University of Alberta

Caribou Habitat Selection in Relation to Lichen and Fire in Jasper and Banff National Parks

by

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Dedication

This thesis is dedicated to my family, especially Brenda and Skylar: Skylar for putting up with her dad being at work too much and Brenda for her tireless support and for taking us away on so many grand adventures.

Abstract

Woodland caribou (*Rangifer tarandus caribou*) populations in Jasper (JNP) and Banff National Parks (BNP) are small and declining. Absence of recent fire has been suggested to have detrimentally affected terrestrial lichens, the main forage of caribou. I examined winter habitat selection by woodland caribou at multiple scales and used models including stand origin, topography, and stand structure data to explore relationships among caribou, lichen, and fire history. At a coarse scale, caribou selected old forest (> 75 years) in landscapes that burned less frequently, whereas the abundance of *Cladonia* spp. influenced caribou selection at fine scales. Lichen occurrence models suggested *Cladonia* established sufficient abundance to attract caribou after 75 years. Abundance of arboreal lichens required the presence of older trees (>150yrs), but abundant arboreal lichens could be retained following low-severity fires. Caribou ranges in JNP and BNP are predicted to be negatively affected for at least 75 years following fire.

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Chapter 1: General Introduction

Both data chapters of this thesis (Chapters two and three) have introduction sections that contain much of the information presented in this general introduction chapter. Each data chapter is meant to be a stand-alone document for eventual journal submission. This chapter serves to provide a background to the thesis.

Woodland caribou (*Rangifer tarandus caribou;* hereafter caribou) in Alberta, Canada are listed federally and provincially as a threatened species (Alberta Wildlife Act 2002, COSEWIC 2003). Several factors have been identified as causes of caribou population declines: direct disturbance from human activities; increased predation due to predator access along anthropogenic linear features and increased predator abundance, which follows increases in abundance of alternate prey in recently cleared forest; and, habitat loss associated with industrial activity (Emonds 1988, Seip 1992, James and Stuart-Smith 2000, Oberg 2001, Kuzyk, 2002, Thomas and Gray 2002, McLoughlin et al. 2003, Wittmer et al. 2005). Jasper and Banff National Parks (JNP and BNP) contain the most southerly distribution of woodland caribou in Alberta. Despite protection from industrial development, the south JNP population is now in serious decline, while the northern BNP population is considered functionally extirpated (Flannigan and Rasheed 2002, Mercer 2002). Canada's recent Species at Risk legislation and Parks Canada's management plans identify population recovery of threatened species as a priority (Parks Canada 2000, COSEWIC 2003). To determine the most effective population recovery actions, and to evaluate how to protect critical habitat, Parks Canada is investigating several potential causes of local caribou population decline. My research focused on the effect of past fire events on caribou habitat.

Evaluating Caribou Habitat

Within caribou range in the national parks, Parks Canada suspects caribou population declines are partly related to habitat deterioration from human activity and infrastructure (primarily hotels, campgrounds, roads and trails; Parks Canada 2000) and/or a lack of recent fire events (Smith pers. comm.). JNP has experienced few fires over the past century compared to the later part of the 19th century (Tande 1979, Achuff et al. 1996, Rhemtulla et al. 2002). It has been suggested that successional processes, leading to a dominance of the landscape by older forest, have been detrimental to forage resources for caribou (Klein 1982, Schaefer and Pruitt 1991, Payette et al. 2000, Coxson and Marsh 2001). My study focused on caribou habitat selection and lichen forage availability relative to past fire events. Results from my analysis are used to evaluate whether fire management within caribou range can be adjusted to improve or maintain important habitat elements for caribou, as part of a comprehensive caribou restoration strategy. Concurrent research in JNP is investigating the impacts of predator access to caribou range via plowed roads as well as impacts of disturbance associated with human use.

There is historical evidence to suggest that robust populations of caribou persisted into the 1970's in JNP (Rogers 1925, Stelfox 1974). This suggests that the reasons for caribou decline may be associated with changes that have occurred in the latter half of the 19th century. The most significant landscape-level change during this period has been a lack of large fires (Achuff et al. 1996). During the 1900's, both JNP and BNP experienced a decline in area burnt by wildfires compared to previous centuries (Tande 1979, Van Wagner 1995, Achuff et al. 1996, Rhemtulla et al. 2002). Some research has suggested that long periods without fire may cause habitat deterioration for caribou (Klein 1982, Schaefer and Pruitt 1991, Coxson and Marsh 2001) while other researchers have found that caribou select older forest (Apps et al. 2001, Szkorupa 2002, Joly et al. 2003, Saher 2005). This apparent discrepancy between results pertaining to caribou habitat needs and time since fire is further complicated by variation in specific life strategies among caribou populations. JNP and BNP lie in the Rocky Mountains along the border between the provinces of Alberta and British Columbia. Animals in JNP and BNP behave differently than other mountain caribou in Alberta in that they are non-migratory (Emonds 1988). They also differ from British Columbia mountain caribou because their main food source is terrestrial lichen (Thomas and Armbruster 1996, Thomas et al. 1996b) rather than arboreal lichen (Poole et al. 2000, Apps et al. 2001, Johnson et al. 2004). Habitat needs of caribou in JNP and BNP are likely specific to these populations; for this reason, it was important that I determine local habitat relationships for caribou in JNP and BNP. To do this, I performed a use/availability habitat selection analysis, a technique that has commonly been used for assessing habitat for caribou (Johnson et al. 2001, Szkorupa 2002, Johnson et al. 2004, Saher 2005).

Several recent studies of caribou habitat selection have concluded that it is necessary to examine habitat selection at different spatial scales (Rettie and Messier 2000, Schaefer et al. 2000, Apps et al. 2001, Johnson et al. 2001, Szkorupa 2002, Johnson et al. 2004, Saher 2005). Accordingly, I carried out habitat selection analysis at two scales. At a coarse or landscape level, I evaluated caribou habitat by creating a robust, predictive habitat selection model using parameters related to recent fire history (eg. stand origin date, stand type) along with parameters that influence fire occurrence and behavior (slope, aspect, elevation). Saher (2005) and Rettie and Messier (2000) determined that caribou habitat selection at fine scales related primarily to foraging needs. Consequently, I created fine scale habitat selection models that focus on caribou selection related to lichen abundance, but also included topography, stand origin, and more detailed data on stand structure and composition. Finally, I developed models that would predict availability of both terrestrial and arboreal lichen, again as a function of parameters related to fire history. Knowledge about how caribou and caribou forage respond to historical fires in JNP and BNP will help Parks Canada determine how to manage fire in caribou range.

Relationship of lichen abundance to time-since-fire

The two growth forms of lichen that caribou use for forage are fruticose or foliose terrestrial lichens (*Cladonia* spp., *Cladina* spp., *Stereocaulon* spp., *Cetraria* spp., *Flavocetraria* spp., and *Peltigera* spp.; Thomas and Hervieux 1994, Thomas and Armbruster 1996, Thomas et al. 1996a, 1996b, Terry et al. 2000) hereafter referred to as terrestrial lichens, and fruticose arboreal lichens (*Alectoria spp., Bryoria spp.,* and *Usnea spp.*; Edwards et al. 1960, Van Daele and Johnson 1983, Thomas et al. 1996b) hereafter called arboreal lichens. Arboreal lichen has been reported to have significant abundance only in older forests (minimum 50 years; Edwards et al. 1960, Arseneau et al. 1997, Terry et al. 2000, Apps et al. 2001), or in proximity to old forests (Sillet and Goslin 1999, Dettki et al. 2000). Arboreal lichens accumulate in a forest slowly over time, and this process begins only after the lichens first colonize trees (Stevenson and Enns 1992). New forests can only be colonized once their branches reach above an area's yearly snow line (Edwards et al. 1960), and this may take many years, especially in high elevation forests. Arboreal lichen abundance is further expected to change over time due to variation in microclimate as stand density and canopy closure change with increasing time since fire (Campbell and Coxson 2001, Coxson et al. 2003). This change in abundance could be positive or negative, depending on whether the arboreal lichen was moisture limited (southerly aspects) or light limited (northerly aspects; Stevenson and Enns 1992, Coxson et al. 2003). Proximity to older forests allows young stands to receive lichen fragments, which greatly speeds up arboreal lichen colonization (Stevenson and Enns 1992).

