QUANTITATIVE OBSERVATIONS ON EPIDENDRIC LICHENS USED AS FOOD BY CARIBOU[1]

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Caribou, *Rangifer arcticus* (Richardson), in Wells Gray Park (lat. 52°N., long, 120°W.) British Columbia, eat epidendric lichens of the genus *Alectoria* Ach. in winter. During winter these lichens provide most of their food (Edwards and Ritcey 1960), and appear to be the only food available in quantity. Survival of caribou in this area, therefore, depends in part upon the availability of *Alectoria* in winter. This study was undertaken to explore how much *Alectoria* is in the park, and the proportion of its total stand available to caribou. Partial answers to these questions are basic to determining the forest management best suited to perpetuate caribou.

Intensive field work was done in the summer of 1957. More general observations were made since 1952 when it was first apparent the arboreal lichens were an important caribou food.

There appear to be 5 species of the genus *Alectoria* in the park. The following nomenclature is taken from Howard (1950). One, *Alectoria sarmentosa* Ach., is light green in color. The remaining 4 (*A. fremontii* Tuck; *A. oregona* Tuck; *A. chalybeiformis* (L). Rohl; *A. jubata* (L.) Ach) are dark brown. The last three are difficult to separate in the field. In this study these are considered together as the *Alectoria jubata* complex, and any reference to this species is meant to indicate the complex.

These plants consist of linear, threadlike filaments which branch dichotomously and decrease in diameter distally. Aggregations of finer threads resemble coarse hair. They may occur luxuriantly on branches and foliage of trees; some species are predominantly pendulous, others are prostrate and form tangled masses among twigs and needles.

METHODS

We chose for study 4 tenth-acres in 4 kinds of forest. Within each study area 11 to 13 trees were chosen by a forester (Soos) as representative, in aggregate, of the forest type. From these, within each successive 10 ft. height interval, 2 representative branches were arbitrarily selected. From each branch all *Alectoria* were removed by hand, the species composition estimated in percentages by volume, and the mass of lichen then oven-dried and weighed. Collecting lichen from the branches of one large tree involved hours of work to separate fine strands of lichen from bark, twigs and foliage.

STUDY AREAS

Areas 1 and 2 were in a region not frequented by caribou. They were chosen for their accessibility and suitability for perfecting techniques and gathering ecological data on lichens. Areas 3 and 4 were in regions regularly frequented by caribou, the former on the valley floor, the latter near timberline.

Area 1, at 2600 ft., had an uneven aged stand of mixed conifers at the edge of a 20 year old burn. Most trees were 80 to 130 years old. Douglas fir (*Pseudotsuga menziesii*) was dominant. Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) the most numerous co-domi-

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nants. Regeneration, predominantly cedar (*Thuja plicata*), was common where fallen trees had opened the stand. Seventy per cent of the forest floor was covered by mosses. Most common herbs were *Linnaea borealis*, *Cornus canadensis* and *Clintonia uniflora*. Deciduous shrubs were scarce except for some scattered *Pachistima myrsinites*. This area was centrally located on the floor of a broad valley.

Area 2, at 2600 ft., had an even aged stand of mixed lodgepole pine (*Pinus contorta*), Douglas fir, trembling aspen (*Populus tremuloides*), Engelmann spruce, subalpine fir and paper birch (*Betula papyifera*). Most trees were 50 to 60 years old. Spruce regeneration was common where the intolerant aspen and willows had died. The shrub layer was low and composed of *Rosa* spp., *Shepherdia Canadensis, Spirea lucida, Rubus parviflorus, Juniperus communis*, and *Vaccinium membranaceum*. Common herbs were *Cornus Canadensis, Linnaea borealis, Chimaphila umbellate, Aralia nudicaulis*, and *Pyrola secunda*.

