# A synthesis of scale-dependent ecology of the endangered mountain caribou in British Columbia, Canada

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*Abstract*: Mountain caribou are an endangered ecotype of woodland caribou (*Rangifer tarandus caribou*) that live in high-precipitation, mountainous ecosystems of southeastern British Columbia and northern Idaho. The distribution and abundance of these caribou have declined dramatically from historical figures. Results from many studies have indicated that mountain caribou rely on old conifer forests for several life-history requirements including an abundance of their primary winter food, arboreal lichen, and a scarcity of other ungulates and their predators. These old forests often have high timber value, and understanding mountain caribou ecology at a variety of spatial scales is thus required to develop effective conservation strategies. Here we summarize results of studies conducted at three different spatial scales ranging from broad limiting factors at the population level to studies describing the selection of feeding sites within seasonal home ranges of individuals. The goal of this multi-scale review is to provide a more complete picture of caribou ecology and to determine possible shifts in limiting factors across scales. Our review produced two important results. First, mountain caribou select old forests and old trees at all spatial scales, signifying their importance for foraging opportunities as well as conditions required to avoid alternate ungulates and their predators. Second, relationships differ across scales. For example, landscapes dominated by roads and edges negatively affect caribou survival, but appear to attract caribou during certain times of the year. This juxtaposition of fine-scale behaviour with broad-scale vulnerability to predation could only be identified through integrated multi-scale analyses of resource selection. Consequently we suggest that effective management strategies for endangered species require an integrative approach across multiple spatial scales to avoid a focus that may be too narrow to maintain viable populations.

**Key words:** caribou, endangered species, landscape, lichen, predation, old-growth forest, *Rangifer tarandus*, spatial scale.

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## Introduction

Either passively or actively, many organisms appear to select locations to spend their time and exploit resources in a hierarchical manner, ranging from where the species occurs to where individuals rest or even what part of a plant or animal they consume (Johnson, 1980; Wiens *et al.*, 1986). At broad scales, the distribution of a species is often limited by coarse factors such as climate and geology. From the applied perspective of maintaining endangered species, understanding these broad limiting factors can provide strategic information to help decision-makers prioritize core areas for recovery within a species' range (Channell & Lomolino, 2000).

At intermediate scales, such as within a home range, individual animals may select habitat attributes such as a specific forest type or terrain feature. When linked to demographic information, this scale of habitat selection can reveal how individual choice affects the fitness of the population (Fretwell & Lucas, 1970). Translating such habitat-specific information into management prescriptions often forms the basis of local land-use plans, which specify amounts and types of certain habitat features that should be maintained (e.g., KBLUPO, 2002; RHLPO, 2005; RIP, 2005).

At the finest scales, resource selection for features such as nesting, bedding, and feeding sites and corresponding diet may indicate functional requirements of both applied and theoretical value. Examining these finer scales often reveals ecological mechanisms that explain broader-scale descriptions of habitat selection (Wiens, 1989). In an applied sense, this level of knowledge helps to focus conservation actions to specific areas that contain critical habitat attributes or to modify activities to either maintain or recruit these attributes.

The woodland caribou (*Rangifer tarandus caribou*) is a subspecies of concern in British Columbia, particularly the endangered "mountain caribou" ecotype that lives in the interior wetbelt[1] (Heard & Vagt, 1998). The distribution and abundance of mountain caribou has declined significantly over the past several decades. In 2006, the entire population consisted of approximately 1900 individuals (Hatter, 2006) distributed over 18 distinct subpopulations (Wittmer *et al.*, 2005a), although two are thought to be recently extirpated (Hatter, 2006).

Mountain caribou (Heard & Vagt, 1998) differ from other woodland caribou ecotypes (e.g. Bergerud & Elliot, 1986; Rettie & Messier, 1998; McLoughlin *et al.*, 2003) in that they feed almost exclusively on arboreal lichen, particularly late in winter (mid January to mid April) when deep snow (1–4 m) covers all terrestrial foods (Rominger & Oldemeyer, 1989, 1990; Seip, 1992; Rominger *et al.*, 1996).

Mountain caribou are confronted with at least 2 management challenges: First, unsustainable predation has recently been the major factor causing population declines (Wittmer *et al.*, 2005a). Apparent competition (Holt, 1977, 1984) leading to high predation rates appears to be the proximate mechanism of the current decline (Seip, 1992; Wittmer *et al.*, 2005a, b). Apparent competition occurs where the abundance of one prey species negatively affects the abundance of another through a shared predator. Although not thought to be currently limiting caribou (Wittmer *et al.*, 2005b), the second challenge is to maintain a continuous supply of available and efficiently obtained forage. Because snow is substantially deeper in areas occupied by mountain caribou than elsewhere within woodland caribou range, winter foraging opportunities are more limited. These caribou forage mainly on arboreal lichen, but because trees with sufficient lichen accumulation are older than will be grown during a typical forestry rotation, a conflict exists between forests managed primarily for fibre extraction and for caribou winter foraging habitat (Rominger & Oldemeyer, 1989; Kinley *et al.*, 2003; Serrouya *et al.*, 2007).

