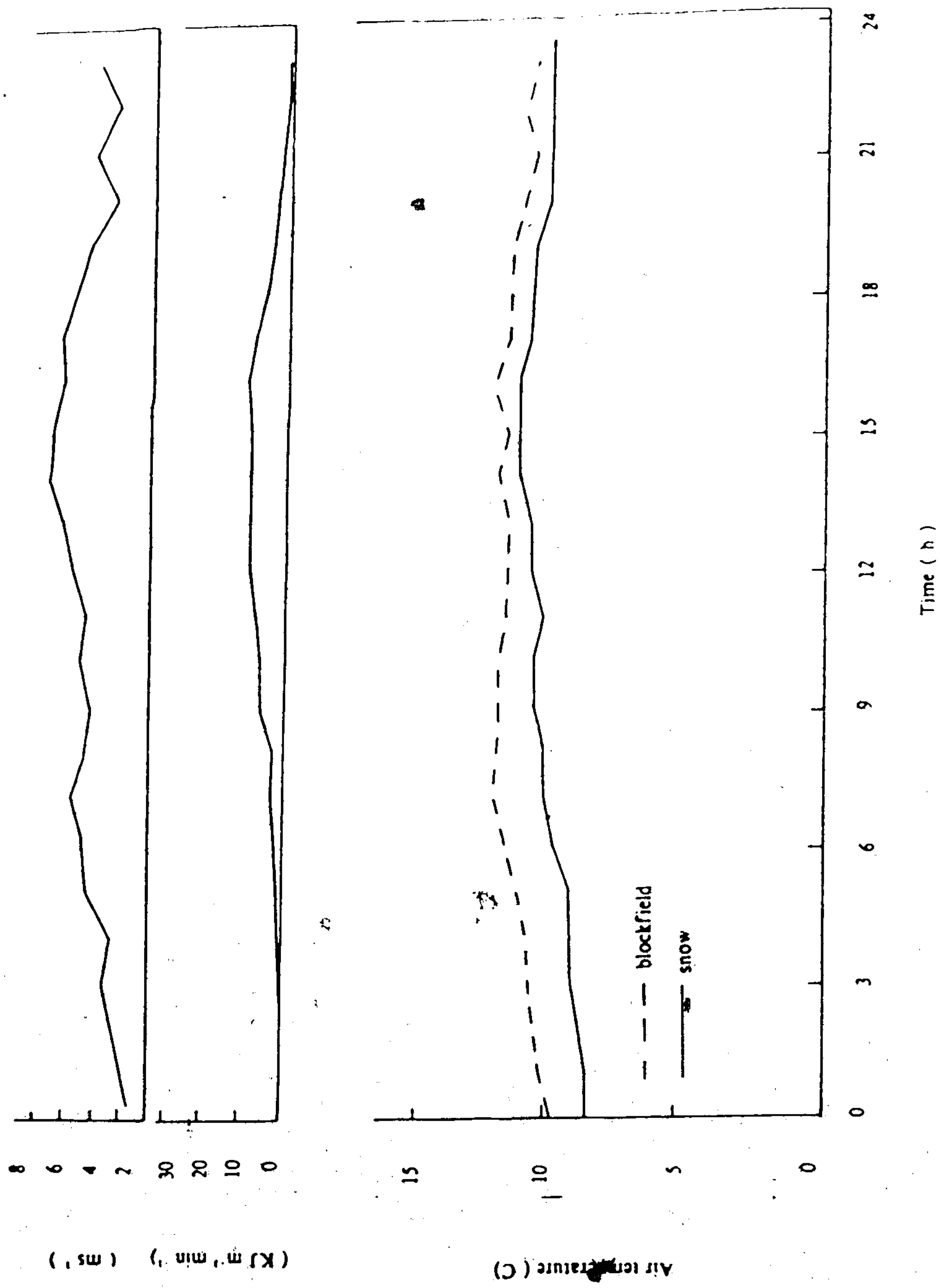


Figure 5.5 Diurnal fluctuation in the Snow/Blockfield air temperature difference under cyclonic conditions. July 27.

generate winds across the margin. In view of the small surface area and volume of the largest snowpatch and the strong winds at high, exposed sites where snowpatches occur, it is highly unlikely that horizontal pressure difference forces across the snowpatch margin were sufficient to initiate any air motion. Under clear, calm conditions with horizontal temperature differences at their maximum of around 3°C no such winds were sensed by anemometers located either side of the snowpatch margin. (Anemometer threshold = $0.5\ m\ s^{-1}$). Pruitt's theory that snow may represent a favoured habitat because of this horizontal motion may be discounted for the snowpatches under study for this reason. His theory is further discredited by the fact that during the period of snowpatch use any horizontal air motion would be *away* from the snowpatch and not in the reverse direction as he postulates. Any benefits in terms of the advection of odour (as Pruitt hypothesized) would be to potential predators as opposed to the caribou.

In terms of the advective influences arising from spatial heterogeneity the snowpatch margin represents the "leading edge". Air passing across this boundary is modified by the new surface. This "internal boundary layer" extended above 1.5 m over the snowpatch as evidenced by the consistently cooler air temperatures at this height over snow compared to the corresponding height over the blockfield. According to Oke (1978) in the lowest 10% of this layer conditions are fully adjusted to the properties of the new surface. The significance of this will be discussed with reference to the behavioural analyses of caribou on snow.

Winds crossing the leading edge at the snowpatch margin experience a change in surface roughness. Theoretically, air moving from a rough to a relatively smooth surface will experience a decrease in surface shearing stress with the result that wind speed will be increased. However, anemometers positioned at 0.5 m either side of the snowpatch margin registered no significant variations in speed under weak and strong winds ($t = 1.14$, $n = 20$, $p = N.S.$). The transition in terms of surface roughness from the blockfield to the snowpatch was thus not very great.

As air moving onto and across the snowpatch is cooled from below, this influence may extend beyond the snowpatch margin downwind. The advection of moist "plumes" of cooled air downwind of the shores of water bodies is well documented in the microclimatic literature. Largely dependant upon the area of the snow surface, a similar effect would be expected downwind of the snowpatches. Although this was not quantitatively assessed, the extent and penetration of any "snowpatch effect" would probably be most strongly expressed under a high radiant flux density, strong wind speeds and a consistent wind direction. This was not thought to be a significant factor in animal distribution although caribou were frequently observed in close proximity to snowpatches if not directly upon them (Plate 9).

5.3 Microclimatic Variation with Elevation

The analysis of climatic parameters either side of the snowpatch margin provided an insight into its distinctive microclimate. Similarly, the comparison of data between the high station and low stations can be used to draw conclusions about climatic variation within the extensive study area. This is not intended to provide a "model" of climatic variability within the study area but to illustrate any changes in microclimate that accompany diurnal shifts in elevation undertaken by caribou in the study area (Section 6.4). In the analysis of snowpatch microclimate, temperature and wind speed were identified as key variables and these form the basis of comparison between the two stations at high and low elevations. The limitations of drawing conclusions based on data from just two stations should be understood. A much more extensive network of continuously operating stations would be necessary to fully appreciate the intricacies of mountain climates (Olsen 1983). As with the snowpatch analyses, emphasis was placed upon the general pattern summarized from the period when the stations were simultaneously collecting data. This was supported by specific 24 h examples.

The comparison of temperature and wind speed data at the high and low stations reinforce the view of mountain climates as largely unpredictable (Barry and Chorley 1978). Averaged hourly values of climatic differences between the sites exhibited considerable variation

(Figures 5.6 and 5.7). Contrary to the expected pattern of an adiabatic lapse in temperature with increasing elevation, air temperatures at 0.5 m over the blockfield were consistently warmer at the high station than the corresponding height at the low station. This apparent anomaly may be explained with reference to the respective surface albedos calculated at the stations. The albedo of the high blockfield site (0.11) was slightly lower than the low Lichen-Heath site (0.19) which, together with the higher thermal conductivity of rock surfaces ensured that the blockfield experienced a warmer diurnal regime. Taken as an average, the high blockfield site was only 1.1°C warmer than the low Lichen-Heath site although considerable variation was evident. Sudden changes in air temperature at the exposed high station were frequently responsible for fluctuations in the elevational temperature difference. Analysis of wind direction data supported the hypothesis that these fluctuations were often due to sudden changes in wind direction causing the advection of air cooled over the snowpatch onto the blockfield.

Analysis of wind speed data (Figure 5.7) leads one to the conclusion that, as is to be expected of such an exposed location, speeds were generally higher at the high station. The difference between the two sites averaged 0.8 m s^{-1} with maximum values of 4.1 m s^{-1} recorded. However, the reversed difference of strong winds at the relatively sheltered low station was also frequently recorded. Analysis of specific occurrences showed this to be the result of sudden gusts rather than extended periods of increased advection. The wind speed difference between the two stations exhibited a steady increase in the afternoon which corresponded with the general increase in wind speeds (Figure 5.8). This was possibly due in part to the influence of daytime upslope (anabatic) winds which were frequently experienced along the ridge on which the high station was located. The predominance of daytime winds from the south and southeast supported this view (Figure 5.16) although it should be noted that anabatic and katabatic winds could not be accurately assessed due to equipment limitations.

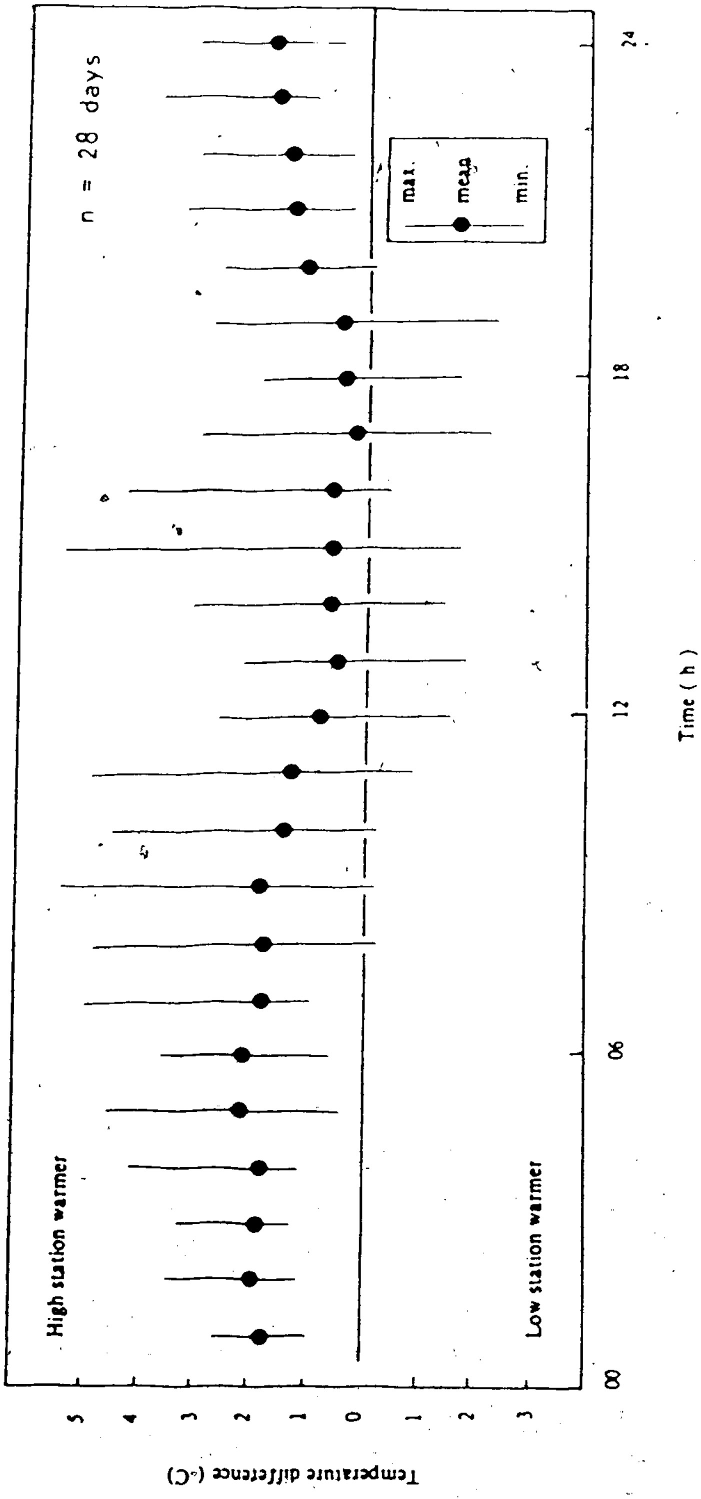


Figure 5.6 Summarized air temperature differences between the Blockfield and Lichen-Heath stations. July 10 to August 6.

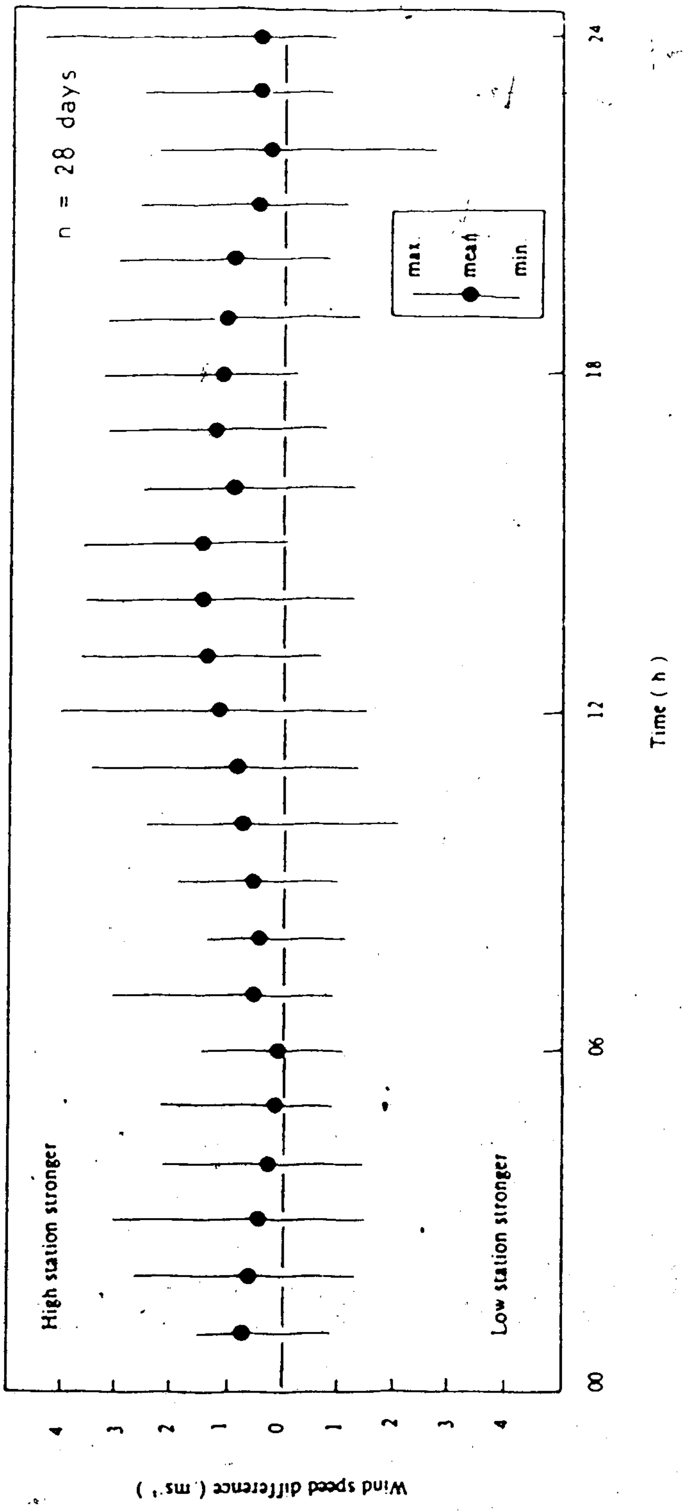


Figure 5.7 Summarized wind speed differences between the Blockfield and Lichen-Heath stations. July 10 to August 6.

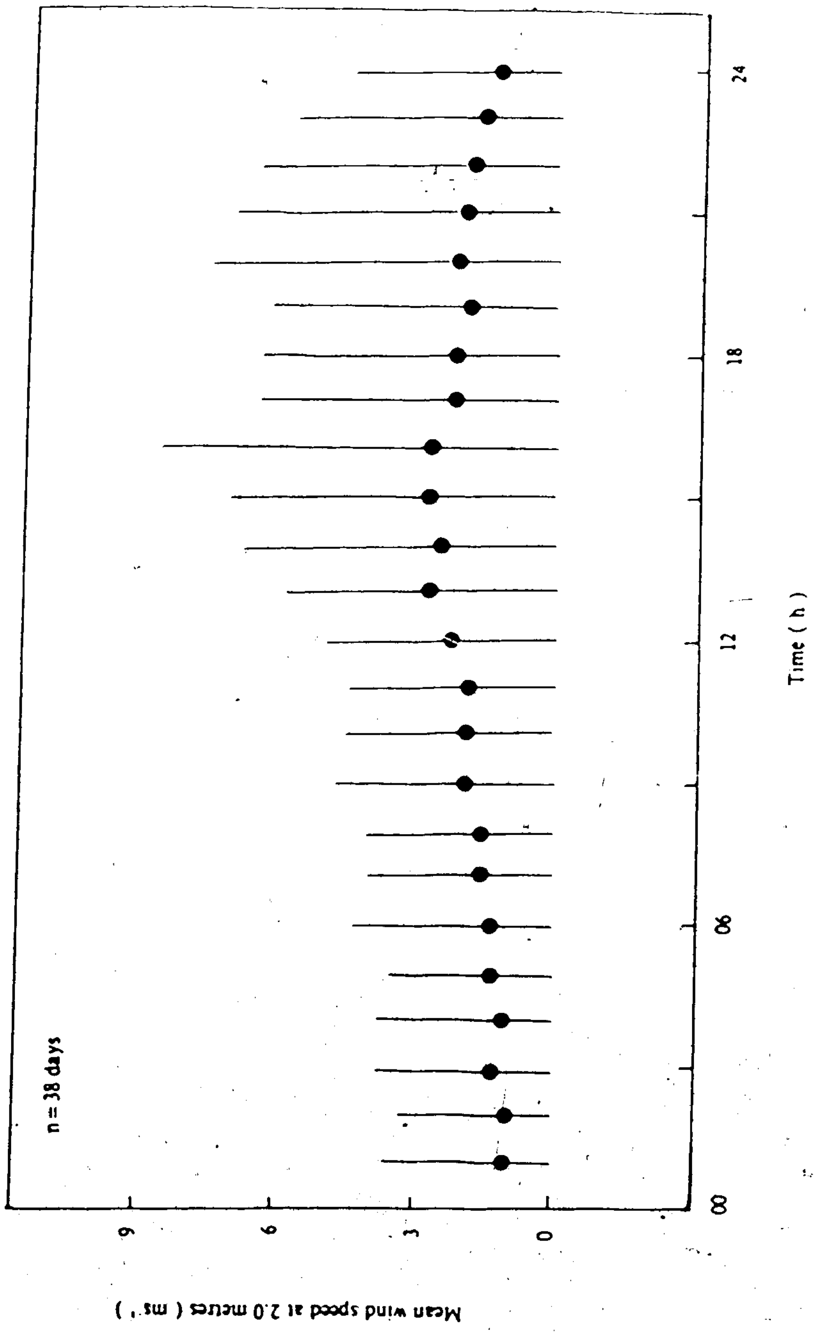


Figure 5.8 Summarized wind speed data at the Blockfield station. July 10 to August 16.

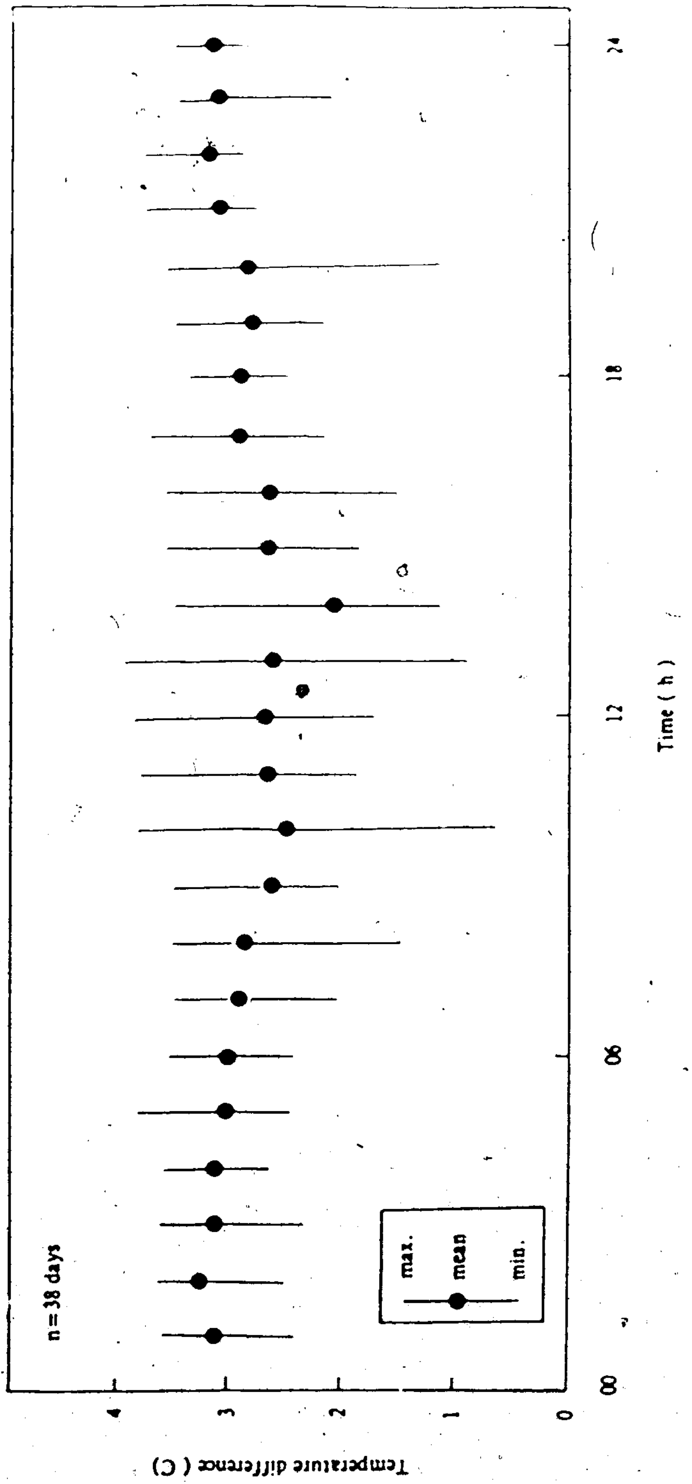


Figure 5.9 Summarized Snow/Blockfield air temperature differences at the High station. July 10 to August 16.

Topography may contribute to the modification or generation of surface winds within the study area. The random sampling of wind speeds at various locations within the study area consistently indicated higher velocities on exposed ridges. Along the ridge bordering the eastern wall of the Main Valley wind speeds averaged 29% stronger than the valley floor. The relatively deep, straight nature of this valley with a north-south orientation (maximizing differential heating due to aspect) and the drainage of cold air from the glacierette at the valley head would all help generate local slope winds.

On August 6, the low station was relocated into a Willow-Forb community at 1601 m, 75 m lower than the Lichen/Heath site. This was to more accurately assess microclimatic regimes between night-time and daytime habitat selection (See Section 6.4). Comparison of data between this and the Blockfield site (Figures 5.10 and 5.11) indicated that temperature differences between these two sites had a similar diurnal trend to that of the Lichen-Heath site but with a greater fluctuation around the 'equilibrium' level. Analysing the mean hourly data for the two sites, air temperatures over the blockfield remained warmer during the morning with a reversal of this difference in the afternoon. This pattern may be explained through the "drainage" of cold air downslope at night onto valley floors and depressions creating inversion profiles. Daytime warming and the generation of winds break down this pattern and the temperature difference showed greater variation.

Wind speeds were consistently lower at the sheltered Willow-Forb site. Between 12:00 h and 21:00 h during the 10 days of data collection only one hourly value had a stronger wind at the low station (Figure 5.11). The pattern of diurnal fluctuation in wind speed and air temperature between the exposed high station and the sheltered low station is exemplified in Figure 5.12. Reduced night-time winds allow the drainage of cold air to lower elevations. The influence of sudden changes in wind speed and its importance in conducting heat away from the surface is illustrated in the period between 17:00 h and 19:00 h in Figure 5.12. This reinforces the highly changeable nature of microclimate in mountainous environments further complicated by varying surface and site characteristics.

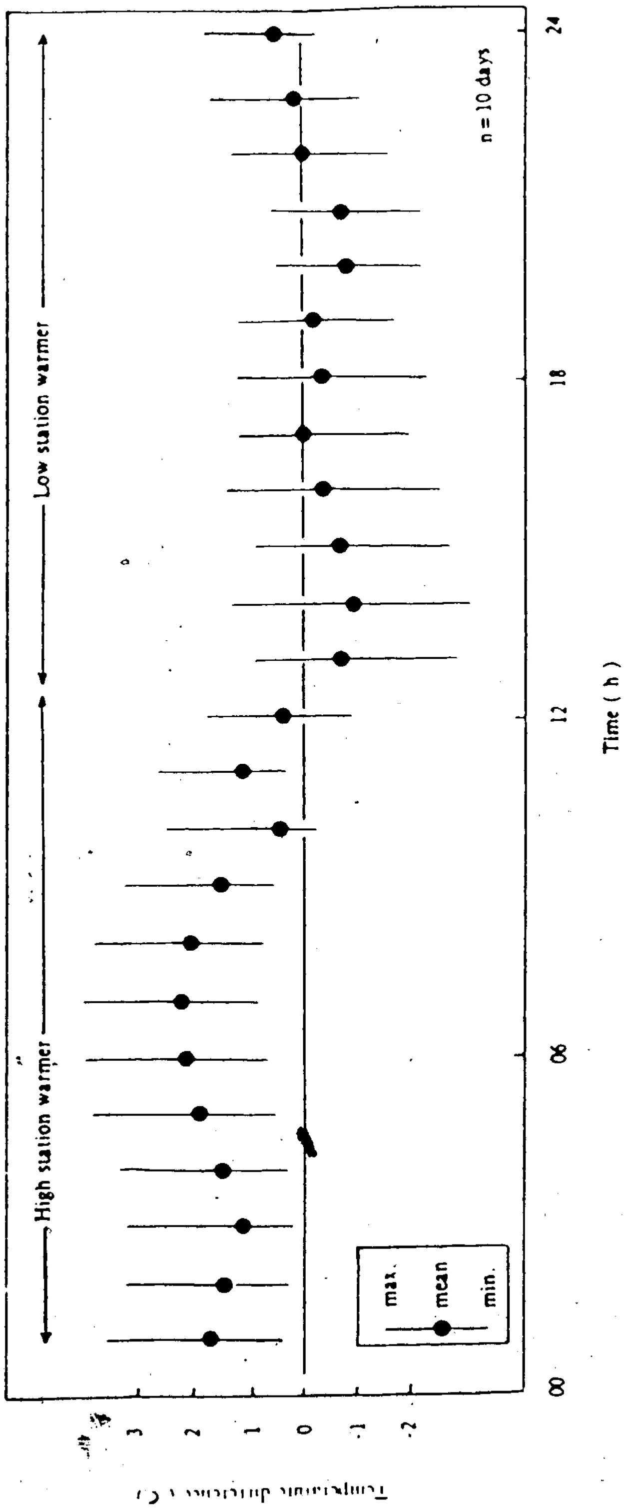


Figure 5.10 Summarized air temperature differences between the High Blockfield and Low Willow-Forb sites at 0.5 m. August 6 to 16.

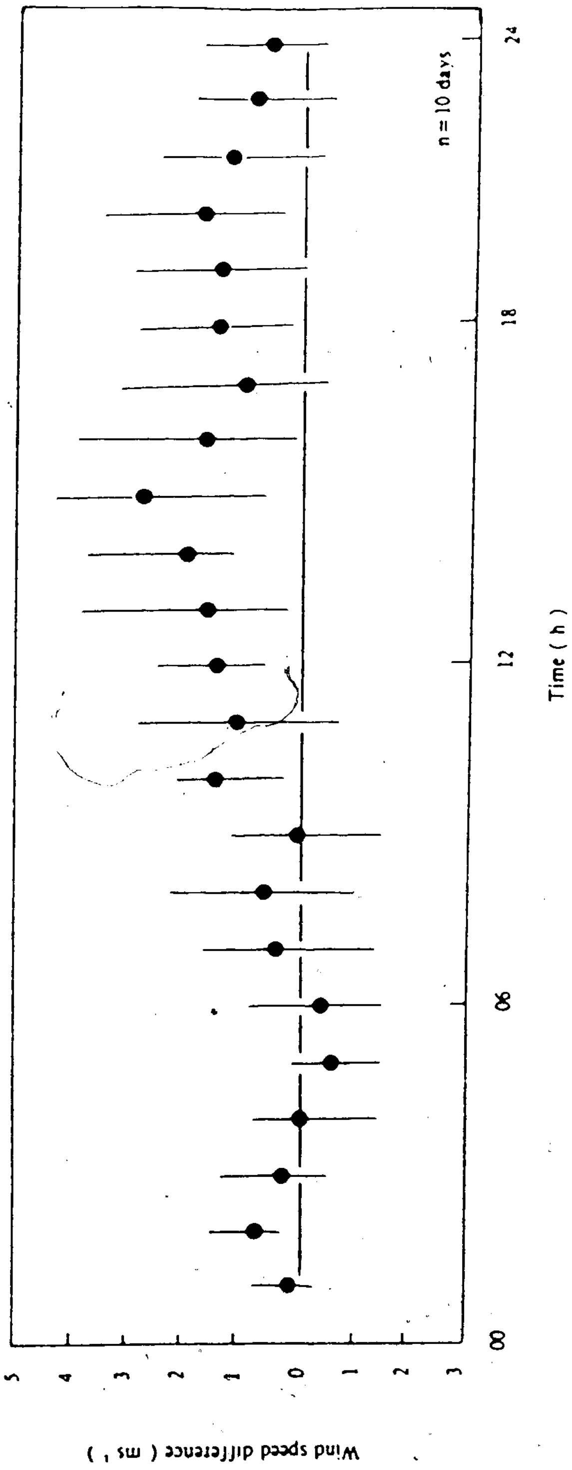


Figure 5.11 Summarized wind speed differences between the High Blockfield and Low Willow-Forb sites at 0.5 m. August 6 to 16.

