

The influence of variable snowpacks on habitat use by mountain caribou

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Abstract: Mountain caribou (*Rangifer tarandus caribou*) in southeastern British Columbia subsist for most of the winter on arboreal hair lichen, mostly *Bryoria* spp. Foraging occurs mainly in old subalpine fir (*Abies lasiocarpa*) forests near treeline. Here, the lower limit of *Bryoria* in the canopy is dictated by snowpack depth because hair lichens die when buried in snow. *Bryoria* is often beyond the reach of caribou in early winter, prompting caribou to move downslope to where lichen occurs lower in the canopy and other foraging modes are possible. Snowpacks are normally deep enough by late winter that caribou can reach *Bryoria* where it is most abundant, at high elevations. Extending this to inter-annual comparisons, *Bryoria* should be less accessible during late winter of low-snow years following normal winters, or of normal to low-snow years after deep-snow winters. We hypothesized that when maximum snowpack in late winter is low relative to the deepest of the previous 5 years, mountain caribou will use lower elevations to facilitate foraging ("lichen-snow-caribou" or LSC hypothesis). We tested this with late-winter data from 13 subpopulations. In the dry climatic region generally and for minor snowfall differences in wet and very wet regions, caribou did not shift downslope or in fact were at higher elevations during relatively low-snow years, possibly reflecting the ease of locomotion. The LSC hypothesis was supported within wet and very wet regions when snowpacks were about 1 m or more lower than in recent years. Elevation declined by 300 m (median) to 600 m (25th percentile) for snowpack differences of at least 1.5 m. Greater use of lodgepole pine and western hemlock stands sometimes also occurred. Management strategies emphasizing subalpine fir stands near treeline should be re-examined to ensure protection of a broader range of winter habitats used by caribou under variable snowpack conditions.

Key words: *Bryoria*, elevation, forage, forest management, lichen, locomotion, *Rangifer tarandus caribou*, winter.

Rangifer, Special Issue No. 17: 93-102

Introduction

Woodland caribou (*Rangifer tarandus caribou*) inhabiting the high-snowfall region of southeastern British Columbia, Canada, are known provincially as mountain caribou¹ (Heard & Vagt, 1998). Mountain caribou and other woodland caribou falling within the Southern Mountains national ecological area are considered threatened nationally (Thomas & Gray, 2002). Mountain caribou have recently undergone a rapid population decline (Wittmer *et al.*, 2005) and are provincially "red-listed" (Conservation Data Centre, 2006).

Mountain caribou are defined largely by their reliance for winter forage on arboreal hair lichen of the genus *Bryoria*, which they obtain mainly in old

treeline forests dominated by subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*; Edwards and Ritcey, 1960; Simpson *et al.*, 1987; Rominger *et al.*, 1996; Terry *et al.*, 2000; Kinley *et al.*, 2003). Hair lichens as a group are sensitive to prolonged wetting (Goward, 1998; Coxson & Coyne, 2003). Presumably because of this, the lower limit of *Bryoria* in the canopy is dictated by the maximum settled depth of the winter snowpack. Thus, where average snowpacks are deep, *Bryoria* on standing trees tends to be unavailable to caribou in early winter, i.e. until snow has accumulated sufficiently to lift caribou within reach of the lichen. The normal foraging reach of caribou is 1.6 to 2.2 m above the point to

¹ In some other jurisdictions, the term "mountain caribou" refers to another ecotype of woodland caribou inhabiting mountainous areas but not primarily reliant on arboreal lichen.

which they sink into the snowpack (Antifeau, 1987). When the *Bryoria* trimline is higher than this, caribou must adopt additional or other foraging modes. Alternatives include using lichen from wind-thrown trees or fallen branches, or using terrestrial plants or lichens. These options are normally accompanied by downslope movement to areas of lower snow depth, where hair lichens occur lower in the canopy and cratering for terrestrial forage is also feasible (Antifeau, 1987; Simpson *et al.*, 1987; Rominger & Oldemeyer, 1989, 1990; Apps *et al.*, 2001; Stevenson *et al.*, 2001). In most of western North America, *Bryoria* is most abundant at upper forested elevations where its most copious growth (at least in the lower canopy) is in well-spaced old growth forests (Goward & Campbell, 2005). Compared to *Alectoria* – the other dominant hair lichen genus in mid- to high-elevation forest – *Bryoria* is strongly preferred by caribou (Rominger *et al.*, 1996), perhaps because of its higher protein levels (Antifeau, 1987). Given that *Bryoria* increases in abundance at higher elevations while *Alectoria* is more common in valley bottoms, and perhaps also because of the higher incidence of predators in valley bottoms during winter (Kinley & Apps, 2001), caribou minimize their time at lower elevations, despite the greater availability of terrestrial vascular forage there (Rominger & Oldemeyer, 1989, 1990).