Because mountain caribou have been studied at varying intensities across their entire distribution, researchers have been able to examine factors that affect mountain caribou ecology across multiple scales. Multi-scale investigations are important because what is considered available to an animal affects the interpretation of results, as much as what the animals actually use (Garshelis, 2000). Habitat relationships may change, sometimes dramatically, when considered across different scales. As animals appear to select resources hierarchically across

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. See Heard & Vagt (1998) or Wittmer *et al.* (2005a) for a range map.

spatial scales, managers that operate at different spatial scales (from recovery prioritization among populations to deciding which tree is cut) require information appropriate for each scale. Therefore, our goal in this review is to summarize factors affecting mountain caribou ecology at three spatial scales (Johnson, 1980): 1) Factors limiting distribution and abundance (first order); 2) habitat selection within the range of a subpopulation (second order), and 3) selection of feeding sites and foraging intensity of different forage items within seasonal home ranges (third and fourth order). Not only does this multi-scale approach provide a more complete view of caribou ecology, but it enables an examination of how factors may shift in importance across scales as the perspective of investigation changes.

## Methods

Mountain caribou have been monitored using radio-telemetry across their entire range. In some areas caribou have been studied more intensively using snow-trailing and forage investigations, whereas others were limited to periodic telemetry investigations. We reviewed 17 mountain caribou[2] papers (Appendix I) and classified them into three categories: 1) those dealing with broad-scale limiting factors, either through the spatial extent of the analysis area, or factors that directly limit population growth; 2) those dealing with intermediate scales of habitat selection within subpopulation bounds, and 3) those dealing with field measurements of fine-scale resource selection and intensity of forage selection. Although more intermediate- and fine-scale studies have been done, for brevity we restrict the details of this review to those listed.

2 In addition to these 17 papers, other woodland caribou papers are also referred to in the text for comparison.

## Results and discussion

*Broad scales: caribou distribution and limiting factors*

Woodland caribou were once much more numerous and widespread in British Columbia as well as Idaho, Montana, and Washington State. Early verbal and written accounts of large herds of caribou that were of great significance to native North Americans have been summarized by Spalding (2000). Based on these early accounts, it appears that populations have declined dramatically in all portions of their range. In the south and southwestern portions of their range the major declines and extirpations occurred near the end of the 1800s and first two decades of the 1900s. In the central and northern portions of the range, the major declines occurred in the 1930s (Spalding, 2000). Overhunting by both native peoples who recently acquired repeating rifles and for some groups that had also lost bison (*Bison bison*) as a major component of their diet (McDonald, 1996) and newly arrived miners and settlers, undoubtedly had an effect on caribou in many areas (Bergerud, 1974, 1978; McDonald, 1996; Spalding, 2000). In addition, an increased frequency of wildfires in the first portion of the 1900s that removed caribou wintering habitat and may have partially led to great increases in moose (*Alces alces*) and apparently wolf (*Canis lupus*) numbers likely had an effect on mountain caribou (Spalding, 2000). There has been the suggestion that a similar increase in mule deer (*Odocoileus hemionus*) in the southwestern portion of their range in the 1880s (McDonald, 1996) may have led to increased cougar (*Puma concolor*) numbers that were partially blamed for the disappearance of the southwestern groups of caribou (Munro, 1947).

Using the above historical accounts to help delineate where mountain caribou once occurred, Apps & McLellan (2006) evaluated factors that potentially limit the distribution of existing subpopulations by comparing these to previous distributions. Static factors that explain the inherent landscape potential to support mountain caribou include the distribution of wet ecosystems, alpine areas and cedar/hemlock (*Thuja plicata* / *Tsuga heterophylla*) forests. Wet ecosystems infer deep snow and long fire-return intervals, which is generally unfavorable for deer and moose, and these forests produce an abundance of arboreal lichen. Alpine areas were significant because early seral ungulates are associated with low elevation winter ranges, so areas with more alpine likely have fewer of these species. These findings imply that caribou are increasingly restricted to mountainous, wet ecosystems where it is more difficult for alternate prey and predators to become established year-round. Dynamic factors that influenced landscape potential included increasing distributions of old forests (>140 yr), remoteness from human influence, lower proportions of mid-seral forests, decreasing road density and less motorized recreation. Extensive areas of old forests provide winter foraging habitat for mountain caribou and contain fewer other ungulates because of a lack of early-seral forage species. Mid-seral forests generally do not support high densities of caribou or other ungulates but reflect a more frequent fire history with adjacent higher quality deer and moose winter ranges.