Area 3, at 3700 ft, was in a mature stand of Engelmann spruce and subalpine fir opened by selective cutting 20 years before. Most trees were 150 to 180 years old with dominants 90 to 120 ft high. Regeneration was mainly spruce and subalpine fir, with some cedar and hemlock (*Tsuga heterophylla*). There was a moderately dense shrub layer, dominated by *Menziesia ferruginea* with *Lonicera involucrata, Rubus parviflorus, Oplopanax horridus*, and *Ribes* spp. Ground flora was dominated by oak fern (*Gymnocarpium dryopteris*) in July, with Linnaea *borealis*, *Cornus canadensis, Rubus pedatus*, *Tiarella unifoliata, Aralia nudicaulis, Clintonia uniflora* and *Lycopodium* sp. This area was in a narrow valley and part of an extensive tract of mature forest. Precipitation is heavier than in Areas 1 and 2. Caribou frequent this area in fall, winter and spring.

Area 4 was near 6000 ft. Here a mature stand of Engelmann spruce and subalpine fir had a shrubby understory composed almost entirely of regenerating spruce and fir. This low growth was almost impenetrable at the forest edge adjacent to natural timberline meadows. The main deciduous shrub was *Vaccinium caespitosum*. Ground cover, chiefly mosses with a few lichens, was sparse. Openings and edges had a variety of herbs and dwarf shrubs, among them *Phyllodoce empetriformis, Luetkea pectinata, Veratrum eschscholtzi*i, and *Arnica latifolia*. This area, near timberline, has snow depths up to 7 ft in late winter.

TOTAL WEIGHTS OF ALECTORIA

Total weights in kg per acre for the 4 study areas appear in Table 1. Area 4 was by far the heaviest producer. *Alectoria* when dried seems light in weight, yet this area had nearly 1.5 tons per acre. This confirms casual observation that timberline forests in this region have heaviest stands of lichen.

Study area	Kilograms of lichen per acre	Kilograms per acre and percent of total lichen below three heights from ground		
		10 ft.	15 ft.	20 ft.
1	339.2	5.5 (2%)	51.5 (14%)	89.1 (24%)
2	114.4	11.0 (10%)	27.7 (24%)	44.5 (39%)
3	305.9	26.1 (9%)	56.2 (18%)	128.2 (42%)
4	1332	169.6 (13%)	329.2 (24%)	156.7 (34%)

TABLE 1. Weights of lichen *Alectoria* on study areas.

The relatively young forest, mainly of lodgepole pine, in Area 2 had the lightest stands of lichen. *Alectoria* is a common genus on pines in the region and seems especially common on pines in boggy areas. However, if Area 2 is typical, lichen loads are not heavy. Perhaps a false impression of abundance results from the lichen being easily visible in the open crowns of these trees.

Originally we thought that Area 3 had a heavier stand of lichen than Area 1. Data show the reverse is true, although the figures suggest no great difference. These figures are from restricted areas, however, and further sampling might confirm our original opinion.

VERTICAL DISTRIBUTION OF ALECTORIA

A meaningful picture of lichen loads on trees must include some indication of vertical distribution. Feeding caribou would derive little benefit from a lichen abundance of a ton per acre if it was confined to the tops of tall trees. To investigate vertical distribution, lichen loads in each study area were calculated for successive 10 ft intervals from the ground. These data appear in Figure 1 for the species of *Alectoria* treated collectively, and in Figure 2 for each species separately. Patterns of distribution are the result of several factors controlling abundance. It is a temptation to regard them solely as reflections of microclimate affecting lichen growth. The figures may be valuable from this viewpoint, but there are additional controls on abundance which complicate analysis.

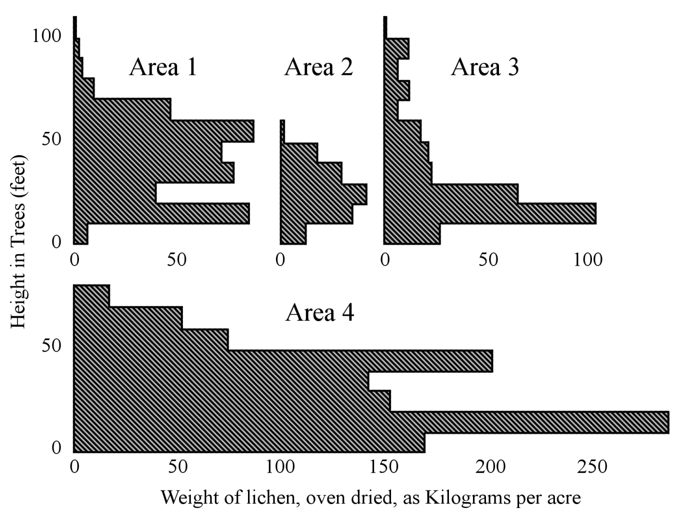

FIG. 1. Histogram showing the weights and *Alectoria* occurring in trees at successive ten foot intervals from the ground.