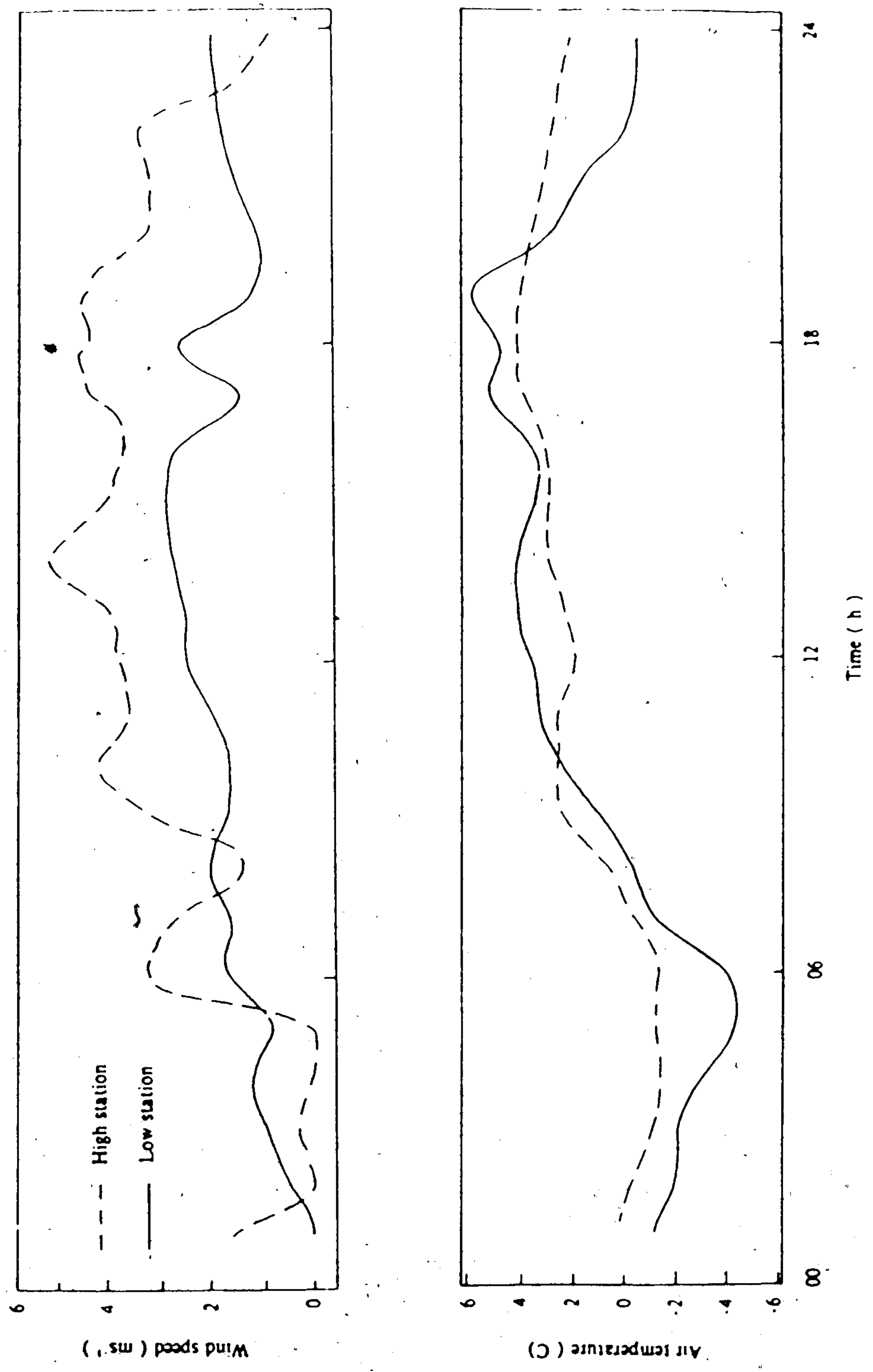


Figure 5.12 Diurnal fluctuation in air temperature at 0.5 m. and wind speed at the High Blockfield and Low Willow-Forb sites — August 8.

5.4 Climatic Conditions — Summer 1984

5.4.1 Introduction

Climatic conditions throughout most of Northern British Columbia and the Yukon during the summer of 1984 were influenced by the inland penetration of cool, moist air masses from the Pacific Ocean. The general circulation produced a westerly flow over the Mackenzie Mountains. A series of low pressure cells originating over the Gulf of Alaska moved inland, periodically replaced by anticyclonic high pressure systems. In this respect, synoptic scale conditions did not vary considerably from previous years (Bryson 1966). The Mackenzie and Selwyn Mountains present a topographic barrier to the prevailing west and south westerly winds. The modifying influence of orography was evidenced in the diversity and variability of specific climatic parameters. The significance of each is discussed separately.

5.4.2 Global (short-wave) Radiation

Radiation flux is the major mode of energy exchange within the biosphere. As such, its importance in explaining the relationship between ecosystem components cannot be underestimated. Within the study area predictable variations in daily radiation receipt such as the season, aspect and slope angle are substantially modified by meteorological variables (e.g. cloud cover) and site-specific variables (e.g. snow cover). Changes accompanying snowmelt at the tundra surface are considerable in terms of radiation exchange and energy budget. Net radiation was not quantified during this study, but would be expected to show a sudden increase with the decreased albedo of the tundra surface associated with snowmelt. Studies attempting to quantify the energy budget of Low Arctic tundra describe rapid increases in latent heat flux (QE) as the partitioning of energy is channelled towards snowmelt and the evaporation of surface water (Weller et al. 1972, Rouse 1982).

Figure 5.13 illustrates the pattern of radiation receipt at the low station during the study period. A maximum value of 53.2 KJm^{-2} min^{-1} was recorded on June 22. These high

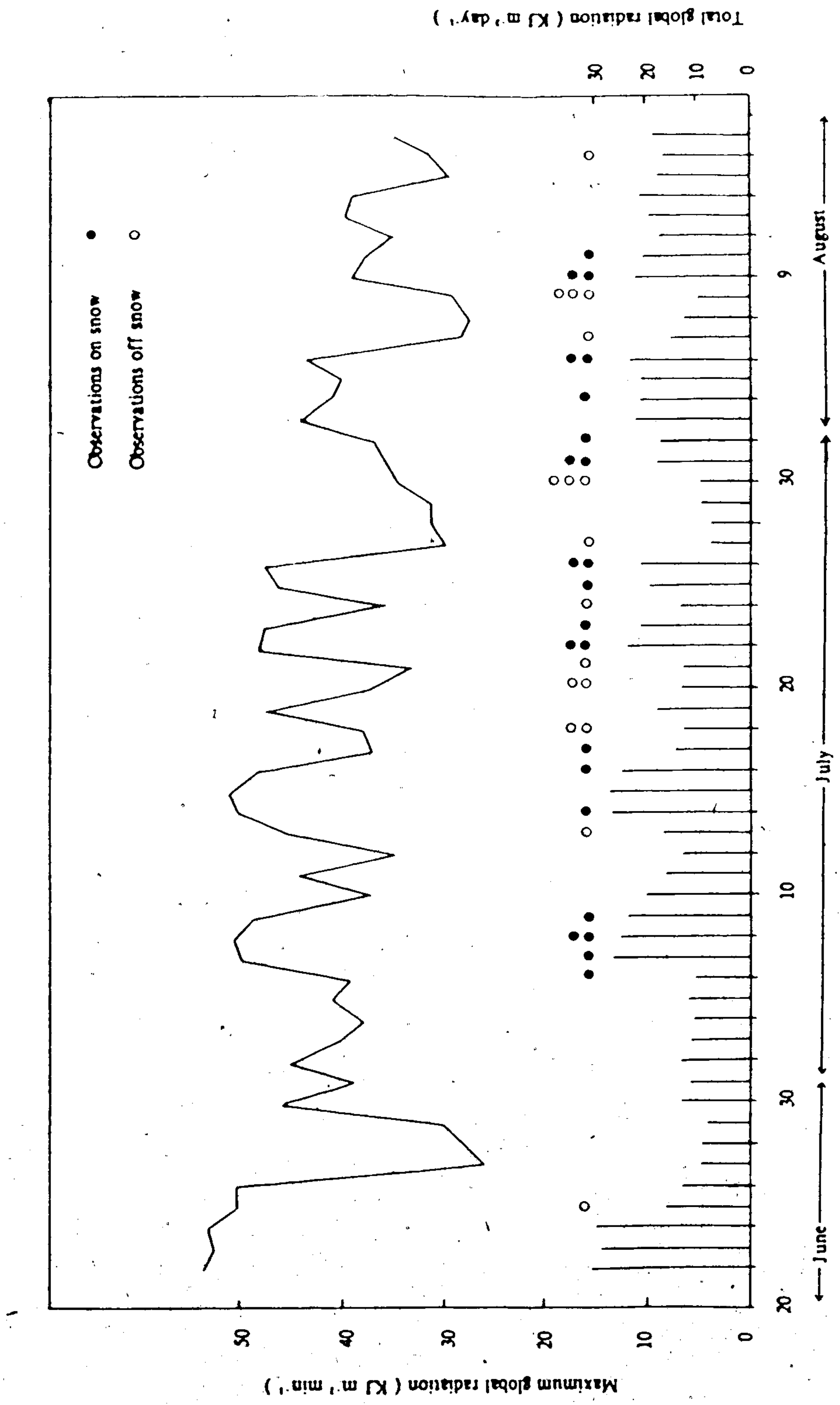


Figure 5.13 Maximum and total daily global radiation for the study period at the Lichen-Heath and Willow-Forb stations.

values on and around the summer solstice are due to a combination of a high solar zenith and high altitude (reducing the attenuation of solar radiation within the atmosphere). Daily maxima declined thereafter with maximum values of around 35 KJm^{-2} min^{-1} recorded at the end of the study period in mid-August. Maximum values of incoming short-wave radiation provide an insight into potential levels of heat loading, but total or "accumulated" levels are a superior measure of that amount of energy available for surface heating on a daily basis. (Furthermore, daily maxima may occur during periodic breaks in cloud cover and provide values which are not representative of conditions throughout the day).

The highest daily totals of incoming radiation were recorded between June 22 and June 24. A combination of uninterrupted, clear skies, high solar angle and long daylength produce totals of around 30 000 KJm^{-2} day^{-1}. Under contrasting cyclonic conditions typified by continuous, dense cloud cover daily totals averaged approximately 10 000 KJm^{-2} day^{-1}. The accumulated daily totals are of value in demarcating the study period in 'sectors' dominated by contrasting general weather conditions. Although small scale diurnal variations in climate will be shown to be an influential factor on animal behaviour, the study period may be sub-divided into twelve 'sectors' (Figure 5.14). With the exception of a nine day period between the end of June and the first week of July in which a succession of low pressure cells passed over the study area, these sectors were usually of three to five days duration.

5.4.3 Air Temperature

On a diurnal basis, temperature maxima generally occurred between three and five hours after maximum solar input. This lag was most pronounced under anticyclonic conditions and less so under cyclonic conditions. The mean air temperature at 0.5 metres at the Lichen-Heath site for the study period was 9.1°C. An absolute maximum of 24.0°C and a minimum of -5.2°C were recorded at the same site on 4 and 13 August respectively. Both values occurred under anticyclonic conditions associated with clear skies and low wind speeds. Diurnal temperature fluctuations were generally reduced under cyclonic conditions due to reduced levels

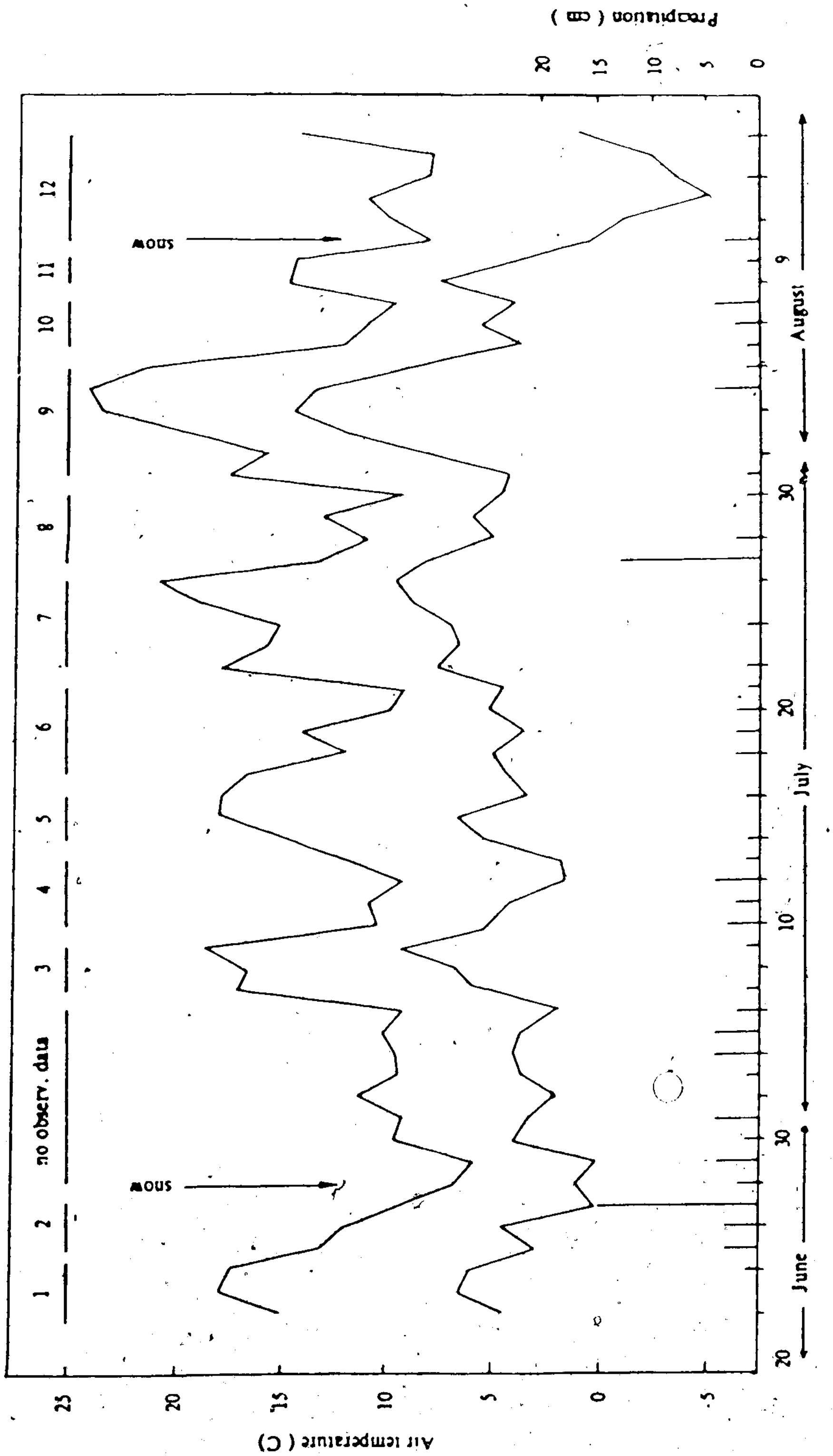


Figure 5.14 Air temperature extremes and total daily precipitation for the study period at the Lichen-Heath and Willow-Forb stations.

of incoming short-wave radiation during the day and retarded outgoing long-wave radiation at night. These variations in radiative flux produced a mean maximum temperature of 13.3°C and a mean minimum of 4.2°C (Figure 5.15).

The highest levels of incident radiation occurred in the last week of June with temperature maxima in the first week of August. This is a typical situation for most continental mid- and high-latitude stations (Hage pers. comm. 1985). The first is that the extensive snowcover around the low station in June with its high surface albedo greatly reduced net radiation and the amount of energy available for conversion to sensible heat. Secondly, meltwater from snowpatch ablation around the low station ponded at the surface due to the persistence of seasonally frozen soil at this time. Consequently, a high proportion of available energy would be converted to latent heat and be unavailable for surface heating. A combination of these two factors was thought to be responsible for the relatively low maximum temperatures in June and the gradual increase into August when the disappearance of snow below 1700 metres and the 'drying out' of the tundra surface combined to enhance local heating.

Such changes in energy partitioning in the summer from relatively low to high Bowen ratios (the ratio of sensible to latent heat flux) have been quantified during snowmelt at other Low Arctic sites at Barrow, Alaska (Weller et al. 1972) and Churchill, Manitoba (Rouse 1982). Seasonal variation in energy balance components may also explain why maximum annual temperatures occur in June on the Tsichu River Valley floor (Kershaw and Kershaw 1983b) and in August in the surrounding mountains (bearing in mind the limitations of comparing an eight year data base with that of one summer). There is no obvious explanation for this anomaly without an analysis of local site characteristics where the climatic data were obtained. Although no data are available for the periods immediately before and after the June to August study period this was thought to represent the warmest time of year within the study area and thus the most critical in terms of relief habitat to Woodland caribou.

5.4.4 Relative Humidity

The inland penetration of cool, maritime air masses from the Pacific Ocean producing a cool, moist regime is reflected in a high mean relative humidity of 72.8% for the study period (Figure 5.15). Daily maxima of 100% were frequently recorded under conditions of intense rainfall with a minimum of 29.6% recorded during the afternoon of June 23 at the daytime temperature maximum. In addition to the moisture advected from the Ocean in air masses, the water content of the lower atmosphere within the study area would be increased by the evaporation and transpiration of standing water from the tundra surface during snowpatch ablation. Under high levels of solar input, sublimation from the snow surface further adds to the water content of the lower atmosphere. Relative humidity as an independant climatic variable was not thought to be an important factor in explaining animal behaviour although no tests of signficant correlations were attempted.

5.4.5 Wind Speed and Direction

Together with air temperature, wind speed was one of the more important climatic variables within the study area. Analysis of the wind speed differences between the exposed, high station and the relatively sheltered low station showed speeds to fluctuate widely in space and time. As is typical of mountainous terrain, topographic asymmetry and subsequent unequal local heat loading combine to produce highly variable wind regimes. This variation was found to be highly significant in explaining animal behaviour.

The mean wind speed at the Lichen-Heath station was 2.33 m s^{-1}. That for the Blockfield station was 3.41 m s^{-1}. Mean daily wind speeds varied from 0.8 m s^{-1} to 4.3 m s^{-1} at the Lichen-Heath station (Figure 5.16). The importance of exposure in an alpine environment is reinforced by the percentage of calms recorded at each station - 1.6% for the high station and 5.9% for the low station. A maximum wind speed of 9.6 m s^{-1} was recorded at the high station under cyclonic conditions on July 27. A maximum value of 8.3 m s^{-1} was recorded under similar conditions at the low station on June 27. Wind speeds were generally stronger under cyclonic

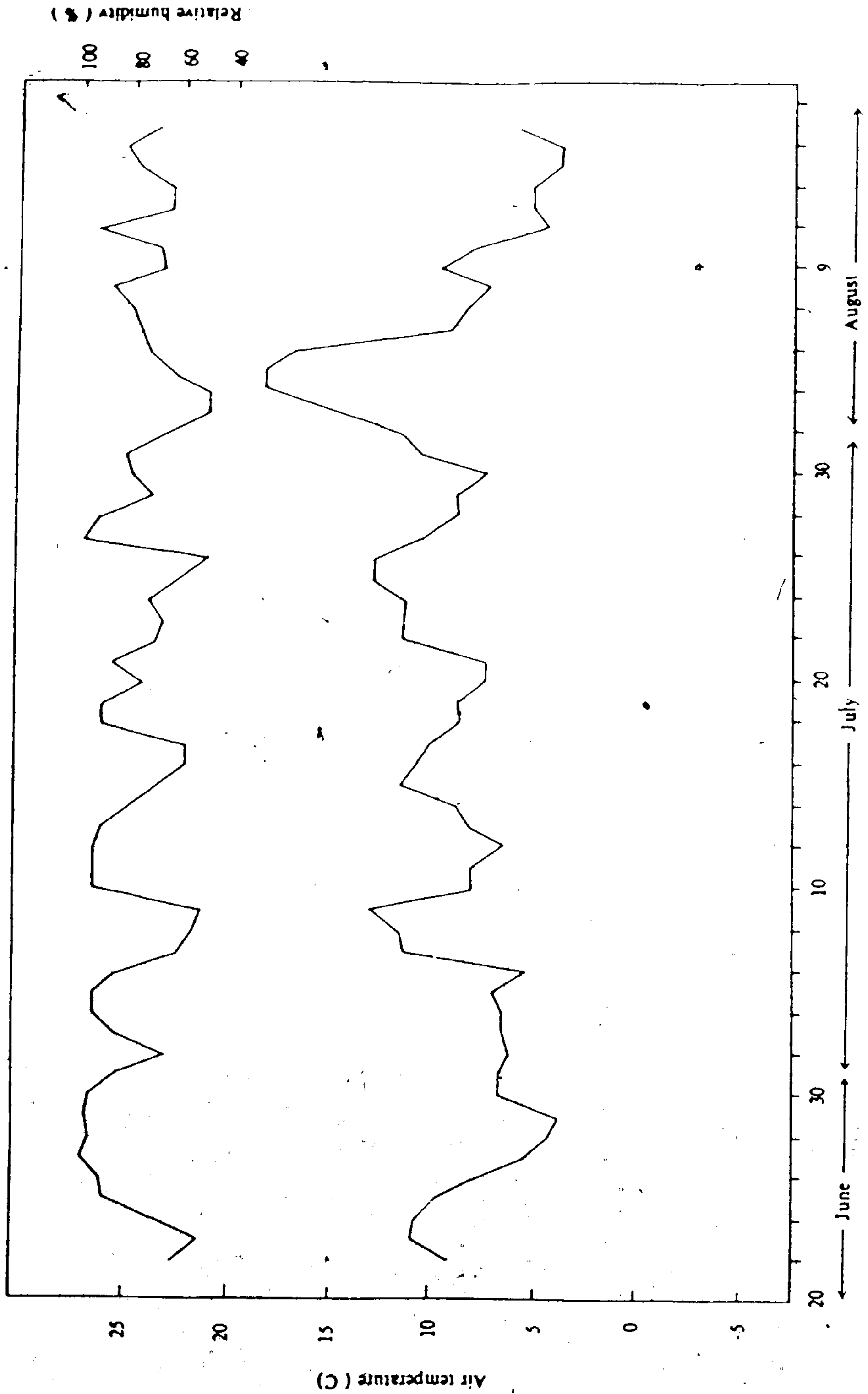


Figure 5.15 Mean air temperature and relative humidity data for the study period at the Lichen-Heath and Willow-Forb stations.

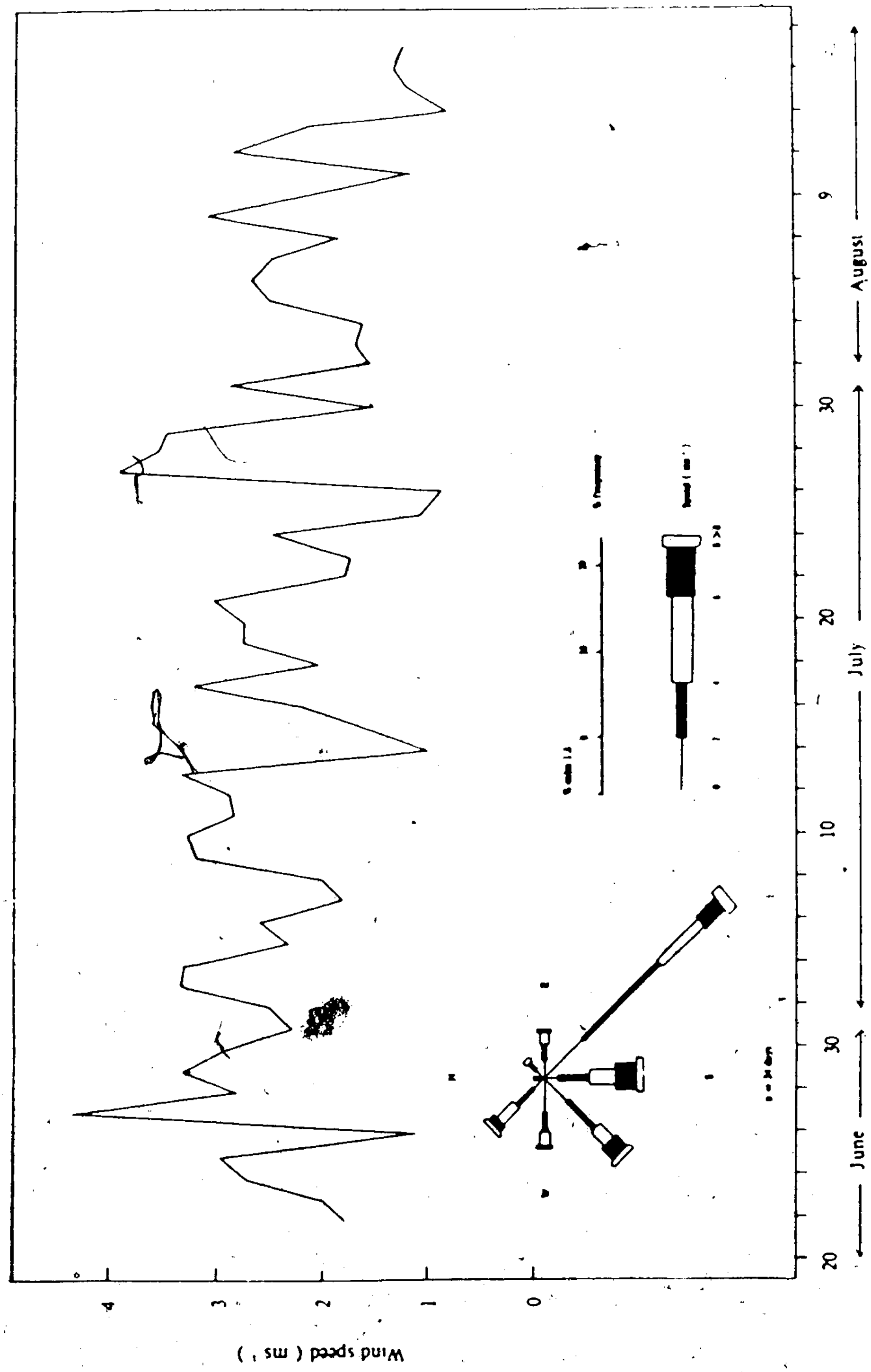


Figure 5.16 Mean wind speed at the Lichen-Heath and Willow-Forb stations (line graph) and wind rose for the Blockfield station.

conditions with the approach and passage of frontal systems. Lower values were recorded under anticyclonic conditions although numerous variations from this pattern were observed. Intense daytime heating generated strong afternoon winds within the study area.

As only one wind direction sensor was employed in the study, conclusions drawn about this variable are essentially limited to one exposed location. In view of the highly variable nature of mountain wind systems the limitations of extrapolating data from one location to another should be recognized. Figure 5.16 illustrates how wind varied considerably in both speed and direction. Speeds in excess of $8\ m\ s^{-1}$ were recorded from the north-west but more frequently from the south, south-east and south-west. The predominance of winds from the south-east (31.1% of total) is difficult to explain but may be due to strong upslope and upvalley winds from the valley south of the high station. This view is reinforced by the higher percentage of winds from the south-east (41.0%) during the afternoon between 12:00 h and 18:00 h when anabatic winds occurred. Night-time winds were generally lower and more variable in direction.

5.4.6 Precipitation

Orographic influences on precipitation are complex. A mountain barrier may trigger convective instability by giving an initial upward motion or by differential heating of the mountain slopes. The funnelling effect of valleys on airflow may also cause convergence and uplift. Cyclonic precipitation may be further increased at any one location by the retarding effect of the mountain barrier on the rate of movement of a depression system. During the summer in continental locations the main effect of relief is the occasional triggering of brief but intense periods of precipitation.

The summer precipitation regime at Macmillan Pass is essentially one of extended periods of cyclonic activity interspersed with frequent squalls. Total precipitation for the study period recorded at the low Lichen-Heath site was 102 mm. At least 1 mm. of rain was recorded on 39 of the 56 days. A maximum daily total of 15 mm was recorded under continuous and intense rainfall associated with cyclonic activity on 27 June. Under similar conditions 13 mm fell on 27 July. With these two exceptions, daily totals never exceeded 4 mm (Figure 5.14). The intense squalls of short duration generally showed up as 1 mm totals or were insufficient to register on the tipping bucket gauge. These sudden showers were found to be important in determining habitat selection for caribou (see Section 7.4). Daily totals give no insight into the form of precipitation. For example, six hours of light and periodic drizzle registered as 4 mm on 12 July whilst an intense 45 minute shower in the late evening of 4 August produced the same amount. Short duration, intense hailstorms were also quite common and were registered

It is difficult to assess whether the summer precipitation regime of 1984 represented an above- or below-average year. The seven year data base at the Tsichu River station reported 53 mm. as an average for July. During July of 1984, 54 mm fell at the low station. This suggests that the summer precipitation of 1984 was average. Data collected at the Tsichu River station describe trace levels of snowfall in the three months of June, July and August. Snow fell on two occasions during the study period. Continuous rain and sub-zero temperatures during the morning of 28 June left 1.5 cm of snow at the low station. Snow fell throughout Macmillan Pass at this time with little remaining below 1600 m after 15:00 h. Within 24 h no fresh snow remained in the high ground around Macmillan Pass (C. Beuhler, Northern Mountain Helicopters, pers. comm.). A lighter snowfall during the morning of August 12 (1 cm) left a snow cover above approximately 1500 m which gradually retreated to 1800 metres by 16:00 h (Plate 8). Strong radiational heating ensured that this snow had completely melted within 36 h. The role of this second snowfall in reducing insect activity is discussed in Section 7.2.

5.4.7 Summary

In view of the general paucity of observational data, knowledge of the physical climatology of alpine tundra areas is scant (Barry et al. 1981). Analysis of data collected during the summer of 1984 at Macmillan Pass generally supports the conclusions drawn from data collected from other tundra zones during snowmelt. High altitude and long day length combine to produce high maximum and total daily levels of incoming radiation. The high frequency of cyclonic activity and local orographic effects produce highly variable radiation regimes. The partitioning of available energy will show considerable seasonal variation essentially related to a diminishing snow cover. Air temperatures closely correspond to the radiation regime with local cold air drainage and other advective effects explaining small scale variations. Wind speeds are strongly influenced by storm frequency and degree of exposure. Precipitation of varying duration and intensity as rain, hail or snow either as part of a low pressure system or a brief squall under clear skies perhaps exemplifies best the highly variable nature of alpine tundra climate such as that at Macmillan Pass. The study area comprised numerous microhabitats, a result of changes in altitude, aspect, exposure, slope and other surface variables (e.g. albedo). An analysis of all these factors is essential to gain a full appreciation of the variety of topoclimates and microclimates within the study area.

6. BIOTIC COMPONENTS : POPULATION CHARACTERISTICS AND LOCAL MOVEMENTS

6.1 Observation Data — Summer 1984

Between 17 June and 17 August, 94 separate observations of individuals or groups were made within the Extensive Study Area for 168.05 h in total (1509 individual animal observations). With the exception of one set of tracks in snow close to the basecamp (Plate 7) there was no evidence that caribou moved into the study area in any significant numbers prior to 17 June.

The first observation within the study area was made on June 22 (an unclassified individual). On June 24 the first post-calving aggregation was observed in the eastern sector of the extensive study area, one mile west of No Fail Lake (Plate 6). This supports the view of a westward migration from winter range to the east of Macmillan Pass. Thereafter, sightings were made on most days within the extensive study area (Figure 6.1). No observation data were collected between June 29 and July 4 as technical problems necessitated movement out of the study area. Reconnaissance with other researchers in the Tsichu River valley around Camp 222 between August 2 and 4 precluded collection of observation data within the extensive study area (E.S.A.) although one observation north of the E.S.A. boundary on 3 August was included in later analysis.

The snowfall of 12 August was thought to be of some importance in triggering a movement of caribou out of the E.S.A. and from the Macmillan Pass area in general. (Several authors claim that permanent snow is necessary to trigger migration to winter range). Between August 12 and 17 only two observations totaling 5 caribou were made within the E.S.A. Both of these were of animals moving eastward. Between August 18 and 20, observations were conducted from Camp 222. No sightings were made in the three day period. One bull was observed on the southern face of Mount Allen on August 19. The lack of observation data in the week following the August 12 snowfall led to the termination of the study.

