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THE SELECTION OF SNOWPATCHES AS RELIEF HABITAT BY WOODLAND CARIBOU (*RANGIFER TARANDUS CARIBOU*), MACMILLAN PASS, SELWYN/MACKENZIE MOUNTAINS, N.W.T., CANADA

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ABSTRACT

Woodland caribou (*Rangifer tarandus caribou* Gmelin) occupy the Mackenzie and Selwyn Mountains of the Yukon and N.W.T., Canada. During the warm weather months they move into alpine areas and are frequently observed to utilize late-lying snowpatches. Microclimatic observations confirm that at 0.5 m height the snowpatch is consistently 3°C cooler than adjacent areas. Insect trap data indicated that significant differences in numbers and species occur between snowpatches and adjacent snow-free areas at the same and lower elevations. Indices of harassment correlated with biting insect numbers and with higher air temperatures (11.3 to 20.4°C, shielded temperatures) and below-average wind speeds (<2.5 m s^{-1}). Group size on snowpatches was significantly greater than on adjacent snow-free areas. While on snowpatches animals ingested snow and otherwise spent most of their time standing or lying. These activities we interpreted as behavioral thermoregulation. However, based on our data it was not possible to separate definitively microclimatic conditions from insect harassment as cause for snowpatch selection as relief habitat.

INTRODUCTION

Permanent snowpatches occur at high elevations in the Selwyn and Mackenzie Mountains of the Yukon and Northwest Territories. Woodland caribou (*Rangifer tarandus caribou* Gmelin) have been observed to congregate on these in large numbers (Archibald, 1973; Gill, 1978; Kershaw and Kershaw, 1983a). This type of behavior appears common in other parts of the North American range of *R. t. caribou* (Edwards and Ritcey, 1959; Bergerud, 1978; Stelfox et al., 1978; Oosenbrug and Theberge, 1980; Fuller and Keith, 1981) and of *R. t. groenlandicus* Borowski (Kelsall, 1968; Skoog, 1968; Elliot, 1972; Curatolo, 1975; Jakimchuk and McCourt, 1975; Calef, 1981). Although less widely reported, the observation has also been made in the alpine ranges of Eurasian reindeer (*R. t. tarandus* L.) (Formozov, 1946). We hypothesized that permanent snowpatches are selected as a form of "relief habitat." Relief from heat stress and/or insect harassment are the most likely causes.

The albedo of fresh snow can reach 0.95 (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 (Schwerdtfeger and Weller, 1967). The snowpatch zone therefore possesses a relatively cool microclimate. The first hypothesis is that caribou use snowpatches as a cool resting area for thermoregulation. This hypothesis may be subdivided into behavioral thermoregulation (selection of a cool resting area) or physiological thermoregulation (the ingestion of ice, snow, or meltwater) (Figure 1).

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The low air temperature immediately above the snow surface is thought to inhibit the activities of blood-sucking insects that harass caribou during the summer months (White et al., 1975; Calef, 1981). Furthermore, the snowpatches, at least in alpine regions, occur in high and exposed locations where wind speeds are generally higher than at lower elevations. Strong winds significantly reduce insect activity (White et al., 1975). These two possibilities form the basis of the second hypothesis that caribou use snowpatches because insect harassment is reduced while animals remain on them (Figure 1).

Study Area

Macmillan Pass, at an elevation of 1350 m is located in the Selwyn/Mackenzie Mountains at the Yukon/N.W.T. border (63°15′N, 130°02′W). The center of the 50.7-km² Extensive Study Area (ESA) was 11 km east of the territorial boundary and 8 km southwest of the Tsichu River Airstrip and meteorological station (1974 to 1981) (Figure 2). A 9.8-km² Intensive Study Area (ISA) could be monitored continuously from a centrally located, permanent base camp.

Macmillan Pass experiences a Continental climatic regime modified by the alpine environment (Kershaw, 1983). Between 21 June and 17 August 1984, 102 mm of rain fell within the study area, with at least 1 mm recorded on 39 of the 56 days (Ion, 1986). Light snow was recorded on 27 June and 11 August. A mean air temperature of 9.1°C was recorded at 1676 m with absolute maxima and minima of 24.0 and −5.2°C. Daily relative humidity maxima of 100% were frequently recorded and the mean of 72.8% reflects a cool, moist regime. At exposed, ridgetop locations, wind speeds in excess of 8.0 m s⁻¹ were frequently recorded although mean values were significantly lower in sheltered, lowland sites.