Terrestrial lichen occurs in a wide range of stand ages (13-250 years post-fire; Yarranton 1975, Snyder and Woodard 1992, Thomas and Armbruster 1996, Thomas et al. 1996a, Eversman and Horton 2004). The relationship between fire occurrence and development of terrestrial lichen is complicated by the long periods needed for lichen recovery and confounding effects of forest succession. Some researchers have argued that fire is necessary, in the long term, to maintain terrestrial lichen cover for caribou because in the absence of fire competing cover of feathermosses or forest litter will eventually overtop lichen (Klein 1982, Schaefer and Pruitt 1991, Payette et al. 2000, Coxson and Marsh 2001). Balancing this positive effect of forest renewal by fire, other research suggests that for caribou, terrestrial lichens do not benefit from fire events because a very long recovery period (often centuries) is required for preferred forage-lichen species to reach ideal abundance levels (Thomas and Armbruster 1996, Thomas et al. 1996a, Arsenault et al. 1997, Joly et al. 2003). Since terrestrial and arboreal lichen likely differ in peak abundance relative to time since fire, it is important to examine each lichen type separately.

Thomas et al. (1996b) found that arboreal lichen made up only one percent of a caribou's diet in JNP and west-central Alberta. In most of British Columbia, however, arboreal, rather than terrestrial, lichen is the primary food source for mountain caribou (Edwards et al. 1960, Van Daele and Johnson 1983, Servheen and Lyon 1989, Apps et al. 2001). Even in British Columbia, where it provides the majority of a caribou's diet, researchers found that arboreal lichen abundance sometimes did not prove to be a good predictor of caribou habitat preference because a small caribou population size made it a non-limiting resource (Servheen and Lyon 1989). In areas that typically have drier climates and lower snow cover, however (e.g. east of the continental divide), arboreal lichen is more scarce and becomes a critical food source when snow depth or hardness prevents caribou from readily accessing terrestrial lichen (Thomas et al. 1996b, Johnson et al. 2001, Szkorupa 2002). It is therefore important to evaluate arboreal lichen resources for caribou in JNP and BNP despite their small contribution to diet.

Terrestrial lichen provides the main forage for caribou in JNP and BNP (Thomas et al. 1996b). Studies of forage selection by caribou in northeastern British Columbia found that caribou select for whichever lichen is present in the greatest abundance (Poole et al.

2000, Johnson et al. 2001). Saher's (2005) findings in a recent study of mountain caribou in West-central Alberta also support this result. She found the most abundant lichen species (*Cladina mitis* and *Stereocaulon* spp.) were significant predictors of caribou foraging preference. *Cladonia* spp. is the most common of the terrestrial lichen forage genera in JNP (Thomas and Armbruster 1996), and establishes much faster than *Cladina* spp. following fire. It has been reported that *Cladina* spp. take more than 100 years to establish in west central Alberta (Snyder and Woodard 1992) and 150-250 years to reach peak abundance in the western boreal forests of northern Canada (Thomas et al. 1996a). In contrast, Thomas et al. (1996a) estimated peak abundance of *Cladonia* to occur 40-60 years post fire in the northwestern boreal forest of Canada, while Yarranton (1975) marked its appearance in Northern Ontario 25 years after burning with rapid increases occurring soon after establishment. Following large fires in 1988 in Yellowstone National Park in Wyoming, Eversman and Horton (2004) found that *Cladonia* was the primary colonizing lichen genus, appearing just 13 years after the fires. Thomas and Armbruster (1996), similarly report that *Cladonia* spp. establishes first (relative to other lichens) in JNP, appearing around 20 years post-fire. The relative abundance and rapid recovery of *Cladonia* spp. following fires may make this genera particularly important to caribou in JNP and BNP, and of particular interest with respect to the effect of time since fire on caribou habitat selection.

Relationship of stand characteristics to topography, time-since-fire, and fire severity

I used stand origin dates from JNP (Tande 1979, Parks Canada File Data) and BNP (Rogeau 1996, Parks Canada File Data) as direct historical evidence of fires in my analysis. I also needed to examine stand characteristics influenced by past fires and by topography (which has influenced fires), to further explore the relationship between fire, caribou, and lichen. Stand characteristics and topography can have a direct influence on lichen development but can also provide indirect information about probable historical fire events.

As forests age following a stand replacing event, stand density usually decreases (La Roi and Hnatiuk 1980, Arseneault 2001, Schoennagel et al. 2003). However, canopy cover is more variable than tree density. The forest canopy may become more dense and closed (Northern Interior British Columbia; Coxson and Marsh 2001), become more open (JNP and BNP; La Roi and Hnatiuk 1980) or remain relatively constant (Kananaskis provincial park and Kootenay National Park in Alberta; Bessie and Johnson 1995). Coxson and Marsh (2001) found that successional increases in canopy cover were negatively correlated with terrestrial lichen abundance. For JNP and BNP, La Roi and Hnatiuk (1980) and Thomas and Armbruster (1996) characterized terrestrial lichen dominated sites as being open forest. La Roi and Hnatiuk (1980) further reported that thinning occurred as forests aged. In sites that had been selectively harvested, terrestrial lichen was found to increase with a reduction of canopy if there had been no soil disturbance (Snyder and Woodard 1992, Coxson and Marsh 2001). This is likely because disturbed soil promotes an increase in vascular plant cover (Cornelissen et al. 2001, Coxson and Marsh 2001). In areas where canopy was becoming less dense as a result of forest succession alone, terrestrial lichen cover was found to remain stable (Carroll and Bliss (1982) in Coxson and Marsh 2001, Thomas and Armbruster 1996).

Fire severity can have a lasting impact on vegetation composition (Halpern 1988, 1989, Schimmel and Granstrom 1996). Severity can affect the density of tree regeneration (e.g., lodgepole pine; Sirois 1993, Kashian et al. 2004). Severity also may affect understory composition. In western Canada, the most severe fires (greatest depth of burn) were found to produce a co-dominance of non-vascular species with herbaceous plants, while fires of lower severity resulted in increased dominance of woody-stemmed and herbaceous plants (Wang and Kemball 2005). In Douglas-fir forest of the Pacific northwest, Halpern (1988) found that severity of disturbance directly related to the amount of compositional change in the understory. Fire severity therefore potentially affects lichen establishment both directly through influence on the understory and indirectly through canopy cover and composition.

Topography can influence stand characteristics, fire frequency, and fire behavior. Elevation often defines the climax canopy species for a region (Krajina 1965, Holland and Coen 1983)while aspect and slope affect moisture and light availability (La Roi and Hnatiuk 1980, Stevenson and Enns 1992) which greatly influence species composition, abundance, and successional pathways. Species composition may also be affected by hillslope position (Chipman and Johnson 2002). Elevation has been found to significantly influence fire return intervals in some areas such that older stands tend to occur at higher elevations (Veblen 2003). This has been documented in JNP and BNP (Tande 1979, Van Wagner 1995, Rogeau 1996) as well as in Yellowstone National Park (Schoennagel et al. 2003) and southern Colorado (Grissino-Mayer et al. 2004). Aspect, another topographic variable, also accounts for significant variation in frequency and intensity of fire events, with south and southwest aspects receiving fire more frequently (Rogeau 1996, Gavin et al. 2002), and often with higher intensities (Gray et al. 2002, Gavin et al. 2003). Age of a stand at the time of a stand-replacing fire can also have an important influence on the subsequent successional pathways of a forest because of effects on seed availability for regeneration. For example, when older forests burn they are likely to have lower post-burn compositions of seral species like lodgepole pine (Antos and Parish 2002).

The various relationships between past fire events, topography, and stand characteristics demonstrate the importance of considering all three when examining the effects of fire on caribou and lichens. A thorough understanding of all these aspects is necessary if we hope to inform fire management options for Parks Canada within caribou range in JNP and BNP.