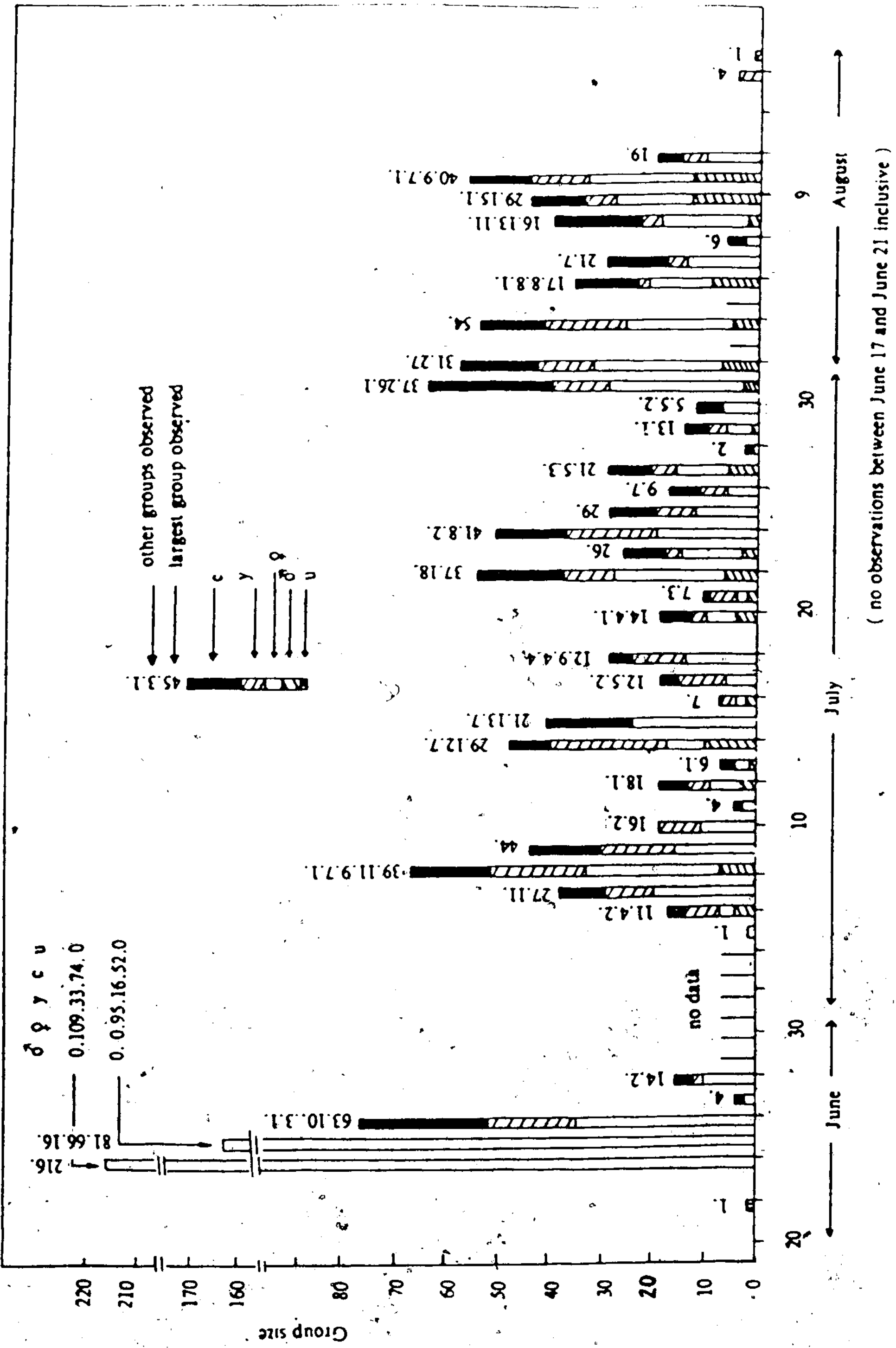


Figure 6.1 Summary of Woodland caribou observed in the E.S.A.

6.2 Population Characteristics

Population composition data collected during the study period cannot be used to describe the status of the Redstone Herd. Repeated aerial surveys would have been necessary to accurately assess the size of the herd. Ground surveys may yield accurate population structure data but are inferior to aerial work which provides more complete information on total population size, composition, distribution and movement. The aerial and ground survey information collected by Archibald (1973) were kept separate. Her ground survey results consistently underestimated total population size. Data from this study are similarly biased.

Estimates of total population size from previous surveys are further complicated by the presentation of data as combined totals from surveys of varying duration and location. Archibald's (1973) totals from a larger study area within the Mackenzie Mountains were sub-divided into periods varying from ten days to three months. No data describing maximum numbers from one aerial survey were given. Records from the aerial surveys flown over a 500 km² area by Kershaw and Kershaw (1983b) had a maximum daily sighting of 407 caribou during the spring (June).

Within the E.S.A. in 1984 the post-calving aggregation of 216 caribou observed on June 24 (Plate 10) was the largest single observation during the study period. This occurred approximately three weeks after the peak of calving. Archibald (1973) also observed large numbers remaining on a proposed calving ground at "Tsichu Mountain" for three weeks. This supports the view of Gill (1978) that the eastern sector of the E.S.A. may overlap with a calving ground and is confirmed by the spring 1982 and 1983 surveys of Kershaw and Kershaw (1983b). Kershaw and Kershaw (1983) calculated a tertiary sex ratio of 20:100 for Mackenzie Mountain caribou in their 500 km² area. In view of this and the proportion of adult females in the largest post-calving aggregations a total population of 500 to 600 head would appear a conservative estimate for animals utilising the Macmillan Pass - Tsichu River area.

6.3 Group Size and Composition in 1984

Within the annual cycle, mean group size in Woodland caribou is usually lowest during late June, July and August (Bergerud 1971). Post-calving aggregations fragment into smaller groups as intense foraging activity favours dispersal. Larger groups are observed during the rut when bull groups rejoin cow/juvenile groups. Although no data were collected to verify the latter, the breakdown of post-calving groups was evident in the last week of June. Groups of 216, 81, 66 and 63 animals were observed between June 24 and June 26. Thereafter, groups of over 45 animals were rarely observed. (It should be noted that no observations were made from June 29 to July 4.) Kershaw and Kershaw (1983b) noted aggregations of up to 68 as late as August 7.

Larger groups generally comprised cows and calves with yearlings. Most of the early observations were of such groups. Cow/calf pairs were frequently observed (Plate 11). Bulls tend to lag behind the adult female cohort of the population in their movements (Kelsall 1968). The arrival of bulls and bull-groups (e.g. adult and sub-adult bulls and yearlings) onto the summer range is thus delayed. The first adult bull was observed within the E.S.A. on July 6. (Kershaw and Kershaw (1983b) noted bulls at lower elevations on the Tsichu River valley floor during early June surveys). Bulls were generally observed alone or in single sex groups of up to eight or in larger groups with yearlings (Plate 12). Groups of mixed age and sex were occasionally observed together. This, and the variation in group size were thought to be largely a function of environmental conditions and is discussed in more detail in Section 7.3.

The under-representation of bulls and bull-dominated groups from surveys in and around Macmillan Pass has been noted by both Archibald (1973) and Kershaw and Kershaw (1983b). Unbalanced tertiary sex ratios were evident in both of these surveys and also from the data collected in 1984. Kershaw and Kershaw's total observation data provides a ratio of 20:100 ; that for the 1984 data is only 15.6:100. In contrast, Gill's (1978) random observations around the Continental Divide above Macmillan Pass were mostly of bull and yearling groups. There is no obvious explanation for these contrasting data. Sexual segregation by elevation was observed by Archibald (1973) with bulls consistently observed at lower elevations during the fly season. Kershaw and Kershaw (1983b) also describe a higher frequency of bulls observed at lower elevations. As the vast majority of observation data were collected above 1600 m in this study, this under-representation of bulls tends to comply with previous surveys.

Bull groups may simply not have been observed as often since they are more solitary at this time of year and thus more difficult to spot. Overselection by non-resident hunters may also be a factor. The higher frequency of bulls observed towards the end of the study period (49% of all bulls observed in observation numbers 72 to 94) tends to support a pattern whereby bulls arrive at Macmillan Pass later than cow groups, move to higher elevations later in the fly season to form pre-rut aggregations and begin the return journey towards winter range some time later than the rest of the herd.

6.4 Diurnal Distribution

Regular patterns of seasonal distribution in Woodland caribou have been described (Chapter 4). Movements within summer range are often described as more transient and nomadic (Cringan 1957). Analysis of data documenting daily movements shows that, contrary to this opinion, movements on a daily basis are often directed and purposeful. Figure 6.2 illustrates the elevational distribution of caribou within the 24 h cycle in the E.S.A. Each line on the graph represents one observation of a group or individual. Sub-dividing the data by month illustrates how observations in time were more variable in that no recurring pattern of movement is evident. Data for July and August however describe a trend of repeated observation at elevations of around 2000 m during the late morning and afternoon with a movement down to below 1700 m in the evening (Plate 13). Mossing (1980) studying Norwegian reindeer made similar observations:

> "H[illegible] summer temperatures, leading to severe mosquito plagues ... force the reindeer to seek refuge on higher ground during daylight". (p. 6)

The majority of caribou observed on snow in July and August were at a height of 2010 m on

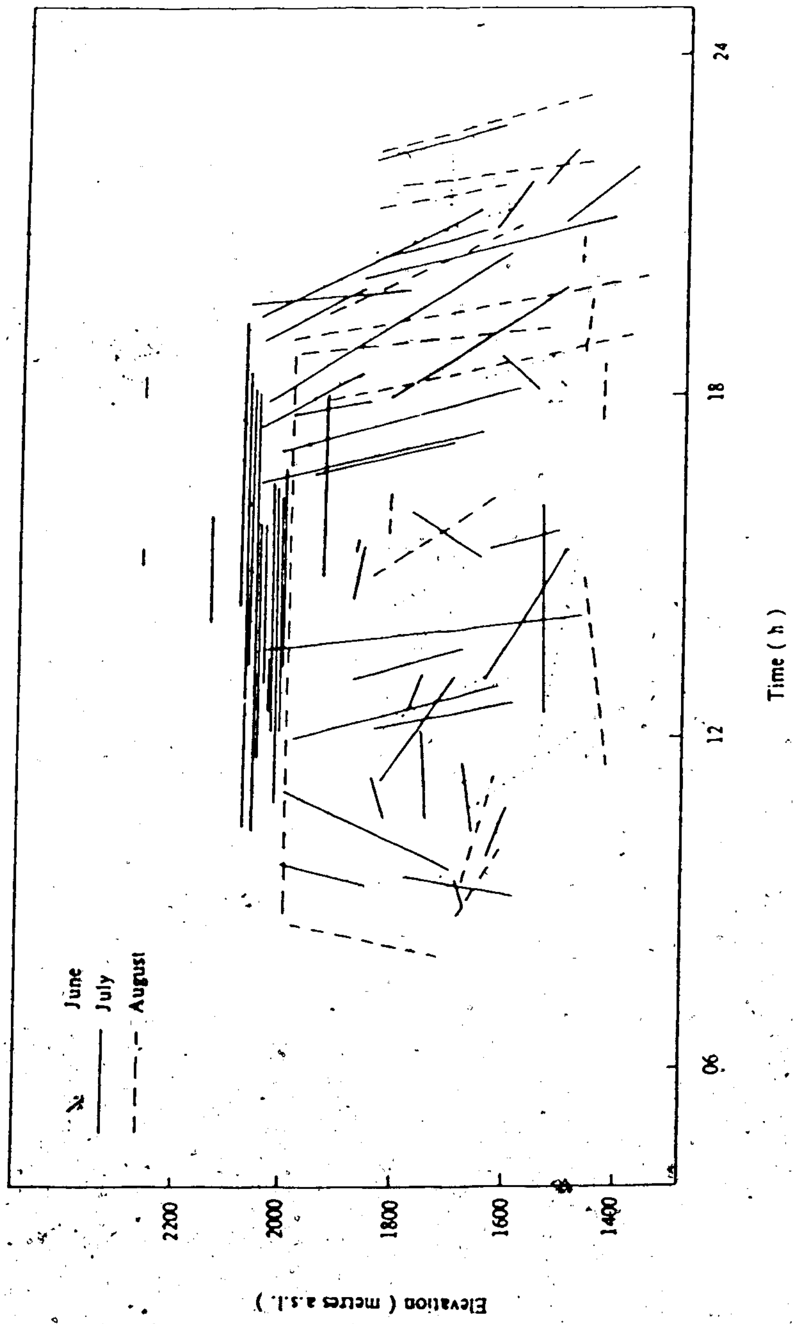


Figure 6.2 Diurnal distribution of Woodland caribou in the Extensive Study Area with respect to elevation.

snowpatch number 13 - the "main aggregation site". As the most effective means of data collection was to concentrate on the first sighting of the day and in view of the increased visibility of caribou on snow, data are possibly biased towards animals on this snowpatch. This also explains why fewer observations of morning ascents were made.

Although nocturnal data were not collected, the daytime data supports a pattern of an ascent from valley floors and land below 1700 m to ridges and snowpatches at and above 2000 m in the late morning, extended periods spent on snow in the afternoon and a descent to land below 1700 m in the evening. As subsequent analysis will show, this highly generalized pattern varies considerably with ambient temperature and other climatic conditions. This does illustrate however, that activity rhythms are influenced by external time cues — zeitgebers — such as the photoperiod. The onset and termination of diurnal and nocturnal activity have been found to be largely in synchrony with sunrise and sunset in many Arctic and Subarctic species (Remmert 1980) and has been documented for caribou in Alaska (Curatolo 1975, Roby 1978). Although this could not be accurately assessed from data collected in this study, the general pattern of ascent and descent as a response to heat and/or insect activity does represent a marked and recurrent cycle of activity.

This pattern is exemplified with reference to specific examples. Of the 94 observations during the study period, 23 were of individuals or groups that undertook some form of vertical migration involving snowpatch selection. Fourteen of these were of caribou aggregating on snowpatch 13. Movement off snow to lower elevation was documented for all but one of these fourteen observations. Four of the longest and most complete observations describing this pattern of aggregation on snow and subsequent descent to lower ground are illustrated in Figure 6.3. The following descriptions illustrate the importance of weather conditions in influencing patterns of movement.

On July 14, a group of 29 caribou moved onto snowpatch 13 at 12:19 h. The entire group remained on the snowpatch at 2010 m until 19:20 h for a total duration of 7:01 h. Movement off snow preceded a slow descent along the ridge above the Main Valley before the

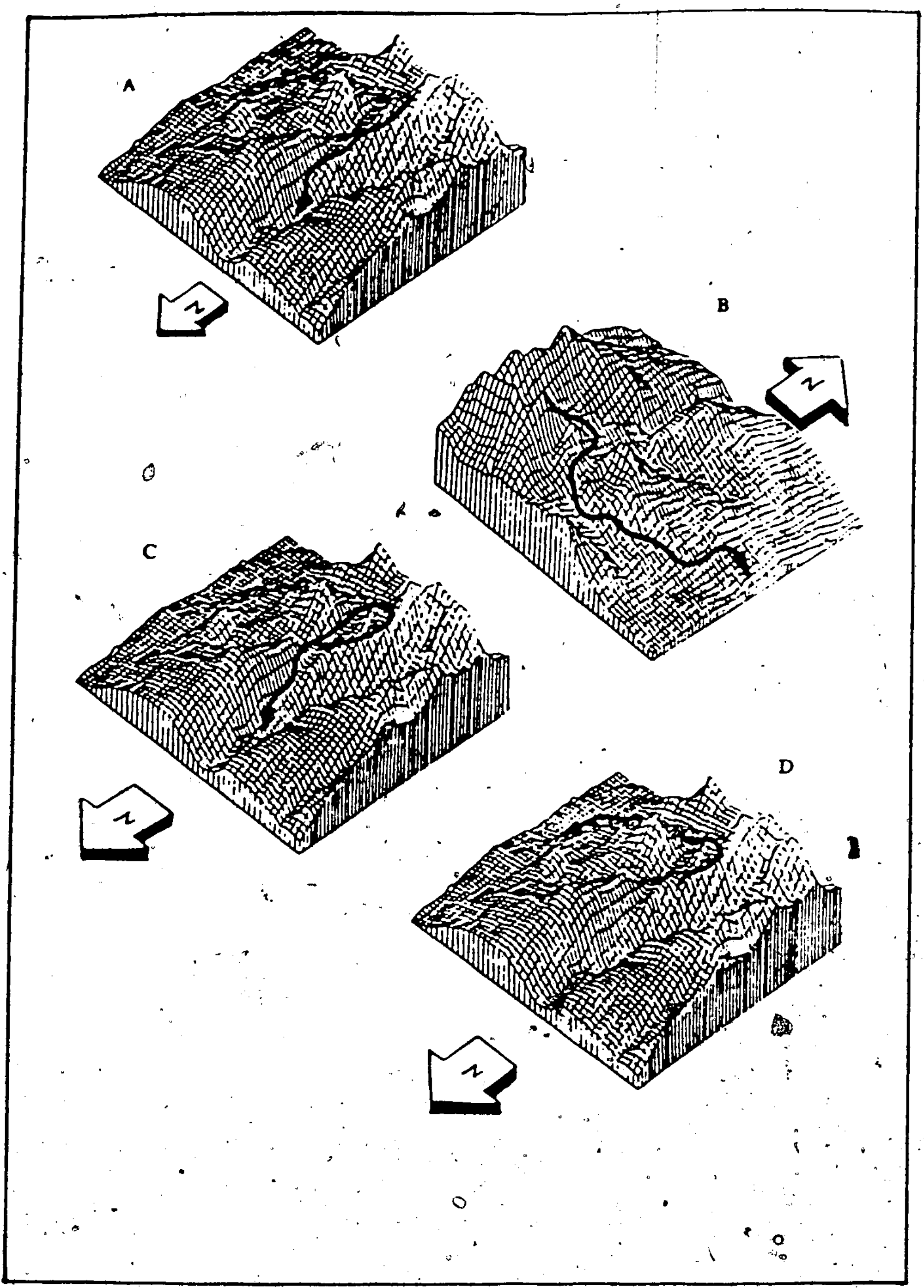


Figure 6.3 Woodland caribou movements within the E.S.A. under anticyclonic conditions. A-July 14, 29 caribou. B-July 23, 26 caribou. C-August 1, 27 caribou. D-August 10, 40 caribou.

group dropped down to the valley floor below 1500 m (Figure 6.3a). During the observation, under anticyclonic conditions, an air temperature maximum of 14.8°C and a mean wind speed of 1.0 m s⁻¹ were recorded at the high station.

On July 23, a group of 26 were observed at the main aggregation site at 10:39 h. Movement off snow occurred at 18:07 h, 7:28 h later. This group approached the centre of the E.S.A. before dropping down into the low-land below 1400 m around No Fail Lake when viewing distance terminated the observation at 19:31 h (Figure 6.3b). Mean and maximum air temperatures during the observation were 11.2°C and 15.8°C respectively with a mean wind speed of 1.7 m s⁻¹.

The longest single observation occurred on August 1 when a group of 27 animals were tracked for 12:04 h. This group was first observed on the ridge to the west of the basecamp at 8:08 h. There followed a slow ascent to snowpatch 13 with movement onto snow at 11:17 h. Anticyclonic conditions prevailed with mean and maximum temperatures of 11.7°C and 15.5°C and a mean wind speed of 1.6 m s⁻¹ recorded during the observation. The group collectively moved off the snowpatch at 19:19 h (8:02 h later) and began a northward descent through the E.S.A. into the Main Valley. The group was last observed at 1490 m at 20:12 h (Figure 6.3c).

On August 10, a group of 40 were observed on the ridge to the west of basecamp at 8:41 h. The last animal in this group had moved onto snowpatch 13 by 10:59 h. All animals had moved off snow by 17:48 h and began a descent towards No Fail Lake. During this observation, the animals remained on snow for 6:49 h. A maximum air temperature of 14.4°C, mean of 8.3°C and mean wind speed of 1.1 m s⁻¹ were recorded for the duration of this observation (Figure 6.3d).

These four case studies illustrate consistent patterns of movement under anticyclonic conditions with relatively high air temperatures and low mean wind speeds. Similar directed movements towards and away from snowpatches were observed on several other occasions under similar macroclimatic conditions. Movements under cyclonic conditions typified by lower air temperatures and stronger wind speeds were generally more random. Figure 6.4 illustrates movements during four of the longer observations where snowpatches were not selected.

On July 20, a group of 14 caribou were observed moving west within the valley in the southern sector of the E.S.A. (Figure 6.4a). During the observation between 11:18 h and 13:51 h, air temperature at the high station averaged 7.7°C with a mean wind speed of 3.6 ms $^{-1}$. A light drizzle fell intermittently. On July 21, between 10:50 h and 15:58 h, a group of seven caribou were observed to traverse almost the entire length of the E.S.A. (Figure 6.4b). No significant changes in elevation were undertaken with a general drift towards No Fail Lake. Conditions throughout were dry with a mean air temperature of 7.9° C and a mean wind speed of 3.0 m s $^{-1}$ recorded at the high station.

Figure 6.4c illustrates the movement of a group of 21 caribou between 15:21 h and 19:07 h on July 27. A north to south movement through the centre of the E.S.A. occurred under intense and continuous precipitation (4 mm fell during the observation) with a mean air temperature of 10.7°C and a mean wind speed of 4.8 m s $^{-1}$. Five animals were observed to descend from the top of a gently sloping hill in the north of the E.S.A. between 15:41 h and 17:28 h on July 30 (Figure 6.4d). During this period dry, overcast conditions prevailed with air temperatures averaged at 7.5°C with a mean wind speed of 2.2 m s $^{-1}$ recorded. Comparison of movement under contrasting general weather conditions illustrates the importance of macroclimate in snowpatch selection. Several other observations were made supporting the contrast illustrated in Figures 6.3 and 6.4.

To facilitate later analyses, observational data were sub-divided into those occurrences in which snowpatches were and were not selected. "Long" observations were differentiated from "short" observations on the basis of the inclusion of focal animal samples. Of the 74 observations, 23 were classed as "long observations on snow" (e.g. those included in Figure 6.3), 17 were of "long observations off snow" (e.g. those in Figure 6.4). The remaining 64 "short" observations were usually of less than one hour duration and comprised scan sample data. These data and the relationship with abiotic variables are discussed in Chapter 7.

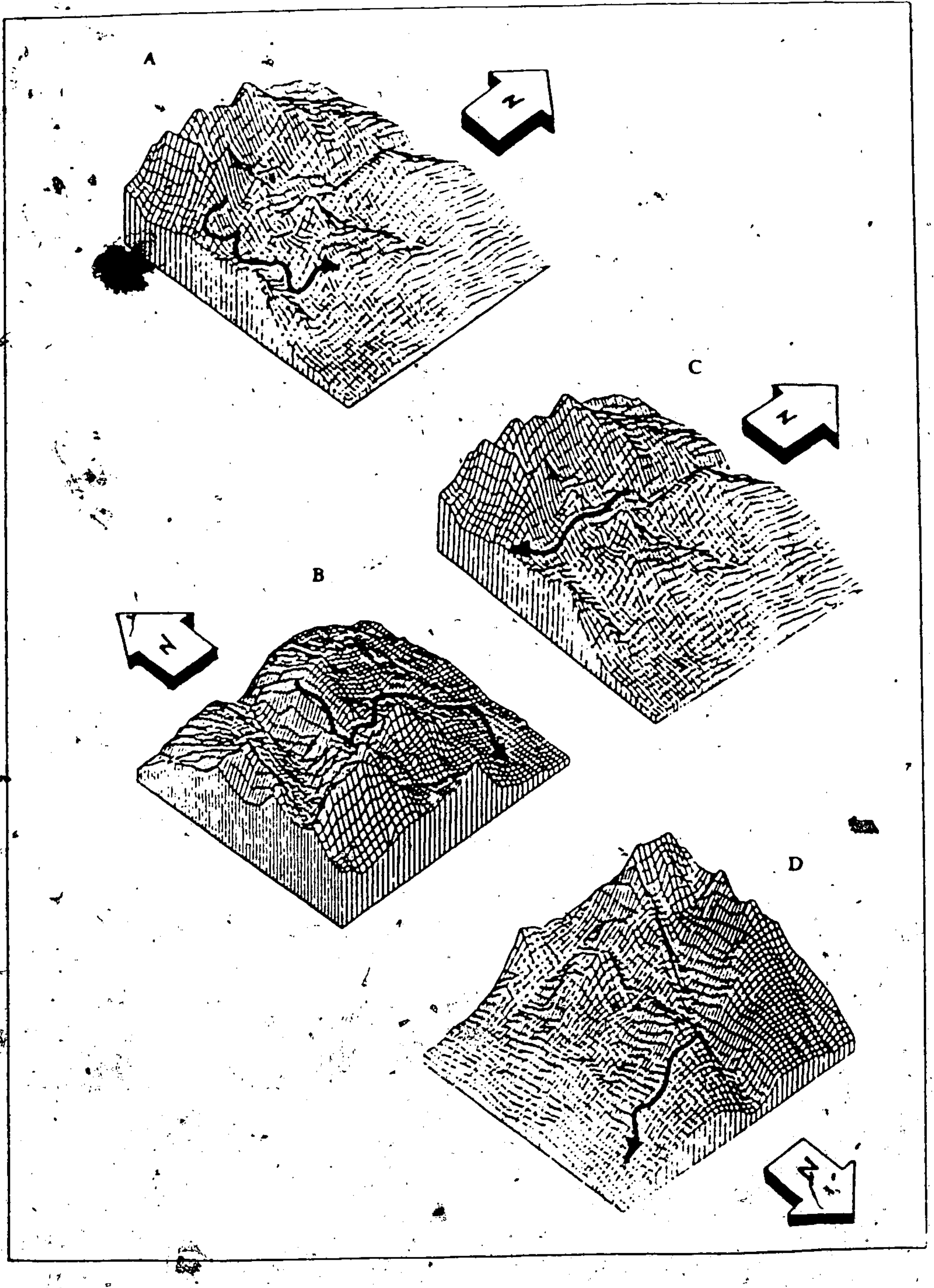


Figure 6.4 Woodland caribou group movements within the E.S.A. under cyclonic conditions. A-July 20, 14 caribou. B-July 21, 7 caribou. C-July 27, 21 caribou. D-July 30, 5 caribou.

6.5 Summary

Data collected during 1984 support the results of previous surveys in that Macmillan Pass is used as traditional summer range for Woodland caribou. The first post-calving aggregations consisting of cows, calves and yearlings were observed south of the Tsichu River on June 24. Group fragmentation ocurred during July and August. Adult bulls were not observed in the study area until early July. The under-representation of bulls was consistent with the results of previous surveys and may be attributed to sexual segregation with respect to elevation.

Analysis of distribution on a daily basis suggests a pattern of ascent to elevations above 2000 m during the morning followed by extended periods spent resting or standing on snow. Descent to lower elevations occurred generally between 18:00 h and 2000 h. This pattern of movement was common under anticyclonic conditions typified by clear skies, high mean air temperatures and low mean wind speeds. Group movements under cyclonic conditions with overcast skies, low mean air temperatures and high mean wind speeds were less pronounced and snowpatch selection was not observed.

7. ABIOTIC : BIOTIC RELATIONSHIPS

7.1 Introduction

In the preceding chapters the abiotic and biotic components of the study were summarized. This goes some way towards providing a solution to the problem of "when" and "where" Woodland caribou selected permanent snowpatches within the F.S.A. Any attempt at answering the question "why" snowpatches are selected at this time of year must involve the combined analysis of both abiotic and biotic variables. Three variables are identified for this analysis : "climatic variables" (wind speed and air temperature for the most part), "insect variables" (numbers) and "caribou variables" (various individual and group-averaged parameters).

Figure 1.1 illustrates the relationship between the three variables as they relate to the hypotheses outlined in Chapter 1. Quantified climate/insect and insect/caribou relationships are used to assess the reduced insect harassment hypothesis, whereas direct climate/caribou relationships are used to elaborate upon the various forms of thermoregulation that are hypothesized to explain snowpatch selection. Throughout the analysis, emphasis is placed upon the comparison and contrast between observed behaviour on and off-snowpatches. As a source of reference for subsequent analyses, basic data for the "long" observations on and off snow are presented in Tables 7.1 and 7.2. As before, analysis will concentrate upon the general pattern with reference to specific examples.

7.2 Climate-Insect Relationships

7.2.1 Trapping Success

The total number of all 'non-biting' insects trapped at the Lichen Heath site on a daily basis together with the number of mosquitoes trapped at the same site is illustrated in Figure 7.1. This site was visited every day for a total of 45 days. No totals are available for the June

Table 7.1 Summary of "Long Observations" of Woodland caribou on snow within the E.S.A.

Date	Group Size	Group Composition (Sample Composition) (♂	♀	y	c)	F.A. Samples	Start of Observation	Start of Observation on snow	End of Observation on snow	End of Observation	Total Observation time on snow	Total observation time	Snowpatch number
06.7	11	4(3)		7(3)		6	1304	1304	1525	1541	2.21	2.37	22
07.7	27		13(4)	5(4)	9(4)	12	1249	1249	1631	1717	3.42	4.28	13
08.7	11	2(1)	6(2)		3(1)	4	943	943	1100	1107	1.17	1.24	23
08.7	39		16(5)	14(4)	9(4)	13	1201	1201	1616	1719	4.15	5.13	13
09.7	44		16(8)	14(8)	14(7)	23	1051	1051	1712	1809	6.21	7.18	13
14.7	29	7(4)	5(4)	12(4)	3(3)	15	1201	1219	1920	1944	7.01	7.43	13
16.7	7	2(3)	2(3)	3(3)		9	1414	1453	1831	1906	3.38	4.52	NP
17.7	12		5(6)	4(5)	3(5)	16	1111	1111	1647	1746	5.36	6.35	13
22.7	37	6(4)	12(4)	10(4)	9(3)	15	1044	1049	1741	1817	6.52	7.33	13
22.7	18		10(4)		8(1)	3	2020	2020	2131	2153	0.51	1.33	19
23.7	26	3(5)	12(6)	3(5)	8(4)	20	1039	1039	1807	1931	7.28	8.52	13
25.7	29		12(3)	8(3)	9(3)	9	1303	1303	1744	1848	4.41	5.45	13
26.7	9		4(1)	1(1)	4(1)	3	1210	1219	1322	1429	1.03	2.19	1
26.7	7		2(1)	4(1)	1(0)	2	1802	1802	1842	1928	0.40	1.26	NP
31.7	26		11(2)	5(1)	10(0)	3	910	1041	1200	1202	1.19	2.52	1
31.7	37	3(2)	13(3)	6(3)	13(4)	12	1419	1434	1807	1931	3.33	5.12	13
1.8	27	7(6)	8(6)	4(5)	8(5)	22	808	1117	1919	2012	8.02	12.04	13
3.8	54	5(1)	21(1)	13(1)	15(1)	4	1729	1729	1831	1831	1.02	1.02	1
5.8	8		4(2)	1(1)	3(2)	5	1401	1401	1549	1619	1.48	2.18	19
5.8	8	8(10)				10	1412	1412	1730	1802	3.18	3.50	14
9.8	29	12(1)	6(0)	6(1)	5(0)	2	917	917	947	1111	0.30	1.54	20
9.8	15		9(6)		6(4)	10	1051	1051	1604	1718	5.13	6.27	13
10.8	40	8(3)	15(6)	9(6)	8(5)	20	1031	1059	1748	1910	6.49	8.39	13
Totals	549	67(43)	204(75)	130(63)	148(57)	238					87.18	111.24	

Table 7.2 Summary of "Long Observations" of Woodland caribou off snow within the E.S.A.