The study area lies entirely above treeline. Lichen-encrusted blockfields occur above 1900 m and are dominated by *Rhizocarpon* spp., *Umbilicaria hyperborea, Agyrophora lyngii, A. rigida,* and *Omphalodiscus virginis* (Kershaw and Kershaw, 1983b). Below this major zone are areas of cushion plant tundra dominated by *Dryas integrifolia* and *Arctostaphylos rubra* with scattered *Hierochloe alpina, Luzula confusa,* and *Vaccinium uliginosum.* Nonvascular plants include *Pogonatum alpinum, Polytrichum piliferum,* and *Cetraria cucullata.* Lichen-grass communities occur on more gently sloping ground and are dominated by graminoids such as *Deschampsia caespitosa, Festuca altaica, Poa arctica,* and *Carex atrofusca. Artemisia arctica* and *Salix arctica* occur as well and nonvascular plants are common (*Polytrichum juniperinum, P. strictum, Cetraria cucullata, C. nivalis, Cladonia mitis,* and *Stereocaulon alpinum*). North-facing sites, often associated with snowdrift areas and late-lying snowpatches, are occupied by lichen–heath communities dominated by *Cassiope tetragona* and *Cladonia mitis.* Below 1600 m, birch–lichen communities predominate.

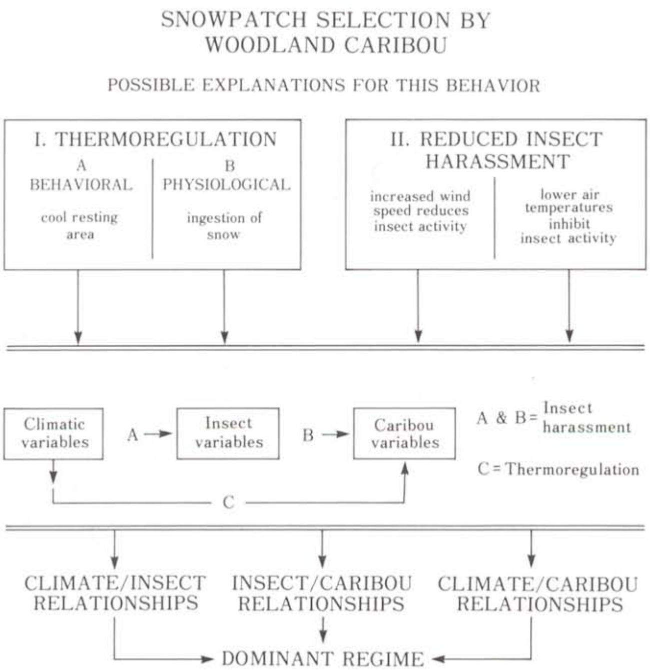

Figure 1. Theories as to why caribou select snowpatches as relief habitat have been hypothesized. *Thermoregulation* has a behavioral and physiological component while *reduced insect harassment* relates primarily to microclimatic variables and their effects on insects. All variables used to test these hypotheses are interrelated and so it is difficult to determine which hypothesis is valid or whether both operate at the same time.

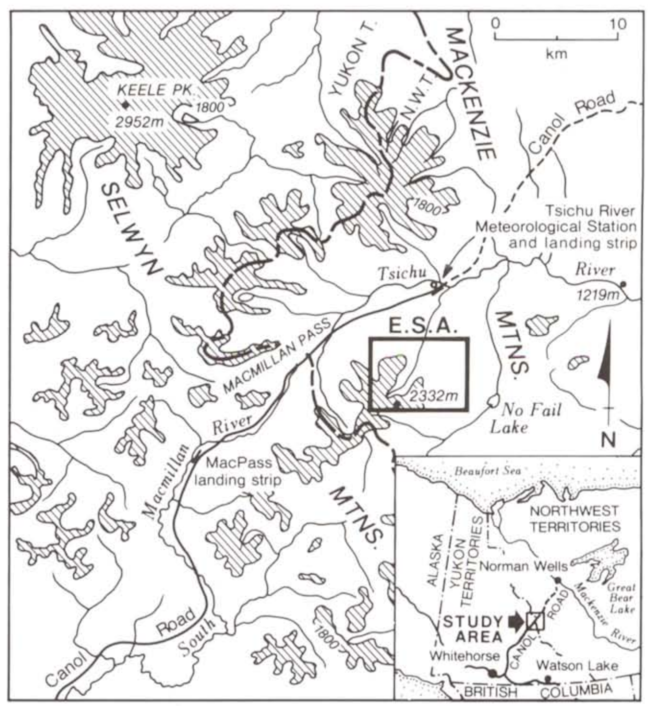

Figure 2. Location of the Extensive Study Area (ESA) near Macmillan Pass, Selwyn/Mackenzie Mountains, N.W.T.