In the first study to address proximate factors limiting mountain caribou populations based on demographic rates, Seip (1992) examined the influence of predators on two caribou subpopulations by comparing seasonal ranges of caribou, moose and wolves. Moose and wolves were sympatric throughout the year and moose were the wolves' primary prey. The caribou population with year-round exposure to wolves was declining, with high adult mortality and low calf survival. In contrast, the population that migrated to a summer refuge in rugged mountains, where moose and wolves were absent, was stable or increasing. Seip's (1992) results supported those of Bergerud & Elliot (1986) that the greatly increased moose population in central British Columbia since the 1920s likely resulted in greater wolf numbers, which consequently meant that caribou, particularly those living without access to summer refuge, were more vulnerable than they had been in the past. Seip (1992) concluded that wolves were the major limiting factor for caribou in areas where no refuge existed.

Since Seip (1992), additional data across the distribution of mountain caribou have been collected including subpopulations not exposed to moose-wolf dynamics. In the southern portion of their range, cougar-deer (*Odocoileus* spp.) dynamics were more dominant processes (Kinley & Apps, 2001; Wittmer, 2005a). The further use of GIS has permitted additional exploration of hypotheses related to recent declines in caribou numbers across markedly different predator-prey systems. Because digital basemaps are limited, variables often used in GIS analyses are assumed surrogates of the more direct parameters such as winter food abundance and predator and prey distributions. In particular, because arboreal lichen is much more abundant in old forest than young, old forests (> 140 yeas old) was used as a surrogate for suitable mountain caribou winter range (Wittmer *et al.*, 2005b). Similarly, the abundance of early to mid-seral forests within or adjacent to caribou range is considered to reflect the abundance of ungulates (moose, deer, or elk [*Cervus canadensis*]) and their predators that tend to be associated with these conditions. The amount and configuration of old and young forests, as well as roads (James & Stuart-Smith, 2000), may also affect predator foraging efficiency. Finally, climatic variables reflect temperature and precipitation, both of which affect ungulate distributions through snow depth and fire-return intervals. These surrogate variables are currently the only means of evaluating influential factors at a range-wide scale.

Using these surrogate variables and other factors, Wittmer *et al.* (2005b) tested competing hypotheses of the cause of the current decline in mountain caribou abundance. Was it likely due to a shortage of forage resulting from the removal of old forests causing starvation or reduced fecundity, or was it increasing predation due to apparent competition? They found that mountain caribou were rarely dying of starvation or even dying in winter when their habitat was being reduced by forestry activities and fire, but by predators during summer when food is abundant and hasn't been affected by people or natural disturbance. Furthermore, subpopulations with the most old forest per individual caribou were declining fastest (Wittmer *et al.*, 2005b). Thus, the greatest support was for increasing predation rates causing the current decline of mountain caribou.

Wittmer *et al.* (2007) found the variation in adult female survival rates among 10 subpopulations was best explained by the amount of early-seral stands within subpopulation ranges and by subpopulation density. They also found that the home ranges of caribou killed by predators had lower proportions of old forest and more mid-aged forest as compared home ranges where caribou were alive. Results of this study remain consistent with the apparent competition hypothesis and, notably, transcend the disparate predator-prey systems outlined above. Wittmer *et al.* (2005b, 2007) suggest that early-seral forests are affecting caribou through the greater alternate prey and predator populations they support. McLellan *et al.* (2006) hypothesized that rapid declines in alternative prey abundance due to severe winters may have resulted in increased searching time by predators and thus greater encounter and kill rates of caribou until predator numbers declined or other ungulates increased. Although this hypothesis remains untested, they suggested that instability of the predator/prey system is why caribou trends often show rapid declines followed by a period of apparent stability (Seip & Cichowski, 1996; McLellan *et al.*, 2006).

*Intermediate scales: habitat selection within subpopulations*

The first published GIS-based habitat model for mountain caribou was done by Apps & Kinley (1998) in the southern Purcell Mountains. They developed a preliminary habitat assessment tool based on a habitat suitability index (HSI) that used telemetry information and a subjective combination of habitat classes to produce maps with relative habitat ratings. Stand age was the main component in the HSI, but elevation, canopy cover, slope and cover type also factored in the analysis. Subsequently, Apps *et al.* (2001) applied an empirical GIS-based modeling approach to evaluate caribou habitat selection across 4 spatial scales in the Columbia Mountains. A main goal of this study was to map the probability of each "pixel" being used by caribou and in doing so quantify relationships that influenced caribou habitat selection within a subpopulation. Scales were defined by "used" and "available" landscape radii ranging from 0.35 to 13.7 km. From this analysis, predictive, seasonal models that integrate relationships across scales were developed and used with other information to delineate habitat for local-land use plans (RHLPO, 2005).