Date	Group Size	Group Composition (Sample Composition)				F A Samples	Start of observation	End of observation	Total observation time
		(♂	♀	y	c)				
24 6	216		109(0)	33(0)	74(0)	0	1112	1544	4.32
13.7	6		3(2)		3(2)	4	1237	1410	1.33
18 7	9		6(2)		3(2)	4	1102	1214	1.12
18 7	12		4(3)	6(3)	2(3)	9	1231	1612	3.41
20.7	14		6(2)	2(2)	6(2)	6	1118	1351	2.33
20.7	1		1(3)			3	1510	1701	1.51
21.7	7	2(3)		5(6)		9	1050	1558	5.08
24 7	41		17(2)	12(1)	12(1)	4	1928	2111	1.43
27.7	21	2(2)	9(3)	3(3)	7(3)	11	1521	1907	3.46
30.7	5		3(1)		2(2)	3	1207	1319	1.12
30 7	5		3(2)		2(2)	4	1541	1728	1.47
30.7	2		1(2)		1(3)	5	1910	2112	2.02
6.8	21		9(2)	3(1)	9(1)	4	1455	1625	1.30
8.8	11		5(1)	1(1)	5(1)	3	841	957	1.16
8.8	16	2(2)	6(2)	2(2)	6(3)	9	1129	1441	3.11
8.8	13		6(2)	1(1)	6(1)	4	1930	2100	1.30
15.8	4			4(3)		3	1651	1807	1.16
Tot	414	6(7)	188(29)	72(23)	138(26)	85			39.43

28 to July 5 period due to the destruction of the traps by marmots. A three day total is included for the period August 2 to 4 inclusive. It was unfortunate that observations within the E.S.A. could not be made between August 2 and 4 as the data suggests that this was the period of greatest insect activity. The vast majority of the 'non-biting' insects were small, midge-like insects (order *Diptera*) that were not thought to harass caribou. Specimen removal from the traps often rendered identification impossible. The inclusion of this data does provide some idea of the variation in insect activity during the study period and how climatic conditions (specifically wind speed) dictate insect members. The number of mosquitoes trapped (the number above the bar on Figure 7.1) is plotted separately to emphasize the difference in terms of actual numbers and temporal distribution.

The daily totals as illustrated in Figure 7.1 describe an "insect season" between June 28 and August 12. Relatively few insects and no mosquitoes were trapped either side of this time period. The sudden appearance of mosquitoes around the source of the South Macmillan River, 11 km west of the E.S.A. was noted on June 4 (L. Saindon, Northern Mountain Helicopters, pers. comm.). The sub-zero temperatures and snowfall of August 12 were thought to be largely responsible for the low insect counts thereafter. Furthermore, no mosquito activity was noted in the Tsichu River valley around Camp 222 between August 18 and 20. No blackfly activity was recorded either. Thus, the "mosquito season" within the E.S.A. was probably no longer than 40 days in 1984.

Within the mosquito season the total number of trapped 'non-biting' insects varied between 39 on July 27 and 488 on July 9. Mosquito numbers fluctuated from zero on several occasions to 8 on August 9. Daily totals exceeded this maximum value on at least one occasion between August 2 and 4 (3 day total of 33 trapped mosquitoes). Including the three day total for August 2 to 4, 7936 insects were trapped during the study period. 138 mosquitoes were trapped in total. Although the limitations of basing conclusions on the data from such a small sampling framework (i.e. one trap in one habitat) should be noted, it was evident that the total number of insects trapped and the number of trapped mosquitoes did not always closely

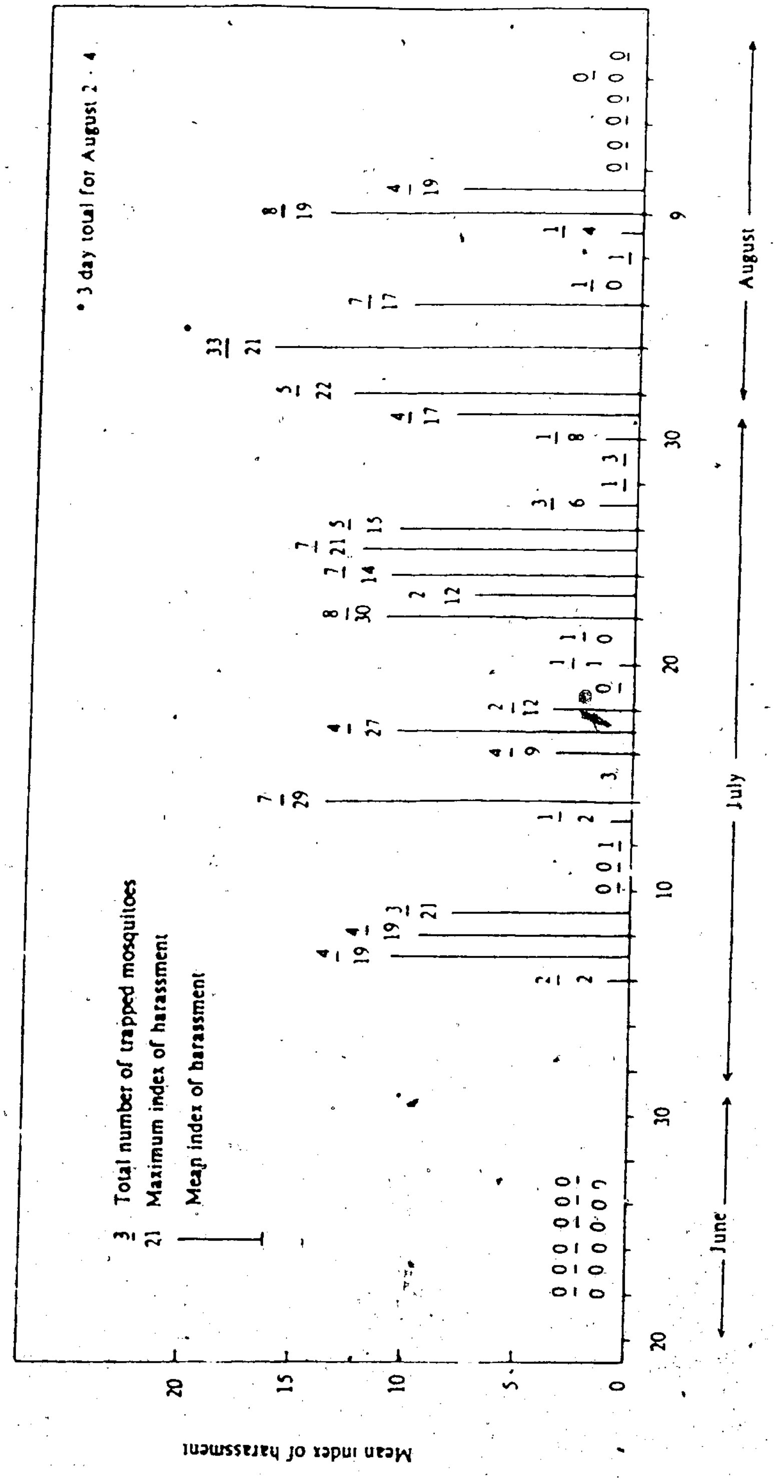


Figure 7.1 Summarized insect data for the study period.

correspond on a daily basis.

7.2.2 Insect Density and Climatic Variation

Air temperature and wind speed were considered to be the most important climatic variables influencing insect activity. Mean values for the period 08:00 h to 20:00 h were calculated for each day on which insect counts were made. This 12 hour interval was thought to be more representative of conditions during which insects were potentially most active and ensured that night-time extremes, especially wind speed variations, were not included (i.e. strong night-time winds blowing insects onto the trap may have produced anomalously high totals for a day with low daytime wind speeds). Use of such "biologically active period" (BAP) data has been made in other studies assessing insect activity (e.g. White et al., 1975).

The total number of non-biting insects trapped during the mosquito season were plotted against mean BAP air temperature (0.5 m at the Lichen-Heath station) and mean BAP wind speed (2.0 m at the same site). in Figure 7.2. Analysis of the distribution of the daily totals about the mean air temperature and wind speed data describes a clustering into the upper left and lower right sectors (24 out of 33, or 72.7% of the daily totals). This illustrates the distinction between cyclonic and anticyclonic conditions with reference to these two climatic variables. A high proportion of days with above-average mean air temperatures also possessed below-average mean wind speeds and *vice versa*.

Theoretically, total insect activity would be greatest under high air temperatures and low wind speeds associated with anticyclonic conditions. The high totals trapped under these conditions (lower right sector of Figure 7.2) supports this theory. However, large total insect counts were also made on days with above-average mean wind speeds (upper left sector of Figure 7.2). There are two possible explanations for this. The first is that high wind speeds inhibit flight and force insects to remain on or within 0.5 m of the tundra surface where they would be entrained on the trap. The second is that stronger winds simply force more insects onto the trap. The high proportion of insects entrained on one side of the trap (see Plate 5.1)

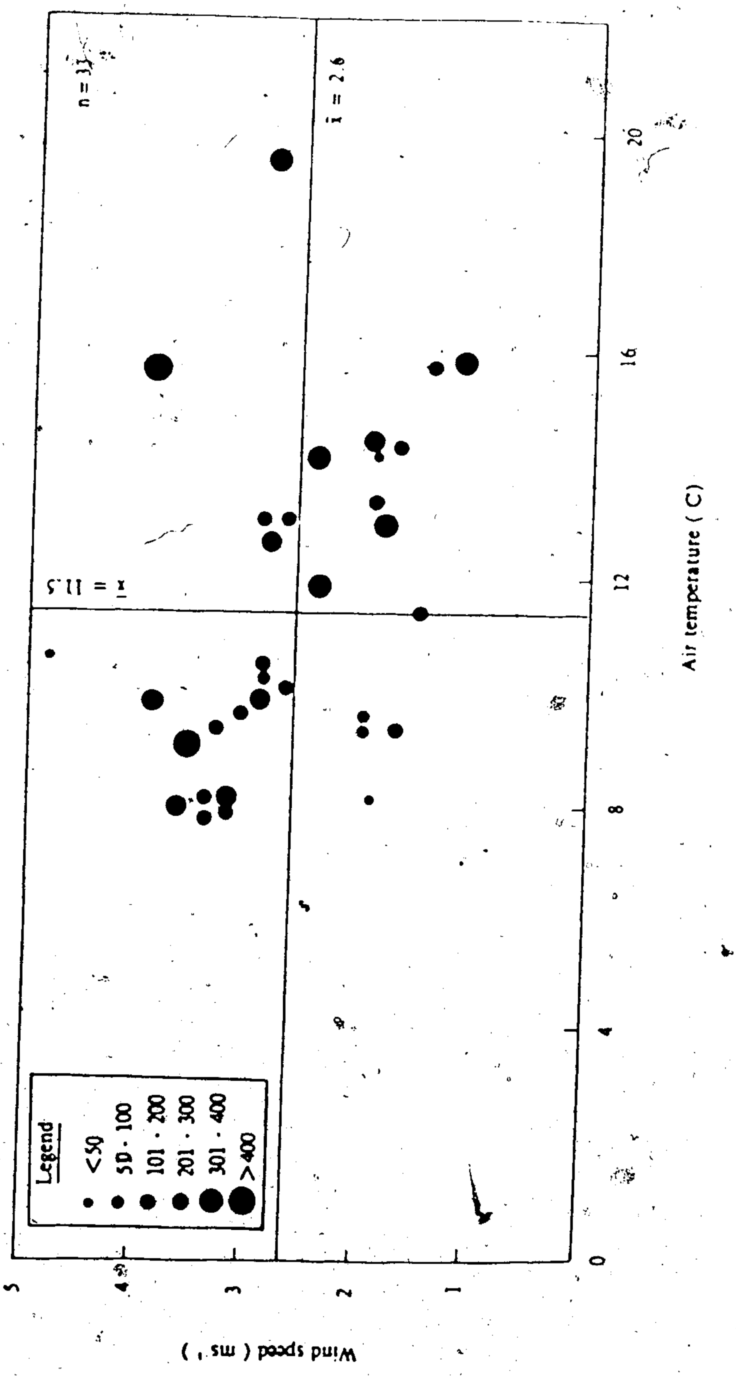


Figure 7.2 Total number of insects trapped at the Lichen-Heath site with respect to air temperature and wind speed. July 11 to July 31 and August 5 to August 16 1984.

(maximum = 93.7%, mean = 52.9% for the 19 days with above average wind speeds) tends to support the second explanation.

Thus it appears that wind speeds were more important than air temperatures in explaining the total number of insects trapped on a daily basis. The reverse relationship holds for the total number of trapped mosquitoes (Figure 7.3). As expected, the highest daily totals were recorded under high mean air temperatures and low mean wind speeds. In contrast to the total insect counts however, relatively few mosquitoes were trapped on days with high mean wind speeds (upper left sector of Figure 7.3). It may be inferred from these data that mosquito activity was greatest under high air temperatures and remained "anchored" on the tundra surface under high wind speeds.

7.2.3 Inter-Site Variation

In this section, comparative data on numbers trapped at the four sites are presented. The number of all insects and mosquitoes trapped are plotted in Figure 7.4. as two day totals corresponding to the frequency at which data were collected from the high elevation traps. Eighteen two-day totals representing 38 days (August 1 to 4 included as one total) were calculated for the Lichen-Heath, Blockfield and Snowpatch sites, and 5 two-day totals (10 days) at the Willow-Forb site.

The total numbers trapped at each site varied considerably on a daily basis. At the Lichen-Heath site a total of 6408 "non-biting" insects and 133 mosquitoes were trapped between July 10 and August 16. At the high Blockfield site 2198 "non-biting" insects and 7 mosquitoes were trapped in total. Over snow, numbers were significantly lower at 41 and 0 respectively. Total numbers of all insects trapped on snow were only 0.63% of that at the Lichen-Heath site. On a daily basis, the total number trapped on snow never exceeded 2.6% of that at the Lichen-Heath site and never exceeded 3.9% of that number trapped at the adjacent Blockfield site less than 20 metres away. Statistical tests for paired samples were applied to these data to illustrate the extent of this variation. Significant inter-site differences were

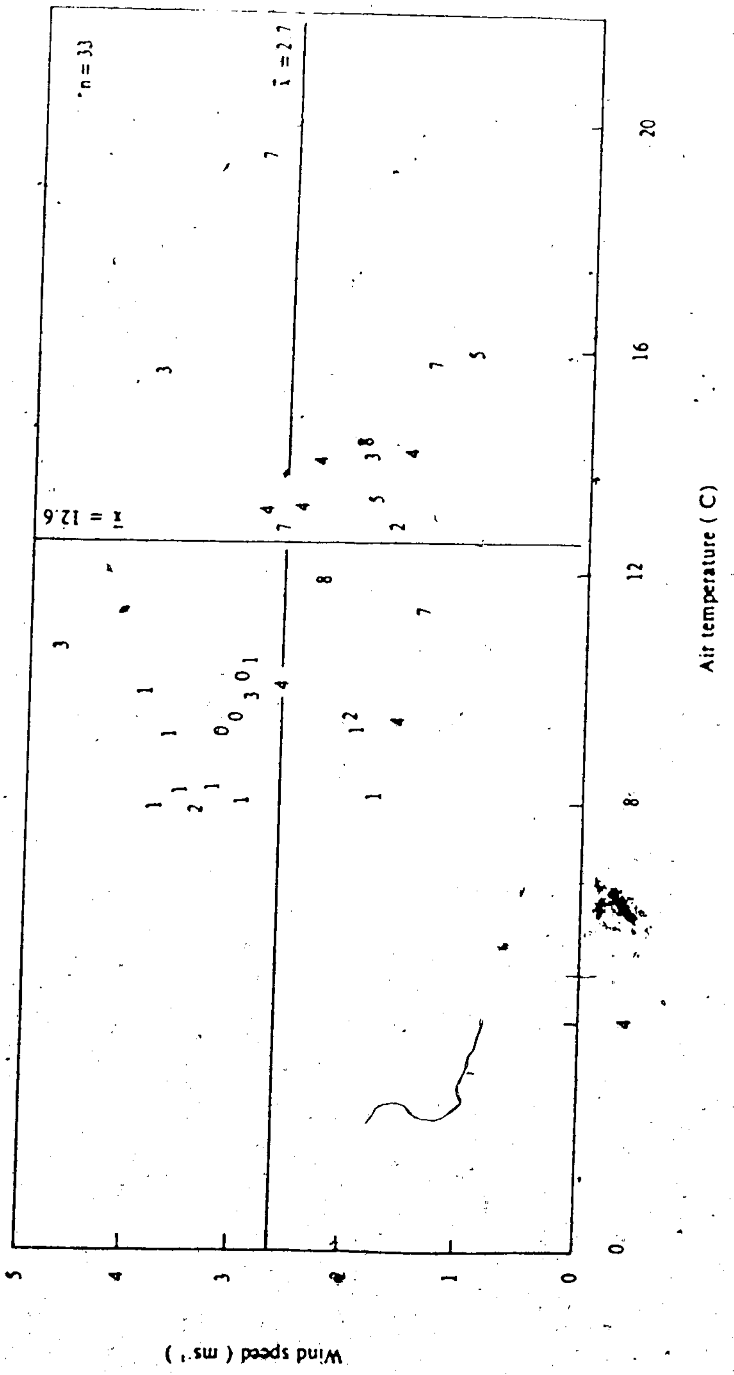


Figure 7.3 Total number of mosquitoes trapped at the Lichen-Heath site with respect to air temperature and wind speed. July 11 to July 31 and August 5 to August 16 1984.

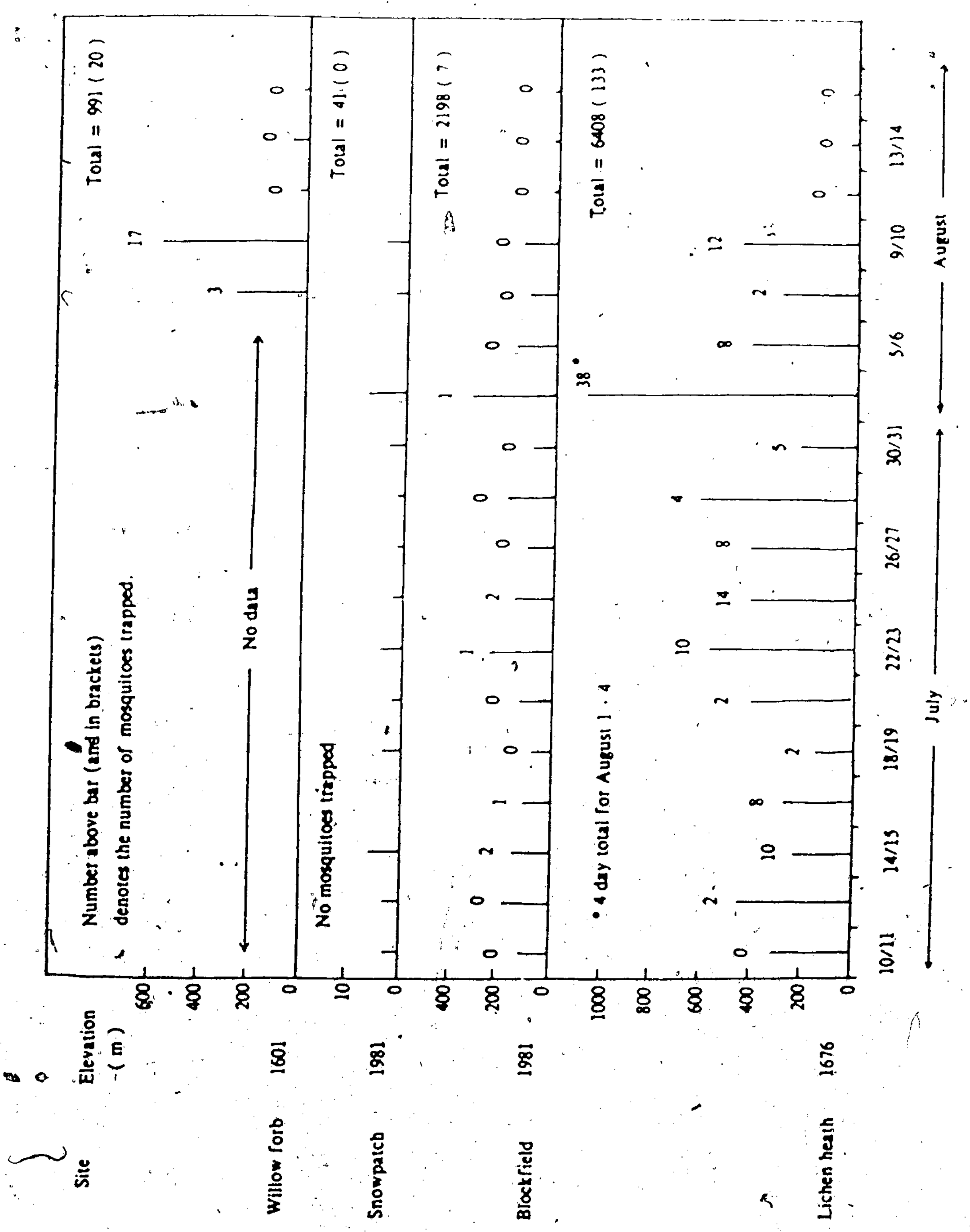


Figure 7.4 Inter-site variation in the number of all insects and mosquitoes trapped.

calculated for total numbers trapped between the Lichen-Heath and Blockfield sites ($t = 5.56$, $S.E.d = 42.12$, $n = 18$, $p < 0.001$), the Blockfield and Snowpatch sites ($t = 6.33$, $S.E.d = 18.96$, $n = 18$, $p < 0.001$) and the Lichen-Heath and Snowpatch sites ($t = 8.98$, $S.E.d. = 59.13$, $n = 18$ $p < 0.001$).

Although less data were available for the Willow-Forb site (10 one day totals), total insect counts were significantly greater than the Lichen-Heath site ($t = 3.52$, $S.E.d = 9.58$, $n = 10$, $p < 0.01$). A total of 991 "non-biting" insects and 20 mosquitoes were trapped between August 7 and August 16 at the Willow-Forb site. This compares with 837 and 14 at the Lichen-Heath site for the corresponding period. These data describe significant variations between the four sites. The Willow-Forb site represented the most favourable "insect habitat" followed by the Lichen-Heath and Blockfield sites with the snowpatch the least favoured. The numbers of all insects and mosquitoes trapped thus suggests a decline in insect density with both the structural complexity of plant cover and increasing elevation.

7.2.4 Discussion

Tundra provides an ideal breeding habitat for mosquitoes. Long, cold winters and short, cool summers ensure that continuous permafrost is widespread above treeline and timberline. A permanently frozen sub-surface produces small, stagnant pools during snowmelt. Heated by the intense insolation and long daylength of the Sub-arctic summer, these pools and waterlogged areas become productive hatcheries.

Studies assessing fluctuations in mosquito densities describe an emergence in late June, a peak in activity in July and a decline in late July and August. In this respect, 1984 was a typical year at Macmillan Pass. The exact duration and intensity of the 'mosquito season' is influenced by several local factors. Roby (1978) studying the summer ecology of the Central Arctic Herd in the foothills of the Brooks Range, described the emergence of mosquitoes on June 21 in 1975. In the same study as evidenced by harassment, numbers did not become "bothersome" until July 6 on the Arctic Coast around Prudhoe Bay. In the following year, mosquitoes were described as "moderately active" on June 12 inland with "few" present near Prudhoe Bay by July 5. The pattern of an earlier emergence inland is supported by data from Curatolo (1975) for the Tanana Hills in west central Alaska, constituting part of the summer range of the Steese-Fortymile herd. In 1973, high densities were first observed on the evening of June 12 with an even earlier emergence along the Yukon River (June 8) where warmer air temperatures and an earlier thaw probably enhanced the date of hatching. It is thus possible that some caribou groups may suffer low levels of harassment during and immediately following calving at inland locations.

White and others (1975) described July as the peak month for insect harassment at Prudhoe Bay during summer surveys in 1972 and 1973. Between 20 and 25 days in July were described as "mild" enough for harassment. In 1975, "severe" harassment was not noted until July 18 at Prudhoe Bay by Roby (1978). Numbers (as evidenced by harrassment) declined considerably during the first week of August in 1972 and 1973 (White et al. 1975) and also in 1975 (Roby 1978) Mosquitoes persisted until August 8 in the Tanana Hills in 1973 (Curatolo 1975).

Sound conclusions on the duration of the mosquito season cannot be drawn using qualitative data gathered from three localized studies from non-successive years. The absence of quantitative data describing insect numbers makes any comparison of intensity somewhat spurious. The Alaskan data does, however, suggest an earlier emergence and slightly longer (although apparently less intense) mosquito season inland compared to the Arctic coast. (Densities within the Tanana Hills were described as "generally lower" than those at Prudhoe Bay by Curatolo). Some tentative conclusions may be drawn. The flat, coastal plain underlain by continuous permafrost at Prudhoe Bay is ideal breeding habitat for large numbers of mosquitoes. The cool climatic regime experienced at the Arctic coast (due to the persistence of sea ice) compared to continental alpine regions reduces the 'potential' insect season. Lower latitude alpine tundra such as that in central Alaska will provide relatively few opportunities in terms of ideal breeding habitat but with a warmer summer climate. A longer, less intense mosquito season is thus more likely.

The date of emergence at Macmillan Pass in 1984 - the first week of July — in comparison to the Alaskan data was relatively late. This is most likely due to a combination of the high mean elevation and late snowmelt. (En route to Macmillan Pass, high mosquito densities were noted at low elevation in north eastern British Columbia on June 11). The end of the mosquito season at Macmillan Pass on August 12 does not seem unduly premature in view of the Alaskan data. It was thought unlikely that many mosquitoes would have survived beyond this date in view of the adult's average life cycle of three weeks. (Canadian species overwintering as adults may survive for 8 or 9 months, however).

The relative intensity of the mosquito season at Macmillan Pass in 1984 is impossible to assess in comparison to Alaskan data in view of the purely qualitative descriptions of harassment in these studies. Surveys of insect harassment of the Porcupine barren-ground caribou herd on the Yukon's North Slope and adjacent mountains (approximately 600 km northwest of Macmillan Pass) were undertaken in July 1984. Russell (1984) described low levels of harassment and generally an "excellent summer" for caribou. Local climatic and site variables are not comparable to Macmillan Pass and so similar conclusions cannot be drawn for data presented here.

Relatively little is known about what constitutes favourable "mosquito habitat". Calef (1981) thought that barren-ground caribou may frequent sand dunes and gravel deltas because these areas, devoid of plants, offer fewer places for mosquitoes to hide and breed than does the wet vegetation of the tundra. Helle and Aspi (1984) found that sand dunes were avoided by mosquitoes and so represented a favoured relief habitat for Finnish reindeer. Data describing total numbers of all insects and mosquitoes trapped supports Calef's view. Trapping success was significantly higher at the Willow-Forb and Lichen-Heath sites. (Figure 7.4) The greater surface roughness of the sites with higher and structurally more complex plant cover would probably also reduce wind speeds at 10 cm above the surface, compared to unvegetated sites. This would further favour these areas as 'mosquito habitat'. The cool air temperatures and stronger wind speeds immediately above the snow surface would inhibit flight to a greater degree. Snow surfaces also possess fewer 'anchor' points for mosquitoes to rest. Despite an adaptation to ice and snow (larvae may be ice bound for several months in the High Arctic) it may be said that mosquitoes consciously avoided snowpatches during the summer of 1984 at Macmillan Pass.

The numbers of mosquitoes trapped on a daily basis in relation to climatic conditions generally supports the findings of White and others (1975) describing harassment at Prudhoe Bay. High mean air temperatures and low mean wind speeds are most suitable for insect flight. Although qualitatively assessed, White et al. described increasing levels of harassment with high air temperatures and an accompanying increased tolerance for strong winds. The small sample size (daily totals) precludes any comparison with these data.

Mosquitoes were trapped at the Lichen-Heath site under mean air temperatures ranging from 7.8 to 21.6°C. Kelsall (1975) described an optimum temperature range for flight in warble fly — a common parasitic fly — of 15 to 27°C. High levels of insolation may raise insect body temperature by 7 to 9° thus lowering the temperature range favoured for flight. This gives a 'threshold' air temperature of 6°C for warble fly flight for Kelsall's (1975) data. White and others (1975) calculated that mosquitoes became active at Prudhoe Bay at air temperatures greater than 6°C in "still" air. A finer resolution of sampling (e.g. hourly counts) is necessary for comparison with Macmillan Pass data. Mean daily air temperatures ranged approximately from 8 to 16°C during the mosquito season. The only occasion on which significantly higher mean daily air temperatures were experienced was between August 2 and August 5. Seven mosquitoes were trapped at the Lichen-Heath site on the 5 August with a mean daily air temperature of 19.4°C. 33 mosquitoes were trapped over August 2, 3 and 4 when mean air temperatures were 16.7°C, 21.4°C and 21.6°C respectively. This exemplifies the paramount importance of air temperature in regulating mosquito density. In general, data describing the numbers of trapped mosquitoes were not thought to be the most accurate means of assessing levels of harassment. Rather, calculated indices of harassment which are discussed in the following section were deemed more reliable indicators.

7.3 Insect/Caribou Relationships

7.3.1 Behavioural Responses to Harassment

In addition to the insect trap data, "indices of harassment" were calculated at each focal animal sample. This involved the notation of individual behavioural responses to insect harassment. Four categories were defined: 'stamping' (front or hind legs), 'head shaking' (any sudden horizontal and/or vertical movement of the head), 'shivering' (sudden bodily contractions) and 'aberrant running' (directed and undirected running at high speed). Such behaviour is recognized as a response to insect harassment (Curatolo 1975, White et al. 1975, Roby 1978). Tail wagging, thought to be a response to mild insect harassment (White et al. 1975) was not quantified. 'Coughing' and 'sneezing' were also infrequently noted when viewing distances were short. The significance of this is discussed later.

Combining all data for the 39 long observations on and off snow, a total of 323 focal animal samples were taken. This breaks down as 23 long observations on snow (238 focal animal samples) and 16 long observations off snow (85 focal animal samples). A total of 2506 individual behavioural responses were recorded (Table 7.3). Head shaking was the most common response (47.0%) followed by stamping (39.4%), shivering (12.6%) and aberrant running (1.0%). Calculations of mean indices of harassment for each of the four age/sex classes suggest that bulls were harassed the least, or exhibited the least response to harassment. By contrast, calves responded the most to insect harassment. This difference is difficult to explain other than to attribute this to the naturally more precocious behaviour of calves, their experience of harassment for the first time or simply a lower level of tolerance. This is supported by the higher proportion of 'extreme' responses to harassment such as aberrant running exhibited by calves, although this was difficult to differentiate from play behaviour. Other than this, variation in the level of harassment with age and sex were not found to be

Table 7.3 Summary of Woodland caribou behavioural response to insect harassment. June 24 to August 16 1984.

	bull	cow	yearling	calf	
Head shaking	149	383	325	321	1178 (47.0%)
Stamping	140	309	255	283	987 (39.4%)
Shivering	35	83	87	111	316 (12.6%)
Running	0	3	7	15	25 (1.0%)
Total.(n)	324(53)	778(100)	674(88)	730(82)	2506(323)
Mean	6.11	7.78	7.66	8.90	7.76

significant.