Parks Canada's Fire Management Program

Parks Canada uses prescribed fire as a management tool to achieve multiple park objectives, including habitat restoration for fire-dependent species, reducing risk of insect infestation, and facility protection (Van Wagner and Methven 1980, Achuff et al. 1996, Parks Canada 2000, 2005.). In JNP and BNP it is also important to ensure that fire does not negatively affect caribou, and this restriction potentially conflicts with other fire management goals (D. MacDonald pers. comm., D. Smith pers. comm., C. White pers. comm.). Parks Canada has adopted a policy of trying to burn an area equivalent to 50% of each Park's calculated long term fire cycle (Parks Canada 2000, 2005). Logistically, planning prescribed fires is much easier in valley systems that have less infrastructure, are narrower, and are segmented by numerous natural fuel breaks like rockslides, avalanche paths, and steep, stream-eroded gulleys (R. Kubian pers. comm., D. MacDonald pers. comm.). These features are more commonly found in the smaller, high elevation valleys that are favoured by caribou (Mercer et al. 2004), rather than in the low elevation, and wider, main valleys. As of 2005, there were several burns planned for JNP and BNP that either included portions of known caribou range, or were immediately adjacent to known caribou range (A. Dibb pers. comm., D. Smith pers. comm.). While a temporary fire exclusion policy for all potential caribou habitat was implemented in 2004 and 2005, there has been significant ecological (for fire–dependent species) and political (for mountain pine beetle management and facility protection) pressure to resume prescribed fire operations in terrain that is used by caribou (A. Dibb pers. comm., D. Smith pers. comm.). Determining whether and how prescribed fire can be used to help maintain or recover caribou and promote forage lichens will be important in assisting Parks Canada to achieve fire management goals.

Thesis Overview

The goal of my research was to determine how caribou habitat selection and occurrence of preferred lichen forage genera in JNP and BNP were affected by fire-related forest conditions (primarily forest age, structure, location, and composition), and to use this information to recommend appropriate fire management activities in caribou range. To do this, I created habitat selection models (RSF models) for caribou and predictive models for lichen occurrence based on stand age, topography and stand structure parameters. Data were acquired using Geographic Information System (GIS) data layers, and by conducting fine-scale field sampling of vegetation and forest characteristics. I then explored how significant variables from my models were related to stand age, fire behavior, and likelihood of fire occurrence.

In chapter 2, I used Generalized Linear Models (GLMs) to create caribou occurrence models (RSF models) for caribou habitat selection during winter (Oct. 15-April 15), when caribou tended to stay below treeline. I modeled caribou habitat selection at both fine and coarse scales. For coarse scale analysis, I used independent caribou location data to validate my coarse scale models. For fine scale models, I used a K-fold cross validation technique (Boyce et al. 2002). These models were used to determine what fire-related forest conditions were being selected by caribou.

In chapter 3, I used GLMs to create probability models for *Cladonia* spp. occurrence and Zero Inflated Negative Binomial (ZINB) models to simultaneously predict occurrence and abundance of Class 3 arboreal lichen trees (trees with greater than 50 grams of fruticose arboreal lichen within browsing reach of caribou; Stevenson et al. 1998). I validated my *Cladonia* models with a K-fold cross validation (Boyce et al. 2002) and my ZINB models with a K-fold technique for probability of occurrence prediction, and a correlation validation for predicted counts. These models were used to determine fire-related forest conditions that promote caribou forage lichens.

In chapter 4, I present management recommendations for fire management based on my research results and relevant literature. I also suggest further areas of inquiry for evaluating indirect effects of fire on caribou populations in JNP and BNP.

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Chapter 2: Caribou Habitat Selection in Relation to Lichen and Fire in Jasper and Banff National Parks

Introduction

Woodland caribou (*Rangifer tarandus caribou;* hereafter caribou) in Alberta, Canada are listed federally and provincially as a threatened species (Alberta Wildlife Act 2002, COSEWIC 2003). Several factors have been identified as the most likely reasons for population decline: direct disturbance from human activities, increased predation due to predator access along anthropogenic linear features and increased predator abundance due to alternate prey population increases, and habitat loss, primarily as a result of industrial activity (Emonds 1988, Seip 1992, James and Stuart-Smith 2000, Oberg 2001, Kuzyk, 2002, Thomas and Gray 2002, McLoughlin et al. 2003, Wittmer et al. 2005). Jasper and Banff National Parks (JNP and BNP) contain the most southerly distribution of woodland caribou in Alberta. Despite protection from industrial development, the south JNP population is in serious decline, while the northern BNP population is considered functionally extirpated (Flannigan and Rasheed 2002, Mercer 2002). Canada's recent Species at Risk legislation and Parks Canada's management plans identify population recovery of threatened species as a priority (Parks Canada 2000, COSEWIC 2003). Within caribou range in the national parks, Parks Canada suspects caribou population declines are partly related to habitat deterioration from human use infrastructure (primarily hotels, campgrounds, roads and trails; Parks Canada 2000) or a lack of recent fire events (Smith pers. comm.). While other research is examining the potential impact of predation and human disturbance on caribou in JNP and BNP, my study has focused on caribou habitat selection relative to past fire events. Resultant patterns will be used to evaluate whether fire management within caribou range can be adjusted to improve or maintain important habitat elements for caribou, as part of a comprehensive caribou restoration strategy.

Determining how to manage fire for caribou within a protected area must be considered within the broader context of other fire management objectives. In national parks prescribed fire is used as a management tool to achieve multiple management objectives, including habitat restoration for fire-dependent species, reducing risk of insect infestation, and facility protection (Van Wagner and Methven 1980, Achuff et al. 1996, Smith pers. comm.). However, Parks Canada must also try to ensure that fire does not negatively affect habitat that is necessary for providing caribou forage. Research indicating that caribou prefer older forests (Apps et al. 2001, Szkorupa 2002, Joly et al. 2003, Saher 2005), suggests that fire exclusion over the later half of the past century should have benefited caribou, by increasing the proportion of older forest on the landscape. Still, caribou have declined in recent decades. Now, protection of older forests is no longer a Parks Canada objective for JNP and BNP; rather, the Agency has adopted a policy of trying to achieve burning of an area equivalent to 50% of each Park's calculated long term fire cycle (Parks Canada 2000, 2001, 2005). This landscape goal increases the complexity of planning fires within caribou range. Currently, there are several prescribed burns planned that either include portions of known caribou range, or areas that are immediately adjacent to known caribou range (Dibb pers. comm., Smith pers. comm.). While a temporary fire exclusion policy for all potential caribou habitat was implemented in 2004 and 2005, there has been significant ecological (for fire–dependent species) and political (for mountain pine beetle management and facility protection) pressure to resume prescribed fire operations in terrain that is used by caribou (Dibb pers. comm., Smith pers. comm.).

In the Rocky Mountain National Parks, stand structure and forest extent have changed over the past century, from a relatively heterogeneous landscape including a variety of forest ages and types along with non-forested areas, into a more even-aged, and uniformly structured forest composition (Tande 1979, Rhemtulla et al. 2002). Researchers report conflicting evidence for whether caribou habitat is improved or degraded by fire events, and effects have been related primarily to the effect of fire on the primary food source for caribou, terrestrial or arboreal lichens (Klein 1982, Thomas and Hervieux 1994, Thomas and Armbruster 1996, Apps et al. 2001, Joly et al. 2003). The immediate effect of fire on lichens is destruction through combustion (Johnson 1981, Schaefer and Pruitt 1991, Joly et al. 2003). In the longer term, however, terrestrial lichens may depend on fire to reduce the competing cover of bryophytes or overriding forest litter (Payette et al. 2000, Coxson and Marsh 2001). Over time, following disturbance by fire, certain lichen genera re-establish in a sequential pattern *eg. Cladonia spp.* first, followed by genera more commonly preferred by caribou (*eg. Cladina spp.*, *Cetraria spp.;* Johnson 1981, Klein 1982, Thomas and Armbruster 1996, Payette et al. 2000). Relative terrestrial and arboreal lichen abundance also varies widely across geographic regions, with increasing amounts of arboreal lichen found moving westward from Alberta into British Columbia (Apps et al. 2001, Johnson et al. 2001, Szkorupa 2002). Terrestrial lichen may be overgrown by feathermoss mats or buried in needle litter in older stands, such that abundance will likely decline with long-term absence of fire (Payette et al. 2000, Coxson and Marsh 2001,). Arboreal lichen, on the other hand, is usually only found in high abundance in older, presumably long-unburnt, stands (Edwards et al. 1960, Schaefer and Pruitt 1991, Apps et al. 2001). Thus, the two lichen growth forms important as caribou forage may differ in terms of their pattern of development post-fire.