At the broadest scale of their analysis, mountain caribou were associated with rugged terrain, but gentler terrain was selected at progressively finer scales (Apps *et al.*, 2001). Caribou usually forage on relatively flat slopes, but the broad-scale relationship with mountainous landscapes likely is related to the importance of seasonal refuge from predators, as well as an association with deep snow and lower historic fire-return. Dry, Douglas-fir (*Pseudotsuga menziesii*) stands were also selected at fine scales, but not at coarser levels. Fine-scale investigations (see 'Fine Scales' section) revealed that these stands contain high lichen loads relative to cedar-hemlock stands (Serrouya *et al.*, 2007). Old forest (> 140 yr) was consistently selected at each of the four scales examined, regardless of the season.

Another output from the Apps *et al.* (2001) analysis was the reconfirmation of distinct elevational migrations in extreme snowfall areas, used to define caribou seasons, as described by Edwards & Ritcey (1959). In the Columbia Mountains, caribou undergo more pronounced elevational migrations than mountain caribou in more moderate snowfall zones. Early in winter when snow high in the mountains covers forbs and sedges that caribou feed on, they move from higher elevation summer and fall ranges to low-elevation cedar-hemlock forests where timber value is high. Then, later in the winter, they use subalpine forests where timber value, alternate ungulate, and predator levels are low. During spring, mountain caribou often descend to valley bottoms again to feed on emerging vegetation. Habitat relationships vary during summer, but caribou generally prefer high elevations. Overlap with forestry is greatest during early winter, and it is then that caribou habitat management is most emphasized. However, because not all old stands are protected within caribou habitat in the Columbia Mountains, managers still lacked a tool to identify stands that deserved priority for retention (see 'Fine scale' section).

Johnson *et al.* (2004) incorporated the telemetry data of Terry *et al.* (2000) in a GIS environment to evaluate mountain caribou habitat relationships for the North Cariboo Mountains and Hart Ranges east of Prince George. The objectives were similar to the Apps *et al.* (2001) study, whereby the intent was to confirm or modify existing land-use maps that defined caribou management zones. They used both census and telemetry information to derive products at the patch and landscape scale (Johnson *et al.* 2004). The most parsimonious landscape-level model included slope and elevation, whereas the patch-scale model contained vegetation cover types extracted from GIS. Unlike Apps *et al.* (2001), Johnson *et al.* (2004) found that stand age was not a predictive variable in their patch-scale analysis. The authors note that the homogenous distribution of old forest in their study area precluded the opportunity for selection, but they expected that if the area was subject to logging or wildfire, age would likely become predictive at this scale (Johnson *et al.*, 2004). Ultimately, the patch and landscape maps were combined to provide a map that was used in conjunction with other information by land-use planners and caribou recovery groups (RIP, 2005). In discussing the overall applicability of their results, Johnson *et al.* (2004) note "… results of this work are likely to be inappropriate for stand-level habitat management. The resolution of the spatial data and the suspected response of caribou to finer-scale habitat attributes require that site inspections or more refined modeling efforts guide forest harvest prescriptions." Hence, fine-scales investigations are also needed.

*Fine scales: selection of stand-level attributes*

In areas where mountain caribou spend most of the year at high elevations, as in more northern (Terry *et al.*, 2000; Johnson *et al.*, 2004) and southern (Apps & Kinley, 1998) populations, habitat protection is more complete because these forests are less valuable to the forest industry. However, in extreme snow zones in the central portions of their range, mountain caribou spend much of the winter in low-elevation cedar-hemlock forests (Apps *et al.*, 2001), where timber values are great. In these areas, land-use planners have decided to protect portions of the harvestable landbase for caribou by ensuring that 40% of the forests must be older than 140 yr (RHLPO, 2005). It must be decided which of the remaining old stands to retain and which stands should be harvested and managed primarily for sustained timber production. If all old stands were of equal value to caribou, then it would not matter which ones were retained. A relevant question becomes: is there additional variation among old stands that is not accounted for using current GIS forest inventory and elevational models?

Field-based research has revealed that there is considerable variation among old stands. For example, Rominger & Oldemeyer (1989), Terry *et al.* (2000), Kinley *et al.* (2003) and Serrouya *et al.* (2007) found that old stands used by caribou contained five times more windthrow compared to old stands on average. These fallen trees provide an abundant source of easily accessible lichen to caribou, and the upper canopy often contains more *Bryoria* spp., which is the genus generally preferred by caribou. Caribou feed intensively on the lichen from windthrown trees and litterfall (Terry *et al.*, 2000; Kinley *et al.*, 2003; Serrouya *et al.*, 2007). Another important source of variation was the size of trees. In low-elevation cedar-hemlock forests, Serrouya *et al.* (2007) report that caribou foraging paths contained 43% more trees >30 cm in diameter relative to random stands. Kinley *et al.* (2003) reported that caribou in higher elevation spruce/fir (*Picea engelmannii / Abies lasiocarpa*) forests also foraged in areas with larger trees.