Mean indices of harassment were calculated for each long observation. (A numeric value was assigned based on a group average of all individuals selected during the observation.) Extremes of 0 and 16.6 were recorded. Daily mean and maximum indices are plotted in Figure 7.1. Group-averaged indices of harassment were thought to be a more accurate measure of insect activity than the insect trap data. On a daily basis, the two measures of mosquito activity (numbers trapped at the Lichen-Heath site and group-averaged indeces of harassment) were found to correlate closely ($Rs = 0.808$, $df = 24$, $p < 0.001$).

7.3.2 Climatic Variation and the Index of Harassment

As with the insect trap data, calculated indices of harassment were plotted against air temperature and wind speed data. Mean climatic data were calculated for the duration of the observation as this would give a better indication of conditions than the BAP data used for the insect trap data (Figure 7.5). The highest levels of harassment were experienced under high mean air temperatures and low mean wind speeds - conditions proven to be most favourable for insect flight. High indices of harassment (>10.1) were observed under mean air temperatures ranging from 11.3°C to 20.4°C. Low indices (<5.0) were recorded between 7.9°C and 14.9°C. High indices were also recorded under below-average wind speeds (i.e. <2.5 m s^{-1}). 10 of the 11 observations with indices of greater than 10.1 occurred under average or below-average wind speeds. On the one occasion at which a high index of harassment was recorded under above-average wind speeds, air temperature was unusually high at 19.4°C. Although this represents only one group-averaged observation it does support the description of the mosquito's increased tolerance for wind at higher air temperatures as discussed by White and others (1975).

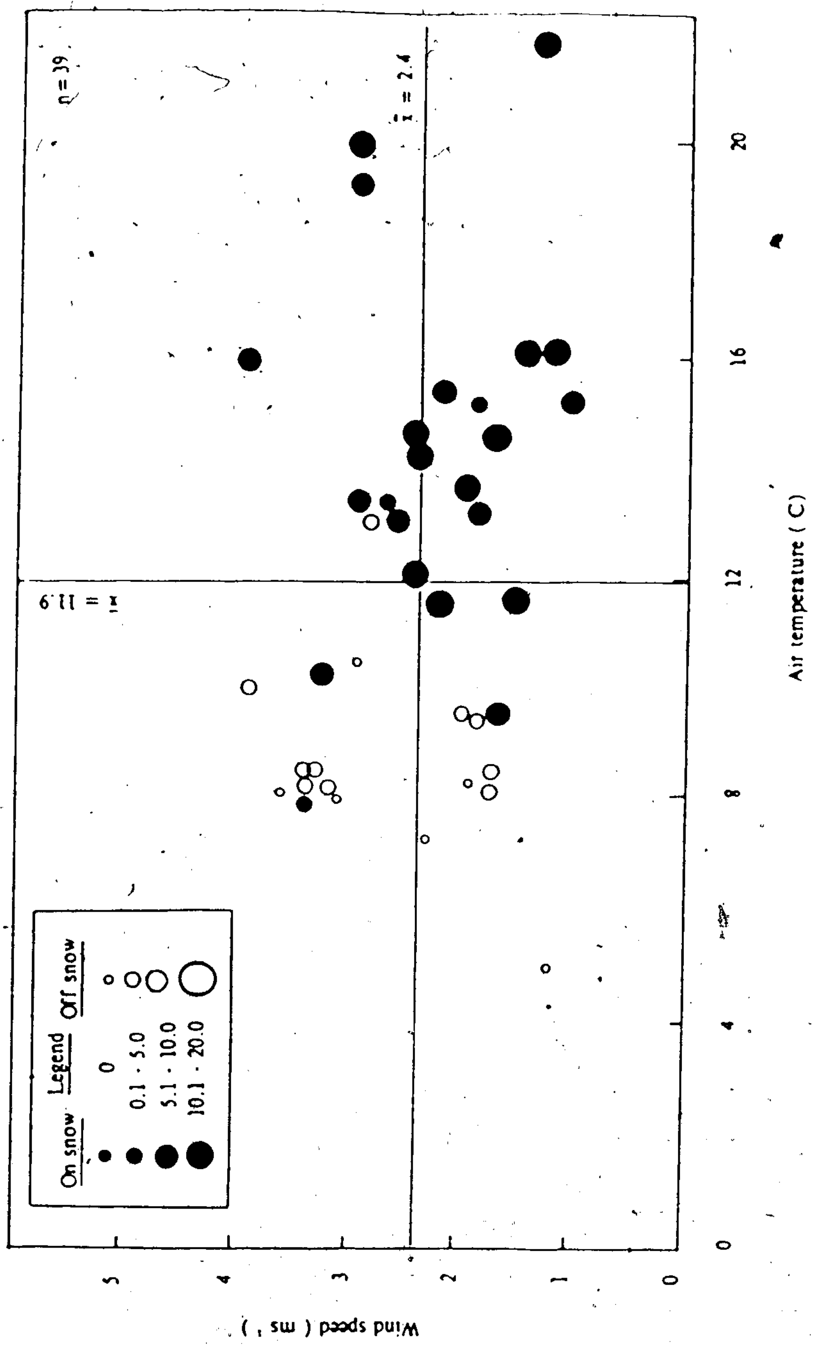


Figure 7.5 Variation in the index of harassment for Woodland caribou with air temperature and wind speed. 24 June to 15 August 1984.

7.3.3 Levels of Harassment On and Off Snow

Comparison of data on and off snow (Figure 7.6) illustrates that harassment was generally higher on snow ($\bar{x}$ = 9.98, n = 23, SD = 4.01) than off snow ($\bar{x}$ = 1.78, n = 16, SD = 2.89). This is in direct contrast to the trap data over snowpatch and snow-free areas. The distribution of 'on snow' and 'off snow' observations about the mean for air tempterature and wind speed explains this apparent contradiction. Previous analysis of climate/insect relationships described greatest insect activity under warm, calm, anticyclonic conditions. The majority of observations on snow were made under such conditions. This raises two points: that snowpatches do not make caribou "immune" to insect harassment and that mosquitoes obviously are capable of differentiating between caribou and an insect trap.

7.3.4 Variation in Group Size and Composition

Observations of caribou on and off snow also describe significant variations in both group size and composition. From the long observation data, the mean group size observed on snow was 23.9. One group of 54 (observed outside the E.S.A.), two groups of 40 or more and three groups of over 30 were observed at the main aggregation site. Mean group size off snow was only 11.9. These variations in group size between observations on and off snow were found to be statistically significant ($t = 4.66$, $p < 0.001$). This was undoubtedly a response to the availability of suitable snowpatches to act as relief habitat. White and others (1975) described similar variations in group size under contrasting levels of insect harassment.

Group composition was also found to vary between observations on and off snow. During the summer, caribou are usually separated into 'cow-dominated groups' (cow/calf/yearling groups) and 'bull-dominated groups' (bull groups and bulls with yearlings). 82 of the 94 observations (87.2%) were of such "segregated" groups. On 12 occasions however (all of which were 'long observations') adults of both sexes were observed together. Such mixed groups were disproportionately observed on snow. Ten from 23 long observations on snow (43.5%) were of mixed groups with only 2 of 16 (12.5%) off snow. This difference was found

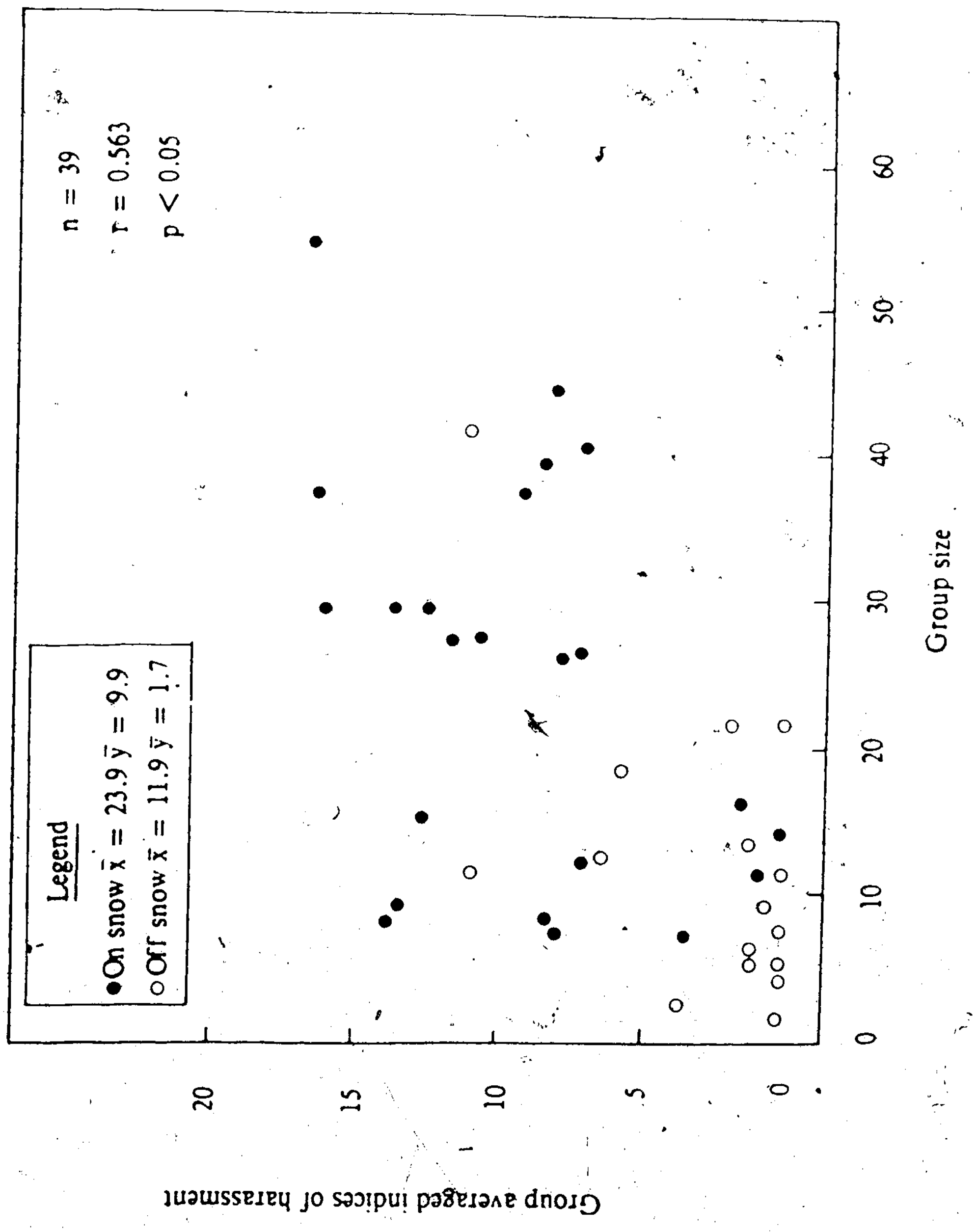


Figure 7.6 Variation in Woodland caribou group size and indices of harassment on and off snow. 24 June to 15 August 1984.

to be statistically significant ($x^2 = 17.12$, $p < 0.001$)

7.3.5 Aggregation as a Response to Harassment

Analysis of the variation of group size and composition illustrated that relatively large groups of mixed sex aggregated on snow under conditions of increased insect activity. It has been theorized that caribou may form closely packed groups as a means of reducing insect harassment *per se*. It may be said that caribou may assure a mutual benefit by "sharing their tormentors". To assess the validity of this theory for the caribou under study, an 'index of aggregation' was calculated which may be used to quantify the degree to which animals coalesced in response to insect harassment.

As inter-individual distances obviously could not be measured, estimates of this variable were made based on a qualitative assessment which was later verified through time-lapse photography taken at the time of specific focal animal samples. Three categories of aggregation were defined : Category 1 - "closely aggregated" ($\leq$ 50% of the group possessed an inter-individual distance of $\leq$1 body length) (Plate 14), Category 2 — "moderately aggregated" ($\leq$ 50% of the group possessed an inter-individual distance of $\leq$3 body lengths) and Category 3 — "dispersed" ($\geq$ 50% possessed an inter-individual distance of $\geq$3 body lengths) (Plate 15). The group was classed into one of these three categories at each scan sample. A total of 1150 scan samples were recorded for the 23 long observations on snow. Each sample was weighted in such a way that a Category 1 observation ("closely aggregated") was multiplied by three, a category 2 by 2 and a category 3 by 1. In this way an index of aggregation was calculated that ranged from 100 (100% of samples multiplied by 1 — "totally dispersed") to 300 ("totally aggregated"). This index of aggregation was found to correlate with the mean index of harassment (Figure 7.7). This provides strong evidence in support of the theory that caribou will aggregate closely (on snowpatches) as a response to harassment. 76.1% of all scan samples taken for observations of caribou off snow fall into category 3 and thus comparison with data on snow is inconclusive.

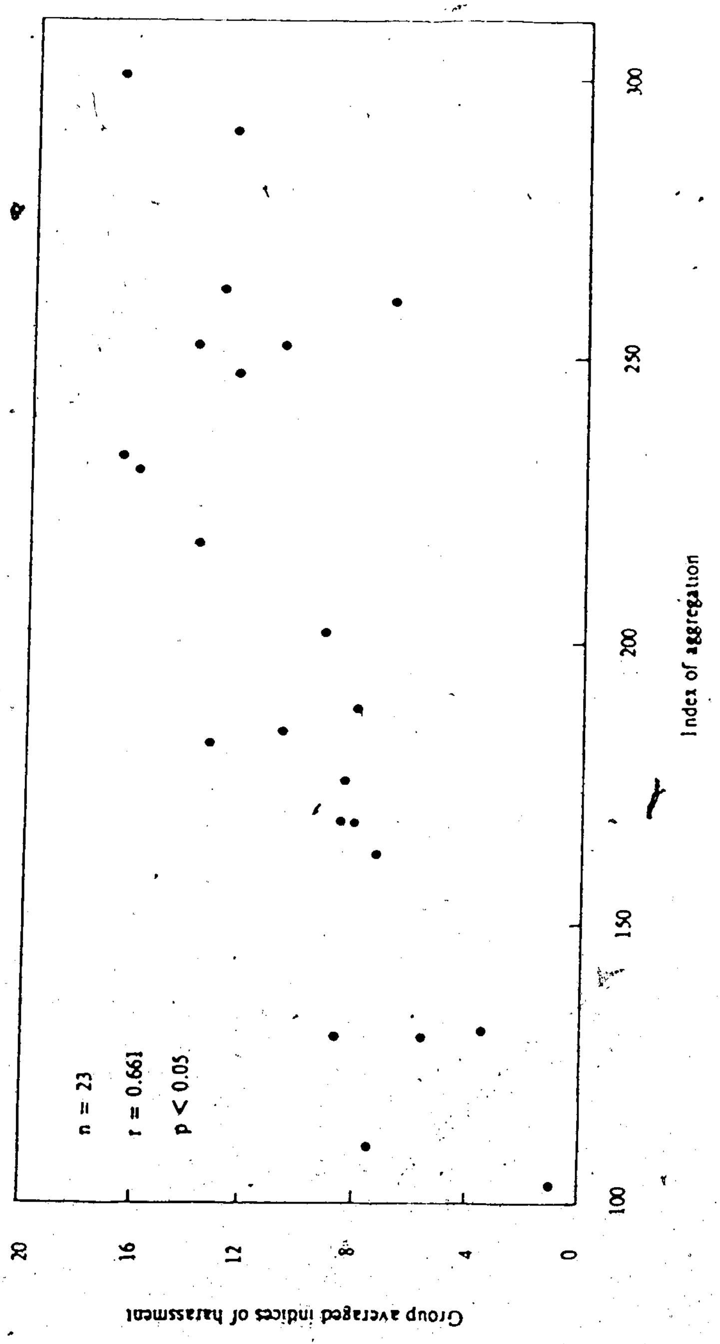


Figure 7.7 Variation in the Woodland caribou index of harassment with the index of aggregation as compiled from observations on snowpatches. July 6 to August 10 1984.

Group-averaged values (such as the mean indices of harassment) tend to overshadow finer-scale variations in group behaviour. The response of individuals and groups to sudden fluctuations in insect harassment was found to be immediate and almost predictable. This is exemplified with reference to a group of 12 caribou observed at the main aggregation site on July 17 (Figure 7.8). This group was observed for 6:35 h between 11:11 h and 17:46 h. The group remained on snow for 5:36 h. During the observation, air temperatures averaged 14.1°C with a mean wind speed of 2.4 m s^{-1}. A mean index of harassment of 10.7 was recorded. Sudden increases in wind speed to 5.0 m s^{-1} at 13:00 h and 15:15 h recorded at the high station resulted in large reductions in the indices of harassment from 27 to 2. Scan sample data for these periods describe an immediate response in the form of a dispersal over the snowpatch. The group resumed a closely aggregated formation when wind speeds dropped and indices of harassment increased again to values over 20 at 14:25 h. This behavioural response is illustrated in Plates 15 and 16.

7.3.6 Harassment in Relation to Group Position

In the preceding section, close aggregation on snow was found to be a group-oriented response to insect harassment. Theoretically, by reducing inter-individual distance until they are touching the caribou will expose a smaller surface area and present less of a "target" to mosquito attack. This section attempts to assess the validity of this theory by comparing levels of harassment to individuals located centrally within a group and those on the periphery. A similar study was attempted by Helle and Aspi (1983).

At each focal animal sample, the individual was categorized into one of three classes: 'centre' (an animal located centrally within a closely aggregated group), 'outer' (an animal located away from the main group) and 'single' (an animal located away from the main group). The distinction is illustrated in Plate 17. Of the 23 long observations, 6 were rejected as no differentiation in terms of group position was possible. All 6 were of groups widely dispersed under conditions of low harassment. For the remaining 17 observations, a total of 216

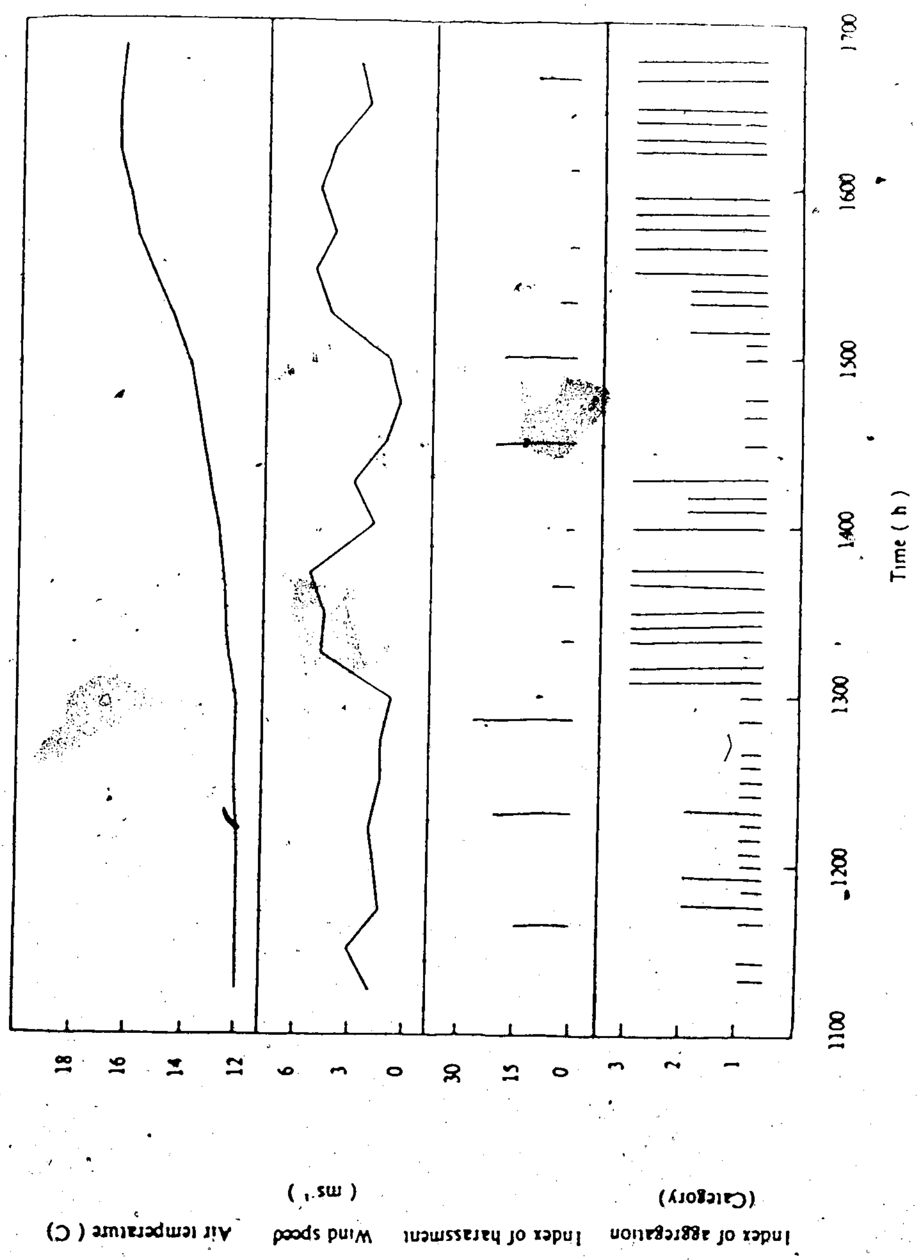


Figure 7.8 Variation in the Woodland caribou index of harassment and index of aggregation with wind speed and air temperature. July 17 1984.

focal animal samples were taken. Whenever possible, individuals were sampled systemmatically with reference to these 3 cateogries to ensure an approximately equal number in each group location category.

A mean index of harassment was calculated for each of the three categories for each of the seventeen long observations. The "single" category ranked the highest index in 11 out of 17 observations (64.7%), ranked second on two occasions (11.8%) and third on four occasions (23.5%). The four occasions on which the 'single' (most exposed) category ranked third (the lowest level of harassment) is significant in that it was on these occasions that sample size was low - 3 to 9 focal animal samples. On those occasions when larger samples were possible (up to 23 samples) the data described a pattern of increasing indices of harassment with increasing distance from the centre of the group. By contrast, the 'central' category never ranked the highest index, was ranked second on six occasions (35.3%) and third on eleven occasions (64.7%). This suggests that a clear advantage exists in terms of reduced levels of harassment to an animal located centrally within a group compared to those on the periphery or located away from the main group. This is statistically verified by comparison of mean indices of harassment for each of the three group locations (Table 7.4).

7.3.7 Activity Patterns in Response to Harassment

Patterns of group activity were recorded to assess any variation in behaviour on and off snow and under varying levels of harassment. Individuals and groups were classified into one of five activity categories: eating (grazing or ingesting snow); walking; standing; lying and running. A group was classed into an activity category if ≥50% of the group members were engaged in that activity. One classification was taken at each scan sample. 1150 samples were taken on snow and 795 off snow for a total of 1945. This incorporates data for both the 'long' and 'short' observations.

Results for all observations rank standing and eating as the two most frequent activities at 44.6% and 33.8% respectively. Lying (15.0%), walking (6.1%) and running (0.5%) were

Table 7.4 Summary of harassment of individual Woodland caribou based upon their relative group position.

Group Location	Single	Outer	Center	Total
Total harassment events	878	721	679	2278
Number of observations	64	77	75	216
Maximum index of harassment	30	29	21	
Mean index of harassment	13.72	9.36	9.05	
T test level of significance	$P<0.05$	$P = N.S.$		
	$P<0.05$			

relatively infrequently observed. Data collected for observations on and off snow however, show some contrast (Figure 7.9). On snow, caribou spent a high proportion of time standing (66.0%), the majority of the remaining time approximately equally distributed between ingesting snow (13.3%) and lying (13.2%). Walking (6.9%) and running (0.6%) were less common group activities. Off snow, grazing activity predominated (63.4%) followed by lying (17.6%), standing (13.6%), walking (5.0%) and running (0.4%).

Patterns of group activity were also found to vary with the level of harassment (Figure 7.10). As the level of harassment was not quantified in the scan samples, values were assigned in one of two ways. For the long observation data, information from the nearest focal animal sample was used. For the short observation data, a qualitative assessment of 'no' or 'mild' harassment was assigned. These data were added to harassment data categorized quantitatively as 'none' (an index of harassment of 0), "mild" (0.1 to 10.0) or 'severe' (above 10.1). It has been described previously that indices of harassment were considerably greater on snow than off snow. This accounts for the disproportionate number of samples falling into two of the three harassment categories (99.0% in "mild" and "severe" for samples on snow and 96.6% in "none" or "mild" for samples off snow). The data for observations on snow describe an increase in eating (ingesting snow), walking and running and a decrease in lying and standing with increased levels of harassment. Likewise, walking, standing and running increased and lying and grazing decreased with increased harassment off snow.

Several studies quantifying activity patterns on a daily basis describe a pattern of alternating periods of feeding and resting (e.g. Fischer and Duncan 1976, Roby 1978). The frequency of resting (lying) behaviour was plotted at 30 minute intervals (Figure 7.11). Resting was found to be most frequent between 13:00 h and 15:00 h, with pronounced variations between data collected on and off snow. Resting behaviour was more common off snow at all times with the exception of the mid-morning period (9:00 h to 10:00 h).

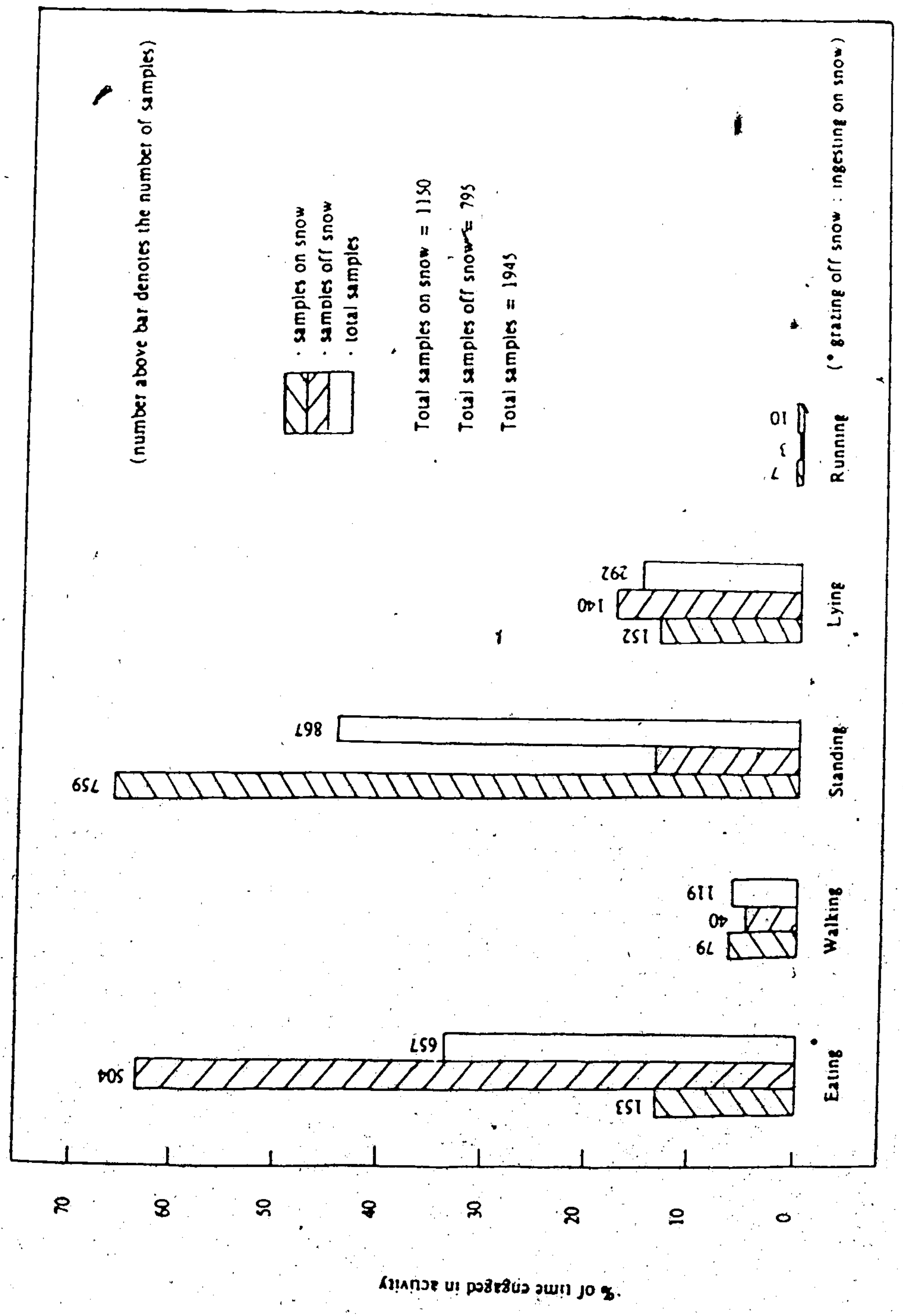


Figure 7.9 Variation in Woodland caribou activity patterns on and off snow.

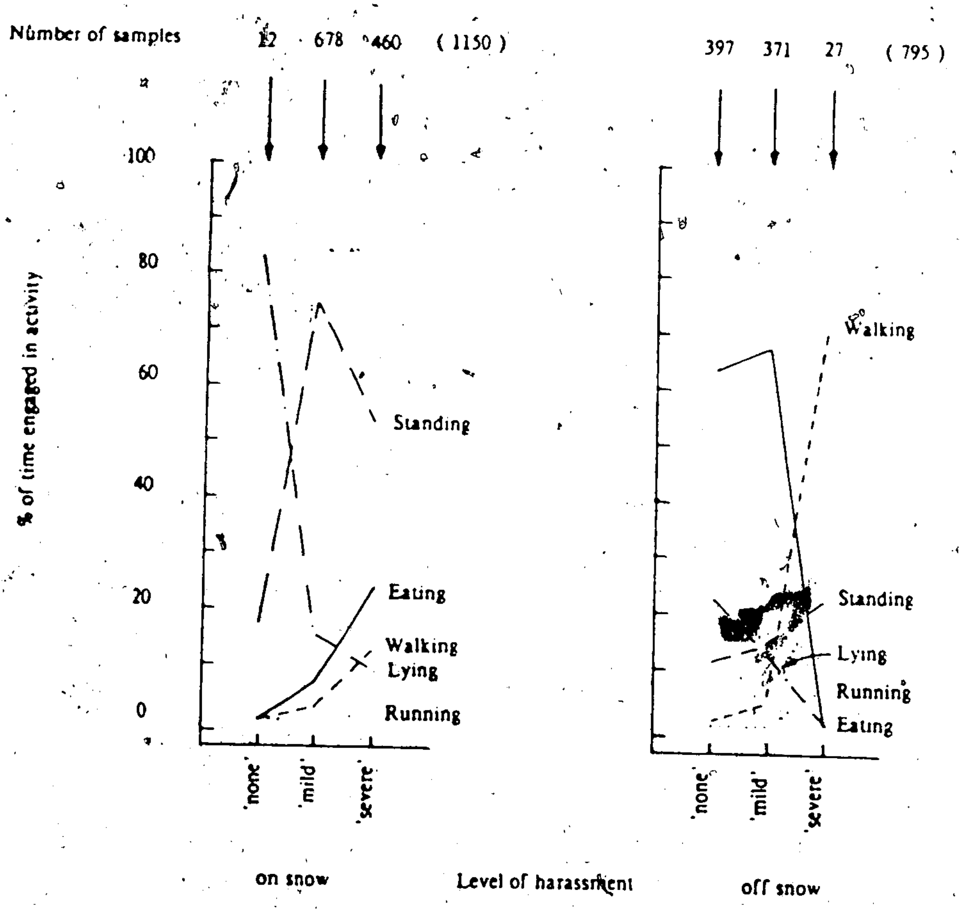


Figure 7.10 Variation in Woodland caribou activity patterns with levels of insect harassment. June 22 to August 16 1984.