They are dominated by *Betula glandulosa, Alectoria ochroleuca, Cetraria cucullata, C. nivalis, Cladonia mitis, C. rangiferina, Stereocaulon paschale,* and *S. tomentosum*. On poorly drained sites and along water courses, willow–forb communities occur with *Salix lanata, S. glauca, S. planifolia,* and *S. reticulata* associated with forbs such as *Artemesia tilesii, Mertensia paniculata,* and *Petasities frigida*.

METHODS AND MATERIALS

Two automatic weather stations were erected within the study area. At first one of these was located in lichen–heath tundra at 1676 m and was operational during most of the field season (21 June to 6 August). Later (i.e., 6 to 16 August) this station was relocated to a lower elevation (1601 m) within a willow–forb community. The second station monitored microclimatic conditions over snow and an adjacent blockfield at 1981 m and operated between 10 July and 16 August. At each station a Campbell Scientific Canada Corp. CR21 datalogger recorded data on global radiation, air temperature, relative humidity, wind speed and direction, and precipitation. Sensors were scanned every minute and summary outputs compiled every 15 min. The weather stations provided: (1) comparative data between the snowpatch and snow-free areas (i.e., blockfield, lichen–heath, and willow–forb sites), (2) comparative data between exposed, upland sites (i.e., blockfield and snowpatch) and relatively sheltered, lowland sites (i.e., lichen–heath and willow–forb), and (3) complementary/background data for animal observation data.

Information on caribou group size and composition, location, and temporal movements were recorded. Time budgeting of focal animals was for 10-min periods (Fischer and Duncan, 1976). Scan sampling of large groups of animals was done by recording an individual animal's current activity at preselected intervals. Between the first arrival of animals in the ESA on 17 June and 17 August when observations ceased, 94 separate observations of individuals or groups were made during a total of 158.05 h (1509 individual animal observations).

"Indices of harassment" were calculated at each focal animal sample. This involved the notation of individual behavioral responses to insect harassment. Four categories were employed: *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 behaviors are recognized as a response to insect harassment (Curatolo, 1975; White et al., 1975; Roby, 1978). A "group-averaged index of harassment" was calculated by computing the average harassment response of all individuals selected during scan sampling of the group.

Simple insect traps were constructed to collect insects over snowpatch and snow-free habitats at each of the meteorological stations (lichen–heath, willow–forb, and blockfield/snowpatch sites). They were dark green, $40 \times 25 \times 25$ cm boxes with a 225-cm² section on each side treated with Tanglefoot, a strong, weatherproof adhesive. No nose bot or warble-fly were taken on these traps, so we can only assume that the method was either inappropriate for these insects or they were absent in the ISA.

RESULTS AND DISCUSSION

Abiotic Components

The Snowpatch Zone

In early June, snow covered 53% of the ESA with the deepest accumulations along water courses, in small valleys, and topographic depressions. By mid-August snow only persisted above 1750 m where there were 30 discrete permanent snowpatches. They covered 0.9% of the ESA for a total surface area of 0.46 km². All but one occurred on slopes with a north, northeast, or east aspect. This is due to the lower irradiance on slopes with a north aspect and the prevailing westerly winds in winter which cause drifting in the lee of mountain ridges on east-facing slopes. These snowpatches appeared in all the aerial photography (i.e., late summer of 1945, 1949, and 1974) available for the area. This and field observations by Kershaw over more than a decade (i.e., 1973, 1974, 1977 through 1984) provide strong evidence for the recurrence of certain snowpatches in the same location over many years.

Snowpatch Microclimate

The unique properties of snow and ice in terms of radiation budget and energy balance provide a distinct microclimate in relation to adjacent snow-free zones. The temperature difference between comparative heights (0.5 m) over the snowpatch and blockfield sites was found to be approximately constant at 3°C (Figure 3). This difference was slightly reduced and more variable on average in the afternoon while higher and less variable at night. This may be attributed to stronger daytime winds generated by continuous heating that break down or diminish horizontal temperature differences. Night-time winds were generally weaker and the temperature difference more constant (hourly values for 0000 to 0600 h were 48.4% of those for 1200 to 1800 h). Air temperature differences also varied with general weather conditions. The snow/blockfield difference of approximately 3°C under anticyclonic conditions reduced to less than 1°C under overcast conditions associated with the passage of frontal systems (Figure 3).