Several other stand characteristics that could respond to time since fire were also examined. As forests age following a stand replacing event, stand density decreases (Arseneault 2001, Schoennagel et al. 2003), and the forest canopy becomes relatively continuous (Bessie and Johnson 1995). Stand characteristics are also influenced by topography, which itself has a modifying influence on fire behavior (Hirsch 1996, Gray et al. 2002). Differences in elevation can significantly influence fire return intervals, with older stands tending to occur at higher elevations. This has been documented in Jasper and Banff National Parks (Tande 1979, Van Wagner 1995, Rogeau 1996) as well as in Yellowstone National Park (Schoennagel et al. 2003). Aspect, another topographic variable, also accounts for significant variation in frequency and intensity of fire events, with south and southwest aspects receiving fire more frequently, and often with higher intensities (Tande 1979, Gray et al. 2002). Age of a stand at the time of a stand replacing fire can also determine the successional pathways for subsequent forest composition, with older forests having higher post-burn compositions of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.; Johnson and Fryer 1989, Antos and Parish 2002, Delong and Meidinger 2003). This occurs because the other main species, lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), is largely dependent on fires for seed dispersal, and does not regenerate in the understory like subalpine fir, or tend to be as long-lived as Engelmann spruce. Time since fire, stand structure and composition, and topography have therefore all been included in my examination of caribou habitat selection.

Several recent studies of caribou habitat selection have concluded that it is necessary to examine selection at different spatial scales (Rettie and Messier 2000, Apps et al. 2001, Johnson et al. 2001, Szkorupa 2002, Saher 2005). At a coarse or landscape scale, my focus was on determining whether I could create a robust, predictive habitat selection model using either fire-determined parameters (eg. stand origin date, stand type) or fire-influencing parameters (slope, aspect, elevation). Saher (2005) and Rettie and Messier (2000) determined that habitat selection at fine scales related primarily to foraging needs. Consequently, my fine scale models focus on caribou selection related to lichen abundance, but also include topography, stand origin, and more detailed stand structure data.

Materials and Methods

Study Area

I conducted my study in the southern half of JNP (North 52 deg 59 min, West 118 deg 03 min) and the northern portion of BNP (North 51 deg 32 min, West 116 deg 02 min) (Figure 2.1), in the Rocky Mountains of Alberta, Canada. Both areas were immediately east of the continental divide and included wide, U-shaped, intersecting glacier carved valley systems. In JNP, a large portion of the park area is rock and glacial ice (19%; Holland and Coen 1983). Forested areas included the montane (7%), lower subalpine (30%), and upper subalpine (37 %) ecological regions, classified by vegetation and elevation (Holland and Coen 1983). The BNP valley systems for this study were all higher elevation valleys and did not include any montane zones. In the vegetated portion of the BNP study area, 44% was alpine, 30% was upper subalpine, and 25% was lower subalpine (Holland and Coen 1983). Montane forest was primarily composed of dominant and mixed stands of lodgepole pine, white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana (*Mill.)B.S.P.), Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco), and trembling aspen (*Populus tremuloides* Michx.). Subalpine forests included lodgepole pine, subalpine fir, Engelmann spruce, black spruce, whitebark pine (*Pinus albicaulus* Engelm.), and subalpine larch (*Larix lyallii* Parl. -BNP only). Stand boundaries in both study areas were determined primarily by stand initiating fire events (Tande 1979, Achuff et al. 1996). In the study area in JNP, stand origin dates ranged from 1600 to 2000 (Tande 1979, Parks Canada file data), and in the BNP study area, stands were generally older ranging from 1390 to 1936 (Van Wagner 1995, Rogeau 1996, Parks Canada file data). Elevations of sample locations in the two parks ranged from 1019m to 2393m a.s.l. in JNP and 1494m to 2589m a.s.l. in BNP.

Study Design

I used Resource Selection Functions (RSF) with a use/availability design to examine habitat selection by caribou at both fine and coarse scales. Fine-scale corresponds to foraging level or third order selection, while coarse-scale corresponds to stand level or second order attributes as defined by Johnson (1980). Previous caribou research has demonstrated the importance of considering habitat selection by caribou at these spatial scales (Apps et al. 2001, Johnson et al. 2001, Szkorupa 2002, Saher 2005). Caribou distribution was based on recent Global Positioning System (GPS) telemetry caribou collar locations (Lotek), radio telemetry locations obtained from previous caribou studies in the park (Brown et al. 1994, Thomas and Armbruster 1996), and/or recorded historical caribou observations (Parks Canada file data). For coarse scale selection, I defined available habitat as the treed, southern half of JNP and the treed northern portion of BNP (Figure 2.2). For fine scale or forage level analysis, I defined available habitat as treed areas within valleys containing caribou use locations. Valleys were delimited by surrounding mountain ranges, and defined as the continuous forest cover on either side of a single main valley-bottom river or stream. I considered this topographical delineation of available habitat to be more biologically relevant to caribou than using an average daily distance traveled, since topography is a more physically-limiting factor for caribou travel in JNP's mountainous terrain than distance. Fine scale sampling was further limited to include only those locations south of Highway 16, since I had no record of collared caribou traveling north of this feature.

Coarse Scale Sampling

For caribou use locations, I chose all GPS positions collected between October 15 and April 15th that fell below the treeline delineated by the stand origin map layers of BNP and JNP. I used caribou location data supplied by Parks Canada, which included radio-telemetry collar data from the first three years of a five-year caribou study in JNP

(Mercer et al. 2004), and from the first year of BNP's caribou telemetry monitoring (Dibb 2004). Parks Canada collared caribou in late fall each year and retrieved the first two animals' collars in the spring of 2002, and all others in October of the subsequent year following collaring. For 2001 to 2003, there were eleven caribou collared, and for the winter of 2003/2004 there were a total of eight (Dibb 2004, Mercer et al. 2004). Collar intervals were set for every six hours. I excluded April 16th to October 14th locations because caribou tended to spend the majority of their time above treeline in the alpine ecological region during this period. Alpine areas in JNP and BNP do not have a measured fire cycle (Tande 1979, Van Wagner 1995).

I used 75-year stand origin categories, to assess stand origin in my RSF models for coarse scale selection patterns. Elevation, slope, and stand origin date summary statistics are listed for each stand origin category in Appendix A. I also evaluated linear and non-linear forms of stand origin, and a binary designation of old stands (>150 years) versus younger stands (<150 years). I chose 75-year intervals based on other related caribou research. Thomas and Armbruster (1996) indicated that 70 years post-fire was the length of time for development of preferred lichen forage in Jasper National Park. Recent research on stand origin dependencies of different lichen species in west-central Alberta (Szkorupa 2002) and northern British Columbia (Coxson and Marsh 2001) also indicated that forage lichen abundance was highest in open pine stands older than 75 years and deteriorated after 150 years. For aspect, I created eight categories that correspond to the eight cardinal and semi-cardinal directions. For aspect, I also evaluated a binary variable that divided each variable into only two distinct categories: south and southwest aspects (157.6

degrees to 247.5 degrees azimuth) versus all other aspects. All variables I evaluated in the coarse scale models are displayed in Table 2.1. For stand origin categories, the oldest time interval is the reference category in the model (1625$_{\mathrm{AD}}$ and earlier) and for aspect categories, North was the reference category. To obtain elevation, stand origin date, slope and aspect for all data points, I used JNP's and BNP's Digital Elevation Models (20m resolution), and their respective stand origin map layers (Tande 1979, Van Wagner 1995, Park File data). I generated this location-based data by using 'Gridspot' and 'Identity' commands in Arc$^{\mathrm{TM}}$ GIS (ESRI GIS Systems) from each park's GIS digital elevation models, stand origin map layers.