“Early winter” is defined as the period from the onset of snow to the time when the snowpack is sufficiently deep to allow foraging of hair lichen from standing trees at high elevations. “Late winter” then lasts until caribou begin seeking terrestrial vascular forage exposed as snow melts in spring (Stevenson *et al.*, 2001). In drier regions where snowpacks are typically shallow, little downslope movement is evident during early winter and that season may be very short, whereas in areas with greater snowfall, caribou may remain at low elevations for nearly half of each winter (Terry *et al.*, 2000; Apps *et al.*, 2001; Stevenson *et al.*, 2001; Kinley *et al.*, 2003).

Such elevational shifts within a subpopulation can be variable within and between years (Antifeau, 1987; Rominger & Oldemeyer, 1990; Apps *et al.*, 2001). Inter-annual differences may relate in part to snow depth in a given winter relative to that of the years preceding. Winters of exceptionally deep snow cause the *Bryoria* trimline to recede upward, thereby potentially placing it beyond the foraging reach of caribou in subsequent years (Goward, 2003). This observation led Goward (2002, 2003) to posit the Lichen-Snow-Caribou (LSC) hypothesis which states that there will be less *Bryoria* within foraging reach of caribou for several years following a season of unusually deep snowpacks, that is, until *Bryoria* re-establishes over lower branches (see also Utzig, 2005).

This pattern should be less true at lower elevations. Despite the lesser abundance of *Bryoria* there (Goward, 1998; Goward & Campbell, 2005), any *Bryoria* or *Alectoria* present is more likely to be within foraging reach of caribou due to the limited variability in snowpack at lower elevations. Therefore, the LSC hypothesis predicts that caribou will tend to use lower elevations, or remain there longer, in low-snow winters following an exceptionally deep snowpack. We predict that this phenomenon may also be detectable during shallow-snowpack years following normal winters, i.e. that *relative* snowpack depth is a key predictor of elevation use. More specifically, we hypothesize that when the maximum snowpack in any winter is low relative to the deepest snowpack of the previous 5 years, mountain caribou will: (1) use lower elevations or spend a greater proportion of their time there, or (2) otherwise shift habitat-use patterns to facilitate foraging. Because mountain caribou in many areas are obliged to use lower elevations during early winter regardless of current snow depth, these predictions apply to late winter. The 5-year effect period is an estimate of the minimum period potentially required for *Bryoria* to recolonize lower branches – mostly from thalli dislodged from higher in the canopy – in amounts potentially usable by caribou (T. Goward, pers. obs.), though full recovery likely takes much longer.

Despite the extensive literature regarding mountain caribou habitat selection, previous authors have not specifically tested the LSC hypothesis. We address differences between years in relation to recent maximum snowpacks, whereas most others compared used habitats to available habitats or compared seasons regardless of inter-annual snowpack patterns (Simpson *et al.*, 1987; Rominger & Oldemeyer, 1990; Terry *et al.*, 2000; Apps *et al.*, 2001; Johnson *et al.*, 2004), looked at single years (Servheen & Lyon, 1989; Kinley *et al.*, 2003), or compared groups of caribou rather than years (Warren *et al.*, 1996). Rominger & Oldemeyer (1989) did compare early-winter habitat use in relation to snowpack accumulation. They found that terrestrial foraging extended longer with slow snow accumulation, but did not specifically address the elevations used in slow- versus rapid-accumulation years. Antifeau (1987) also examined habitat use relative to snowpack, sinking depth, energetics, and lichen availability, pointing to the energetic advantages of using low elevations during early winter when lichen was unavailable at upper elevations, and higher elevations during late winter. He also found differences in elevation use in relation to snow accumulation rate but did not examine the effect of extreme inter-annual snowpack differences.

An alternative hypothesis exists to explain the downslope movements made in many subpopulations

during early winter. Such movements could potentially relate to the difficulty of locomotion in the unconsolidated snowpack typical of that season, rather than or in addition to an inability to access sufficient *Bryoria* then (Edwards & Ritcey, 1959; Antifeau, 1987). Perhaps caribou move downslope in deep-snow regions primarily to reach areas with greater ease of movement until the snowpack becomes consolidated at upper elevations. If so, unusually heavy snowfalls during late winter should also impair the ability of caribou to move at upper elevations. If this locomotion hypothesis were valid, we would expect that caribou would more commonly occur at lower elevations during deep-snow years, rather than during low-snow years as predicted by the LSC hypothesis.

Understanding whether or to what extent shifts in the lichen trimline affect movements and habitat use by mountain caribou has potentially profound implications for habitat requirements, forest management and population viability, particularly in view of changing climates. In this analysis, we reviewed existing telemetry and snow-survey data from throughout the range of mountain caribou to determine whether the LSC hypothesis was supported or whether there was greater support for the locomotion hypothesis. For each of 13 mountain caribou subpopulations investigated, we compared late-winter habitat use during years having shallow versus deep relative snowpacks, to determine whether habitat use was affected by presumed upward shifts in the *Bryoria* trimline.

