Canopy, snow, and lichens on woodland caribou range in southeastern Manitoba

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Abstract: I examined the relationships among snow cover (api), lichen abundance, and canopy composition on the range of the Aikens Lake population of woodland caribou (*Rangifer tarandus caribou*) in southeastern Manitoba. Percent cover of forage lichens (*Cladina* spp.) was positively correlated with maximum total thickness and with maximum vertical hardness of api. Mixed communities of trembling aspen (*Populus tremuloides*), spruce (*Picea* spp.), and balsam fir (*Abies balsamea*) showed the most favourable nival conditions for caribou but had low lichen abundance; those dominated by jack pine (*Pinus banksiana*) were the converse. The results suggest an energetic compromise for woodland caribou when foraging for terrestrial lichens. During winter, caribou exhibited significant selection for jack pine communities whereas mixed communities were avoided.

Key words: habitat selection, foraging, *Rangifer tarandus caribou*, taiga

Introduction

Api (snow on the ground) and lichens are perhaps the most salient habitat features that influence the behaviour of caribou (*Rangifer tarandus*) in winter. Caribou are well-adapted to both. Their broad hooves, low foot loading, and single-file mode of travel are characteristics that qualify them as chionophiles (Russell & Martell, 1984). During winter, lichens provide a unique, highly-digestible energy source and are often exploited as a principal forage (Luick, 1977; Russell & Martell, 1984).

For *Rangifer*, api and lichens are opposing entries on the energetic balance sheet: travelling on and cratering through snow cover are often energetic investments for obtaining terrestrial lichens. Recent studies have begun to explore these energetic costs (Boertje, 1985; Fancy & White, 1985, 1987) and nutritional benefits (Person *et al.*, 1980; Thomas *et al.*, 1984) but, as yet, we know little of the association between these 2 important range features. Such knowledge seems fundamental for managing habitat and modelling caribou foraging behaviour. Here, I examine the relationships between api characteristics, lichen abundance, and canopy composition on the taiga range of the Aikens Lake population of woodland caribou (*R. t. caribou*) in Manitoba.

Materials and methods

Field investigations were conducted in the vicinity of Taiga Biological Station, Wallace Lake, in southeastern Manitoba (51°01'N, 95°40'W). The study area, part of the Northern Coniferous Section of the Boreal Forest Region (Rowe, 1972), was dominated by Precambrian outcrops with numerous intervening bogs and small lakes. Sampling was based on a map recognising 5 vegetation communities (Schaefer & Pruitt, 1991): mature spruce bog, jack pine forest, mixed coniferous forest, jack pine outcrop with intervening black spruce bog, and mixed deciduous forest.

Overstorey and Lichen Abundance
Tree density and lichen coverage of 5 vegetation communities, 90 - 160 years of age, were sampled 12 June to 31 July 1985. Discrete areas of habitat within an accessible area were selected randomly. Within each discrete area, 2 sampling sites were picked randomly with a 1:15840 aerial photo and a grid overlay of points 50 m apart. At each site a 50-m transect was established. Its exact origin was determined by the toss of a stone, its orientation (north or south) by the toss of a coin. At 3 random points along the transect, a 50-m branch transect was established with a random east or west directi-

on. The abundance of lichens of the genus *Cladina* was estimated from 6 quadrats, 20 cm x 50 cm, placed longitudinally at random 1-m intervals along the branch transect; 6 discrete cover classes, i.e., <5%, 5-25%, 25-50%, 50-75%, 75-95%, >95% (Daubenmire, 1968) were used. The mid-point of each cover class was used in the statistical analyses. The density of trees was determined at each quadrat by tallying individuals (> 2.5 m high) within a plot of radius 2.0 m. For analysis, each site was treated as an individual sampling unit and was represented by the average tree density and lichen coverage from 18 plots.

To display relationships between canopy composition and other habitat features, principal components analysis (PCA) was performed using SPSS/PC+ (Norušis, 1986) on the density of tree species. The effectiveness of PCA lies in its ability to reduce the number of dimensions to display such multidimensional data while retaining much of the original information (Pielou, 1984). Using PCA, therefore, density data of each of 5 tree species (*Pinus banksiana, Picea* spp., *Populus tremuloides, Betula papyrifera,* and *Abies balsamea*) were reduced to one axis, the largest principal component (i.e., PCA axis 1).

Api Conditions

I restricted the analysis to the time when api thickness and hardness were maximal (early March) in 1985 and 1986. I selected a 6 x 50 m site, representative of each community type (Schaefer & Pruitt, 1991), where api profiles were placed haphazardly. In each profile, vertical hardness (g·cm⁻²) of the sur-

face layer, using spring penetrometers, and total thickness (cm) were recorded (Pruitt, 1959). During 1985, 5 profiles were taken per site; during 1986, 4 profiles were taken. For each community type, the 2-year averages of maximum total thickness and maximum vertical hardness were extrapolated to all sites of the same habitat type. The lack of independence of api observations means that such sampling is pseudoreplicated (Hurlbert, 1984). Hence, although I used a Bonferonni-corrected α of 0.005 as an indication of significant linear correlations between variables (Norušis, 1986), these statistical inferences should be treated cautiously.