JNP and BNP have ecological land classification digital map layers (Holland and Coen 1983) that define areas to be one of the following vegetation types: lodgepole pine, Douglas-fir, white spruce, poplar, aspen, closed Engelmann spruce/subalpine fir, Engelmann spruce/subalpine fir/whitebark pine, shrub, meadows, or alpine. From these vegetation types, I defined each location as either open canopy (meadow, alpine, or aspen (which was leafless during the winter sampling period), or closed canopy (all other categories). I was not confident that closed sites differentiated well between tree species, so chose not to examine each vegetation type as individual categories.

Fine Scale Sampling

In 2003, I chose field-sampling points for development of fine scale models based on a random draw of sample locations in treed areas, from 787 telemetry locations representing two caribou (38 caribou use locations). For my 2004 sampling season, I chose use sites from 3505 treed telemetry locations by randomly selecting ten locations from each of nine animals successfully collared over the winter of 2002/2003 (90 sample locations in total). As with the coarse scale model, I only used locations recorded between October 15, 2002 and April 15, 2003, to optimize samples from the period caribou tend to remain below treeline. Due to the differences in sample selection, I included data collection year as a variable within my set of candidate models. To build a set of "available" sample locations, I randomly selected locations within valleys containing caribou use locations, while excluding areas within 300m of a use location; 300 meters is one order of magnitude larger than the reported error for a study on uncorrected GPS collar accuracy in mountainous terrain (D'Eon et al. 2002). I chose this value to reduce the possibility of overlap with any use locations that may have had position errors during GPS collar fixes. Since caribou location data from BNP were not available during the 2004 sampling season, fine scale selection analysis used JNP sample data only.

I sampled vegetation at a total of 128 caribou use locations and 64 available locations, over two years. I used two diagonally-adjacent 10m by 10m squares laid out on a North-South by East-West grid to delineate the plot area (Figure 2.3). At each plot site, I recorded local slope in degrees with an inclinometer, and aspect in degrees, corrected for declination (22 degrees). For each tree (defined as minimum 5cm diameter at 130cm above ground) I recorded species, diameter at 1.3m height, and arboreal lichen abundance (in categories, as per Stevenson et al. 1998). For arboreal lichen abundance, I used counts of numbers of trees in different lichen abundance classes as defined by Stevenson et al.

(1998), and also evaluated a binary variable that coded plots as having at least one Class 3 tree (estimated > 50 grams of lichen) or not. I also estimated overall tall (>10cm height) shrub cover (by species) to the nearest 5 percent in each plot. I estimated percent cover to the nearest percent for understory herbaceous plants (to species), lichens (to genus) and dwarf shrubs (<10cm height, to species) using five, 240cm^2 quadrats in fixed corner locations of the plot. To reduce sampling time at each plot I combined all grass species and made a single cover estimate; cover of moss was estimated as either feathermoss (*Pleurozium* spp. or *Ptilium* spp.) or other moss spp. (all other moss genera). I recorded total terrestrial lichen cover as well as cover of individual lichen genera and different combinations of genera (e.g. *Cladonia* and *Cladina* spp. or *Stereocaulon*, *Cetraria*, and *Flavocetraria* spp.) to the nearest percent in each of my quadrats. For all plant cover estimates I averaged values from the five quadrats to provide overall estimates for each plot location. I maintained cover estimation consistency in quadrats by using standardized cover cards and conducted periodic consistency checks among my four field personnel. At the location of the quadrats, I also estimated canopy cover using a convex spherical densiometer (Lemmon, Model A Forest Densiometers), and recorded moss depth and depth from litter or moss surface to mineral soil. Depths used in analysis are the average value from the five measures taken at each plot. From the dominant canopy layer I selected three trees on which I measured height and took cores for aging and measurement of sapwood width. I used my east-west line as a 20m line intersect sample to count number of downed logs, and had a 2m by 2m square microplot off the plot center where I recorded the number and species of saplings (<5cm diameter at 130m height above ground). From the three tree cores taken at breast height from each plot, I used the one with the highest ring count as a conservative measure of minimum number of years since stand replacing fire. Of these measured variables, the ones selected for my ten best performing models are listed in Table 2.2.

Data Analysis

Coarse Scale Selection

I created a candidate set of RSF models in S-PLUS v.6.2 (Venables and Ripley 1999) using Generalized Linear Models (GLMs). I used a combination of forcing of different stand origin variables, with forward and reverse stepwise selection for all other remaining variables (Table 2.2). I used forcing of different linear and non-linear forms of stand origin variables as well as stand origin interactions with topography to determine whether there were significant relationships (beta coefficients of $p<0.05$) between caribou selection and stand origin. I did this to investigate my primary question, the effect of historical fires on caribou habitat selection. No pair of variables had Pearson correlations greater that 0.50, so I assessed all measured parameters during model selection. I compared my suite of candidate models using Akaike Information Criterion values (AIC; Burnham and Anderson 1998) focusing on examinations of the relative change in deviance when additional variables were included. AIC for large sample sizes tends to favor over-parameterization of models, so only significant predictor variables (beta coefficients of $p<0.05$) were included. Using the *groupdata* function in S-PLUS v.6.2 (Venables and Ripley 1999), I designated individual animals to be a random effect to avoid pseudoreplication error from lumping data points from all animals together (Aebischer et al. 1993).

For my training model, use locations were from two caribou collared through the winter of 2001/2002, and nine caribou collared during the winter of 2002/2003 (4288 use locations; 9798 available). For model testing, I used two independent data sets: JNP's 2003/2004 telemetry data (locations from eight animals - 3048 use locations; 11 292 available) and BNP's 2003/2004 data (one animal - 783 use locations; 783 available). Model performance was measured using a Spearman rank correlation test on calculated probability values from the training and validation data sets, which were divided into nine bins of 0.0-0.10, 0.11-.20, 0.21-0.30, 0.31-0.40, 0.41-0.50, 0.51-0.60, 0.61-0.70, 0.71-0.80, and 0.81-1.00. The tenth bin (0.91-1.00) was grouped with the ninth because out of 18 067 data points, only three points had probabilities greater than 0.90. Using the Spearman rank correlation method may underestimate model significance when applied to use/availability data (Boyce et al. 2002), thus I also report the calculated area under the Receiver Operating Characteristic Curve (ROC). The ROC value is a standardized measure of a logistic regression model's ability to distinguish between a one (use location) and a zero (available locations; Hosmer and Lemeshow 2000).

In S-PLUS v.6.2 (Venables and Ripley 1999), designation of categorical variables results in the creation of "dummy" coded variables in a GLM. These "dummy" variables represent different levels within a categorical variable. For determining relative significances of each "level" within a category, I used the Sidak post-hoc multiple comparison test within S-PLUS v.6.2 (Venables and Ripley 1999). This provided 95% confidence interval differences between beta coefficients for the levels within each categorical variable, allowing me to rank these in relation to each other. I summed the number of times each level was selected over another to determine a category ranking. Those most often selected in relation to another were considered preferred by caribou, those least selected were assumed to be avoided by caribou. Ranking of selection preference is recommended by Keating and Cherry (2004) for use/availability RSF studies.

Fine Scale Selection

To assess the significance of independent fine-scale variables, I evaluated each by means of univariate regressions in GLM. Only those variables that accounted for deviance in excess of 1 were included in stepwise selection (summary statistics from evaluated variables are listed in Appendix A). In S-PLUS v.6.2 (Venables and Ripley 1999), I created RSF candidate models using both forward and reverse stepwise methods with GLMs to create candidate models based on biologically-reasonable predictor variables using data from the 192 plots I sampled. I selected the most parsimonious model using AIC corrected for small sample sizes (AICc; Burnham and Anderson 1998). I subsequently evaluated the best model using the Spearman rank, K-fold cross validation technique (Boyce et al. 2002), using a series of ten random draws of 80 percent (154 plots) of my data for model training and the remaining 20 percent (38 plots) for validation. To ensure there would be enough use locations per bin with only 38 plots in my testing set, I used only six probability bins for the Spearman rank correlation test. Most use locations tended to have high predicted probabilities, so bin ranges were scaled larger for low probability values to avoid use counts of zero in lower probability bins.