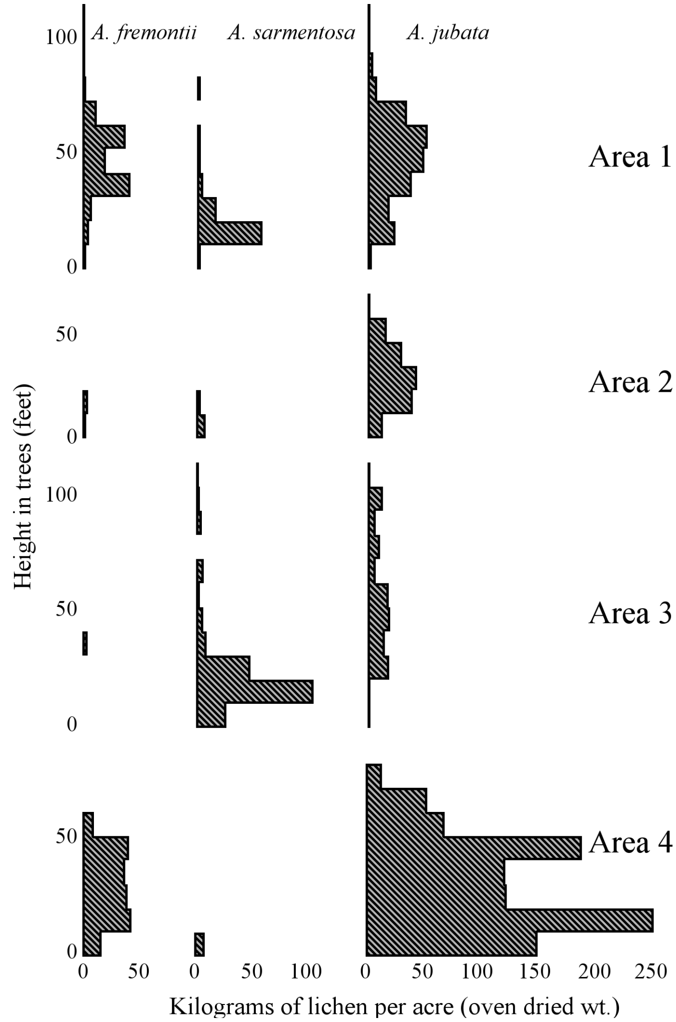

FIG. 2. Histogram showing the weights of three kinds of *Alectoria* in trees at successive 10 foot intervals from the ground.

When snow melts in the spring, the ground beneath heavy lichen loads may be strewn abundantly with fallen lichens. Presumably frozen, brittle lichens are dislodged in quantity by winds, driven snows, and heavy loads of snow on the trees. The more exposed the lichens, the more vulnerable they are to such forces. This may partly explain the light loads in tree tops.

A characteristic feature of most graphs in Figures 1 and 2 is the relatively light lichen loads from 0-10 ft. These may be partly due to caribou and deer feeding upon lichen. Taylor (1922) reported that the scarcity of *Usnea barbata* near the ground may be caused by snow on the ground. He was unaware that he observed mainly *Alectoria* spp. not *Usnea barbata*. Depth of snow may influence the abundance of epidendric lichens in Wells Gray Park, but there is no simple relationship such as Taylor proposes. This is shown by abundant lichen near the ground at timberline, an area with deep snow in winter, and by the confinement of *A. sarmentosa* near the ground in several areas.

Perhaps the most important factors limiting the abundance of *Alectoria* are the shapes of trees, due in turn to the size of their branches. Short branches near the tops provide less space for lichens than do larger branches below, while a paucity of branches near the ground in closed stands could impose the same limitation. For example, data from Area 2 came predominantly from lodgepole pines. The shape of the figure for Area 2 in Figure 1 suggests the shape of a pine tree. Similarly, in Area 4 the spruce and fir tend to be conical in shape with longest branches low and near the ground.