It has been known for some time that arboreal lichens are the only available forage to mountain caribou during late winter (Edwards & Ritcey, 1960; Freddy, 1974; Antifeau, 1987; Rominger & Oldemeyer, 1989). However, in deep snow areas, the manner in which lichen is available to caribou differs greatly among seasons, and quantifying this source of variation reveals differing foraging mechanisms. During early winter, either in low-elevation cedar and hemlock forests in deep snow zones or higher-elevation spruce and fir forests in areas with more moderate snowpacks, standing trees account for >90% of potential forage items, but most (> 85%) of these trees are ignored, with no foraging attempts made (Terry *et al.*, 2000; Serrouya *et al.*, 2007). At this time of year, little lichen on standing trees is available to caribou in areas with deep snow because lichen is killed by prolonged burial in the snowpack (Goward, 1998), so remaining lichens are high in the can-

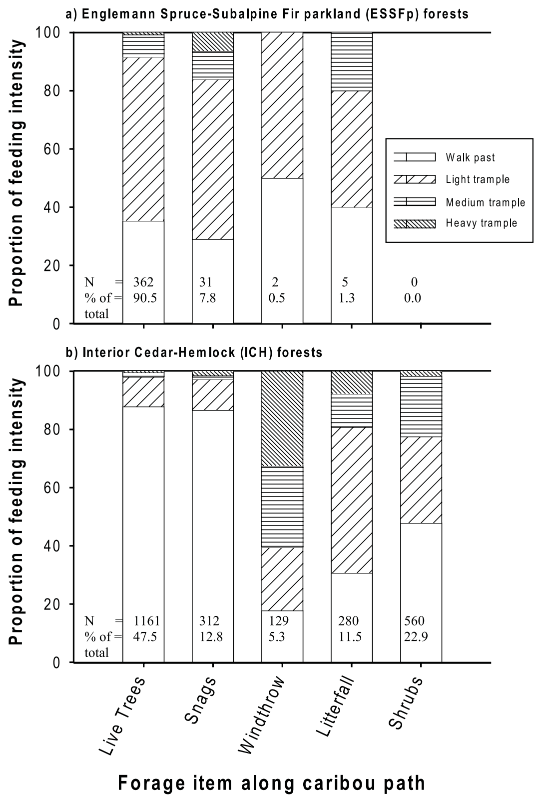



Fig. 1. Proportion of feeding intensity classes for a subsample of forage items available to mountain caribou (*Rangifer tarandus caribou*) in a) Engelmann Spruce/subalpine Fir (*Picea engelmanni / Abies lasiocarpa*) parkland (ESSFp; late-winter habitat) and b) Interior-Cedar/Hemlock (*Thuja plicata / Tsuga heterophylla*) (ICH; early winter habitat) forests. Feeding intensity classes are walk past, step towards, light trample, medium trample, heavy trample. Snow trampling is an index of foraging intensity (see Terry *et al.*, 2000 for details). Number of forage items and per cent of total items are presented in the bar graph. Modified from Serrouya *et al.* (2007).

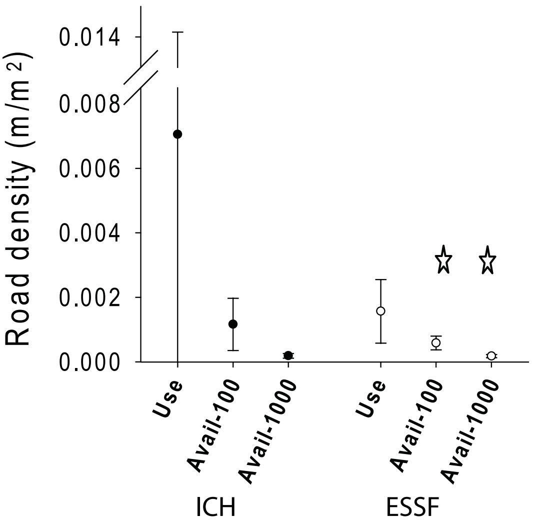
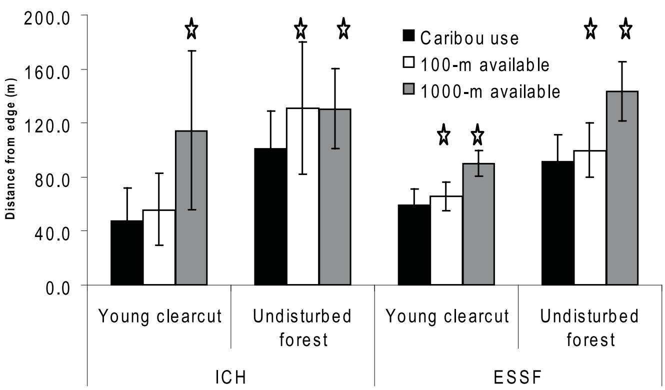