The probability bin ranges were therefore 0.00-0.25, 0.26-0.50, 0.51-0.70, 0.71-0.85, 0.85-0.95, and 0.96-1.00.

Results and Discussion

Coarse Scale Model

The best coarse-scale model, in which all variables were significant, was the model *full1* (Table 2.3). This model included: the linear form of slope in degrees (negative), elevation in meters (positive), the six (75-year) stand origin categories, the eight cardinal and semi-cardinal aspect categories, and a positive association for stands categorized as “closed”. The final model evaluated with independent data was therefore:

$$\mathbf{g(x) = \beta_0 + \beta_1\,(fire.category) - \beta_2(slope) + \beta_3(elevation) + \beta_4\,(aspect.category) + \beta_5(forest.closure)}$$

with **g(x)** as the logit function of the predicted response variable. Of my predictor variables, elevation was the most influential factor, explaining 74% of the variation, and forest closure the least. A full description of the combined data set and its associated parameter estimates are listed in Table 2.4. The model performed quite well, with significant and high Spearman Rank correlations and high ROC values (Table 2.5).

At a landscape scale during winter (mid-October to mid-April), within the forested portion of BNP and JNP, caribou preferred higher elevations, gentler slopes, and closed canopy forest. Based on multiple comparison analysis of the six different fire categories (Table 2.5), caribou preferred relatively older forest, showing the greatest preference for stands that originated between 1701 - 1775$_{AD}$ and those from 1851 – 1925$_{AD}$. Caribou were less likely to select the youngest stands (originating in 1925$_{AD}$ or more recently), and older stands from the intervals 1776 – 1850 $_{\mathrm{AD}}$ or 1626-1700 $_{\mathrm{AD}}$. Multiple comparison analysis of aspect categories (Table 2.6) revealed that the two aspects consistently avoided were the South and Southwest. I also evaluated linear and non-linear forms of stand origin date (*fire*), as well as interactions of stand origin with elevation and slope, however, inclusion of stand origin categories provided the most consistent and informative explanation of habitat selection patterns by caribou.

Avoidance of younger stands by caribou was not observed in a recent summary of studies in the boreal forest (Dunford 2003, Ferguson and Elkie 2004) but is corroborated by Alaskan research (Joly et al. 2003), and recent caribou studies in west-central Alberta (Szkorupa 2002, Saher 2005). Over the broader area of JNP, this avoidance could be explained by the strong correlation of younger stands with lower elevations (Tande 1979, Rogeau 1996), although some recent fires have extended into higher elevation areas within traditional caribou range. Selection for higher elevation forest and avoidance of southwest aspects may have several explanations. High elevations experience fire less frequently, while southwest aspects tend to have more frequent fire (Tande 1979, Rogeau 1996). This is primarily due to variation in snow-free periods and more direct solar incidence on southwest aspects. Caribou are therefore more likely to find older forests at high elevations, and those older forests may have an arboreal lichen-forage benefit (Edwards et al. 1960, Terry et al. 2000). However, Thomas et al. (1996) reported that arboreal lichen only accounts for about one percent of the diet of caribou in JNP and BNP, with the primary forage being terrestrial lichen. Further, Coxson and Marsh (2001) found that terrestrial lichen abundance declined after 150 years in pine forests in northern

British Columbia. Another explanation for caribou preference of higher elevations and avoidance of southwest aspects is predator avoidance. Recent research in JNP found wolves preferred low elevation, southwest aspect terrain (Whittington et al. 2005). In other species, predator avoidance has been demonstrated to be a strong deterrent to selection of preferred forage (Hebblewhite and Pletscher 2002), and caribou are likely more vulnerable to predation pressure than other ungulate species (Oberg 2001, McLoughlin et al. 2003, Wittmer et al. 2005). Predator avoidance may also explain the preference for closed canopied forest over open areas. Closed canopy forests could offer greater hiding cover and at the same time may confer a foraging benefit since snow interception by the canopy would reduce the cratering depth necessary to access terrestrial lichens (Terry et al. 2000). Predation avoidance does not explain the preference for less steep slopes, however, while a fire effect potentially does. Low angle slopes are associated with less intense fires than steeper slopes because direct radiation from flame tilt and convective pre-heating of upslope fuels occurs increasingly with steeper terrain (Hirsch 1996, Gray et al. 2002). Low intensity fires can reduce mosses or vascular plants that compete with lichens (Payette et al. 2000, Coxson and Marsh 2001) while not eliminating preferred closed-forest canopy. Historical evidence of low intensity fires in these areas has not been examined (eg. fire scars, charcoal analysis), and it is possible that the stand origin maps miss significant areas that may have received lower intensity fire within and on the periphery of large stand replacing events. One study in eastern Canada found that the footprint of some large fires was doubled by the inclusion of areas of less-visible, lower severity fire occurrence (Bergeron et al. 2001). Determining the extent of low intensity fires in JNP and BNP is required to assess this further.

Fine Scale Selection

The best fine-scale model of caribou habitat selection related probability of use to: number of saplings (positive), cover of all caribou forage lichens combined (positive), depth through moss and litter (negative), age of oldest tree cored at the plot site (positive), number of downed logs at the site (negative), the percent cover of *Cladonia spp.* (positive), the percentage of uncommon tree species at the site (negative), and the number of arboreal lichen class one trees present (negative; see Table 2.8 and Table 2.9). Caribou selected sites with high lichen cover, (especially *Cladonia spp.* cover), that had older trees and more saplings present, while avoiding areas with deeper duff, more downed logs, more trees with low arboreal lichen abundance, and sites with Douglas-fir or deciduous trees as part of the canopy.

Ten k-fold cross-validation runs of this model yielded Spearman's rho values that averaged 0.921, providing a two-tailed significance of $0.02<p<0.05$ (Zar 1999; Table 2.10). Two of the ten runs were not significant at alpha < 0.05, likely due to the relatively small sample size ($n=192$) that was partitioned for testing. The average ROC value for the model validation data sets was 0.897, indicating excellent model discrimination (Hosmer and Lemeshow 2000) between use and available locations. The next most parsimonious models evaluated had AICc weights of 0.16 and 0.12, only slightly decreased weighting from the addition of either the binary aspect category (negative association with South or Southwest aspects), or basal area (negative), compared to the best model (Table 2.8).

Individual cover and total cover of six different terrestrial lichen genera were examined (*Cladonia* spp., *Cladina* spp., *Stereocaulon* spp., *Cetraria* spp., *Flavocetraria* spp., and *Peltigera* spp.*)*. Among these lichen genera, *Cladonia* spp. were present in the greatest abundance in sample locations, and when examined singly in a univariate model, *Cladonia* spp. cover accounted for the greatest deviance in use compared to all other predictor variables (Table 2.11). Interestingly, *Cladonia* spp. is not recorded in other studies as the primary terrestrial forage genus for caribou (Thomas and Armbruster 1996, Thomas et al. 1996, Szkorupa 2002, Dunford 2003, Saher 2005). In JNP, however, *Cladonia* spp. is the most abundant genera among the terrestrial forage lichens (this study, Thomas and Armbruster 1996). Thomas and Armbruster (1996) noted that Jasper had much less lichen than other areas that supported caribou, in particular the boreal forest and northern Canada, while Poole et al. (2000) and Johnson et al. (2001) found that in northern British Columbia, caribou selected for lichen that was of greatest abundance. The selection for areas with high cover of *Cladonia* spp. in this "lichen-impoverished" environment could be an adapted foraging strategy.