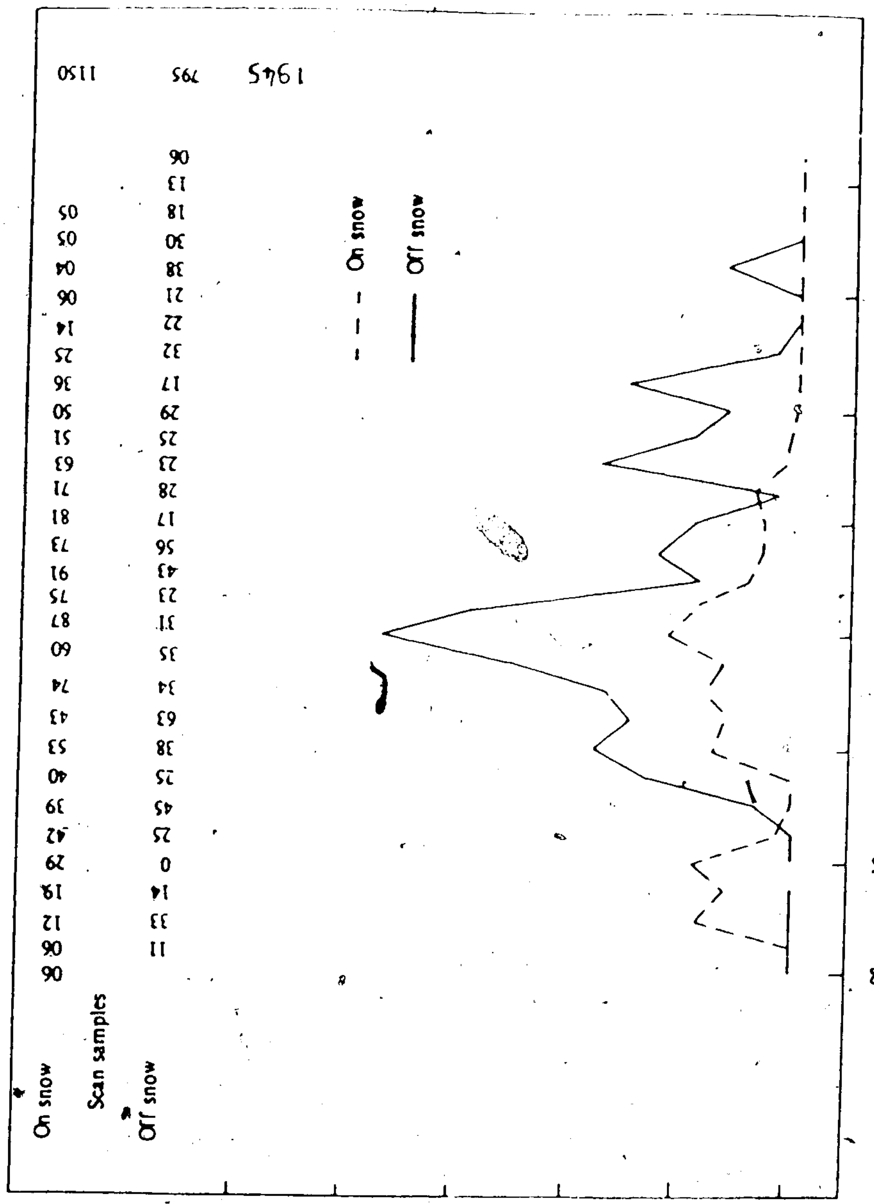


Figure 7.11 Diurnal variation in Woodland caribou resting behaviour on and off snow. June 24 to August 16 1984.

7.3.8 Discussion

Behavioural responses of individual reindeer and caribou to insect harassment have been described in several studies (Skoog 1968, Kelsall 1968, Espmark 1968, Curatolo 1975, Roby 1978). A variety of terminology exists, including "ear-flicking", "tail-wagging", "twitching", "shuddering", "shivering", "head-shaking", "leaping", "bounding", "kicking" and numerous other descriptions. In these studies a circularity problem exists in that it is not insect harassment that is being described, but the response to harassment exhibited by the individual animal. The "effect" is being used to describe the "cause". This is a problem inherent in any field observation assessing harassment either qualitatively or quantitatively. Repeated observation has, however provided much complementary data on response to insect harassment in *Rangifer*. Such indirect methods have been widely adopted in the literature. As an example, Helle and Tarvainen (1984) found a strong negative correlation between insect harassment and weight gain in Finnish reindeer calves. In that study harassment was quantified by the "daytime air temperature (2 p.m.) during the potential insect season", such was their confidence in the relationship between air temperature and the severity of insect harassment.

A further problem with field observations is the difficulty in attributing specific behavioural responses to particular insect species. The majority of studies assessing insect harassment of caribou and reindeer recognize two types of parasitic insect. These are the blood-sucking flies: (*Aedes* spp.) and blackflies (*Simulium* spp.) and oestrid flies: warble flies (*Oedemagena tarandi* L.) and nose-bots (*Cephenoma trompe* L.). Mosquito phenology has been discussed previously. Although common on some caribou ranges (Kelsall 1968) no blackflies were trapped at Macmillan Pass. Little is known of any (if any) specific behavioural response to this species. It was thus assumed that they were of little or no ecological significance to caribou in this study. This is possibly due to the later emergence in mid to late August. Curatolo (1975) found them to be "almost absent" from the Tanana Hills and Roby (1978) never encountered significant numbers on the coastal plain at Prudhoe Bay although they were "occasionally bothersome".

Supposed reaction to oestrid fly harassment has received considerably more attention in the literature. The adult warble fly - a large, orange and black bee-like fly, about 2 cm in length - attempts to lay eggs on the legs and flanks of the caribou from where they migrate to the back region. The life-cycle of the adult is approximately 3 weeks during July and August although in favourable years the season of activity may cover about 3 months (Hadwen 1927). The nose bot, also a large black insect resembling a bee attempts to deposit larvae in the nasal passages of the caribou where they attach to the sinus cavities and linings. Hadwen (1927), cited in Skoog (1968) described the reaction of reindeer to warble fly attack:

> "... as soon as the fly touches the deer a severe shock goes through the body. The animal jumps or kicks and then looks around and listens for his tormentor. If it feels it again it's jumping and kicking is repeated, and when struck for the third or fourth time the reindeer becomes thoroughly frightened and thinks of flight. At times the reindeer will look and search for the fly, meanwhile stamping with its feet, evidently attempting to destroy its tormentor". (p. 59).

Hadwen described the reaction of reindeer to bot flies:

> "... when the insect is hovering in front of their noses they assume a terror-stricken look, their eyes staring, their mouths open, and their bodies in a tensely strained attitude. When a reindeer is in this rigid state, the slightest touch on any part of the animal will cause muscular contractions which shake the whole body, just like an electric shock. (The deposition of larvae) is succeeded by total relaxation ... The animal appears nauseated and walks a few steps with his head elevated, sneezing and showing signs of nasal irritation". (p. 63).

Several problems hindered the accurate assessment of oestrid fly harassment at Macmillan Pass. First, no warble flies or bot flies were entrained on the insect traps although it was obvious that larger insects were able to pull themselves off the trap. Second, oestrid flies never harassed the observers. This in turn may be attributed to the fact that warble flies and bot flies parasitize only caribou (Skoog 1968). Third, viewing distance was usually too great to identify insects flying around the caribou. For the same reason, "coughing" and "sneezing" - thought to be responses to oestrid fly harassment - could only be heard on very rare occasions under calm, quiet conditions.

Of the individual behavioural responses quantified, "stamping" may be interpreted as a response to warble fly attack (see Hadwen citation above) and Curatolo (1975) described "aberrant running" as a response to this parasite. The "shivering" response could compare with Hadwen's description of 'muscular contractions' but a closer comparison is of an animal responding as if to "rid the body of water" — a response to mosquito harassment according to Curatolo (1975). Furthermore, Curatolo's description of aberrant running as basically wild and undirected does not correspond with observations made in this study. Group running was usually in a straight line downslope (Plate 18) initiated by one animal under extreme mosquito harassment. Theoretically, the more 'extreme' responses to harassment such as stamping and running should occur more often later in the summer coincident upon oestrid fly emergence. As specific behavioural responses were not temporally skewed, and in view of the lack of other supporting data, oestrid fly harassment was not considered a major factor in this study. The strong correlation between the number of trapped mosquitoes and indices of harassment provides further evidence that these insects were the most significant source of harassment to caribou of Macmillan Pass during the period of study although data from the late summer were absent.

Mosquitoes will concentrate their efforts on areas where the fur is thin — legs, lips, muzzle, ears, eyes, 'velvet' — or where it has been shed or rubbed off during the summer moult. In this way blood loss from reindeer to mosquitoes has been estimated at up to 125 g day^{-1} (Zhigunov 1968). These short-term losses may have a greater impact in the long term. It is doubtful that insect harassment is a direct cause of mortality in caribou but it may act as a contributory factor in several ways. Insect harassment occurs at a time in the caribou's life cycle when body growth and the replenishment of fat, mineral and other body reserves is crucial. Behavioural response to harassment may represent a significant expenditure of energy. Energy loss from blood loss, combined with the debilitating effects of warble fly infestation may severely reduce the animal's physical capabilities. The cumulative effects of a severe winter may further weaken the individual and increase its susceptibility to predation. Reimers (1980)

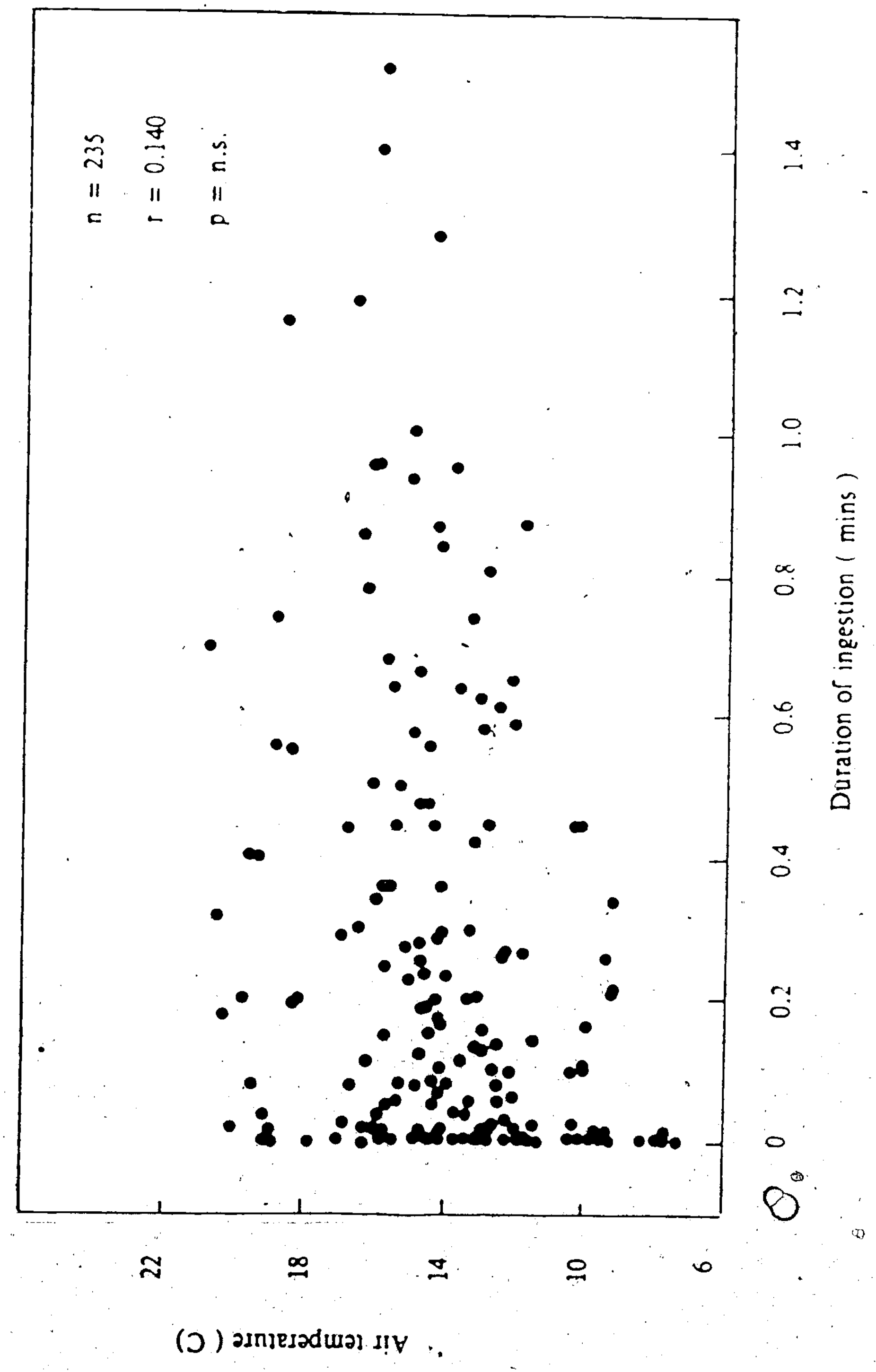


Figure 7.12 Duration of snow ingestion episodes by individual focal Woodland caribou samples as compared with air temperature.

compared the condition to Norweigian wild mountain reindeer (*R. t. tarandus* L.) with Svalbard reindeer (*R. t. platyrhynchus* L.). His conclusions were that the faster growth and greater fat accumulation of Svalbard reindeer is largely due to the absence of insect harassment

The most obvious group response to insect harassment in this study was the coalescence of individuals and small bands into relatively large groups (on snowpatches). It has been seen that the highest indices of harassment were recorded on snow and that mean group size was significantly higher on than off snow. Aggregation on snow can thus be proposed as a likely response to insect harassment.

Significant increases in group size under increasing intensity of harassment have been widely recorded. White and others (1975) calculated a mean group size of 22 animals at Prudhoe Bay under insect-free conditions with an increase to 77 under insect harassment. Roby (1978) described a mean group size of 44 when mosquitoes were absent and an increase to 383 at high levels of mosquito harassment in central Alaska. The results from this study correspond closely with those of White and others in that the increase in group size is largely due to the coalescence of cow-dominated and bull-dominated groups into those of mixed sex. It is noteworthy that this coalescence of the adult sexes during periods of insect harassment is a widespread response in groups varying in size by two orders of magnitude. Helle and Aspi (1983) found significant differences in insect numbers trapped in a 'simulated' herd of 24 animals. In view of this, the postive effects of herd formation should be considerably greater in groups numbering in the hundreds and thousands. In larger herds such as the Porcupine Herd in the northern Yukon, sexual segregation by group position has been observed, with bulls located centrally within the group (Nixon pers. comm. 1985). No consistent patterns of sexual segregation were observed at Macmillan Pass.

Apparent advantages of herd formation in response to insect harassment are several. Cumming (1975) claimed that, assuming an even distribution of insects, clumping behaviour lengthened the average distance between insect and host. The probability of host location was thus reduced. Under bright, calm conditions mosquitoes could be observed flying around the caribou probably in an atempt to locate a landing position. The higher indices of harassment for animals located away from the main group supports the theory of Helle and Aspi (1983) that insects will preferentially select 'objects' (i.e. caribou) with plenty of free space around them but tend to avoid those with limited flying space.

Herd formation has also been proposed as a response to wolf predation (Bergerud. 1974) and the re-establishent of winter bands broken during spring migration (Miller and Broughton 1974). There was no evidence in this study to support these hypotheses in favour of reduced levels of insect harassment. Caribou were observed to coalesce on snow with group fragmentation often occurring as the animals moved off snowpatches to graze in the evening. Aggregation on snow occurred as caribou congregated onto a limited "resource" occupying a small percentage of the surface area of the E.S.A. The close association between levels of insect harassment and snowpatch selection suggests that this behaviour is a "temporary response to an immediate problem". The coalescence and dispersal of groups on a daily basis has been observed in other herds of varying size (White et al. 1975, Roby 1978).

The sudden decline in the number of caribou observed in the Macmillan Pass area in the second week of August may be due to several factors. Reduced numbers of mosquitoes obviated the need for permanent snowpatches as relief habitat. Although no data are available for 1984, permanent snow is thought to be less frequent at increasing distance from the Continental Divide at Macmillan Pass. The fragmentation of groups is commonly observed during August dispersal in Alaskan caribou and is an optimal foraging strategy. Oestrid fly harassment has also been proposed as a major reason for the dispersal of post-calving caribou (Curatolo 1975) perhaps due to the smaller numbers of these parasites and their method of host location (olfactory).

Patterns of group behaviour on and off snow exhibited considerable contrast in response to varying levels of insect harassment. The general pattern of an increase in standing with a decrease in eating and lying corresponds with activity data collected for reindeer in Norway (Thompson 1971) and caribou in Alaska (White et al. 1975, Curatolo 1975, Roby

1978). Standing is thought to be a direct response to oestrid fly harassment (Curatolo 1975) as the animals are more susceptible to attack when lying (Espmark 1968). Increased walking and running at Macmillan Pass also appear to be common responses to higher levels of harassment.

Comparison of overall activity patterns with previously published data is difficult in that these results are not standardized with reference to sampling frequency, group characteristics, climatic and insect variables etc. Some comparative data are presented in Table 7.5. There is a remarkable consistency in activity during insect-free periods between reindeer in the alpine tundra of Hardangervidda in southern Norway and caribou occupying low arctic coastal tundra at Prudhoe Bay. This suggests that during periods of no insect activity, the environment may assume a relatively minor role in dictating activity patterns. Oosenbrug's (1976) data for Woodland caribou of the Burwash Uplands exhibit a greater similarity to those for caribou at Macmillan Pass. This similarity is evidenced in lower percentages for grazing and lying and higher totals for standing. This may be partially due to the inclusion of data recorded under varying levels of insect harassment.

The most striking difference between Macmillan Pass and other published data is in the observation of standing animals (45% in this study, 1% at Prudhoe Bay and 3% at Hardangervidda). This is largely due to the disproportionate number of observations of animals standing on snow. Lying was observed approximately 50% less at Macmillan Pass than the other studies. Other than the possibility that this behaviour was simply not observed as often, it was thought that the lack of night-time data may explain this. Signs of bedding activity (i.e. compressed vegetation) in Willow-Forb and Birch-Lichen communities below 1600 m and the observed pattern of diurnal movements (Section 6.4) suggest a pattern of night-time resting to 'compensate' for extended periods of standing on snow during the day.

Table 7.5 Comparison of activity patterns in various groups of *Rangifer*

Author(s)	White et al.	Thompson	Oosenbrug	This study
Location	Alaska [1]	Norway [2]	Yukon.T [3]	Mac.Pass
Activity				
Grazing	53%	49%	35%	34%.
Lying	33%	30%	11%	15%
Standing	1%	3%	24%	44%
Walking	11%	14%	30% [4]	6%
Running	<1%	3%		<1%
Other	<2%	3%		

1- Adult caribou, 'insect-free data', July.

2- Adult reindeer, 'insect-free data', August

3- 'mid-summer' - 16 July to 20 August

4- Total for all 'travelling' observations

n.b. Thompson's data does not total 100%

7.4 Climate/Caribou Relationships

7.4.1 Introduction

It has been hypothesized that caribou utilize snowpatches as a means of behavioural thermoregulation. This may be achieved in three ways: movement towards a more favourable (less thermally stressful) environment; ingestion of snow, ice or meltwater or by changes in posture. It is known that the snowpatch possesses a cool microclimate in relation to adjacent and lower elevation snow-free zones. Movements towards and away from snowpatches were described in Section 6.4. Analysis of ingestion and posture is thus the focus of this section with the emphasis upon potential thermoregulatory benefits of snowpatch selection.

7.4.2 Ingestion

Under field conditions it was not possible to quantify the volume of snow that an individual animal consumed over a specified time period. A method was therefore devised which involved the analysis of posture with respect to head position. During each focal animal sample if the muzzle was visible above the snow surface the animal was classed in the "head raised" position. An animal was only classed as in the "head lowered" or "ingesting" posture when the muzzle was obscured from view below the snow surface. To exemplify, all the animals in Plate 19 would be classed as "head raised" whereas the animal in the upper left of Plate 15 is in the "ingesting" posture. Visible jaw movement was further proof that an animal was ingesting snow. The total time spent in the "head lowered" position (duration of snow ingestion) for each sample was calculated and correlated with air temperature. This was completed for each individual observation and as group averages for each long observation on snow. The relationship was found to be statistically insignificant for individual observations (Figure 7.12) due to the large number of samples with a duration of zero. Analysis of the individual data confirm that at air temperatures of less than 10.0°C, caribou spent a very small portion of the 10 minute sample period ingesting snow (mean = 0.08 mins, n = 24). Between

10.1°C and 16.0°C this figure increased (mean = 0.19, n = 185) and above 16.1°C caribou ingested snow for a considerably longer duration (mean = 0.37, n = This general trend is supported by the group — averaged values for the long observations on snow (Figure 7.13). A statistically significant positive correlation ($p < 0.05$) existed between the mean duration of snow ingestion for the entire group and the ambient temperature during the observation.

Comparisons of specific activities on and off snow were presented in Section 7.3. "Eating" contrasted considerably on and off snow. Ingestion of snow was a relatively short duration behaviour (both in terms of individuals and group averages) whereas grazing occupied the majority of time that animals spent off snow (Figure 7.14). Although indices of harassment were lower for the observations off snow, grazing activity was generally unaffected by harassment. For example, in Figure 7.14 indices of harassment of over 6 were recorded on only two occasions yet almost continuous grazing occurred when an index of 11.0 was recorded. No statistically significant relationships were calculated for the relationship between indices of harassment and the duration of ingestion either on or off snow. The higher correlation coefficient for observations on snow was thought to be largely a result of higher air temperatures and its influence on mosquito activity.

Analysis of the frequency of individual ingestion "events" on snow revealed a statistically significant ($p < 0.05$) relationship with insect harassment. It was found that under increasing indices of harassment caribou generally increased the frequency with which they ingested snow. This was due to the animals' increased response to insect harassment. Animals continuously harassed by mosquitoes would lift their heads to shake themselves in an attempt to reduce harassment. The frequency of ingesting events was also found to correlate with their duration ($p < 0.05$).

7.4.3 Posture

One of the ways in which caribou thermoregulate behaviourally is in the selection of snowpatches as a cool, resting area. The relative coolness of the snowpatch microclimate has

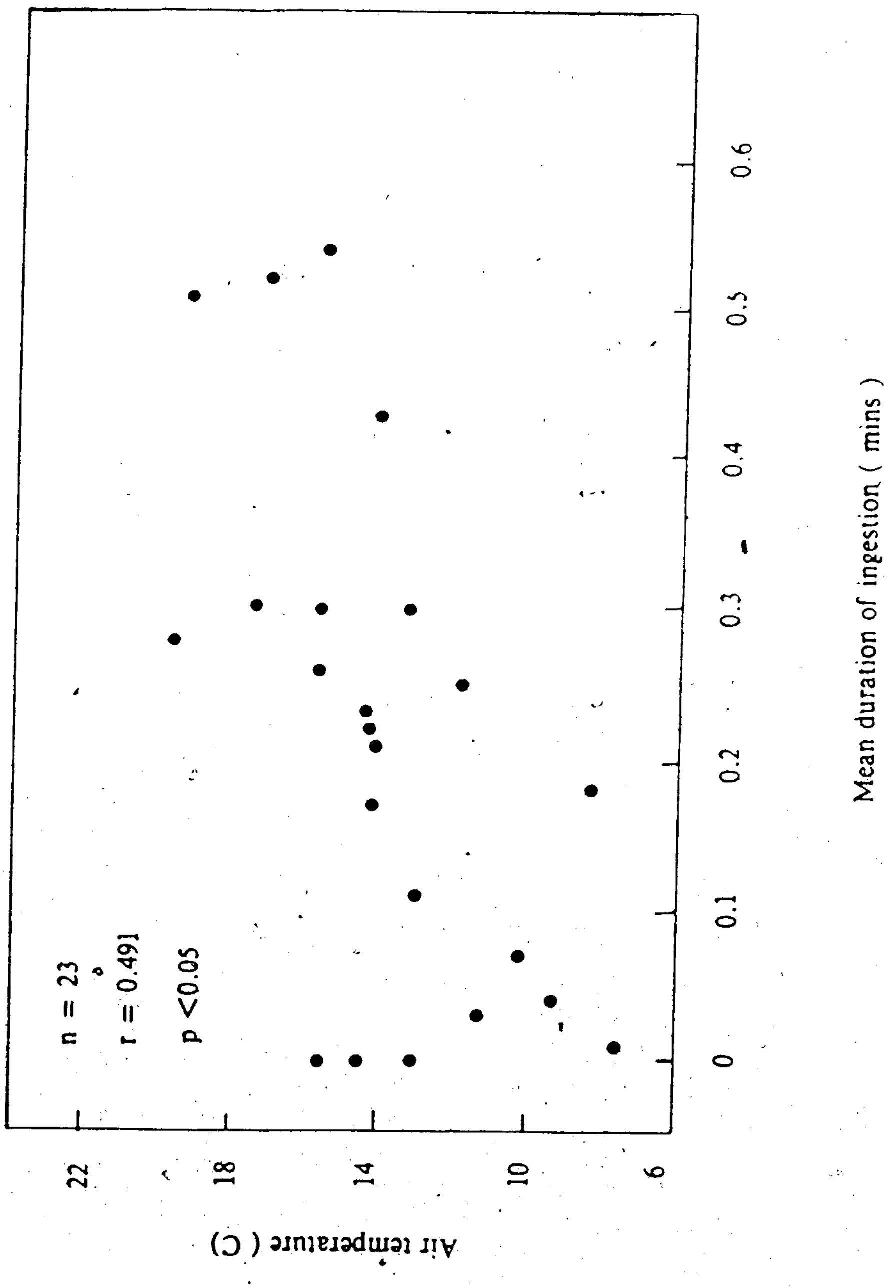


Figure 7.13 Variation in the duration of ingestion of snow by Woodland caribou compared with the index of harassment on and off snow.

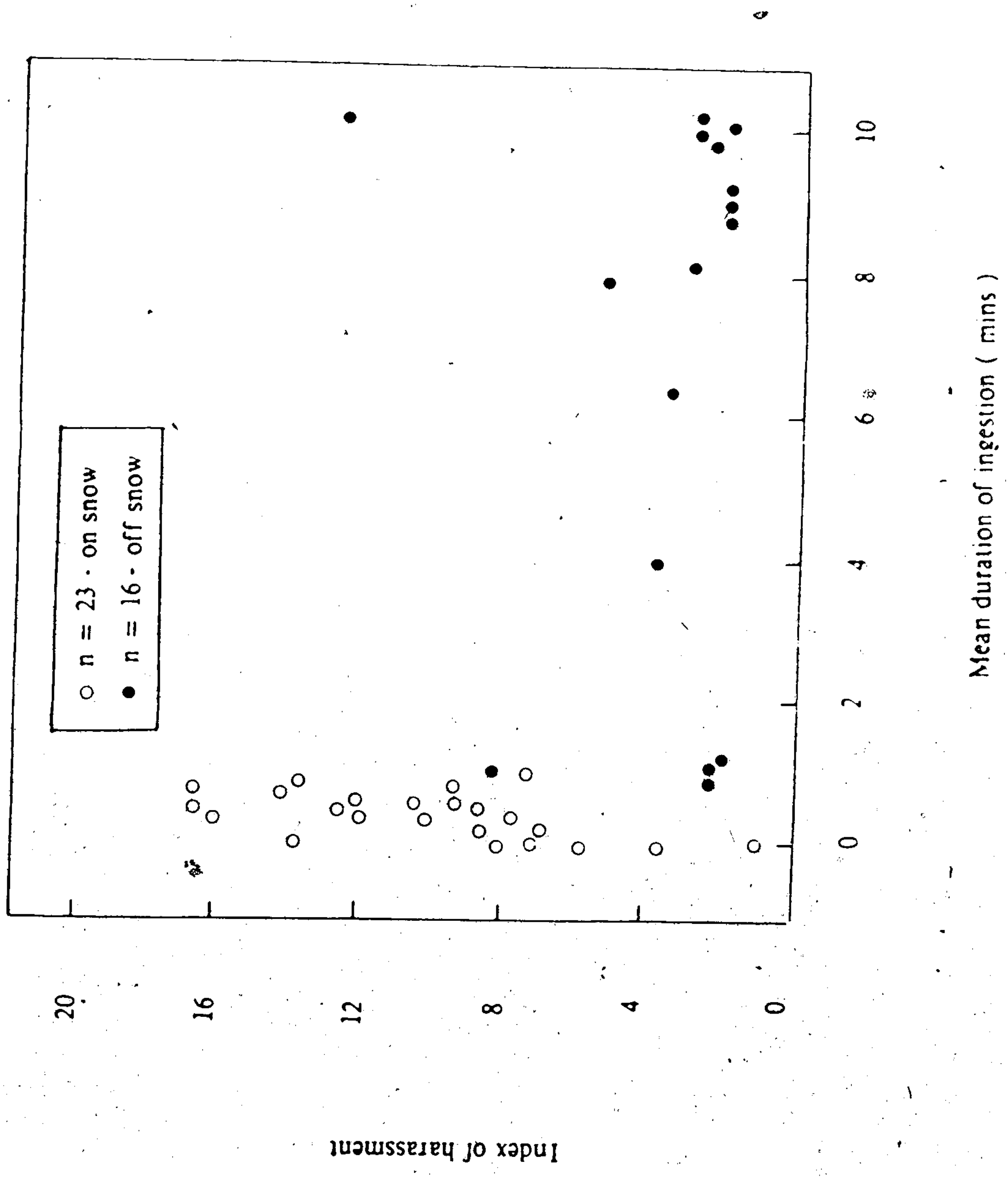


Figure 7.14 Variation in the frequency of ingestion events completed by Woodland caribou compared with the index of harassment.

been discussed. As with the analysis of snow ingestion, the duration and frequency of standing and resting behaviour was quantified for each focal animal sample. The scan sample data for group activity patterns described standing as three times more common than lying (45% to 15%) for all data and over five times more (66% to 13%) on snow. If the grazing/ingesting totals are included in the standing behaviour category, the "resting/standing" ratios increase to 1:5.3 overall and 1:6.3 on snow. This pattern is generally supported by the focal animal sample data. Combining all group-averaged values for the 10 minute sample period, the mean duration of all standing behaviour was 7.9 minutes for all observations and 8.6 minutes for observations on snow.

Resting behaviour was found to be largely dependant upon levels of insect harassment. The mean duration of standing behaviour on snow increased with the level of insect harassment ($r = 0.371$). Under 'severe' harassment (i.e. a mean index > 16.0) lying on snow was not observed at all. Resting on snow at length (e.g. for more than four minutes mean duration) was only observed on two occasions when mean indices of harassment were below 4.0. Observations off snow were less variable in that 10 of the 16 (62.5% observations recorded a mean duration of 10 minutes standing. The predominance of grazing activity off snow provides an explanation for this behaviour. The frequency with which caribou changed posture from standing to resting also varied between observations on and off snow. (Mean frequency for all observations off snow = 0.11; on snow = 0.65). A maximum value of 6 (i.e. 3 separate periods of standing or resting) was recorded on snow. No relationship with insect harassment was evident either for individual or group averages as it became obvious that animals would not bed down at all under severe insect harassment.