Group Size and Composition

Within the annual cycle mean group size in woodland caribou throughout its distribution is usually lowest during late June, July, and August (Edwards and Ritcey, 1959; Freddy, 1979; Bergerud, 1978; Stelfox et al., 1978; Oosenbrug and Theberge, 1980). Presumably, postcalving aggregations fragment into smaller groups as intense foraging activity favors dispersal. Larger groups occur during the rut when bull groups rejoin cow/juvenile groups. In the ESA the breakdown of postcalving aggregations was evident when the larger groups observed in the last week of June (e.g., 216, 81, 66, and 63 animals) were replaced by smaller ones later in the summer that seldom exceeded 45 head (Ion, 1986).

Kerhsaw and Kershaw (1983a) noted that these early-season large groups were generally composed of cows and calves with yearlings. Our data from 1984 confirm that bulls tended to lag behind the adult female cohort so that adult and subadult bulls and yearlings were delayed in moving onto the summer range. The first bull was observed on 6 July, more than a month after cow/calf groups arrived in the ESA. Bulls were generally observed alone or in single sex groups of up to eight or in larger groups with yearlings.

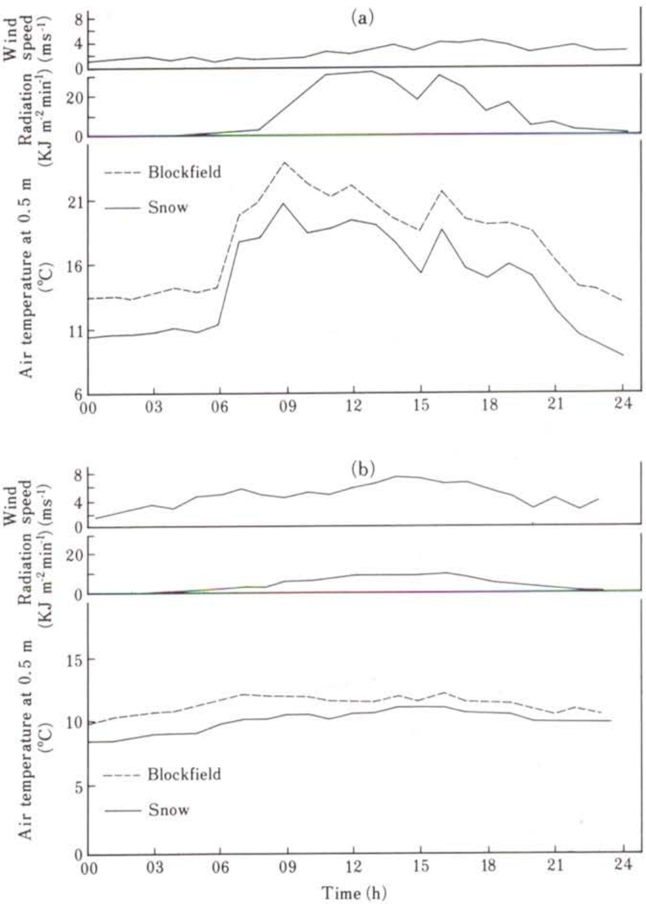

FIGURE 3. A comparison of microclimatic characteristics under anticyclonic (a) and cyclonic (b) conditions on a diurnal basis between a snowpatch and an adjacent blockfield near Macmillan Pass, Selwyn/Mackenzie Mountains, N.W.T.

Diurnal Distribution

The daytime pattern was an ascent from valley floors and slopes 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 late afternoon and evening (Figure 4). This cycle was observed mostly under anticyclonic conditions when high air temperatures and low wind speeds (Figure 3) increased the need for relief habitat. Movements were generally more random under cyclonic conditions.

ABIOTIC/BIOTIC RELATIONSHIPS

Climate/Insect Relationships

Daily totals of trapped individuals describe an "insect season" between 28 June and 12 August. Relatively few insects and no mosquitoes were trapped outside this time period (Figure 5). The sudden appearance of mosquitoes around the source of the South Macmillan River, 11 km west of the ESA, was noted on 4 July. The subzero temperatures and snowfall of 12 August were thought to be largely responsible for the low insect counts thereafter. Thus, the "mosquito season" within the ESA was probably no longer than 40 d in 1984. No blackfly activity was recorded.