Methods

Study area

Mountain caribou exist as a series of 18 subpopulations (Wittmer *et al.*, 2005) in a high-precipitation, mountainous, continental region of southeastern British Columbia, Canada, and small portions of adjacent northern Idaho and Washington, USA. Elevations within this 60 000 km² area range from 450 to 3500 m. Three principal biogeoclimatic zones occur here, defined on the basis of climate and climax vegetation (Meidinger & Pojar, 1991; Meidinger, 2006; Research Branch, 2006). (1) At the lowest elevations, the Interior Cedar – Hemlock zone (ICH) has climax forests consisting of western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*). Other biogeoclimatic zones are intermixed with or replace the ICH in places, including the Montane Spruce (MS) in the extreme southeast, and the Sub-Boreal Spruce (SBS) in the north. In both cases, climax forests are mainly of hybrid white spruce (*Picea glauca* x *engelmannii*). (2) Above the ICH

is the Engelmann Spruce – Subalpine Fir zone (ESSF), in which climax stands are closed-canopied Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) that, near the upper limits of the zone, become more open (“woodland”) and then very open and clumpy (“parkland”). With increasing elevation, subalpine fir is often mixed with whitebark pine (*Pinus albicaulis*) and, in the south, alpine larch (*Larix lyalli*) in the woodland and parkland subzones. (3) The Interior Mountain-heather Alpine zone (IMA) in the south and Boreal Altai Fescue Alpine zone (BAFA) in the north are at the highest elevations and are non-forested. Wildfire and other natural and human-caused disturbances have resulted in variable proportions of non-climax tree species in all zones below the ESSF woodland. Of note is the relative abundance of lodgepole pine (*Pinus contorta*), except in the highest-precipitation areas toward the center of mountain caribou range.

Late-winter habitat generally consists of the uppermost portions of the closed-canopied ESSF along with the ESSF woodland and ESSF parkland, while early-winter habitat normally includes the ICH and closed-canopied ESSF (Stevenson *et al.*, 2001) and sometimes the ESSF woodland.

Snow data

We obtained snow-depth data collected near the first day of each month from January 1980 through May 2004 (River Forecast Centre, 2006). A representative snow course was chosen for each subpopulation based on its location and completeness of data. For months when snow-depth values were missing, we regressed snow-depth against available snow-pillow (mass) data from that snow course for that month in other years, then estimated snow depth based on the current month's snow mass. Where this was not possible, we estimated depth based on values from an adjacent course in a similar biogeoclimatic subzone, in relation to regressions of snow depth between the 2 courses from other years for that month. Because snow courses occurred across a range of elevations, we then adjusted snow depths to values that would be expected at elevations where late-winter habitat normally occurs, defined as local boundaries between the closed-canopied ESSF and the ESSF woodland subzone. We determined this elevation – snow depth relationship by comparing data from all pairs of snow courses within mountain caribou range where the 2 courses were within 5 km of each other but were separated by 390 to 770 m of elevation. We developed regression equations of mean snowpack difference (cm) per elevation (m) for 6 pairs of courses from very wet or wet subzones of the ESSF and separately for 2 pairs from dry subzones (Research Branch, 2006). We then

used the slope of the appropriate equation (0.1811 cm snow/m of elevation for wet and very wet subzones and 0.0849 cm snow/m of elevation for dry subzones) to extrapolate snow depth from the snow course elevation to the local ESSF woodland lower boundary. While acknowledging the simplistic assumptions inherent in this approach, we feel the resulting approximations reflect trends in snow depth.

Each winter was then assigned to categories of either low relative snowpack (hereafter “low-snow years”) or normal to deep relative snowpack (hereafter “deep-snow years”) based on the following criteria. If the maximum snow depth during the winter (regardless of month) was 50-99 cm lower than that of any year within the previous 5 years and was also lower than the 25-year mean of maximum annual snow depths, it was considered to be a low-snow year. If it was within 25 cm of the maximum recorded during each of the previous 5 years (or exceeded that value) and was also greater than the 25-year mean of maximal snow depths, it was considered to be a deep-snow year. If it did not fit either of these categories, it was disregarded. This process was then repeated, replacing the 50-99 cm “cutpoint” with 100-149 cm and then 150+ cm (only 2 data points fell beyond 200 cm). Deep-snow years remained unchanged in each case. This allowed us to compare low- to deep-snow years based on up to 3 definitions of “low-snow”, thereby making it possible to evaluate the sensitivity of caribou to various classes of relative snow-depth.