Notable for its lack of importance in predicting caribou habitat selection was the number of heavily laden arboreal lichen bearing trees (Class 3 trees) at a site. While arboreal lichen has been identified as an important forage resource for caribou in west-central Alberta (Thomas and Armbruster 1996, Thomas et al. 1996, Szkorupa 2002, Saher 2005), this was not apparent from my selection analysis. As a univariate predictor, the number of class 3 lichen bearing trees accounted for a deviance of only 0.0007. While this result does not seem to match other studies that report significant selection for arboreal lichen bearing trees by caribou during late winter (Szkorupa 2002, Saher 2005), it corroborates previous fecal analysis conducted on caribou pellets in JNP that found arboreal lichens only made up approximately one percent of caribou diet (Thomas et al. 1996). It is possible however, that since my study included early and late winter foraging (mid-October to mid-April), the importance of selection for arboreal lichen was masked, especially if selection for areas with high abundance of arboreal lichens occurred only during a relatively brief period of the winter season. It is also possible that the short duration of my study did not capture a season with late-winter snow conditions that necessitated a greater reliance on, and therefore noticeable selection of, arboreal lichen. In seasons with heavy or long-lasting snow cover, arboreal lichen is recognized as a critical food resource for caribou (Thomas and Armbruster 1996). Possibly, at a coarse scale, caribou are generally selecting sites with higher likelihood of having arboreal lichen, like high elevation areas (Edwards et al. 1960). This is supported by avoidance of Douglas-fir and Aspen sites, which tend to occur at lower elevations (Holland and Coen 1983).

While not in my top model, basal area was a significant predictor in lower-ranked AICc weighted models, and was selected as the second most important variable during forward stepwise selection modeling after *Cladonia* spp. cover. While no other studies of woodland caribou in Alberta have reported basal area to be a significant predictor of caribou habitat selection, two studies in British Columbia's Selkirk Mountains did find increasing basal area to predict mountain caribou habitat selection (Rominger and Oldemeyer 1989, Terry et al. 2000). In contrast, stand density was not a significant predictor of caribou habitat selection, indicating a potential use by caribou of a broad range of stand ages - those with relatively higher density of smaller (and usually younger) trees, to those with fewer large, (and usually older) trees. This is consistent with my coarse scale model findings, which suggested two distinct stand-age ranges (1701-1775_{AD} and 1851-1925_{AD}) were selected by caribou. The maximum tree core variable (fine scale variable) indicates that sites with fewer, but older, trees are most likely selected. Young, dense forest also tends to have fewer high arboreal abundance trees (Sillet and Goslin 1999, Dettki et al. 2000) and since caribou avoided sites with high numbers of Class one trees (< 5 grams of lichen /tree), this also supports selection for sites with fewer, older trees.

Selection by caribou for areas with shallower duff and increased number of saplings could indicate favourable conditions occurring from more recent fire (Coxson and Marsh 2001) or from other less severe disturbances (Antos and Parish 2002). Conversely, a preference for sites with older trees present is consistent with areas having longer fire return intervals or at least fires of low severity. Low severity fire has not been considered the historic norm for the higher elevation sites preferred by caribou (Tande 1979, Van Wagner 1995). In these areas, fire has been characterized as infrequent, severe, and stand replacing (Bessie and Johnson 1995, Veblen 2003). As for coarse scale analysis, determining the extent of low intensity fires in JNP and BNP is required to assess this further.

Avoidance of sites with more logs may have a link to historic fires. Stands do self-thin more while they are younger (La Roi and Hnatiuk 1980), producing more logs. Possibly however, this behavior simply related to physical-barrier avoidance. Downed logs would impede travel, and may have been avoided to save energy, or to perhaps allow easier flight from predators.

Conclusions

My selection models at both scales indicated a preference by caribou for older forest, or sites likely to have older forests. At a landscape scale, caribou selected older forest (1701- 1775_{AD} and $1851\text{-}1925_{AD}$), at higher elevation and lower slopes, i.e., areas that are less prone to fire. In the fine scale model there was selection for sites with older trees present. At this scale, however, there were some characteristics of stands selected by caribou that could indicate a preference for areas with more recent fire (preference for stands with increased number of saplings, increased *Cladonia spp.* cover, decreased moss and litter depth, and decreased number of logs). These conditions may be the result of past fires, but could also be associated with partial disturbances or autogenic processes (Antos and Parish 2002).

My study found that terrestrial lichen abundance was a significant predictor of caribou habitat selection while arboreal lichen abundance was not. Nevertheless, harsher conditions than those encountered during the years of this study could increase the relative importance of arboreal lichens. As reported by Coxson and Marsh (2001), it is possible that terrestrial lichen abundance might decline in forests older than 150 years, in which case fire would be necessary for rejuvenation of lichen cover. Indeed, caribou preference for stands in the 1925-1850$_{\mathrm{AD}}$ category may correspond with the finding by Coxson and Marsh (2001) that lichen abundance was highest in stands 75-150 years old. Lower intensity fires could potentially be used to reduce competing bryophyte and litter cover in older forests, while not destroying other selected stand elements, and this might also allow retention of arboreal lichen. A closer examination of the effect of fire on these selected forage level elements would be a useful follow up to my study.

My habitat selection models do not indicate that the lack of recent fire has been detrimental for caribou. Plans for large prescribed burns within caribou habitat would create areas that caribou would be likely to avoid during the winter for many decades. Caribou habitat would therefore benefit, at least in the short term, from exclusion of prescribed fires and wildfires from caribou range. To achieve other fire management goals and avoid negatively affecting caribou habitat, Parks Canada should focus prescribed burn efforts on lower elevation valleys that do not support caribou.

Tables and Figures

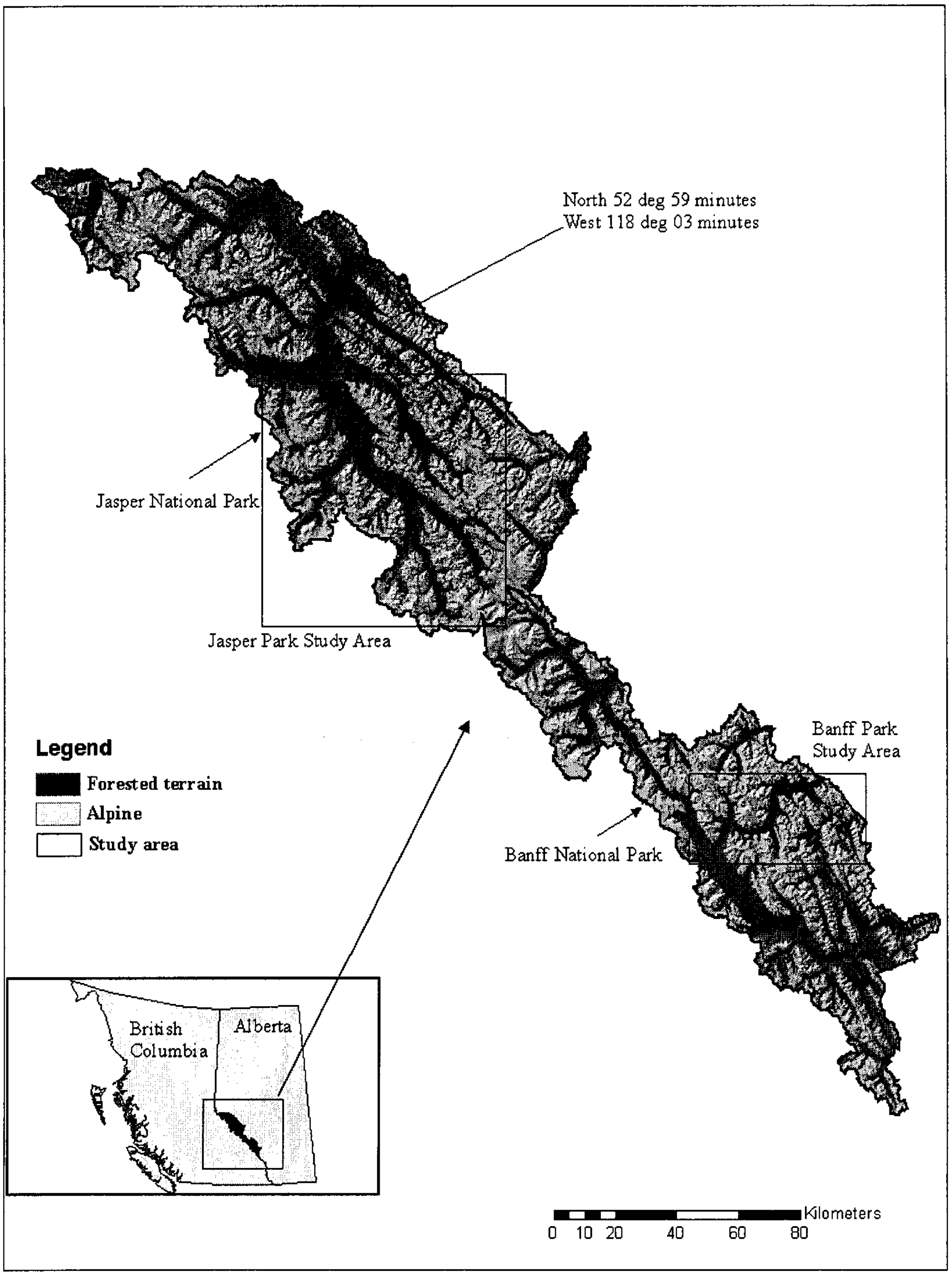

Figure 2.1: Jasper and Banff national parks in relation to Canada and Alberta. Both parks are within the Rocky Mountain range on the East side of the Continental Divide.