Air temperature and wind speed are considered to be the most important climatic variables influencing insect activity (White et al., 1975). The total number of insects trapped during the mosquito season was plotted against mean air temperature and mean wind speed for the period 0800 to 2000 h (the Biologically Active Period) (Figure 5). Theoretically, total insect activity would be greatest under the higher air temperatures and the lower wind speeds associated with anticyclonic conditions. The high totals

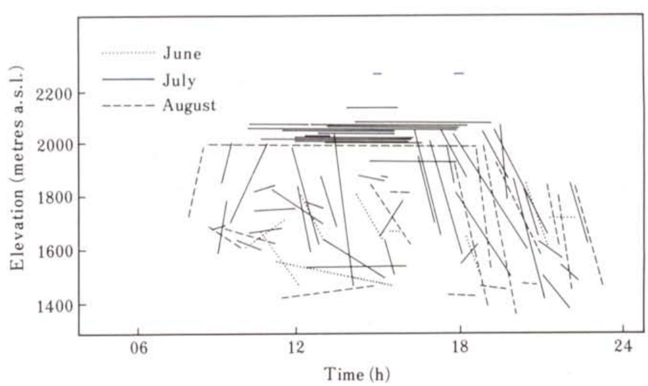

FIGURE 4. Diurnal movements of woodland caribou in the Extensive Study Area with respect to elevation near Macmillan Pass, Selwyn/Mackenzie Mountains, N.W.T. Each line represents an animal or group of animals' movements.

trapped under these conditions support this theory. However, large totals were also recorded on days with above-average mean wind speeds (Figure 5). There are two possible explanations for this. The first is that high wind speeds inhibit flight in mosquito-sized insects and force them 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, the windward, of the trap (maximum = 93.7%, mean = 52.9% for the 19 d with above-average wind speeds) tends to support the second explanation.

Thus, it appears that wind speeds were more important, or at least equal to, air temperatures in explaining the total numbers of insects trapped on a daily basis. The reverse relationship holds for the total number of trapped mosquitoes. As expected, the highest daily totals were recorded under high mean air temperatures and low mean wind speeds (Figure 6). In contrast to the total insect counts, however, relatively few mosquitoes were trapped on days with high mean wind speeds. Mosquito activity apparently was greatest under high air temperatures and they remained "anchored" on the tundra surface under high wind speeds.

Insect numbers also varied considerably between different habitats. At the lichen–heath site, a total of 6408 nonbiting insects and 133 mosquitoes were trapped between 10 July and 16 August (Figure 5). At the high blockfield site 2198 nonbiting insects and 7 mosquitoes were trapped in total. Over snow, numbers were significantly lower at 41 and 0, respectively. Statistical tests for paired samples were applied to these data to illustrate the extent of this variation. Significant intersite differences were calculated for total numbers trapped between the lichen–heath and blockfield sites ($t = 5.56$, SE = 42, $p < 0.001$), the blockfield and snowpatch sites ($t = 6.33$, SE = 18.96, $p < 0.001$), and the lichen–heath and snowpatch sites ($t = 8.98$, SE = 59.13, $p < 0.001$).

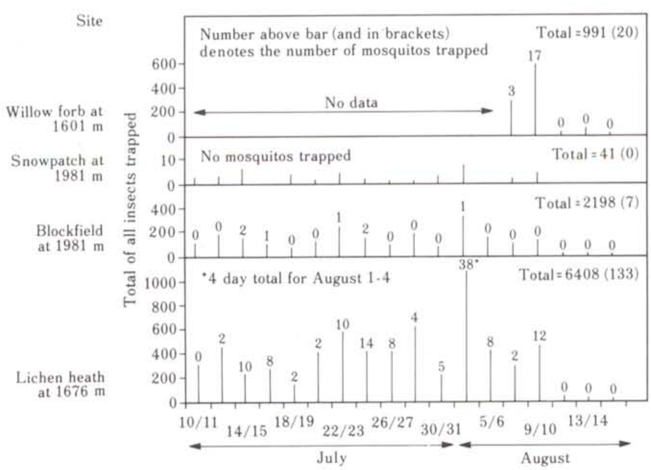

FIGURE 5. Intersite variation in the number of insects and mosquitoes trapped near Macmillan Pass, Selwyn/Mackenzie Mountains, N.W.T.

Although few data were available for the willow–forb site, total insect counts were significantly greater than the lichen–heath site ($t = 3.52$, SE = 9.58, n = 10, $p < 0.01$). A total of 991 nonbiting insects and 20 mosquitoes were trapped between 7 and 16 August at the willow–forb site which compares with 837 and 14 at the lichen–heath site for the corresponding period (Figure 5). 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.

Insect/Caribou Relationships

In addition to the insect trap data, indices of harassment were calculated involving the notation of individual behavioral responses to insect harassment (Curatolo, 1975; White et al., 1975; Roby, 1978). Combining all data for observations on and off snow, a total of 2506 individual behavioral responses were recorded. 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 four age/sex classes (adult bull, adult cow, yearling, calf) suggest that bulls were harassed the least, or exhibited the least response to harassment. Group-averaged indexes of harassment were calculated for extended periods of observation. These 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 indices of harassment) were found to correlate closely (Rs = 0.808, df = 24, $p < 0.001$).