Variations observed in the abundance of lichen through forest canopies will not be adequately explained until detailed studies evaluate the separate effects of many ecological influences.

ECOLOGY OF ALECTORIA

Smith (1921) states that the genus *Alectoria* inhabits the cool temperate zone. In British Columbia it grows in regions with relatively heavy precipitation, and may flourish in dry sites in the maritime climate near the Pacific Coast. Away from the sea dry sites in areas of heavy precipitation may contain *Alectoria* but its vigor may be low.

In his unpublished thesis, Szczawinski (1953) reported that in forests on the eastern slope of Vancouver Island, *Alectoria* spp. were most abundant and vigorous in most open and driest sites, while one species, *A. fremontii*, was confined to these sites. On better sites with less exposed location and more dense forests, *Alectoria* spp. were confined to tops of trees where exposure and other physical characteristics approximated those near the ground in poor, exposed sites. He stated also that "*Alectoria sarmentosa* and *A. jubata* are probably the most prominent heliophytes in corticulous sociations…" in the area studied.

In Wells Gray Park *Alectoria sarmentosa, A. fremontii*, and *A. jubata* differ in their occurrence with elevation. *A. sarmentosa* is common in lowland forests and on adjacent slopes to 5,000 ft, but is scarce at higher elevations. The other species do not appear to have this altitudinal restriction.

Figure 2 indicates that requirements of *A. sarmentosa* differ from those of the other two where all three occur in lowland forests. On all study areas, *A. sarmentosa* was mainly on branches of trees within 30 ft of the ground. In Areas 2 and 4, where this species was scarce, it was mainly within 10 ft of the ground. *A. sarmentosa* appears to favour the lower branches in dense forests as if requiring more sheltered sites where air movement and light intensity are reduced, temperatures are less extreme, humidity is increased, and mechanical injury from the elements is reduced. The separate effects of such a complex are difficult to unravel.

Alectoria jubata is not usually abundant at levels on trees where *A. sarmentosa* occurs (Fig. 2). Still, *A. jubata* appears to have wide ecological tolerance, occurring higher in the trees than other species in all areas. This ability to colonize the tree tops with relative abundance in the open, rather than dry forest of Area 2, and impressive abundance in timberline forests, indicates a considerable tolerance to exposure. It is possible however, that the apparent wide ecological tolerance of *A. jubata* is due to our considering it one species, when in reality it may be a complex of several similar species.

A. fremontii is scarce or absent at levels where *A. sarmentosa* occurs (Fig.2). Levels with relatively abundant *A. fremontii* are immediately above those with abundant *A. sarmentosa*. For example, in Area 3 *A. sarmentosa* abundance decreases sharply about 30 ft above the ground, while *A. fremontii* occurs only from 30 to 40 ft.

A. fremontii is not so successful in invading tree tops as is *A. jubata*. In all 4 study areas there were tree tops free of lichens, but there was much variation in the numbers of such trees, and in lengths of tops devoid of lichen (Table II). The exposed tree tops of a forest are in a drier climate than are more sheltered levels below. Presumably tree tops devoid of lichen are too dry to favour these plants. In Area 2 many tops of lodgepole pine had no lichen for comparatively long distances. This forest was relatively dry so the canopy was probably especially xeric. The absence of lichen in pine tops and the predominance of *A. jubata* below these tops supports *A. jubata* as probably the most xerophytic of the 3 lichens studied.

Contrasting with Area 2, most tree tops had lichen in Area 3, which probably has the most humid climate of the 4 study areas. The climate affecting Area 3 is illustrated by meteorological records from Blue River, B.C.; that for Areas 1 and 2 by data from Park Headquarters. Hythergraphs in Figure 3 illustrate the greater precipitation of the former. There are no meteorological data for Area 4, but from its location near timberline it is safe to say that temperatures are lower than in all other areas, and that precipitation is heavier than in Areas 1 and 2.