Fig. 2. Road density of caribou use trails relative to two scales of available area, 100 m and 1000 m buffers around the use trail, in Interior Cedar/Hemlock (ICH) and Engelmann spruce/Subalpine-fir (ESSF) forests. Error bars are 95% CI and asterisk indicates significant difference between use and availability at $\alpha$=0.05 using a paired *t*-test. Modified from Serrouya *et al.* (2006).

opy yet there is little snowpack to support the animals. Large amount of lichens are mainly available to caribou through litterfall from the canopy and recently windthrown trees. In the lowest snowfall regions with mountain caribou, they appear to feed more on lichen from standing trees early in winter (Kinley *et al.*, 2003) because lichens are more abundant low in the canopy (B.N. McLellan, B.C. Ministry of Forests, unpubl. data).

When caribou in most areas move upslope in late winter, their foraging patterns change. The standing trees they encounter are most-often foraged upon (Fig. 1a), which is in contrast with patterns observed earlier in the winter and in particular from low-elevation cedar/hemlock forests (Fig. 1b). During late winter, snow has accumulated and settled enough to provide the lift needed for caribou to reach branches and lichens in the lower canopy. Because lichens do not grow much below the height of the deepest winter snowpack (Goward, 1998; Kinley *et al.*, 2007), consistent snowpacks become an important mechanism for caribou to access arboreal lichen during late winter in some areas. These findings suggest that lichen biomass alone does not explain caribou foraging behaviour. It is the mechanism of how lichens become available to caribou that determines its level of use. Foraging on lichens growing on standing trees is more important during late winter, whereas substrates on the ground appear to be key during early winter, particularly in areas with very deep snow. Hence, a conflict arises not only between the short rotation ages of forests managed primarily for timber production, but also for salvaging decadent or diseased stands.

Fig. 3. Mean distance into habitat features of caribou paths relative to two scales of available areas, 100 m and 1000 m buffers around the use trail, in Interior Cedar/Hemlock (ICH) and Engelmann spruce/Subalpine-fir (ESSF) forests. Error bars are 95% CI and asterisk indicates significant difference between matched use and availability at $\alpha$=0.05 using a paired *t*-test. Modified from Serrouya *et al.* (2006).



In addition to foraging behaviour, fine-scale investigations have revealed movement patterns and resource selection not identified at broader scales. Serrouya *et al.* (2006) used snow trailing and estimated road densities to be 2.7 and 8.7 times higher along paths used by caribou compared to areas available within 100 m and 1000 m buffers, respetively, around the caribou path (Fig. 2). This pattern reflects field observations of caribou often using roads for traveling during winter. Similarly, at the fine-scale, Serrouya *et al.* (2006) found that forest-clearcut edges were selected in winter (Fig. 3) because of the higher incidence of windthrow and lichen litterfall along these edges. These fine-scale studies are important because they contrast findings at broader scales where roads and edges result in lower caribou persistence (Kinley & Apps, 2001; Apps & McLellan, 2006), hence may reveal a further mechanism of population decline.

*Relationships across scales*

The hierarchical pattern of resource selection by mountain caribou can be summarized by the selection of wet, mountainous landscapes, with relatively little early-seral forest but an abundance of old forest, followed (in winter) by a preference for gentle benches and ridges with old forests, where they select travel routes to encounter larger standing trees and snags but focus their foraging on windthrown trees and litterfall (Fig. 4). That old forests and old trees are selected at each scale signifies their importance for foraging opportunities and the preclusion of forage production for other ungulates. However, multi-scale analyses can also reveal contrasting relationships at different scales (see examples in Wiens, 1989), as is the case for the selection of dry Douglas-fir stands (Fig. 4). At the broadest scale, Apps & McLellan (2006) determined that the current distribution of mountain caribou was restricted to the wettest ecosystems available

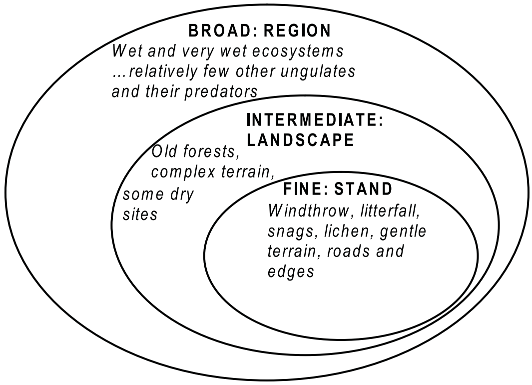



Fig. 4. Conceptual diagram of scale-dependent mountain caribou ecology. Adapted from Bunnell & Huggard (1999).