The highest levels of harassment were observed under high mean air temperature and low mean wind speeds—conditions thought to be the most favorable for the flight of small or light insects (Figure 7). High indices of harassment (> 10.1) were observed under mean air temperatures ranging from 11.3 to 20.4°C (Figure 7). Low indices (< 5.0) were recorded between 7.9 and 14.9°C. High indices were also recorded under below-average wind speeds (i.e., < 2.5 m s^{-1}). Ten of the 11 observations with indices greater than 10.1 occurred under average or

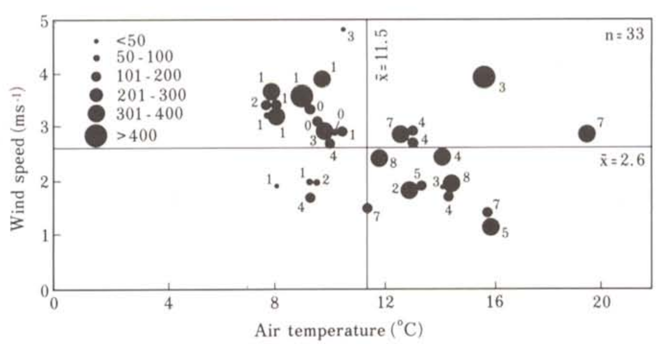

FIGURE 6. Total number of insects (legend) and mosquitoes trapped (value beside symbol) at the lichen–heath site (1676 m) with respect to air temperature and wind speed near Macmillan Pass, Selwyn/Mackenzie Mountains, N.W.T. (11 to 31 July and 5 to 16 August 1984).

below-average wind speeds. On the one occasion when 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 described by White et al. (1975).

Harassment was generally higher on snow (mean = 9.98, SD = 4.01, n = 23) than off snow (mean = 1.78, SD = 2.89, n = 16) (Figure 7). This contrasts with the insect trap data over snowpatch and snow-free areas. The distribution of on-snow and off-snow observations about the mean for air temperature and wind speed helps to explain this apparent contradiction. Previous analysis of climate/insect relationships described greatest insect activity under warm, calm, anticyclonic conditions. Caribou have moved onto snow to avoid the greater number of insect pests occurring at these higher temperatures and calmer conditions. The majority of observations on snow were made under such conditions. This raises two points: snowpatches do not make caribou immune to insect harassment, especially when climatic conditions are optimum for the pests; and mosquitoes obviously are capable of differentiating between caribou and the insect traps we used. The lack of success in trapping larger insect pests, such as warble and bot flies, make it impossible to draw conclusions regarding their possible role, assuming they were present in the area.

Specific activities also contrasted considerably on and off snow. Ingestion of snow was a relatively short-duration behavior whereas foraging occupied the majority of time that animals spent off snow. Although indices of harassment were lower for the observations off snow, foraging activity was generally unaffected by harassment. Indices of harassment of over 6 were recorded on only two occasions off snow, yet almost continuous foraging occurred when an index of 11 was recorded. No statistically significant values were calculated for the relationship between indices of harassment and the duration of head lowered posture (i.e., ingestion of snow or foraging) either on or off snow.

Significant variations in group size and composition occurred. From the observation data, the mean group size observed on snow was larger (mean = 23.9, n = 16) than off snow (mean = 11.9, n = 23). These variations 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. For example, some snowpatches may be too small to create a significant microclimate difference from snow-free areas, or perhaps they are too steep, etc. Furthermore, snowpatches occupy a relatively small area compared to snow-free habitats. Consequently, animals are forced to congregate in larger groups on those snowpatches which offer relief habitat.

Sex composition also varied between observations on and off snow. In summer, caribou are usually separated into cow-dominated groups (cow/calf/yearling groups) (Figure 8) and bull-dominated groups (bull groups and

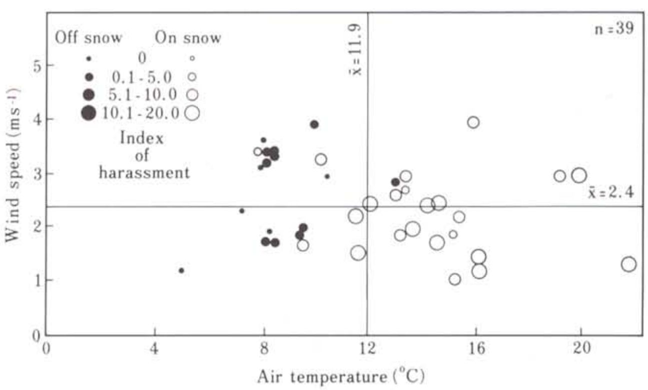

FIGURE 7. Variations in the index of harassment for woodland caribou with respect to air temperature and wind speed near Macmillan Pass, Selwyn/Mackenzie Mountains, N.W.T. (24 June to 15 August 1984).