Lichens usually grow best in exposed places (Smith 1921), but the poor lichen growth found in Area 2, the pine forest, suggests the limitations of this requirement. These pines had the most open crowns of any trees sampled, yet *Alectoria* grew more luxuriantly in all other areas. An important

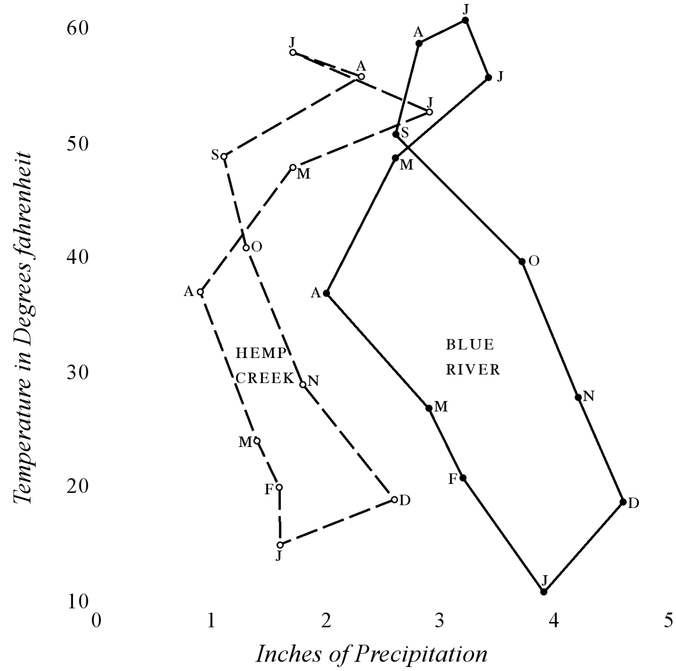

FIG 3. Hythergraph for Blue River, near the eastern boundary of Wells Gray Park, and for Hemp Creek, in the southwest portion of the park.

factor here was probably moisture. Lodgepole pine forests are relatively xerophytic, while other areas, especially 3 and 4, give floristic evidence of much higher humidity.

These ecological considerations have been mainly comparative among the species studied. Such terms as "xeric" are relative, and here apply only to the region studied. Szczawinski (1953) found in Douglas fir forests of Vancouver Island that *Alectoria* spp. were most successful in the driest forests, while their occurrence near the ground was confined to such forests. Since he was working in a region quite different in climate from that of Wells Gray Park, allowance must be made for these differences when comparing relative statements.

AVAILABILITY OF ALECTORIA TO CARIBOU

On standing trees. -- Only lichens on lower branches of standing trees may be reached by caribou. The height that caribou can reach to gather food is thus of importance. In winter, when caribou feed heavily on lichen, the ground is covered with snow, variable in depth and ability to bear weight. Caribou may ordinarily be able to reach up to 8 ft from the ground while standing erect but snow may increase this distance. In Area 4, which in late winter may have snow depths of 7 ft or more with crust hard enough to support caribou, their effective reach may approach 15 ft. This maximum must vary, however, depending on snow depths and crust strengths. These are variables which complicate any measurement of lichen available to caribou. As Figure 1 shows, in all plots the amount of lichen growing from 10-20 ft is greater than that within 10 ft of the ground. In some plots the lichen load just above 10 ft is the heaviest on trees, so the effect of snow on caribou reach above 10 ft is one of primary importance.

An additional variable affects lichen within reach. In this study, distances from the ground for branches bearing lichen were measured from points of attachment of branches to trunks. Lower limbs of most conifers droop so that most foliage is 1-3 ft below the attachment point. Thus caribou with a reach of 8 ft can reach limbs attached approximately 10 ft from the ground.

Table II shows how height of reach would affect amounts of food available. With a reach of 10 ft, probably a generous allowance for caribou standing on bare ground, relatively small amounts of lichen are available. Reach to 15 ft would at least double the food available on all plots. In one plot this additional reach would increase the available lichen 9 times. A reach of 20 ft would increase available food 3 to 16 times, and make up to 42% of the total lichen food available. We believe that deep snow providing a firm footing for caribou is a variable determining the quality of this caribou range in winter. Successively higher reach as snows deepen enables caribou to obtain fresh supplies of lichen.