Calves were generally more precocious and changed posture most frequently. One calf bedded on snow and stood up again immediately on three separate occasions within a seven minute period. Often this was a response to harassment as evidenced by "shivering" and stamping when standing. On several occasions however, no behavioural responses were observed upon standing which may suggest that movement was related to the physical comfort of the individual. Caribou were observed on occasion to lie with the underside or side of the head resting on the snow surface for brief periods (Plate 20). This behaviour was not quantified but may represent a definite thermoregulatory response which is discussed later. Snow ingestion was rarely observed when animals were lying.

It is possible that caribou orient themselves as a means of behavioural thermoregulation. Analyses of group and individual orientation with reference to wind direction and solar azimuth were thus attempted. Individual animals were classed as parallel to the wind (facing towards or away from the wind), perpendicular to it, or with no specific orientation. (This third category included those observations when wind speed was zero, i.e. no direction). A group was classed as oriented parallel or perpendicular to the wind when 50% or more of the group were oriented in the same direction. Between July 10 and August 16 (when the high station and wind direction sensor were operational) a total of 1579 scan samples specifying oreintation were taken - 925 on snow and 654 off snow. Observations off snow were differentiated in terms of group that were travelling and those adjudged to have no directed movement. (Group members naturally assumed a common orientation when travelling).

For groups on snow, orientation parallel to the prevailing wind direction was observed more frequently than perpendicular or those with no specific orientation (Table 7.6). Employing the same methodology to quantify scan samples with respect to insect harassment as before, almost half (49.6%) of the scan samples, under conditions of 'severe' insect harassment, were of groups oriented either into or away from the prevailing wind (Plates 21). Orientations were generally more random under lower levels of harassment.

Orientations were more random off snow. Although sample size was small, caribou groups did not consistently orient movements into the wind. Random orientations were also more commonly observed than either orientation class for 'static' animals. 22.9% of observations off snow were of individuals or groups oriented parallel to the prevailing wind direction. Levels of insect harassment were significantly lower for these observations. On July 20, a lone cow was observed standing on an exposed ridge for 111 minutes during which time it

Table 7.6 Orientation of Woodland caribou with respect to wind direction.

Orientation									
Surface	On Snow			Off Snow					
Movement	'Static'			Travelling			'Static'		
Level of harassment	none	mild	severe	none	mild	severe	none	mild	severe
Parallel to wind	0	58	191	0	5	4	80	58	4
Perpendicular to wind	0	39	45	2	9	11	66	32	4
No orientation	12	431	149	0	0	0	161	214	0
Total # of scans	12	528	385	2	14	19	307	304	.8
% of observations parallel to wind direction	0.	11.0	49.6	0	35.7	21.0	26.1	19.1	50.0

remained essentially motionless (Plate 21). No signs of insect harassment were recorded throughout the observation with the animal facing into a wind averaging at 4.2 m s^{-1}. It is not possible under field conditions to determine if caribou orient themselves parallel or perpendicular to the wind as a means of cooling the body. It may be postulated that a parallel orientation downwind increases the animal's sensitivity to sound and/or smell. Their awareness of potential predators is thus enhanced.

Exposed, windswept ridges were also selected during observations on snow. Snowpatch number 13 — the main aggregation site — was located on either side of an arete ridge (Plate 8). Within the snowpatch boundaries this was a favoured location for caribou either standing (Plate 19) or resting (Plate 20). Although a microclimate station was not erected at this location (due to potential 'disturbance' effects), sampling at regular intervals permitted the derivation of a mean wind speed 31% higher at the ridge crest than at the centre of the snowpatch. Evidence from direct observation and the degree of disturbance at the snow surface suggested that the ridge at the main aggregation site was the most frequently selected zone within the E.S.A.

The orientation of individuals and groups was also analysed with reference to solar azimuth. Similar classifications of orientation were attempted with the data sub-divided into observations on and off snow and under clear skies (direct and diffuse beam radiation) and overcast skies (diffuse only). On snow, of the 744 scan samples under clear skies, 41 (5.5%) were of groups oriented parallel to the sun, 205 (27.6%) were of perpendicular orientations with the remaining 498 (66.9%) possessing no specific orientation. Observations off snow occurred mostly under overcast skies (83.9% of the samples) with 73.2% of these with no specific orientation. No statistically significant relationships were found among any of these data. Wind direction and solar azimuth were thought to be only partly responsible for animal orientation. The majority of observation data on snow were collected at the main aggregation site. In view of the steep slope angle of this snowpatch (28°) it is likely that an individual standing at this site for long periods would select a posture that placed least physical stress upon it. With the added ease of snow ingestion, theoretically, an animal facing upslope would be in the "optimal posture".

Previous analyses have identified air temperature, wind speed and wind direction as factors influencing animals' behaviour and snowpatch selection. Caribou were also observed to exhibit specific responses to precipitation. Individuals and groups were frequently observed to continue grazing during intense and heavy rainfall with sporadic hail showers also eliciting no specific behavioural response. On two separate occasions however, groups were observed to move off snow in direct response to the onset of a storm. On August 10 at 17:48 h a mixed group of 40 caribou were observed to move off snowpatch # 13 on which they had been observed for over 6 hours. A sudden heavy rain shower fell on the mountain at this time. The entire group descended through the centre of the study area towards the Tsichu River valley at a brisk trot. On July 14 a group of 29 animals moved off snowpatch number 15 at the onset of a brief rain shower. There followed a period of continuous grazing throughout the duration of the shower and an almost immediate return to the snowpatch as rainfall ceased. Coincident observations of insect harassment on and off snow explain this behaviour. The immediate reduction in insect activity during the shower allowed caribou to move off snow and graze in areas adjacent to the snowpatch. Similar patterns of behaviour were observed by Archibald (1973).

7.4.4 Discussion

In theory, caribou in the vicinity of Macmillan Pass may attempt to thermoregulate behaviourally in several ways. They are capable of physically moving to an environment that, fo~~r the~~ moment, places the least stress upon them — their "preferendum". The snowpatch (zone) clearly represented the preferendum of the animals under study although this was shown to be largely dependant upon macroclimate. The ability of animals to further alter their environment by changing position with respect to topography was also evident in the selection of relief habitat such as exposed and windswept ridges. Group and individual orientation and other postural changes were found to be of some importance in this study. The ingestion of snow, ice or meltwater was a voluntary response to potential heat stress and thus also represented a form of behavioural thermoregulation. The limitations of the field situation precluded any analysis of physiological (involuntary) means of thermoregulation.

It was not the intent of the field study to monitor,the "climate" of the animal. Nor is it the objective of this discussion to "model" the situation. As Oke (1978) states, "The interactions between the atmosphere and animals represents one of the highest levels of complexity in the boundary layer" (p. 160). Analysis of energy flux over the body surface is further complicated by spatial variability in heat transfer. Most experimental and theoretical studies of the 'climates of animals'' employ simplified models of energy balance and body geometry which assume uniform fluxes averaged over the body surface (Monteith and Mount, 1974). An integrated approach incorporating individual analyses of local micro-scale energy balances is essential to a complete understanding of the interaction of animal and environment.

The energy balance of the caribou may be written as:

$$Q^{*} + QM = QH + QE + QG + \Delta QS \qquad (7.1)$$

The sign convention follows that of equation 5.1 with QM being the rate of heat production by metabolic processes and ΔQs the net change of body heat storage. Q^{*} usually represents a channel of heat loss but may become a heat source during periods of strong radiant heat loading (Oke 1978). In fact, solar radiation intercepted by an animal in bright sunlight is often the largest single factor in the total energy balance and may exceed total metabolic heat production by an order of magnitude (Cena, in Monteith and Mount 1974). The shade-seeking response of caribou adjacent to the Trans Alaska Pipeline System as observed by Roby (1978) and at the mining camp at Macmillan Pass may represent an attempt to reduce irradiation. Cooler air temperatures (and subsequent reduction in insect activity) may also be of some importance however.

Theoretically, Q^{*} as a heat source is increased by snowpatch selection. The short-wave irradiance of a dark animal on snow is higher than adjacent vegetated or unvegetated surfaces of lower albedo. The disproportionate selection of snowpatches under conditions of high insolation suggests that caribou are tolerant of high levels of radiant heat loading.

Metabolic processes always act as a source of heat. Thermoregulation through increased metabolic heat production has been assessed in the literature largely in response to cold stress. Increased activity (and the generation of metabolic heat) has been proposed as a response to low ambient temperatures and low wind chill values (Moen 1968, Ozoga and Gysel 1972). Heat generated through metabolic processes would be absorbed in raising ingested snow to body core temperature. Net heat storage (ΔQS) remains close to zero as fluctuations in body temperature are low under a wide range of temperature extremes (Yousef and Luick 1972). Heat loss is thus essentially partitioned through convection (QH), conduction (QG) and evaporation (QE). Loss of heat by evaporation is the principal means by which homeotherms avoid heat stress (McLean, in Monteith and Mount 1974). Evaporation occurs from the moist surfaces of the respiratory tract in caribou. Although recorded rarely in other herds (e.g. Curatolo 1975) no animals in this study were observed to engage in prolonged periods of panting. Barren-ground caribou have been observed to wade into the frigid waters of the Arctic Ocean (White et al. 1975) and stand in shallow water bodies on Baffin Island (Elliot 1972). Surface wetting of the skin will increase evaporative heat loss. No caribou or caribou sign were observed around any of three small lakes within the E.S.A. This may be attributed to the suitability of such areas as mosquito breeding habitat.

The influence of the environment on non-evaporative heat exchange other than heat gain by solar radiation is best described by Newton's Law of Cooling, which states that ".. The rate of heat loss (from an object) ... is proportional to the temperature difference between the object and its surroundings." Sensible heat loss is reduced by the high insulative value of the fur. The shedding of the heavy winter pelage was evident with discarded hair visible on the snow surface. The thinner summer coat facilitates sensible heat loss. (Absorption of radiant energy is also reduced by the lighter tone of the coat). The cooler air temperatures above the snow surface will increase the animal - environment temperature difference and thus increase sensible heat loss.

In comparison to other exchanges, heat loss or gain by conduction is usually negligible (Oke 1978). Heat loss by conduction through contact with the ground should be increased by standing on snow compared to snow-free areas. (The lower temperatures maintained at the peripheral regions serves to minimize this heat loss). Lying down would bring a larger surface area of the animal into contact with the snow and enhance heat loss by conduction.

Much of the literature describing thermoregulation in caribou has been concerned with responses to cold stress. Blix and others (1979) described heavy mortality among reindeer calves when wind and rain occur early during the calving period. Hart and others (1961) found that caribou calves steadily increased their metabolism as ambient temperature fell. Cottle (1959) found that cold temperature thermoregulation was well developed in caribou calves with the rate of heat loss dictated by wind speed and air temperature.

It was not possible under field conditions to quantify the volume of water that an animal ingested. The ingestion of snow as a response to heat stress represents a plausible hypothesis but one which cannot be accurately assessed under anything other than controlled laboratory conditions. Caribou adopted a variety of heat postures. Selecting one of these as a criterion for snow ingestion may be criticised. Animals were observed resting or standing with their muzzle and nose either on the snow surface or within a crater. The snowpatch depth and unvegetated substrate precluded digging for forage as an explanation for this behaviour. It is possible that this may be a direct response to nose bot harassment. Epsmark (1968) often observed small groups of Swedish reindeer closely aggregated "in a curved formation with heads lowered and pointing towards the centre of the group, thus making the nostrils approachable with difficulty" (p. 162). Epsmark's observations were reinforced by filming idividual cases of oestrid fly harassment and reindeer response. Similar group behaviour was observed on snowpatches at Macmillan Pass (Plate 14).

Snow ingestion as a means of thermoregulation was not thought to be as important to caribou as originally hypothesized. Although it was not possible to assess the temperature regime of the individual animals, ambient temperatures over snow were not thought sufficient to initiate high levels of heat stress. Air temperatures over 20°C were rarely recorded over snow. Under laboratory conditions, Yousef and Luick (1972) found that physiological responses (e.g. oxygen consumption, heart rate, respiratory frequency and rectal temperature) were only found to show a marked increase at environmental temperatures above 30 °C. Rosenmann and Morrison (1967) found no increase in the rectal temperature of summer-acclimatized reindeer exposed to temperatures of 43°C for 7 hours. The concensus within these two studies was that reindeer possessed a good capacity for heat resistance when water was available but a poor resistance to water deprivation. The occasional ingestion of snow may help fulfil this requirement for caribou at Macmillan Pass.

Standing has been proposed as a direct response to insect harassment (Curatolo 1975, Roby 1978). Epsmark (1968) described the increased susceptibility of resting reindeer to warble-fly attack. Standing may also increase body heat loss. The long, slender limbs of caribou are well suited to heat exchange. The sensitivity of standing animals to cooling factors in the environment has been noted (especially for newborn calves) by several authors (Cottle 1959, Hart et al. 1961, Hissa et al. 1981). All of this work is concerned with the possible influences of cold stress. Increased wind speed decreases the insulative value of the fur which increases sensible heat loss from the animal. Standing on exposed areas with relatively high wind speeds such as the arete ridge of the main aggregation site may thus represent habitat selection for optimal heat loss.

Oritsland (1974) devised an index for homeotherms in which the solar heat load upon the animal was calculated as a function of irradiance and wind chill. Solar radiation and wind are thus thought to be of considerable importance upon the thermal regime of warm-blooded animals. Orientation with reference to these parameters may be of some thermoregulatory benefit to caribou. Some doubt exists as to whether caribou orient themselves into the wind. Skoog (1968) found no association. Data in this study support Curatolo's observation that caribou orient into the prevailing wind only when insect harassment is high. Presumably, strong winds keep insects away from the sensitive facial areas (where the fur is thin). Under experimental conditions with a calf pelt attached to a hot plate, Lentz and Hart (1960) described maximum heat loss when air flow occurred perpendicular to the "grain" of the fur. Although no information on fur grain was available for the animals under study, it is likely that an orientation into the prevailing wind would maximize heat loss. In winter, resting caribou orient themselves with their backs facing into the prevailing wind to protect sensitive areas and conserve body heat (Henshaw 1968).

Orientation into the sun has been described as a means of body temperature regulation in poikilotherms (Kevan et al. 1982). No complementary data have been collected for homeotherms from caribou at Macmillan Pass. Joubert (1972) claimed that Hartmann Zebra (*Equus zebra hartmannae*) regulated body temperature by orienting their bodies to change the light-dark ratio of their stripes. Thermography data have illustrated higher skin temperatures recorded for black patches on domestic cattle. In view of the dark coat colouration of caribou, orientation parallel to the sun would result in a lower solar heat load on the animal than a perpendicular orientation, especially for caribou standing on snow.

Studies attempting correlative analyses between behavioural and environmental variables for caribou in summer reinforce the overall importance of insect activity in influencing activity patterns. Direct climate/caribou relations appear somewhat more spurious. Part of the problem lies in the autocorrelation between weather variables. For example, a specific behavioural response positively correlated with increased air temperature will be negatively correlated with relative humidity due to the inverse relationship between these two climatic variables. The negative correlation between air temperature and the incidence of lying described by Curatolo (1975) for Alaskan caribou is explained by the positive correlation between air temperature and standing, itself a direct response to increased insect harassment. Similarly, a positive correlation between wind speed and feeding activity, described by Roby (1978) is almost certainly due to the influence of wind in regulating insect numbers. Wind speed and lying were also found to positively correlate in Curatolo's data.

Other climatic variables were not thought to be of equal significance to wind speed and air temperature. Cena in Monteith and Mount (1974) found relative humidities of between 35% and 70% to have no influence upon domestic cattle although higher humidities were thought to influence the passage of air through the respiratory tract. Darling (1937) thought that varying levels of atmospheric water vapour influenced the olfactory perception of red deer (*Cervus elaphus* L.)

Caribou at Macmillan Pass were found to be generally tolerant of summer precipitation in accordance with other unpublished data (Curatolo 1975, Roby 1978) with behaviour generally corresponding to expected patterns as a result of reduced insect activity (e.g. increased feeding).

In view of the limitations imposed by field methods, it is difficult to supply conclusive evidence that Woodland caribou select snowpatches primarily as a means of thermoregulation. Several theoretical statements may be proposed describing relationships between caribou physiology and behaviour and environmental variables. The extension of experimental or laboratory-proven results to the natural setting is highly spurious. The intricacies of heat transfer between the animal and the environment cannot be fully understood under field conditions. However, a high tolerance for climatic extremes is a characteristic of all homeotherms. Published data describing upper critical temperatures for both domestic and wild ungulates define air temperatures at least 10°C higher than those at Macmillan Pass. Yousef and Luick (1972) found reindeer to be almost as heat tolerant as some desert ungulates. Similar behavioural responses to changing weather conditions have been documented for different caribou groups. During the summer months these relationships consistently reinforce the importance of insect harassment in dictating activity patterns. The role of wind speed and air temperature in regulating insect activity in this study supports the general concensus within the literature that climatic variables essentially modify as opposed to directly influence caribou behaviour. The fundamental problem is in separating behavioural responses from climatic variation or variations in insect harassment (Chapter 6).

8. CONCLUSIONS

In several respects this is a unique study. Snowfall and snow cover have been widely discussed as an integral part of caribou range in relation to winter ecology. In contrast, no previous work has attempted to document, describe and explain snowpatch selection during the summer-fly season despite the recognized importance of this habitat in several circumpolar populations.

The literal treatment of the hypotheses proposed in an attempt to explain this behaviour was of value in isolating variables for subsequent analysis. However, the underlying problem throughout the thesis was in identifying specific cause-and-effect relationships. High air temperatures were coincident with high levels of insect harassment. Snowpatch selection occurred most frequently under such conditions. Attributing this behaviour to one specific cause was not possible under field conditions. Of the two hypotheses identified, snowpatch selection as a means of reducing insect harassment was favoured over thermoregulation for three reasons :

1. Indices of harassment for individuals were consistently greater on snow than off it. Movements towards and away from snow were observed as an immediate response to fluctuations in insect activity. For example, sudden rain squalls temporarily suppress insect flight and animals move off snow to graze under reduced levels of harassment. (The coincident benefits of reduced heat stress should also be acknowledged).

2. Aggregation as a response to insect harassment was more frequently documented on snow than off snow. Behavioural analyses of individuals and groups (e.g. standing with head lowered onto the snow surface) are consistent with other documented evidence of response to oestrid fly harassment.

3. The documented tolerance of *Rangifer* for ambient temperatures well above those at Macmillan Pass during the summer of 1984 suggest that caribou were unlikely to suffer unduly from heat stress.

The snowpatch environment did provide a source of water to potentially heat stressed animals and individuals were frequently observed to ingest snow. It should be stated therefore, that although individual and group behaviour suggest that snowpatches were sought primarily under conditions of high insect harassment, the coincident benefits of snow ingestion cannot be rejected as insignificant.

The conclusions from any study of this nature are limited by the methods adopted in the field. The sampling procedure of concentrating upon the first sighting inevitably omitted a large portion of the population. The representativeness of these data for the entire population may be questioned. Quantitative, ground survey work supplemented by repeated aerial transects would provide a more complete regional perspective. Similarly, a more complete climate monitoring network is essential to understand the variability of mountain microclimates. This may also reduce the margin of error in attributing behavioural response in individuals and groups to changes in microclimate recorded at a station located away from the group under study. Studies such as this and the work of Helle in Finland, in attempting to test specific hypotheses through quantitative analysis should be used as a basis to formulate standardised procedures applicable to other groups and locations.

Potential disturbance to northern mammals has been the focus of considerable research over the past ten years. The implications of this for caribou summering at Macmillan Pass have also been studied (Collin 1983, Kershaw and Kershaw 1983b). This study adds little to this aspect of caribou ecology other than to reinforce the view of potential conflicts arising from increased human activity at Macmillan Pass. The tungsten mine at Mount Allen on the Continental Divide is located within the snowpatch zone. Observations at the minesite in 1984 supported previous studies in concluding that caribou become habituated to certain disturbances. Limited development such as the Mactung mine does not appear to have drastically affected caribou although data prior to disturbance are non-existent. The current dichotomy in the caribou/development issue (Miller and Gunn 1985) illustrates the uncertainty that exists concerning long term impacts of human activity on caribou populations.

Furthermore, a full scale mine with associated developments (mill, townsite, transport routes etc.) would certainly exceed the level of present day-activity.

Should the recreational and tourist viability of Macmillan Pass be fully realized; the influx of human activity of a different magnitude to the minesite may be more detrimental than present levels. The mountains around the Continental Divide provide excellent hiking opportunities into the snowpatch zone. The increased visibility of caribou on snow may attract recreationists towards these areas. Repeated disturbance may lead to displacement from traditional summer range. At present, the frequency of snowpatch distribution, the availability of alternative relief habitat (e.g. windswept alpine ridges) and the documented adaptability of caribou suggest that groups occupying Macmillan Pass in summer are in no immediate danger of summer range reduction.

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APPENDIX 1

SELECTED PLATES

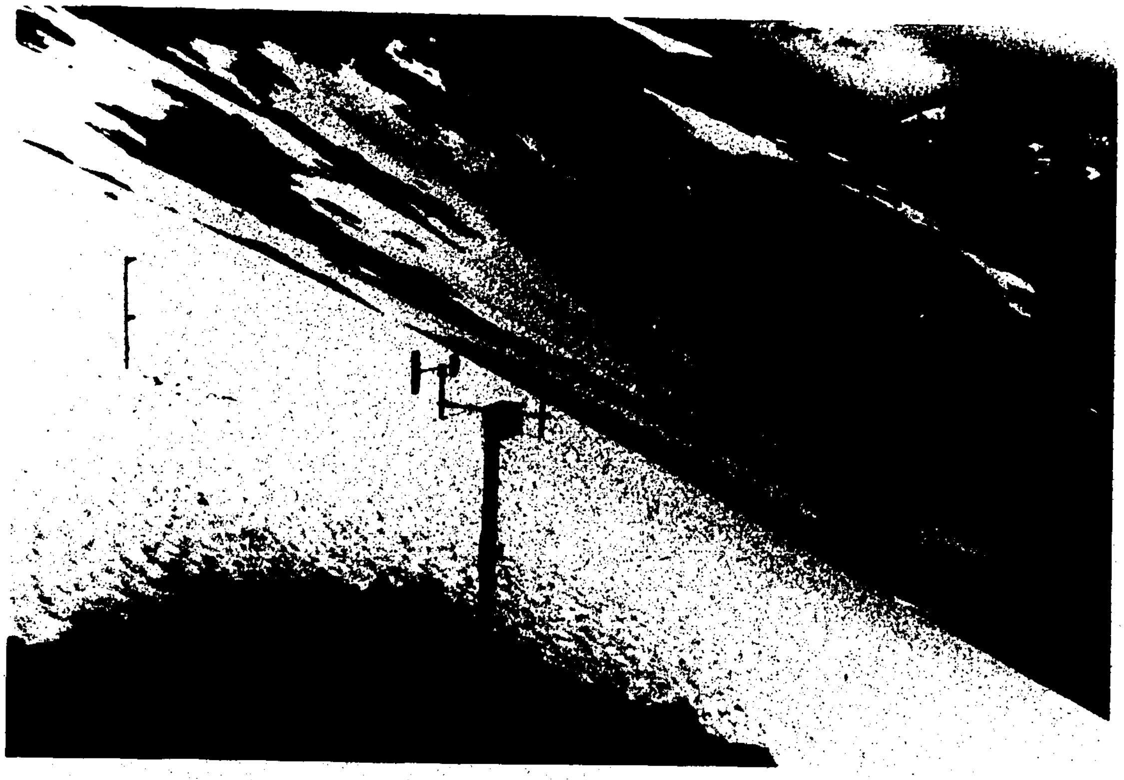

Plate 1. At the exposed High Station climatic data were collected over snow and lichen-encrusted felsenmeer at heights of 0.5 and 1.5 m. The Main Aggregation Site lies beyond the ridge in the middle distance.

Plate 2. At the High Station data were transferred from sensors to the internal memory of a CR21 micrologger and dumped to magnetic tape and an SM64 solid state storage module.

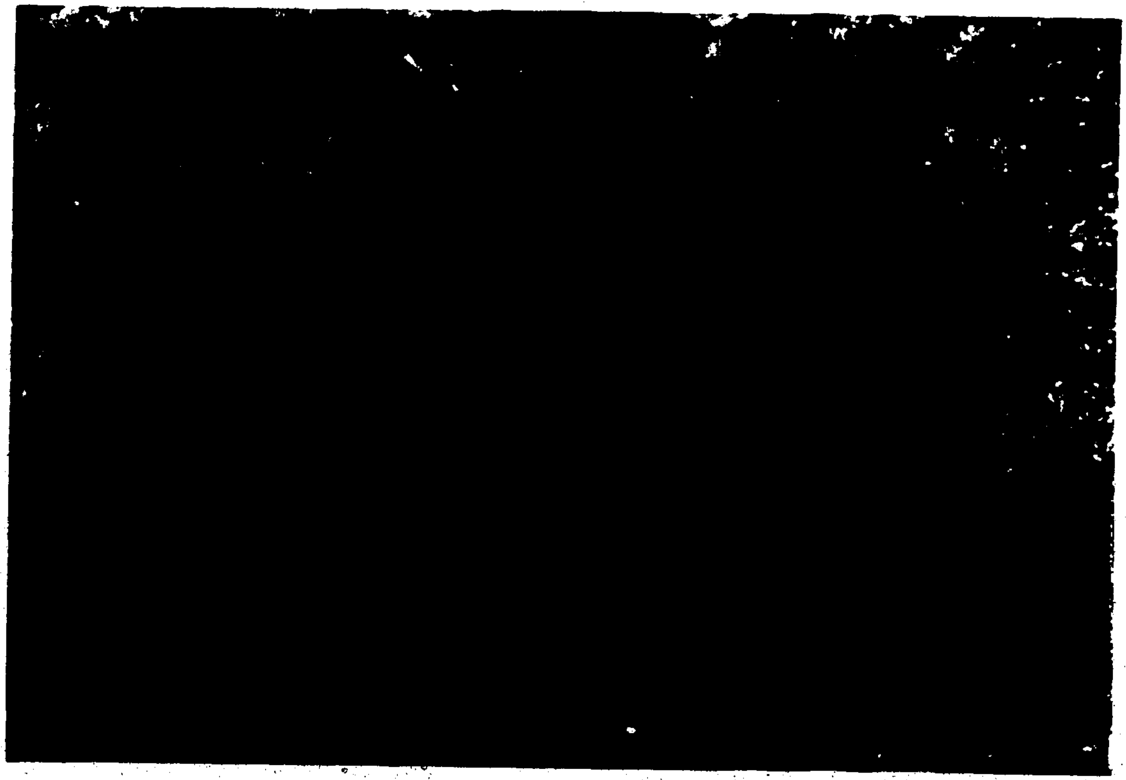

Plate 3. Simple insect traps were located in selected habitats such as this Lichen-Heath community.

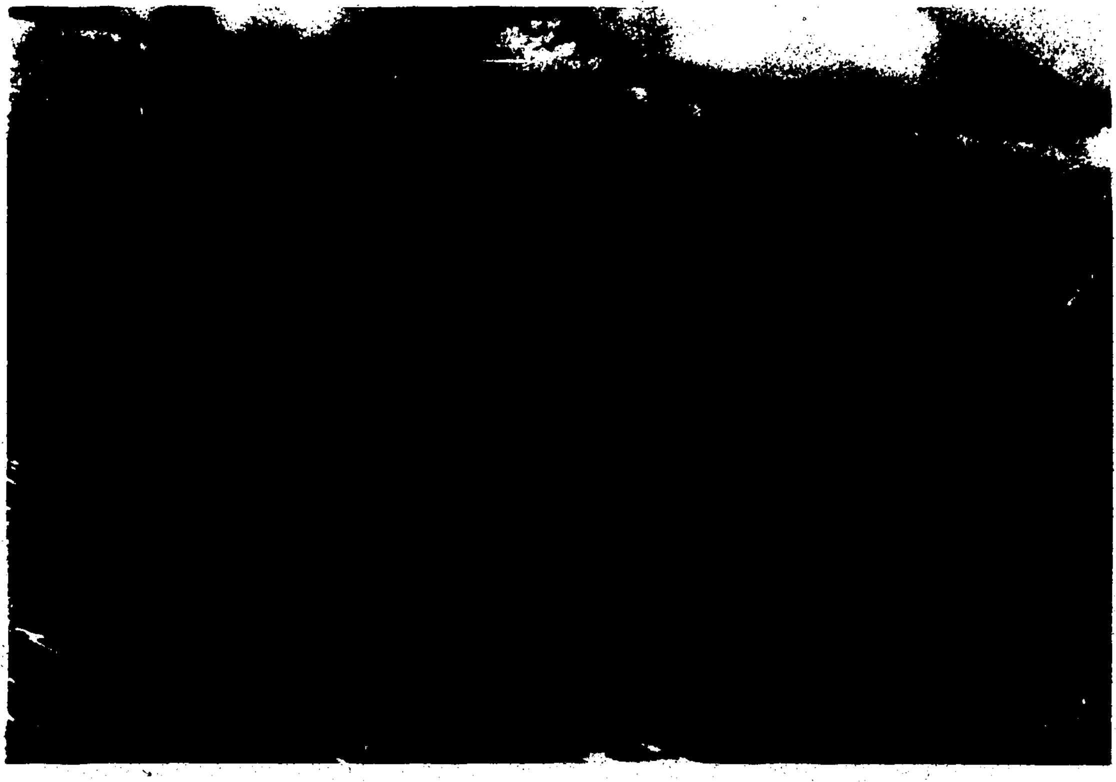

Plate 4. Snow cover within and to the north of the Extensive Study Area. [illegible] 17 1984. Note the icing on the Tsichu River at left of centre.

Plate 5. Snow cover within and to the east of the Extensive Study Area. Basecamp was located at lower left of centre. June 17 1984.

Plate 6. The eastern sector of the Extensive Study Area. June 20 1984. No snow remained on the south-facing slopes (centre) with sinuous patches extending to No [illegible] Lake (upper right). Note the game trails etched into the talus at left of centre.

Plate 7. Snow cover in the southern sector of the Intensive Study Area at the beginning of the study period June 17 1984. No evidence of caribou activity was recorded at this time other than the single trail in the snow at left of centre.