Caribou location data

We collated radiotelemetry data gathered from 411 caribou between 1987 and 2004 under previous or existing research projects within all subpopulations. We divided the Wells Gray subpopulation as defined by Wittmer *et al.* (2005) into 3 groups based on major physiographic and caribou habitat-use differences (Apps & Kinley, 2000). These new groups included Wells Gray-Mountain, Wells Gray-Highland North and Wells Gray-Highland South. Adult caribou on which conventional VHF radiocollars were deployed were of both sexes and were captured using net guns fired from helicopters. They were monitored aerially during the winter, using standard radiotelemetry techniques (Fuller *et al.*, 2005) on a roughly weekly to monthly schedule. Where GPS collars were also deployed they were generally also monitored using the collars’ VHF beacons, so we used such manually collected data because it was most comparable to the VHF-collar data. Where GPS collars were not aerially monitored, we used locations logged by the collars, but rejected records based on fewer than 4 satellites or not obtained between 8 AM and 5 PM (the approximate period in which aerial telemetry occurred). We then

thinned the remaining GPS-collar data to get 1 randomly selected point per week (or longer if no data meeting our criteria were available) and added this to data obtained through conventional radiotelemetry. Some of the study animals for the South Selkirks subpopulation had been translocated there. Though habitat use by these animals was similar to that of residents (Warren *et al.*, 1996) we deleted, as a precautionary measure, any data from the winter of their arrival and the following winter.

We based our analysis on data obtained between 1 January and 15 April. This end date is the earliest among years that animals in the highest-snowfall region of mountain caribou range shifted from late-winter to spring behavior (Apps *et al.*, 2001), so we selected it for all subpopulations to ensure that we were not considering spring foraging behavior. The 1 January analysis start is the approximate mean date at which the shift from early-winter to late-winter foraging begins (Apps *et al.*, 2001; Stevenson *et al.*, 2001; Kinley *et al.*, 2003). While this date is variable among subpopulations and years, it was less critical for our analysis than was the choice of end date because the transition from early to late winter essentially represents a continuum.

Habitat use measures

In a GIS environment, we obtained attributes of each caribou radiolocation in relation to 3 habitat variables (Table 1). Digital data included elevation (Geographic Data BC, 1996) and forest cover projected to 2000 (Forest Analysis and Inventory Branch, 2000). This was true of all but the South Selkirks subpopulation which, because it straddles 3 states or provinces and many land-ownership jurisdictions, was not covered by any single database. Accordingly, we used a forest-cover database developed specifically for that subpopulation (T. Laysen, USDA Forest Service, Priest Lake, Idaho, unpubl. data) which grouped tree species into categories that could be correlated to our 3 species groups. However, it included only a 2-part (forest versus non-forest) rather than 3-part scheme for cover classification, so that variable was not assessed for this subpopulation.

Data analysis

For each subpopulation and for each of the 3 definitions of low-snow late-winters, we compared all caribou locations from all low-snow years combined to those from all deep-snow years, using the variables in Table 1. Comparisons were made only when a subpopulation had at least 10 telemetry locations in each of low-snow and deep-snow years. In addition, we pooled all subpopulations falling entirely within wet or very wet subzones of the ESSF (i.e. excluding

Table 1. Habitat variables derived for each caribou radiolocation.

Variable	Description	States or Range	Scale
Elevation	metres asl	continuous	250-m pixels
Cover	broad cover class	<ul style="list-style-type: none"> • NF: non-forest (generally alpine) • AF: alpine forest (open canopied, near treeline) • F: forest (\approx commercial forest) 	1:20 000
Leading Tree Species	most common species in over-story, grouped in ecological classes (only for AF and F cover types)	<ul style="list-style-type: none"> • B: subalpine fir (<i>Abies lasiocarpa</i>), whitebark pine (<i>Pinus albicaulis</i>), alpine larch (<i>Larix lyalli</i>), Engelmann and hybrid white spruce (<i>Picea englemannii</i> and <i>P. glauca</i> x <i>englemannii</i>), mountain hemlock (<i>Tsuga mertensiana</i>) • H: western hemlock (<i>Tsuga heterophylla</i>), western redcedar (<i>Thuja plicata</i>), Douglas-fir (<i>Pseudotsuga menziesii</i>), all broadleaf species • P: lodgepole pine (<i>Pinus contorta</i>), western white pine (<i>P. monticola</i>), western larch (<i>Larix occidentalis</i>) 	1:20 000

Purcells-Central, Purcells-South and South Selkirks) to examine the aggregate effect for caribou in the deeper snowpack regions. For each of low-snow and deep-snow years, this pooled sample included an equal, random selection of telemetry locations from each subpopulation, based on the subpopulation with the lowest sample size (minimum 10 locations per year type). We tested nominal data (cover and leading species) with chi-square tests and elevation data with Wilcoxon rank sum tests to assess significance, using the program JMP IN 5.1 (SAS Institute Inc., Cary, North Carolina). We used the nonparametric Wilcoxon test rather than the parametric t-test because elevation distributions were not normal, and because we were more interested in differences in the median and associated indicators of distribution (percentiles) than in the mean. We report differences in responses between low-snow and deep-snow years, rather than the absolute values of each, to facilitate comparisons among subpopulations. To adjust for multiple comparisons from the same dataset, we define P_{CRIT} as 0.05/the number of tests per population. For each year of data for each subpopulation within the wet and very wet climatic regions, we also compared snowpack (in relation to the deepest in the previous 5 years) to median relative elevation of caribou locations. Relative elevation was the absolute elevation of caribou locations scaled to the elevation range used by that population, which was the difference between the 1st and 99th percentiles of elevation used by any animal of that population during early winter or late winter (1 Nov – 15 Apr) of all years combined.