Study area	No. trees examined	No. trees lichenless in top 5 feet	Average distance lichenless, in feet
1	11	6	8
2	13	8	25
3	12	0	—
4	11	3	5

TABLE II. Treetops without *Alectoria.*

On fallen trees. -- Only a variable and frequently small fraction of lichen loads on standing trees is available to caribou; over half the load remains out of reach. Periodically, however, standing trees are felled by wind breakage and root decay. The full lichen load on the tree is then more or less available to caribou. Fallen trees are a major attraction to caribou, as noted in Ontario by Cringan (1956) and in the present study. Even near timberline where lichen loads near the ground on standing trees are particularly heavy, freshly fallen trees in winter may attract caribou, creating the greatest concentrations of feeding activity noted in our studies.

Cringan (1956) has postulated that in mature or other forests in which large trees are falling with some regularity, lichen carried to the ground may be an important source of food for caribou. He notes that enough falling trees could result in a sustained delivery of lichens to caribou from an abundant and growing supply held out of reach in trees, and so in no danger of being eaten in excess of growth increment. There is no doubt that this mechanism is in operation in Wells Gray Park. From timberline to lowest forests inhabited by caribou in winter, trees with their lichens fall every winter, many are found by caribou, and the lichen on them is eaten.

A major question is whether falling trees bring down enough lichen to make a major contribution to the supply of available food. It is possible to make some estimates of this contribution using weights of lichen obtained in this study.

In a forest typified by Area 3, there are 940 trees per acre with dbh of 2 in. or more. Table III shows the number of these trees by ages, their mortality and the lichen loads they carry. These figures are approximate, and indicate only roughly the amount of lichen that might fall with trees.

Ages of trees (years)	No. trees per acre	No. trees dying in 25 years	Lichen load per tree (gms)	Lichen load on falling trees through 25 years (kg)
50-75	450	200	50	10
76-100	250	90	100	9
101-125	160	110	700	77
126-150	50	35	1600	56
151-175	15	5	3100	155
176-200	10	5	1600	23
201-225	5	5	8600	43
Totals	940	450		373

TABLE III. Theoretical tree mortality on Area 3, and lichen loads on falling trees, in 25 year period.

These figures on tree mortality are obtained by subtracting the number of trees in one age group from the number in the previous age group. For example, the group of 450 trees 50-75 years old will lose 200 trees in 25 years, and there will then be 250 trees 75-100 years old. This calculation assumes there is no change in the structure of the forest with time, but trees are germinating, aging, and dying, in such a manner that the age structure of the forest is more or less constant. This is an ideal concept, familiar as theory in forestry. Such a uniform age structure is found rarely in nature, although some uneven-aged forests approach this theoretical condition.

Table III shows that about 450 trees die in a 25 year period, or 18 trees die per acre per year. If the calculation went back to age zero, rather than age 50, the mortality figures would be much higher. Most mortality in trees takes place at an early age. Our data purposely excluded trees under 50 years old because they carried relatively unimportant quantities of lichen.

If the total load of lichen on trees falling over a 25 year period was 373 kg per acre (Table III), this represents and annual fall of lichen per acre of about 15 kg, oven dry weight. As seen in Table II, the lichen available per acre on standing trees in Area 3 is 26 kg below 10 ft and 56 kg below 15 ft. It appears that falling trees could be important to caribou, as Cringan's hypothesis suggests.

The importance to caribou of 33 kg of falling lichen per acre depends on whether other foods are plentiful or scarce at the time. If most trees fell in winter storms when snow was soft and food difficult to obtain, fallen trees with their lichen would be much more important to caribou survival than if most trees fell in the spring when melting snow was uncovering food on the ground. Limited field data suggest that most trees fall from January to April when food supplies may be critical. The importance of the lichens thus made available may be far greater than is suggested by the weight of caribou food involved.

On the ground. -- When the snow melts in spring, in some forests of Wells Gray Park, considerable quantities of *Alectoria* appear on the ground. These have fallen from trees during the winter, and have accumulated at various depths in the deep snow. Data on the quantities of lichen involved suggest that the amounts made available to caribou in this way may be considerable.

In the spring of 1959, lichens on the snow in 85 plots 1 m sq were collected, dried, and weighed. Plots were arbitrarily scattered through the forests inhabited by caribou in spring. Lichens collected were mainly *Alectoria* spp. but 28 samples contained small quantities of *Cetraria* sp. The weight of fallen lichen on each plot averaged 2.1 ± 1.9 g. This represents an occurrence of available tree lichens on the ground of 8.5 kg per acre. Over small areas this fallen lichen may exceed 50 kg per acre.