where Douglas-fir forests are rare. In landscapes where caribou occurred historically and Douglas-fir is common, such as the Okanagan Highlands or the southern Rocky Mountains, snow depths are shallow, precipitation is light, and fire is more frequent (Meidinger & Pojar, 1991) and consequently, deer and elk are abundant (Shackleton, 1999; Hudson *et al.*, 1976). Caribou are now absent from these areas, and, although arboreal lichen (*Bryoria* spp.) is locally abundant (McLellan, unpubl. data), predators that are sustained by other ungulates are likely too numerous for caribou to persist. However, at finer scales, Apps *et al.* (2001) and Serrouya *et al.* (2007) found selection of dry, Douglas-fir leading stands. This result appears to contradict the broader-scale analysis and the general perception that mountain caribou are a "wetbelt" species. Hypotheses regarding the mechanism underlying the apparent change in selection across scales have been tested using fine-scale field investigations and revealed greater lichen biomass in Douglas-fir stands than cedar-hemlock stands at similar elevations. Douglas-fir have more dead branches lower in the canopy that are suitable for lichen attachment relative to other tree species, and thus lichen is more available to foraging caribou (Serrouya *et al.*, 2007). In wet ecosystems, these stands are too rare to support enough other ungulates and their predators to exclude caribou from the larger area over the long term. Hence, in small amounts, dry Douglas-fir stands provide additional foraging opportunities (Serrouya *et al.*, 2007), but in landscapes dominated by these stands, caribou are excluded (Apps & McLellan, 2006).

Understanding other examples of contrasting relationships of caribou habitat selection across scales, such as road densities and forest-clearcut edges is even more significant for forest managers. This attraction to roads and edges by caribou has only been investigated in winter (Serrouya *et al.*, 2007), when mountain caribou infrequently die (Wittmer, 2005a). However, if this attraction were also to occur in summer, the potential for increased mortality exists because others have found that increased predation risk occurs along roads and edges (James & Stuart-Smith, 2000; Apps *et al.*, in prep.). The phenomenon of animals being attracted to certain habitats because of a short-term benefit (i.e. a foraging or movement opportunity) but experiencing increased mortality risk (i.e. "ecological traps") is the subject of theoretical research and debate (Van Horne, 1983; Remes, 2003; Robertson & Hutto, 2006). Landscapes dominated by recent changes due to human activities are likely prone to ecological traps as animals have not had time to adapt to these changes.

In his review on spatial scaling in ecology, Wiens (1989) points out that fine-scale investigations are more likely to reveal biological mechanism underlying observed patterns, whereas broader scale studies are more likely to provide generalizations across systems. Our review of mountain caribou ecology suggests that mechanisms may be best revealed through integrated analyses across scales. Fine-scale analyses may explain why animals make shorter-term decisions related to foraging and cover requirements, while broader-scale features may explain longer-term decisions such as those that reduce encounter rates with predators (Rettie & Messier, 2000).

*Management implications*

For mountain caribou, the obvious management implication is that maintaining large tracts of old forests will be the most secure way to serve the dual role of reducing predation risk and provide foraging opportunities. However, this solution is presently of little value because after decades of forest harvesting, the current age distribution of the forest will take many decades to return to more natural conditions. Broad-scale investigations such as those dealing with factors limiting distribution and abundance (Seip, 1992; Apps & McLellan, 2006; Wittmer *et al.*, 2005b, 2007) have revealed that predation is currently the main limiting factor and must be managed in some way to maintain most subpopulations.

These findings are consistent with those of other ecotypes of woodland caribou (Bergerud & Elliot, 1986; Rettie & Messier, 1998; McLoughlin *et al.*, 2003). However, if the negative effect on caribou of the altered predator-prey system can be resolved through predator-prey management, then management must focus on maintaining suitable foraging conditions for mountain caribou. It is likely that the availability of arboreal lichen will become the next limiting factor. This lichen is available through litterfall, windthrow, and on standing old trees, but a sufficient amount of these forest attributes typically take longer to develop than a commercial forestry rotation. The studies of fine-scale resource selection that have revealed the types of forests attributes used by caribou during winter have enabled optimal prioritization of stands for retention.