Results

Of the 20 possible caribou groupings, 13 had sufficient data to test the hypothesis for at least 1 of the relative snowpack cutpoints. When late-winter snowpack variability was 50-99 cm, 0 of 11 subpopulations used significantly lower elevations in low-snow years

than in deep-snow years, and the Purcells-Central subpopulation used higher elevations (Table 2). At snowpack variability of 100-149 cm, 4 of 8 subpopulations occurred at significantly lower elevations, 2 had apparently lower but non-significant elevation values, 1 (Columbia-North) had lower 25th and 75th percentile elevations but a non-significantly higher median and caribou in 1 (Purcells-Central, occurring in the dry climate region) used higher elevations. When snowpack variability exceeded 150 cm, caribou in 3 of 4 subpopulations used lower elevations, while median elevation in the other (South Selkirks, occurring partly in the dry climate region) did not differ. Differences between low-snow and deep-snow years were most evident at the 25th percentile of elevation.

At 50-99 cm snowpack variability, use of cover types did not differ significantly between low- and deep-snow years for any subpopulation (Table 2). For differences of 100-149 cm, caribou in Wells Gray-Highland North, Wells Gray-Mountain and Frisby-Boulder used more forested areas. When snowpack differences were greater than 150 cm, Frisby-Boulder caribou used more forested areas, data for Columbia-South and Nakusp were indicative of greater forest use (but were not significant), and no cover data were available for South Selkirks.

When snowpack variability was 50-99 cm, leading tree species among forest and alpine forest cover types differed between deep- and low-snow years only for Purcells-Central, where caribou locations were more commonly associated with subalpine fir during low-snow years (Table 2). At 100-149 cm variability, Purcells-Central caribou were again more commonly associated with the subalpine fir group during low snow years and those in Wells Gray-Highland North were more commonly associated with lodgepole pine and western hemlock, as were caribou in South Selkirks and Nakusp at 150+ cm of negative snowpack difference.

For data from combined subpopulations of the wet and very wet subzones, changes in habitat use were

evident under conditions of greater inter-annual snowpack variability (Fig. 1). At 50-99 cm snowpack variability, little difference was evident between low-snow and deep-snow years, although there was a weak indication of greater use of subalpine fir at the expense of western hemlock. When variability was 100-149 cm, elevation declined, use of cover classes differed (an

apparent shift from non-forest and alpine forest to forest), and data were indicative of greater use of western hemlock during low-snow years. When snowpack variability exceeded 150 cm, low snow years were characterized by lower and more variable elevations (median and 75th percentile declined by about 300 m while the 25th percentile declined by nearly 600 m

Table 2. Late-winter habitat use by mountain caribou in relatively low-snow years. Reported values are differences (elevation) or classes having increased use (cover and leading tree species; including absolute percentage increase) in low snow versus deep-snow years. Significance: * = $P < 0.05$ /tests per subpopulation. Blanks indicate no or insufficient sample, or no habitat data available.