Results

Api variables, canopy composition, and the abundance of *Cladina* lichens were interrelated in the study area (Table 1). Maximum total thickness and maximum vertical hardness of the api were negatively correlated with the density of balsam fir (*Abies balsamea*) and positively correlated with that of jack pine (*Pinus banksiana*). Coverage of forage lichens (*Cladina* spp.) was similarly related; more lichen was associated with increased density of jack pine, less lichen with with increased density of fir.

Correspondingly, greater lichen abundance was positively correlated with both harder and thicker api (Table 1). We can compare the extremes in upland communities: on jack pine outcrops, where coverage of *Cladina* spp. averaged 17%, api was 80 g·cm⁻² (more than 100%) harder and almost 10 cm (32%) thicker than in mixed coniferous forests where lichen coverage was only 1.5%.

The first principal component from the ordination of overstorey species - tending to separate sites dominated by jack pine from mixed stands of balsam fir, spruce (*Picea* spp.), and trembling aspen (*Populus tremuloides*) - accounted for 34% of the total variation. When plotted against *Cladina* spp. abundance, the above interrelationships can be visualised (Fig. 1). The ordination axis, with mixed communities (types 1, 3, and 5) tending to the negative (left) end of the axis and jack pine habitats (types 2 and 4) to the positive (right) end, was positively correlated with lichen coverage (r = 0.69). The superimposed api parameters, hardness and thickness, show relationships to both overstorey and *Cladina* abundance (Fig. 1). Vertical api hardness was better correlated to the canopy ordination axis (r = 0.67), however, than was total thickness (r = 0.38).

Discussion

Snow cover is influenced by the type and density of the trees above it, a relationship which has been widely documented (e.g., Bunnell *et al.*, 1985). In

Table 1. Correlations between density of tree species, api characteristics, and lichen abundance in the Wallace-Aikens lakes study area in southeastern Manitoba, 1984–86. All correlations were significant (Bonferonni-corrected $P < 0.005$).

	Jack pine density	Balsam fir density	Api total thickness	Api vertical hardness
Lichen coverage[a]	0.69	- 0.57	0.51	0.84
Jack pine density		- 0.47	0.44	0.63
Balsam fir density			- 0.44	- 0.57
Api total thickness				0.76

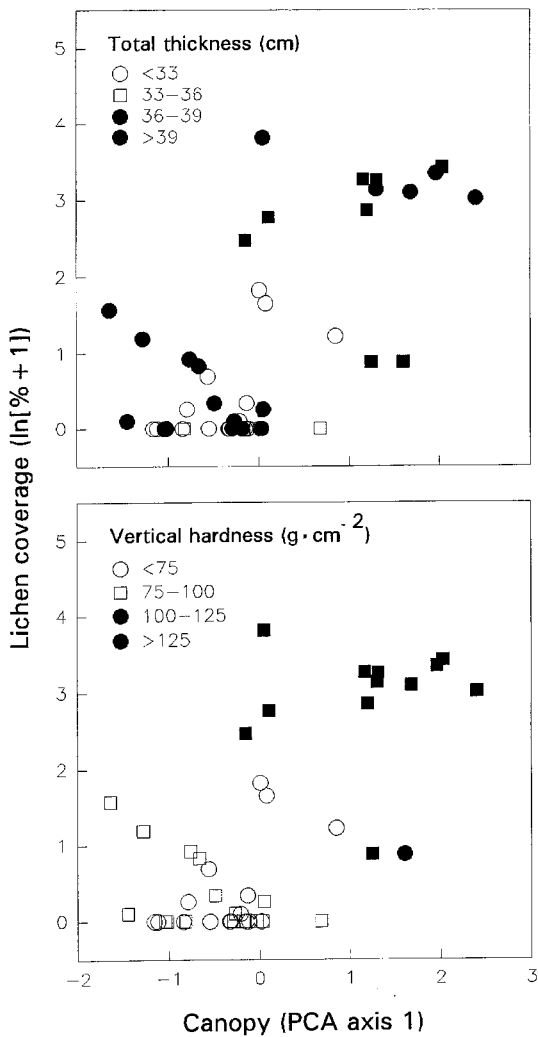[a] Lichen coverage is expressed as ln (% cover of *Cladina* spp. + 1).