An important next step in caribou research and management relates to the possible creation of ecological traps. Several studies have documented increased caribou mortality as a result of linear features (James & Stuart-Smith, 2000; Apps *et al.*, in prep.), but none that we are aware of have documented an attraction to roads and edges by caribou, locations where forage is facilitated but vulnerability to predators is higher (but see McLoughlin *et al.* [2005] where caribou occasionally select uplands where predation risk was higher). This juxtaposition of fine-scale behaviour with broad-scale vulnerability to predation can only be identified through integrated multi-scale analyses of resource selection. If the attraction to roads and edges by caribou holds to seasons where predators and caribou range overlap more completely, then the urgency to address predation in the short term and forest management issues over the longer term is accentuated.

Finally, the hypothesis that stochastic events could cause rapid changes in alternative prey, and precipitate greater incidental predation rates on caribou (McLellan *et al.*, 2006) has not been fully tested (but see Festa-Bianchet *et al.*, 2006). Data on alternate prey abundances following severe winters, along with predator movement and kill rates would help test whether this hypothesis was supported. This information could be of great value to managers because it could provide a trigger to accelerate predator and prey management following a severe weather event, to help reduce predation risk on caribou.

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Skala-avhengig økologi og truet fjellvillrein i Britisk Columbia

*Abstract in Norwegian / Sammendrag*: Fjellvillreinen i de nedbørsrike fjellområdene i sørøstre Britisk Columbia og nordlige Idaho som er en truet økotype av skogsreinen (*Rangifer tarandus caribou*), har blitt kraftig redusert både i utbredelse og antall. Mange studier har vist at denne økotypen er avhengig av vinterføden hengelav i gammel barskog hvor det også er få andre klovdyr og dermed få predatorer. Slik skog er også viktige hogstområder, og å forstå økologien til fjellvillreinen i forskjellige skaleringer er derfor nødvendig for å utvikle forvaltningsstrategier som kan berge og ta vare på denne reinen. Artikkelen gir en oversikt over slike arbeider: fra studier av begrensende faktorer på populasjonsnivå til studier av sesongmessige beiteplasser på individnivå. Hensikten er å få frem et mer helhetlig perspektiv på fjellvillreinen og finne hvordan de begrensende faktorene varierer etter skaleringen som er benyttet i studiet. Oversikten vår frembragte to viktige resultater; 1) Uansett skalering så velger dyrene gammel skog og gamle trær. 2) Dyrenes bruk av et område kan variere med benyttet skalering, for eksempel vil landskap utbygd med veier og hogstflater være ufordelaktig for overlevelsen, men synes likevel å kunne tiltrekke fjellvillreinen til visse tider av året. Forholdet mellom atferd ut fra fin-skalering og stor-skalering sårbarhet hva gjelder predasjon, ville kun blitt avdekket ved flere-skaleringsanalyse av hvordan ressursene benyttes. Ut fra dette foreslår vi at forvaltningsstrategier for truete bestander som eksempelvis fjellvillreinen, må baseres på tilnærminger ut fra ulike skaleringer for å hindre at et for snevert perspektiv kan begrense muligheten for vedvarende levedyktighet.

Appendix I.

Main studies considered in this review, stratified by three spatial scales defined in the text.

| Scale | Author | Relevance |
|---|---|---|
| **Broad** | Seip, 1992 | Caribou growth rates with and without predation |
| | Kinley & Apps, 2001 | Identification of limiting factors contrasted across two sub-populations |
| | Wittmer *et al.*, 2005a | Delineation of subpopulation bounds and identification of limiting factors |
| | Wittmer *et al.*, 2005b | Testing 3 alternative hypotheses of caribou decline |
| | Apps & McLellan, 2006 | Factors explaining persistence, distribution, and vulnerability index among subpopulations |
| | Wittmer *et al.*, 2007 | Habitat components affecting adult female survival |
| **Inter-mediate** | Apps & Kinley, 1998 | Delineation of caribou habitat for local land-use plans |
| | Apps *et al.*, 2001 | Delineation of caribou habitat for local land-use plans |
| | Johnson *et al.*, 2004 | Delineation of caribou habitat for local land-use plans |
| **Fine** | Edwards & Ritcey, 1960 | Caribou foods in Wells Gray Park |
| | Antifeau, 1987[a] | Food habitats and foraging |
| | Rominger & Oldemeyer, 1990 | Shifts in diet selection in relation to snow accumulation |
| | Rominger *et al.*, 1996 | Experimental arena and field trials to study forage intake rates and digestibility |
| | Terry *et al.*, 2000[a] | Identification of key stands within delineated habitat; foraging patterns |
| | Kinley *et al.*, 2003 | Identification of key stands within delineated habitat; foraging patterns |
| | Serrouya *et al.*, 2006 | Resource selection of edges, roads, and partial cuts at fine scale using snow trailing |
| | Serrouya *et al.*, 2007 | Identification of key stands within delineated habitat; foraging patterns |

[a] Also covers intermediate scales, but we only refer to the fine scales for the purpose of this review.