Subpopulation (NW to SE)	Climatic Region ¹	Snowpack Difference (cm)	n (low)	n (high)	Elevation (m)			Cover ²	Leading Tree Species ³
					median	25th %	75th %		
Hart Ranges	wet	50 - 99	71	95				NF (11)	unchanged
		100-149							
		150+							
Barkerville	wet	50 - 99	125	86	-36	-12	-3	NF (2)	B (5)
		100-149	22	86	* -106	-142	-49	F (14)	B(1), P(1)
		150+							
Wells Gray-Highland North	wet	50 - 99	90	205	-22	-36	5	F (5)	unchanged
		100-149	47	205	* -93	-153	-87	* F (41)	* P(12), H(1)
		150+							
Wells Gray-Mountain	wet	50 - 99	132	235	30	24	32	NF (4)	B (13)
		100-149	187	235	* -107	-133	-44	* F (19)	B (7)
		150+							
Columbia- North	very wet & wet	50 - 99	110	203	-86	-198	-2	NF(2), AF(1)	H (13)
		100-149	173	203	-50	111	-53	AF(5), NF(2)	H (3)
		150+							
Frisby-Boulder	very wet & wet	50 - 99	20	25	-92	-20	-105	* F (47)	B (13)
		100-149	10	25	* -236	-492	-212	* F (62)	H (18)
		150+							
Columbia- South	very wet & wet	50 - 99	64	97	-24	81	11	NF(9), AF(1)	B (19)
		100-149	147	97	-89	-75	-39	NF (18)	H (3)
		150+	153	97	* -312	-422	-166	F (7)	B (3)
Kinbasket	wet & very wet	50 - 99	65	71	-113	-228	-2	AF (14)	H (6)
		100-149							
		150+							
Duncan	wet	50 - 99	42	24	-42	-159	-83	F(17), AF(1)	H (1)
		100-149	23	24	* -409	-550	-388	F(28), AF(5)	H (28)
		150+							
Nakusp	wet	50 - 99	111	328	47	24	28	NF(5), AF(3)	P(2), B(1)
		100-149							
		150+	14	328	* -448	-520	-368	F (29)	* H(49), P(15)
South Selkirks	wet & dry	50 - 99							
		100-149							
		150+	98	228	36	-28	69		* P(25), H(10)
Purcells- Central	dry	50 - 99	30	81	* 166	117	128	AF(14), NF(11)	* B (29)
		100-149	30	81	* 128	117	131	AF(24), NF(1)	* B (30)
		150+							
Purcells-South	dry & wet	50 - 99	97	142	-27	-6	-30	AF(4), NF(1)	B (3)
		100-149							
		150+							

¹ based on subzone names within the Engelmann Spruce-Subalpine Fir zone.

² NF = non-forest; AF = alpine forest; F = forest (≈ commercial forest).

³ B = subalpine fir group; H = western hemlock group; P1 = lodgepole pine group.

relative to deep-snow years). There was also a non-significant shift to less use of non-forest and alpine forest and greater use of western hemlock.

Considering all data for the wet and very wet climatic regions as individual data points, the use of the highest relative elevations generally occurred when snowpacks were just below the deepest in recent years (Fig. 2). When snowpack differences were considerably lower (roughly 80-90 cm or greater), relative elevation declined. There may also have been a slight elevation decline when snowpacks exceeded those of recent years (Fig. 2).

Discussion

Snowpack variability of less than about 1 m caused little change in elevation by mountain caribou during low-snow years. Possibly the *Bryoria* trimline was sufficiently irregular within or across stands due to the presence of sheltered microsites (such as within clumps of trees) to sustain caribou when the change in relative snowpack was minimal. Alternatively, moderately low-snow conditions may have been of benefit by improving the ease of locomotion at high elevations and allowing caribou to remain there or even move higher than usual. However, when the maximum snow depth was at least 1.5 m lower than in recent years, subpopulations of the wet and very wet regions used increasingly lower elevations, consistent with the LSC hypothesis. In particular, the lower limit of caribou activity declined dramatically, with the 25th percentile of elevation shifting nearly 600 m downward during the lowest-snow years. This disproportionately low 25th percentile in comparison to declines in the median and 75th percentile of about 300 m indicated greater variability in elevation during low-snow years.

The downward shift during low-snow years was not evident for subpopulations occurring at least partly within the dry climatic region. Caribou of the only subpopulation completely in the dry region (Purcells-Central) were actually higher during low-snow winters. Drier areas typically have lower snowpacks so *Bryoria* would be expected to be available early in the winter there. Thus, snowpack variability in such areas may have little impact on the availability of *Bryoria* to caribou, obviating the need to move downslope during winters with relatively low snowpacks. Foraging for terrestrial food sources can occur at high elevations in dry regions (Kinley *et al.*, 2003) so low-snow winters may allow caribou to travel more easily and extend ground-foraging for longer periods while also taking advantage of the greater total *Bryoria* biomass at upper elevations. Also, the uppermost elevations correlate roughly with windswept slopes and ridges where

Bryoria occurs lower in the forest canopy (T. Goward, pers. obs.) and where there should be reduced upward movement of the *Bryoria* trimline during deep-snow years. Therefore, even if *Bryoria* availability does decrease somewhat during relatively low-snow years in dry regions, shifting to windswept sites at very high elevations could mitigate that effect. Overall, patterns observed in shallow-snowpack regions are not obviously consistent with the LSC hypothesis and may in