Fig. 1. Maximum total thickness and vertical hardness of api superimposed on a scattergram of lichen (*Cladina* spp.) abundance and the first principal component of canopy species. Jack pine communities tend to the right, mixed spruce/fir/aspen communities to the left.

general, greater coniferous cover reduces api thickness by providing greater snow interception and qali (Pruitt, 1957) formation. It reduces the surface hardness through wind interference and shading of the forest floor (Bunnell *et al.,* 1985).

In this study, the relation between maximum thickness of snow cover and jack pine abundance was counter to this general trend and, initially, appears counter-intuitive. The result may stem from the low sample size, but I offer 2 further, tentative explanations. First, the form of the jack pine - api relationship may not be strictly linear across the full range of jack pine densities. The extent of densities studied here

(approx. $0.5 - 1.0 \times 10^3$ stems·ha⁻¹) was well below that in younger (37-year-old) stands in the study area (approx. $2.5 - 3.5 \times 10^3$ stems·ha⁻¹ [Schaefer, unpubl. data]). Such dense, intermediate-aged stands, although not used by woodland caribou, appeared on cursory inspection to have thinner snow cover than old-growth communities. Coverage of *Cladina* spp., however, was similar (Schaefer & Pruitt, 1991).

Second, and perhaps more fundamental to our understanding, is that the relationships outlined here are probably scale-dependent. Results from many ecological studies (reviewed by Wiens, 1989) suggest that such correlations may depend on scale, i.e., the size of the sampling unit and the extent of sampling chosen by the investigator. Schaefer & Messier (1995), for example, found that correlations between arctic vegetation and snow cover (upsik) appeared stronger when larger sampling units were used in analysis. In this light, the positive association of jack pine and api may be counter to expectations only at the finer, microsite level. The extent of sampling for vegetation in this study was at the 'stand' level; i.e., I used a potential sampling area of 50 x 100 m at each site. At this scale, the increasing amount of jack pine at the expense of other species may be indicative of a relatively more open canopy.

LaPerriere & Lent (1977) have noted a hierarchical nature of habitat selection by caribou: animals first choose regional areas (such as a watershed), feeding areas (such as an outcrop), and finally a crater site (such as a lichen patch). This suggests that the present study of range relations has implications for the feeding area level of habitat selection, but may not validly be extrapolated to higher or lower scales. In general, there is a need for studies of how scale affects the interpretation of ecological phenomena. See Wiens (1989) for an excellent discussion on spatial scaling in ecology.

Nonetheless, the present results are in agreement with previous reports that tree species differ in their efficacy at altering snow cover (Bunnell *et al.,* 1985). In the study area, balsam fir appears to be the most effective species at providing favourable api for *Rangifer*. This accords with the findings of Lull & Rushmore (1961, in Bunnell *et al.,* 1985: 323) who found that balsam fir intercepted a relatively high proportion in snow.

Yet, interestingly, those habitats dominated by fir also contain a paucity of *Cladina* lichens as well as other winter forages for woodland caribou (Schaefer, 1988; Schaefer & Pruitt, 1991). Jack pine communities in old-growth condition had abundant lichen (*Cladina* spp.) but more severe api conditions. This is consistent with Stevenson & Hatler's (1985) generalisation that, for caribou, a trade-off exists between snow cover and forage abundance.

How do woodland caribou deal with such a energetic compromise? Previous investigations (Pruitt, 1959; Bergerud, 1974) have indicated that caribou select feeding sites primarily for abundance of forage, secondarily for suitability of nival conditions. During 1984-86, Aikens caribou exhibited similar behaviour. Winter activity as measured by travel, feeding sites, and pellet groups was significantly skewed towards jack pine habitats while mixed communities were avoided (Schaefer & Pruitt, 1991). These results imply that added investment of cratering and travelling on harder, thicker api (Fancy & White, 1985; 1987) was adequately compensated by the richer lichen mat. Conversely, Ouellet et al. (1993) suggested that caribou (*R. t. groenlandicus*) on Southampton Island failed to exploit the most lichen-rich habitats because of higher snow accumulation, although they reported only weak correlations of lichen biomass and hardness of upsik.

The results may carry implications for the management of woodland caribou habitat. In particular, because of the influence of trees on snow cover, alteration of the canopy by fire or logging may indirectly affect the winter foraging behaviour of caribou. Logging operations, for instance, may have only negligible effects on the biomass of *Cladina* lichens (Harris, 1992), but removal of the canopy by logging can result in thicker and denser api (Kirchoff & Schoen, 1987; Schwab *et al.*, 1987) and, inferentially, greater energy costs for foraging caribou. In the study area, Schaefer & Pruitt (1991) found that api hardness and thickness were substantially greater in burned (i.e., 5-year-old) than in old-growth stands, even though much *Cladina* lichen remained intact within the burn.

The results here suggest an energetic compromise for caribou while foraging for *Cladina* lichens during winter. Further documentation of the relationship between forages and snow may improve our understanding of caribou foraging behaviour and management of their habitat.

Acknowledgements

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