The extent to which caribou feed upon this temporary source of food is unknown, but fallen lichen could be important in the spring. About half as much lichen falls free of trees in winter as is carried to the ground annually by falling trees. Like the lichens clinging to fallen trees, those on the ground are supplied by a sustained yield process from a source growing out of reach of caribou, and hence free of possible excessive use.

DISCUSSION

An important condition uncovered by this study was the abundance of *Alectoria* on trees near timberline. Lichen loads of over a ton per acre, oven dry weight, constitute an unexpected abundance, even though casual observation had suggested that loads were heavy. This abundance and its concentration close enough to the ground to be available to caribou are probably the major factors influencing caribou migrations in these mountains. As discussed by Edwards and Ritcey (1959), caribou inhabit forests near timberline from February to April when winter conditions are most severe, and when snow at this elevation may be 6-10 ft deep. One important condition enabling caribou to survive in these high elevation forests is that the deep snows are usually firm to walk on by February. The abundance of lichen must be an additional factor enabling caribou survival. *Alectoria* is abundant, a large percentage of the loads grow on branches near the ground, and deep firm snow increases the upward reach of caribou while feeding. A fortunate combination of environmental conditions appears to favor survival of caribou in winter areas which seem anything but favorable at first glance.

Before February caribou are found in valley bottoms after descending from alpine meadows and timberline forests in October. In valley bottom forests (Area 3 is an example) they feed at first on herbs and evergreen shrubs. Later the snow is too deep for caribou to find these foods, and too soft for easy travel. The caribou then feed on *Alectoria*. The species of lichen available in greatest abundance on this early winter range is *A. sarmentosa*, a species scarce near timberline where *A. jubata* is the main form. Thus two species of *Alectoria* provide most food in winter, one in early winter, the other later.

Possibly caribou have no special preference for these lichens. In these forests in winter epidendric lichens are the only food available to caribou except for coniferous foliage which they apparently find unpalatable. Deep snow buries herbs and shrubs, so that conifers and the lichens on them are the only vegetable matter available to large herbivores.

SUMMARY

Caribou in Wells Gray Park, British Columbia, appear dependent on epidendric lichens, *Alectoria* Ach., for food in winter. This study evaluated roughly the amounts of these lichens available to caribou. Lichen was collected from sample branches of trees in 4 study areas. It was oven dried, then weighed. From each sample the percentage composition by species as estimated.

Total lichen loads per acre ranged from 114-1332 kg. The latter value was from forest near timberline.

Vertical distribution of lichen loads varied among the areas. Loads were generally light within 10 ft of the ground, but were heavy immediately above this. Tops of trees had light loads, partly be-

cause branches were small, and partly because of exposure.

The 3 species of lichen, *Alectoria sarmentosa, A. fremontii* and *A. jubata* (the last may be a complex of similar species) showed quite different ecological tolerances. *A. sarmentosa* was confined to lower branches of forests at lower elevations. The *A. jubata* complex was most successful in all study areas and the most successful in exposed tree tops. The abundant lichen near timberline was mainly *A. jubata. A. fremontii* was less abundant than the other two species. In all study areas it was most abundant in branches immediately above those with abundant *A. sarmentosa*.

These lichens are available to caribou: on trees and within reach from the ground, on fallen trees, and on the ground after falling from trees.

Amounts of lichen on trees available to caribou vary according to several factors. Chief among these appears to be depth of snow. The deeper the snow the higher the reach of caribou into trees. If reach varies from 8-15 ft above bare ground, amounts of lichen available in areas studied ranged from 5-128 kg per acre.

A theoretical calculation of lichen available on falling trees, in a forest typified by Area 3, suggests that 15 kg per acre per year are available. Since most trees fall in severe winter weather, this source of food may be available when other food is scarce.

Fallen lichens accumulate in the snow through winter, and become available in quantity as the snow melts. Limited measurements suggest that almost 8.5 kg per acre may be available on the ground in the spring.

The great abundance of lichen on trees near timberline enable caribou to spend much of the winter in this zone of severe climate and deep snow. The settled snow of late winter enables them to reach higher into trees heavily laden with lichen. These high forests with severe winter climate are the most favored habitat in that season.

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