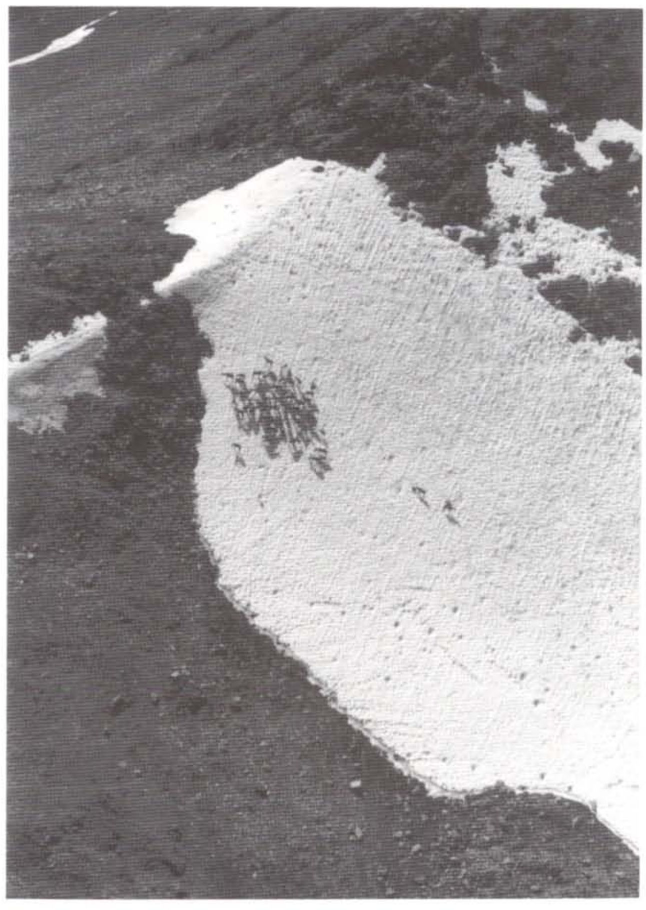

FIGURE 8. This large group of caribou was observed on this snowpatch during a 3.5-h aerial survey on 7 August 1981. It was composed of 40 cows, 23 calves, and 5 unclassified animals. This is the snowpatch on which most of the 1984 observational data were collected. It illustrates the aggregation behavior, posture, and composition for most caribou groups on snowpatch relief habitat.

bulls with yearlings). Of the 94 observations, 82 or 87.2% were of such segregated groups. On 12 occasions, however, adults of both sexes were observed together. Such mixed groups were disproportionally observed on snow: 10 of 23 observations on snow (43.5%); only 2 of 16 (12.5%) off snow. This difference was found to be statistically significant ($x=17.12$, $p<0.001$). These groups, which normally would remain separate at this time of year are drawn together on snowpatches where they utilize them as relief habitat. Since the habitat is restricted, they must share the resource, but snow-free habitats are much more abundant and segregation based on sex/age classes can therefore occur.

Relatively large groups of mixed sex congregated on snow under conditions of increased insect activity. Caribou may form closely packed groups as a means of reducing insect harassment *per se*. Caribou may assure a mutual benefit by sharing their tormentors. Additionally, the central animals could rub off insects such as mosquitoes using their neighbors, and peripheral animals would be subject to attack by newly arriving insects (Thomas, pers. comm., 1988). An index of aggregation was calculated which quantifies the degree to which animals coalesced in response to insect harassment. Closely aggregated groups had <50% of the individuals with interanimal distances less than one body length. Moderately aggregated groups had <50% of the individuals with interanimal distances less than three body lengths. Dispersed individuals had >50% of their number with interanimal distances greater than three body lengths. Each group was classified into one of these three categories. The index of aggregation correlated with the mean index of harassment ($r=0.661$, $p<0.005$) suggesting that benefits are to be gained from forming closely packed groups during peak insect harassment episodes.

Including all observations, regardless of habitat or climatic conditions, standing and eating were the two most frequent group activities at 44.6 and 33.8%, respectively. Lying (15.0%), walking (6.1%), and running (0.5%) were infrequently observed. However, on snow, caribou spent a higher proportion of time standing (66.0%) (Figure 8), the remainder in ingesting snow (13.3%), lying (13.2%), walking (6.9%), and running (0.6%). Off snow, foraging activity predominated (63.4%) followed by lying (17.6%), standing (13.6%), walking (5.0%), and running (0.4%). On snow there was 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 foraging decreased with increased harassment off snow.