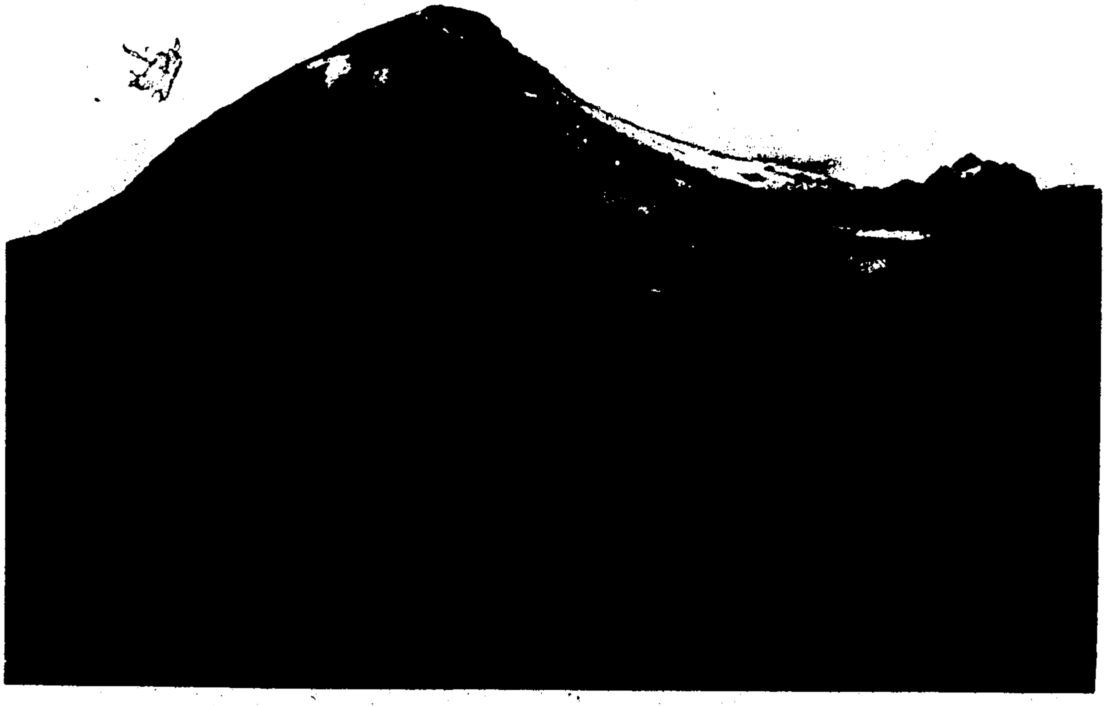

Plate 8. Snow cover in the southern sector of the Intensive Study Area towards the end of the study period. August 11 1984. Fresh snow covers the land above 1900 m. The Main Aggregation Site (Snowpatch # 13) and key observation points are visible.

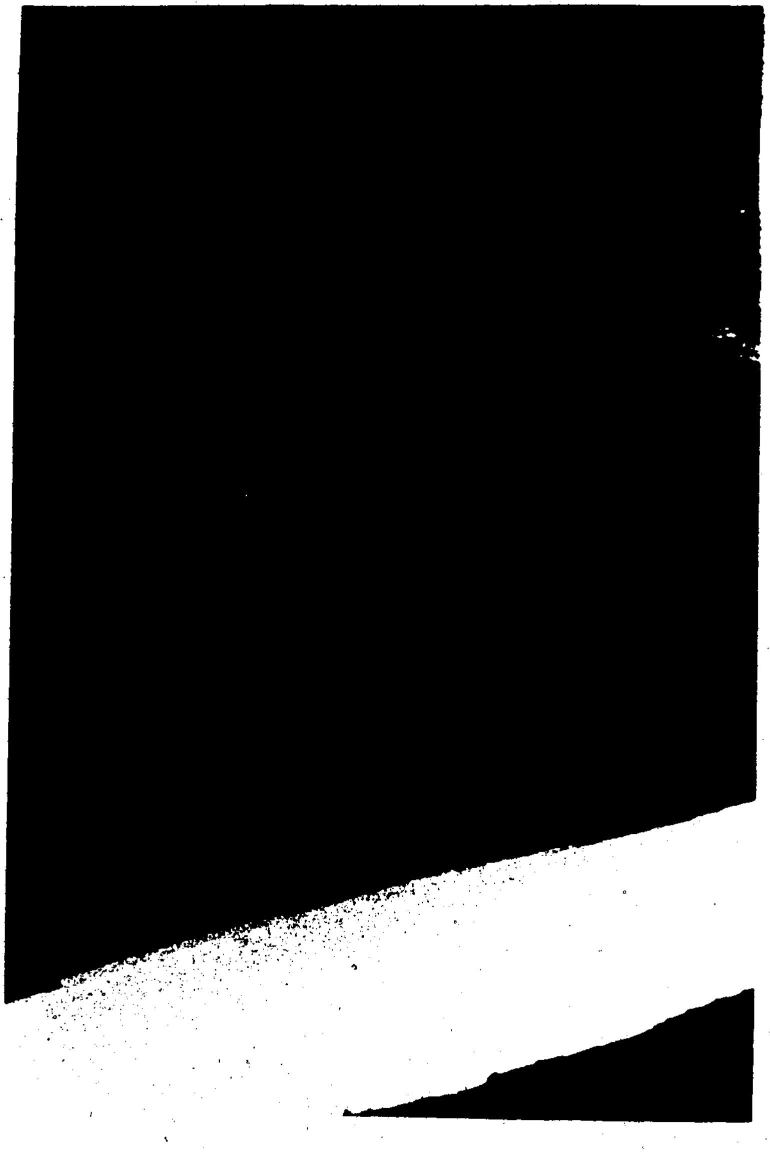

Plate 9. Caribou were frequently observed in close proximity to permanent snowpatches if not always aggregated on the surface. The animal at lower right is ingesting meltwater at the snowpatch margin. July 22 1984.

Plate 10. On overcast and cool days many animals showed no preference for either snowpatches or snow-free areas. This photograph shows part of a post-calving aggregation of 216 animals - the largest observed during the study period. June 24 1984.

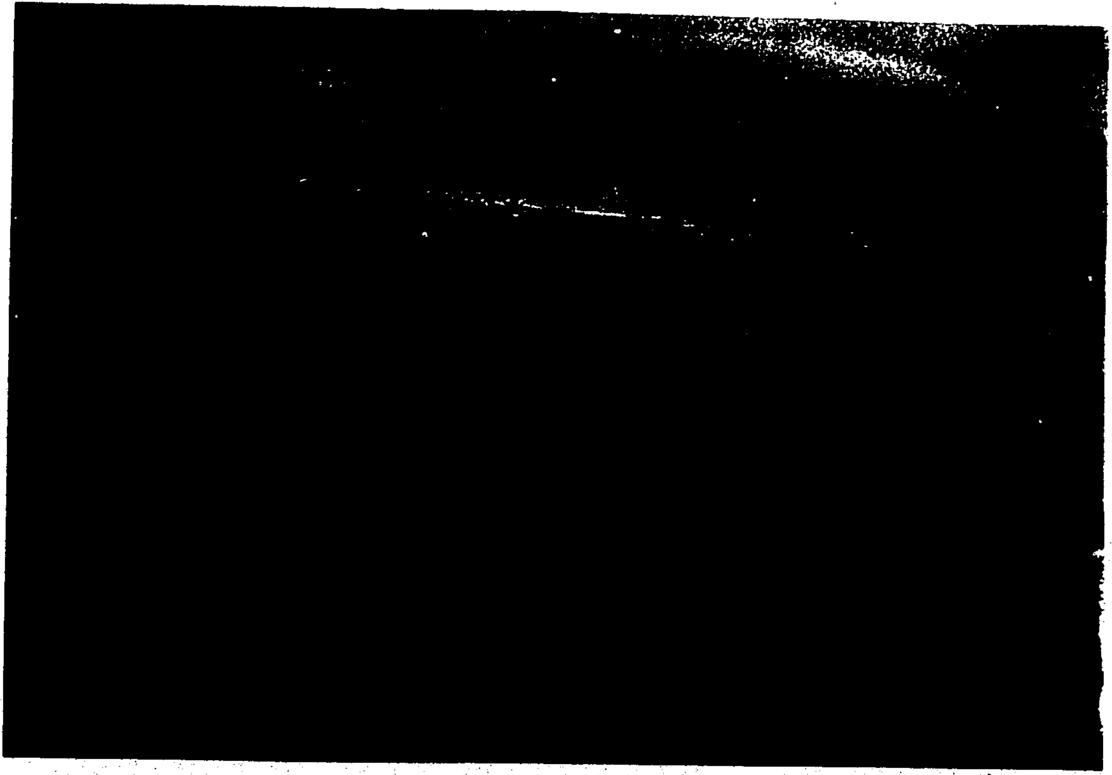

Plate 11. Approximately eight weeks after parturition the development of the newborn calf is rapid. July 30 1984. At this time cow/calf groups are most frequently observed at higher elevations as they leave the calving grounds to the east.

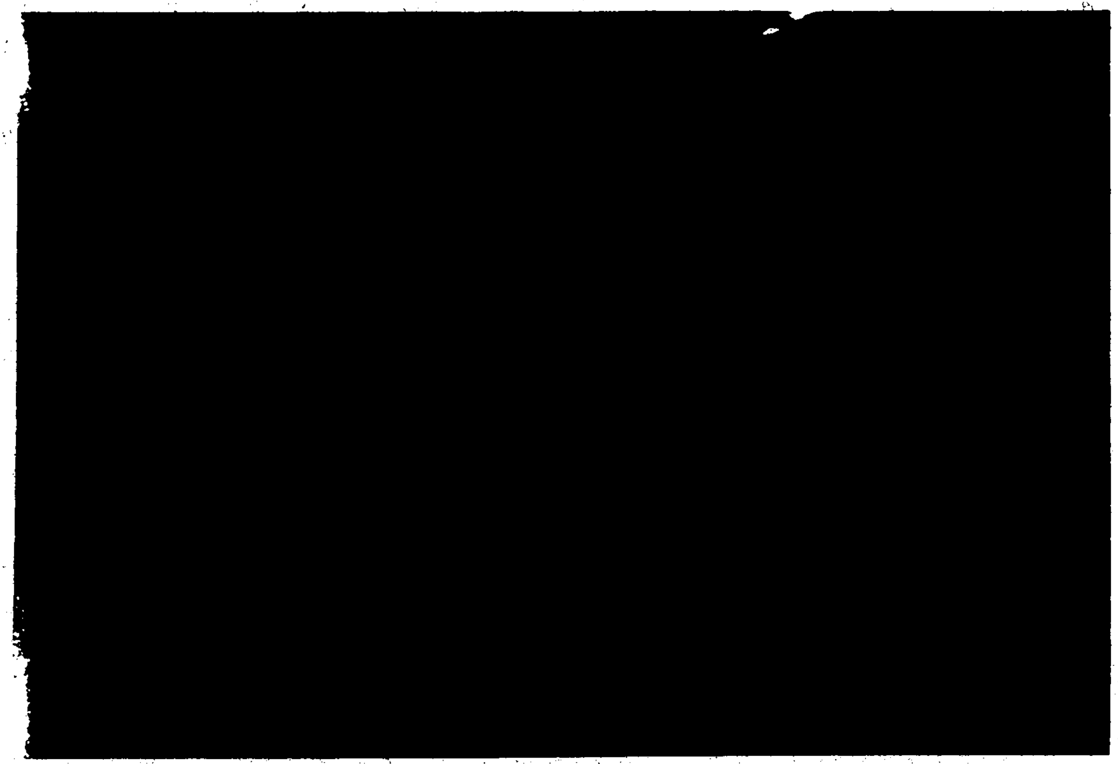

Plate 12. Mature bulls were observed mostly alone or in single sex groups of up to eight. Movement into the study area from winter range occurs later than the cow/calf groups - the first adult bull was observed on July 6.

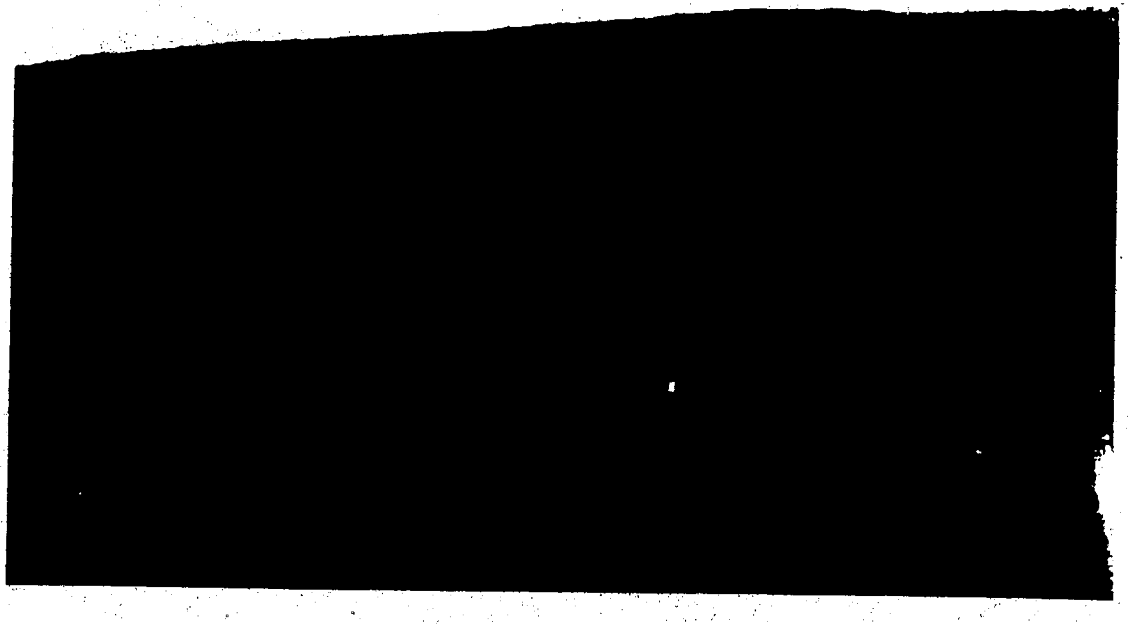

Plate 13. Lowered air temperatures and reduced levels of insect harassment allow caribou to move off snow and graze at lower elevations in the evening. The patches of bare ground at centre are due to late-lying snow occupying hollows and gullies on the tundra surface. July 20 1984.

Plate 14. Groups such as this were classified as being "closely aggregated" with a mean inter-individual distance of less than or approximately equal to one body length. Theoretically, aggregation will reduce insect harassment *per se*.

Plate 15. July 17 13:30 h. With an air temperature of 16.2°C and a wind speed of 5.6 m s^{-1} indices of harassment between 0 and 11 were recorded. The group response to these conditions is to disperse.

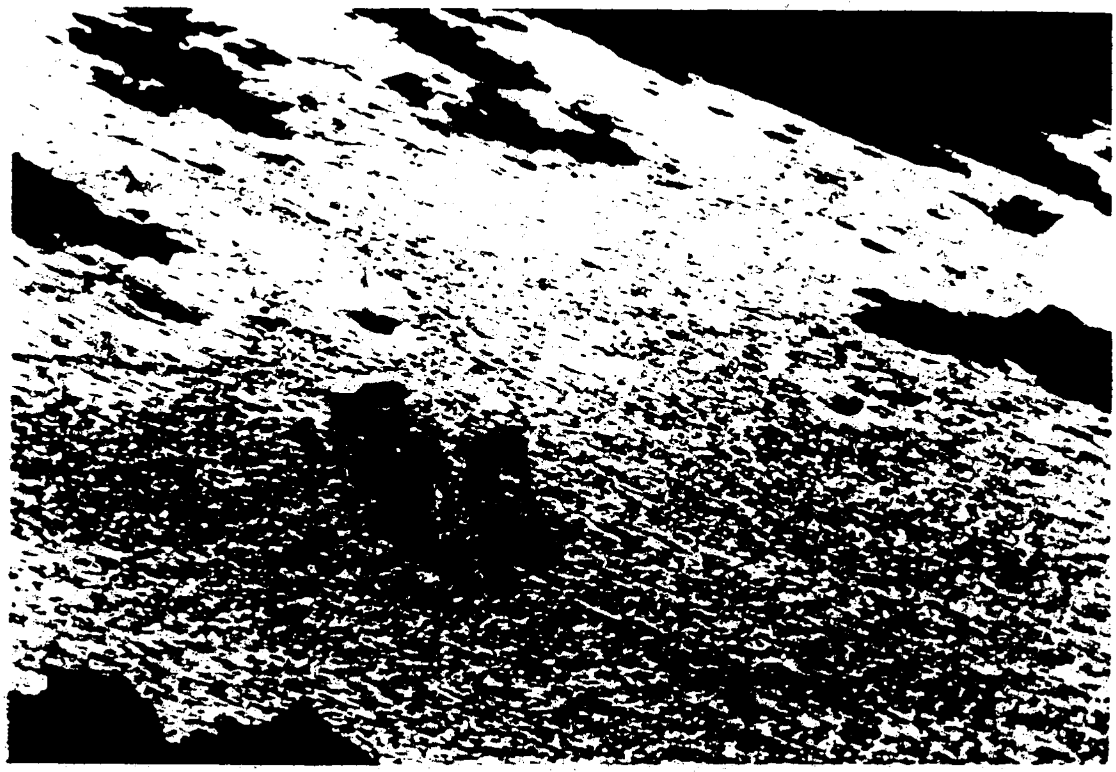

Plate 16. July 17 12:25 h. With an air temperature of 16.[illegible] and a wind speed of [illegible] indices of harassment between 14 and 29 were recorded. The group under study were [illegible] aggregated in response to increased insect harassment.

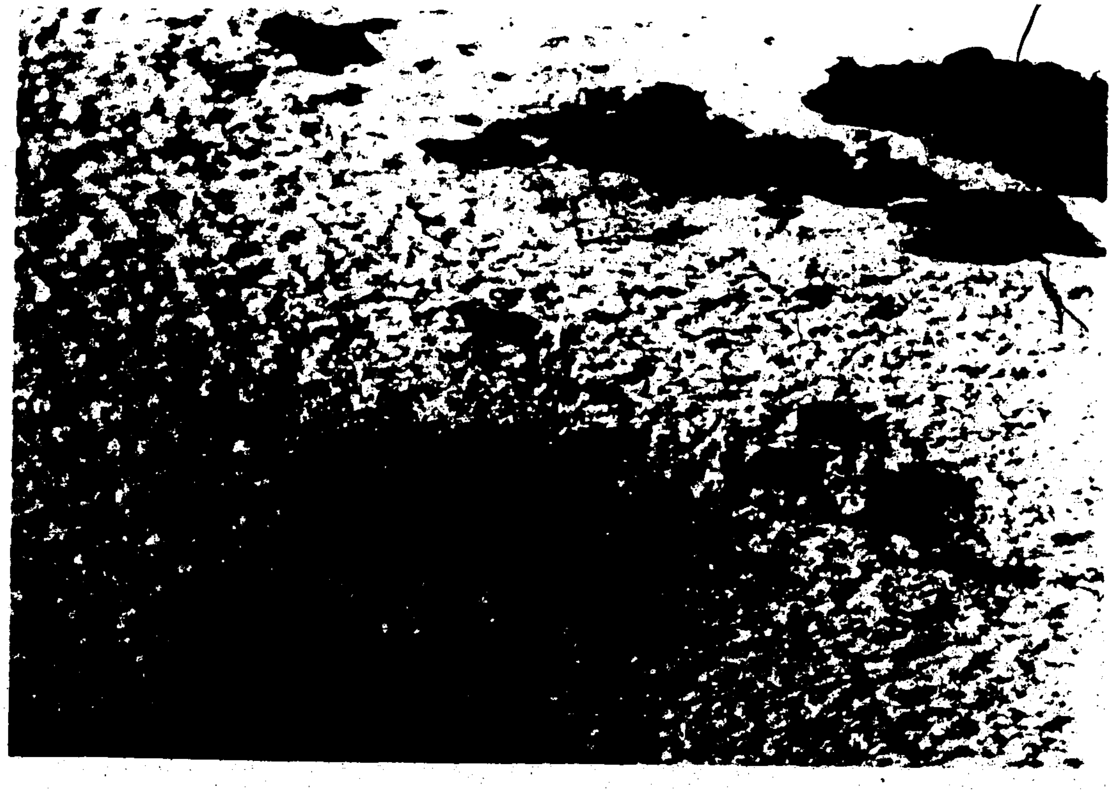

Plate 17. Under conditions of extreme insect harassment mean group size was found to be significantly greater than that under no or minimal levels of harassment. Varying degrees of harassment were also recorded between individuals located in the centre and outer edges of the group.

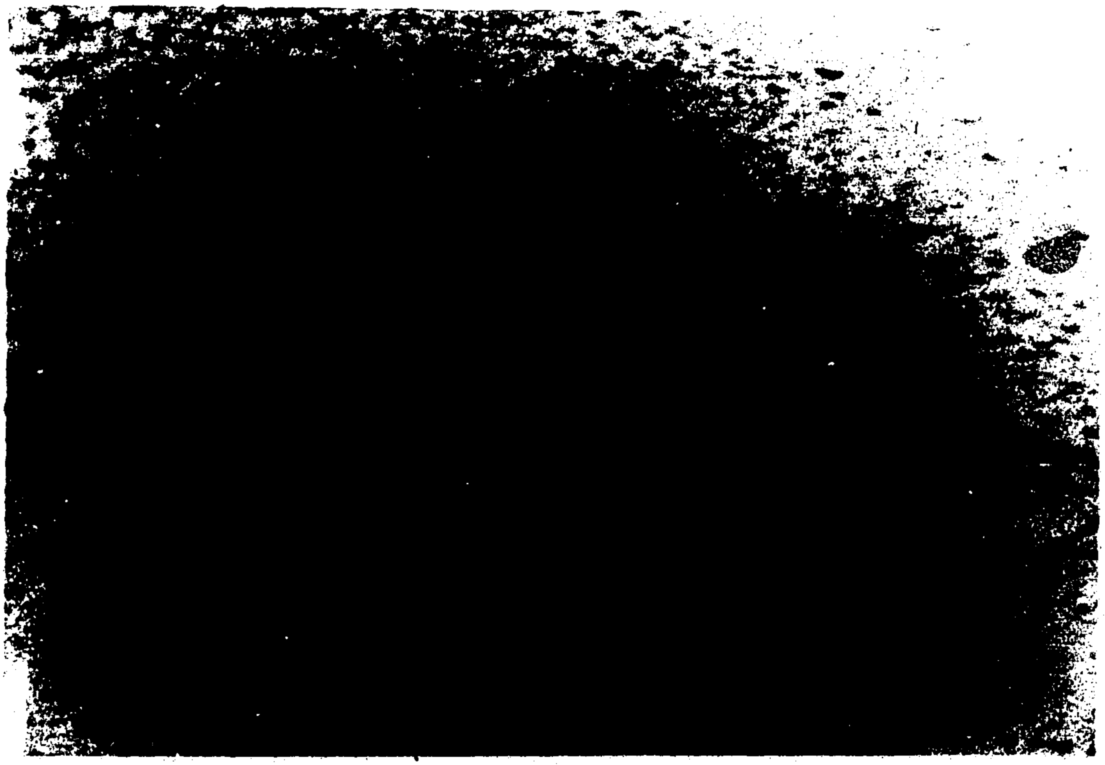

Plate 18. Under conditions of intense and continuous insect harassment one animal may initiate the downhill charge of an entire group. August 1 1984.

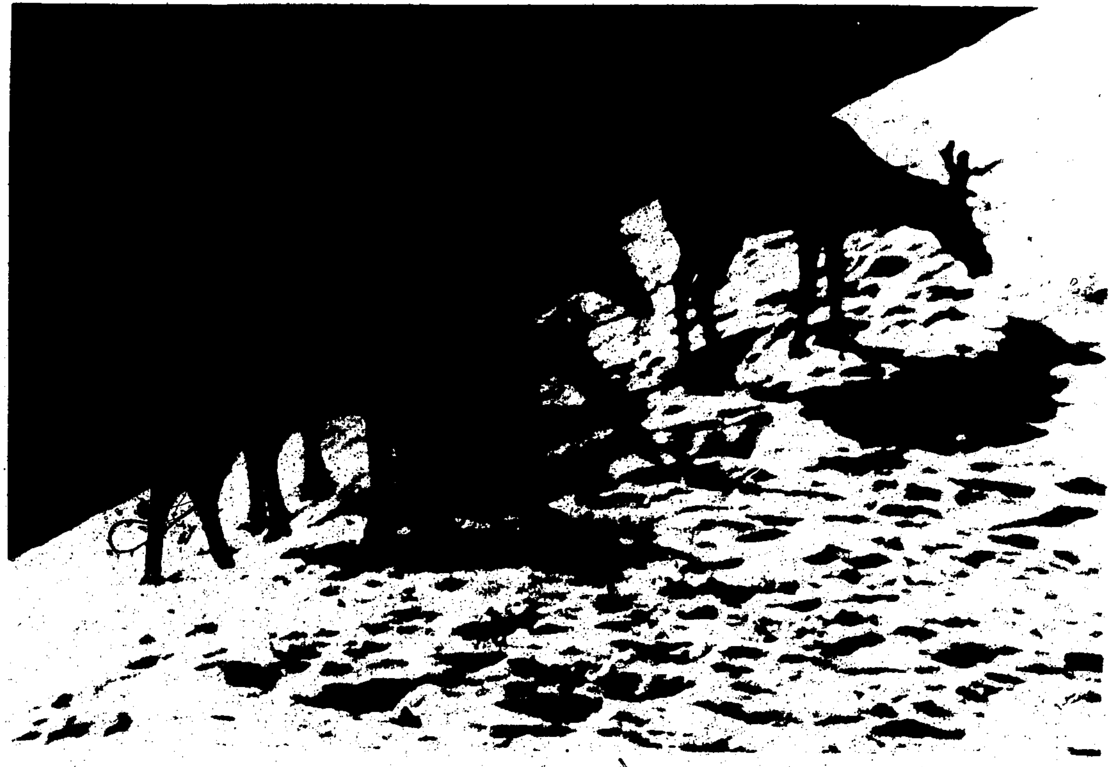

Plate 19. One of the more frequently observed responses to insect harassment was for the individual or group to orient relative to wind direction. In this photograph the animals are oriented into an easterly wind of 5.0 m s^{-1} recorded at the High Station.

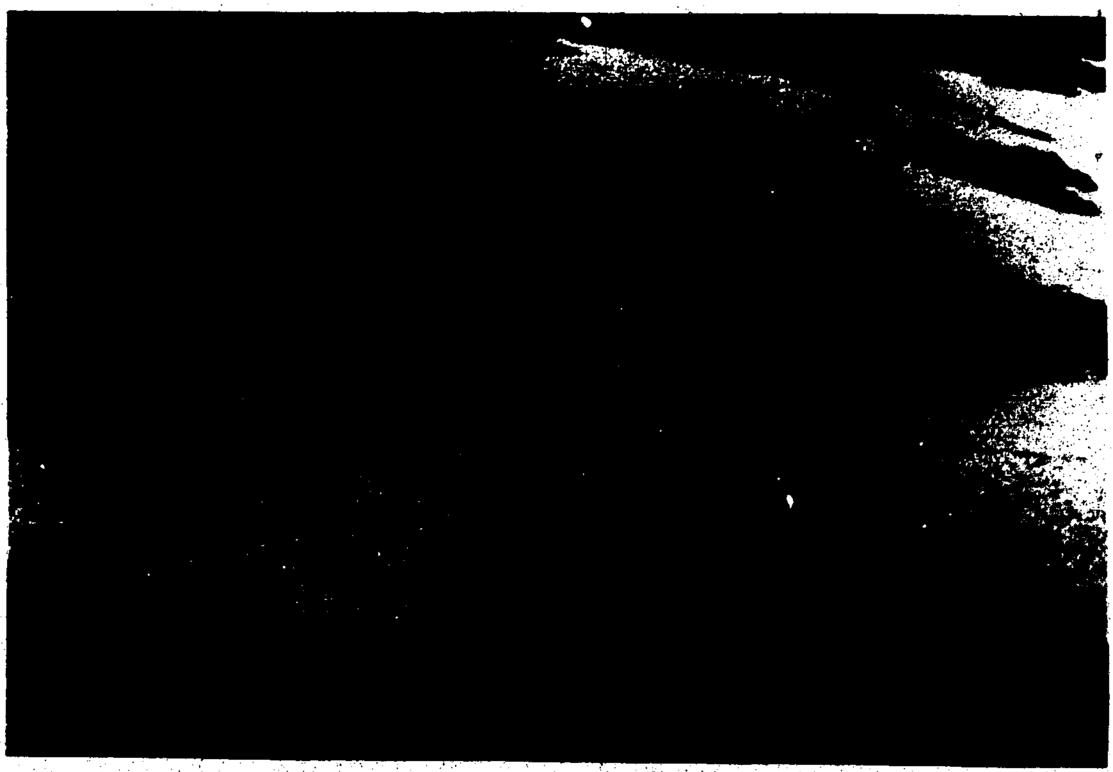

Plate 20. High wind speeds and low air temperatures significantly reduced levels of harassment. Under these conditions caribou spend a higher proportion of time resting. This group of 3 cows and 3 calves bedded down on the exposed ridges of the Main Aggregation Site for [illegible] minutes.

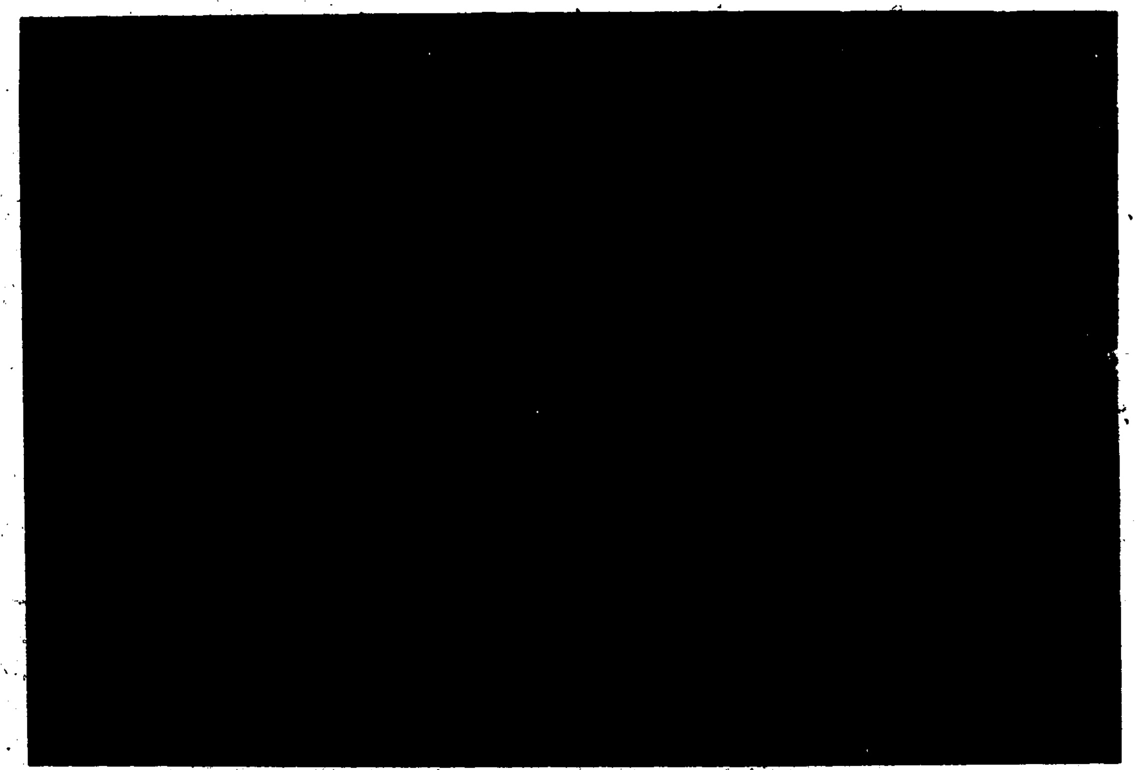

Plate 21. Windswept ridges were used as alternative relief habitat for insect-harassed animals. This animal was observed for 111 minutes during which time it remained essentially motionless and oriented parallel to the wind direction. July 20 1984.