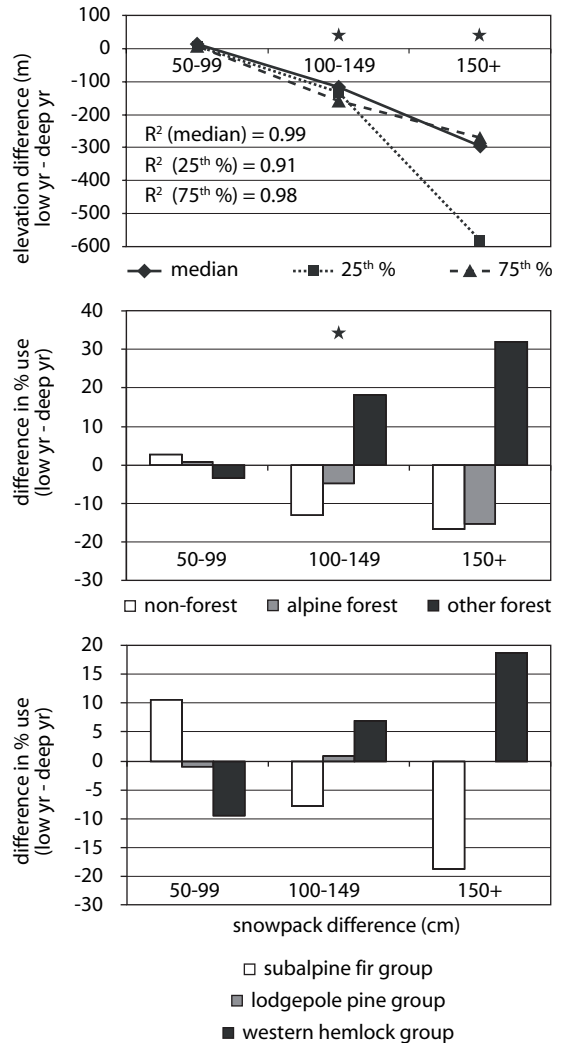


Fig. 1. Late-winter habitat use by mountain caribou in low-snow relative to deep-snow years based on equal random samples from all available subpopulations in wet and very wet ESSF subzones ($n=336$ low/192 deep locations from 8 subpopulations at 50-99 cm, 140/168 from 7 subpopulations at 100-149 cm and 30/75 from 3 subpopulations at 150+ cm; * = sig. difference at indicated snowpack difference).

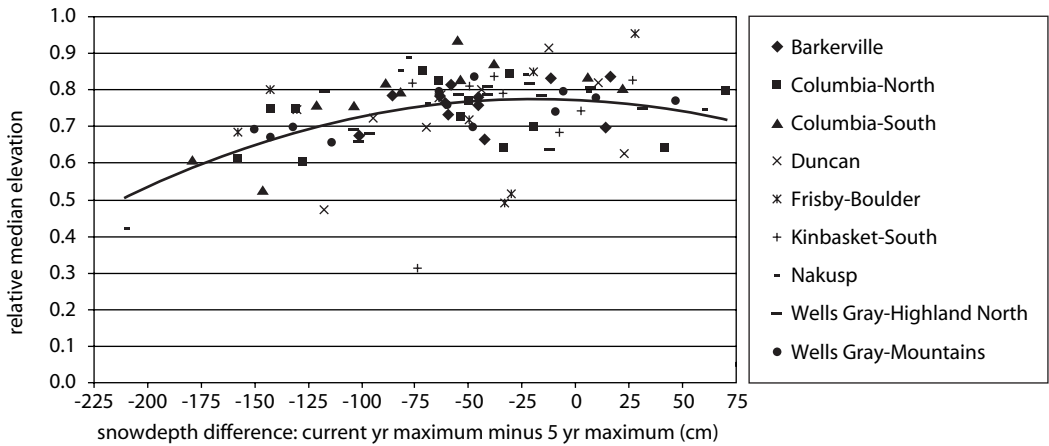


Fig. 2. Relative elevation in relation to relative snow depth for mountain caribou in the wet and very wet climatic regions ($n = 9$ subpopulations, 91 subpopulation-years). Relative elevation = (median elevation for late winter - 1st percentile of winter elevation for all years combined) / (99th percentile - 1st percentile of winter elevation). Trend line is 2nd-order polynomial for all data.

fact reflect the validity of the locomotion hypothesis under certain conditions.

Within the wetter regions, it would be expected that the observed downward shifts in elevation would be accompanied by an increased use of forests, especially hemlock stands, given both the distribution of those habitat types with respect to elevation and previous observations showing that hemlock stands are heavily used when caribou occur at low elevations (Apps *et al.*, 2001). Significant results, while consistent with this expectation, were sparse. This may simply reflect the overarching importance of snowpack with reference to *Bryoria* availability; when conditions necessitate caribou moving downslope, the vegetation they encounter may be of less importance than simply reaching an elevation where snowpack variability is less extreme. There may also be bimodal patterns within individual subpopulations of the wetter regions when snowpacks are only slightly lower than in recent years. In such years, some animals may move downslope while others may move upslope to seek windswept sites, as hypothesized above for caribou of the dry region. This would be consistent with the (non-significant) results indicating that when snowpack variability was minimal caribou in low-snow years actually appeared at least as likely to shift toward greater use of non-forest or alpine forest and stands dominated by subalpine fir.