Climate/Caribou Relationships

Caribou may utilize snowpatches as a means of behavioral thermoregulation. This may be achieved in three ways: movement toward a more favorable (less thermally stressful) environment; ingestion of snow, ice, or meltwater; or by changes in posture. The latter two can be partially assessed by our data.

Under field conditions it was not possible to quantify the volume of snow that an animal consumed over a specified time period. Individuals thus were arbitrarily classified into positions as head raised or head lowered when it was assumed the animal could be ingesting snow. However, we should caution that head lowered posture is also typical for animals being harassed by larger insect pests (Epsmark, 1968). The duration of presumed snow ingestion activity for each sample was correlated with air temperature. The relationship was found to be significant for individual observations ($r=0.491$, $n=23$, $p<0.05$) due to the large number of samples with a duration of zero. Subdividing the data by temperature, however, confirms that at air temperatures of less than 10°C, caribou spent a very small portion of the 10-min sample period ingesting snow (mean = 0.08, n = 24). Between 10.1 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 = 26). Ingestion of snow may also be done to meet water requirements since respiratory water losses increase directly with air temperatures (Cameron et al., 1982). These hypotheses could be further tested with physiological studies.

One of the ways in which caribou may thermoregulate behaviorally is in the selection of snowpatches as a cool resting area. For group activity patterns, standing was three times more common than lying (45 to 15%) and was over five times more common (66 to 13%) on snow. Combining all group-averaged values for the 10-min sample periods, the mean duration of all standing behavior was 7.9 min for all observations and 8.6 min for observations on snow. Resting behavior was largely dependent upon levels of insect harassment. The mean duration of standing behavior on snow increased with the level of insect harassment ($r=0.371$, $p<0.005$). A standing animal will be warmer than one that is lying, particularly on snow. The energy cost of standing is higher than lying (Fancy and White, 1985) and an animal standing on the snow (a high albedo surface) will gain heat from direct as well as reflected radiation. However, an animal that is lying is one that is tranquil and unharassed by insects. Standing animals exhibited stress-related behavior such as foot stamping. We conclude that the higher incidence of standing while on snow compared to off snow is due to the degree of insect harassment and that, in the absence of snowpatches, evidence of harassment would be even greater off the snow.

Under severe harassment (i.e., a mean index of 16.0) lying on snow was not observed at all. Resting on snow at length (e.g., for more than 4 min 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 observations had a mean duration of 10 min standing. The predominance of foraging activity off snow provides an explanation for this behavior since animals were constantly moving in search of food.

Caribou may orient themselves as a means of behavioral thermoregulation. Analyses of group and individual orientation with reference to wind direction was thus attempted. For groups on snow, orientation parallel to the prevailing wind direction was observed more frequently than perpendicular, or those with no specific orientation. Almost half (49.6%) of the samples under conditions of severe insect harassment were of groups oriented either into or away from the prevailing wind. Orientations were generally more random under lower levels of harassment. Orientations were also more random off snow. Although sample size was small, caribou groups did not consistently orient movements into the wind. Of observations off snow 22.9% were of individuals or groups oriented parallel to the prevailing wind direction. Levels of insect harassment were significantly lower for these observations. 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.

CONCLUSIONS

The literal treatment of the hypotheses proposed to explain caribou behavior on and around snowpatches was of value in isolating variables for subsequent analysis. However, the identification of specific cause-and-effect relationships was a problem. In particular, high air temperatures were coincident with high levels of insect harassment. Snowpatch selection occurred most frequently under such conditions. Attributing this behavior to one specific cause or ranking of factors was not possible in this study. Of the two hypotheses identified, snowpatch selection as a means of reducing insect harassment was favored over thermoregulation for three reasons:

(1) Movements toward and away from snow were observed as an immediate response to fluctuations in insect activity. However, indices of harassment for individuals were consistently greater on snow than off it. We conclude that, although caribou were still bothered by insects while on snow, there was still a relative degree of relief compared to snow-free areas where pests were unaffected by the microclimate associated with the snowpatch.

(2) Aggregation as a response to insect harassment was more frequently documented on snow than off snow. Behavioral 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 (Curatolo, 1975; White et al., 1975; Roby, 1978).

(3) The documented tolerance of caribou 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 (Yousef and Luick, 1975). However, active animals, bothered by insect pests, could experience heat stress during running episodes (Thomas, pers. comm., 1988).

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

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