In sum, our results indicate that (1) when snowpacks are considerably lower than those of recent years, mountain caribou in deep-snowfall regions make more extensive use of low-elevation sites, consistent with the LSC hypothesis; (2) this shift is sometimes associated with increased use of stands of both lodgepole pine and western hemlock, and (3) when the negative

snowpack difference is slight for deep-snowfall regions, and for shallow-snow regions generally, low-snow years are characterized by little difference or even an increase in elevation, potentially consistent with the locomotion hypothesis. Thus, it appears that caribou responses to snowpack variability fall along a gradient, with snowpack differences of roughly 1 m necessary to initiate significant downslope movement during low-snow years. It is not clear whether this situation holds at the northern limit of mountain caribou range as there was limited data for the largest and northernmost subpopulation (Hart Ranges) and insufficient data for any analysis of the other 3 most northerly ones (North Cariboo Mountains, Narrow Lake, George Mountain).

Our results for most subpopulations point more strongly than has previous habitat modeling (e.g. Apps *et al.*, 2001) to the potential need for low-elevation habitat in sustaining caribou for extended periods during some winters. The risk of having limited areas protected at low elevations includes the potential lack of forage and the reduced separation from predators inhabiting valley bottoms. Another implication of such shifts is that caribou sightability during late-winter population surveys may be highly variable among years, so using the same correction factor each year may be inappropriate. Our telemetry data spanned only 6 – 13 years per population with maximum expected snowpack variability of just over 2 m, but given the trends observed it is likely that elevation shifts in wet regions would be even larger when extreme inter-annual snowpack differences occur, and at some point should precipitate significant downward movement even within drier regions.

It also appears that the characteristics of low-elevation stands used in late winter may differ from

those used during early winter, even when at roughly the same elevation. Presumably, low-elevation sites used in late winter must provide high volumes of accessible *Bryoria* or have the potential to provide windthrown branches bearing this lichen on a winter-long basis. This is because terrestrial foods are not likely to be available or even detectable later in the winter within wet or very wet regions, even in a shallow-snow year. For example, the Char Creek snow station in the South Selkirks is near the boundary of a dry ESSF subzone and lies at only 1310 m elevation (700 m below normal late-winter habitat), but the lowest maximum snow depth in the 40-year record was 95 cm (River Forecast Centre, 2006). The shift toward lodgepole pine stands during low-snow years within 3 subpopulations (including 2 in the wet climatic region) may reflect the necessity of finding non-terrestrial foods when low elevations are used during late winter. While pine is more abundant at lower elevations, it has not previously been shown to be associated with preferred mountain caribou habitats (Apps *et al.*, 2001; Stevenson *et al.*, 2001; Johnson *et al.*, 2004). However, when forced to move downslope, caribou may take advantage of the short lifespan of lodgepole pine and its preponderance of dead lower branches to find windthrown pine snags or branches bearing *Bryoria*, in addition to gleaning lichen from the pine trunks.

All land-use plans in mountain caribou habitat allow for the preservation or special management of some lower-elevation stands in recognition of their importance for early-winter habitat or as movement corridors (Mountain Caribou Technical Advisory Committee, 2002). However, protected habitat has generally been concentrated in the upper ESSF (*ibid.*), some caribou management plans specifically allow the harvest of lodgepole pine in otherwise protected zones (Abbott, 2005), and no local allocation of habitat protection “budgets” has been explicitly based on the implications of the LSC hypothesis. We therefore recommend that any revisions to land-use plans include consideration for the key role that low-elevation habitat may play under low snowpack conditions, particularly in wetter ecosystems.

It should be noted that telemetry data for our analysis was often limited or unavailable for key years and the scale of our snowpack data was coarse (*i.e.* maximum depth per winter, interpolated over elevations and limited by the availability of snow stations) so our results may not precisely reflect patterns within any given subpopulation. Future analyses based on years with greater environmental variability and with more localized, real-time data on snow depth and caribou sinking depth, combined with field observations of caribou activity, temporal shifts in the *Bryoria*

trimline and within-stand variability in *Bryoria* trimline heights, are required if local habitat protection plans are to more precisely reflect inter-annual differences in habitat use. In particular, the current inability to test the LSC hypothesis for the most northerly subpopulations is a significant gap. There is also a need to determine the time required to redevelop significant loads of *Bryoria* in the lower canopy after an upward shift in the trimline, in relation to the typical interval between years of exceptionally deep or shallow snowpacks.

Acknowledgements

We wish to thank those who provided radiotelemetry data for this project, including J. Almack, K. Furk, D. Hamilton, D. Heard, D. Seip, J. Surgenor, H. Wittmer, and J. Young. M. Eng and G. Utzig were of great help in obtaining and interpreting biogeoclimatic mapping and data. C. Apps extracted habitat attributes for caribou locations. The manuscript benefited from insightful comments by 2 anonymous reviewers. Funding for data compilation and analysis was provided by the Habitat Conservation Trust Fund, project CAT05-4-332.

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