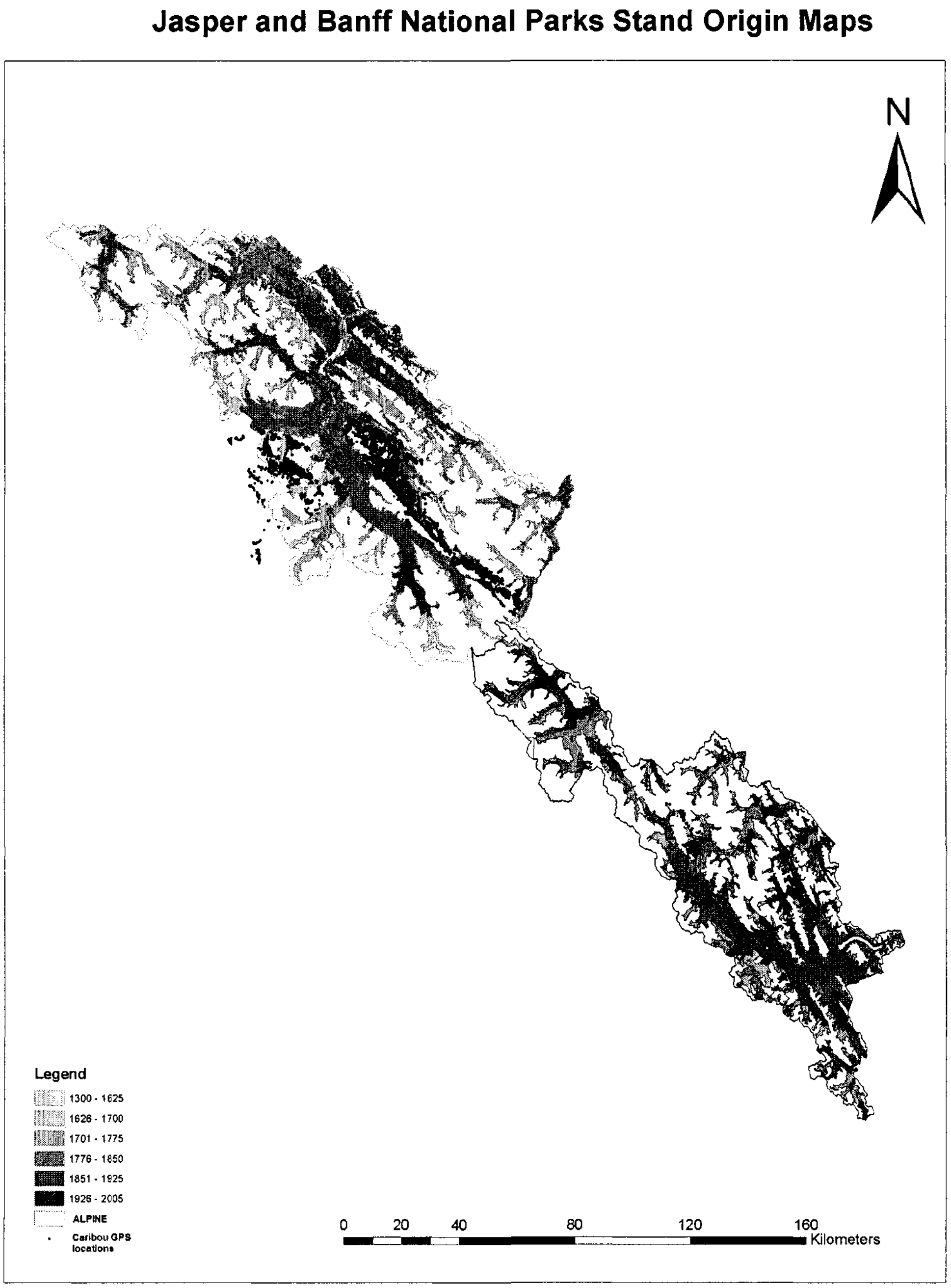

Figure 2.2: Jasper (northern park) and Banff (southern park- black boundary line) National Parks with GPS caribou collar locations indicated on the stand origin map layer. Blue dots represent collar locations from 20 different caribou over three years (2001-2004). Coloured polygons represent stand origin with darker colours representing increasingly younger forest. Jasper Park had no caribou locations in the northern half of the park and Banff Park had no locations in any southern valley systems. Locations in Banff Park are from a single collared animal.

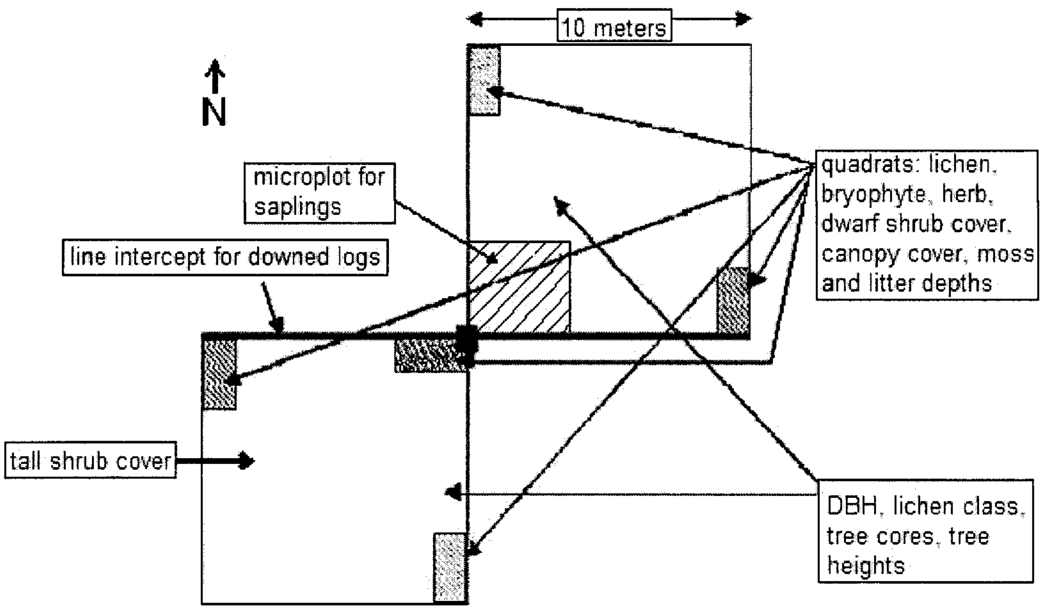

Figure 2.3: Plot layout for fine scale sample plots using a fixed area design with five quadrats (1 m X 2 m) for measuring cover of lichens, bryophytes, and herbaceous vascular plants and dwarf shrubs. Measurements of tree sapling density and cover of tall shrubs were made in the single 2 x 2 m plot. Tree heights, increment cores, # of trees by species, and arboreal lichen abundance were measured in the two 10 meter by 10 meter plots. The 20m east/west line was used as a line intercept for counting downed logs.,Trees were differentiated from saplings as all woody-stemmed perennials with a diameter greater than 5cm at 130cm above ground.

Table 2.1: Definitions of independent variables used in the coarse scale selection models. Fire (stand origin) date was not a significant predictor for the training data set, while fire.old was not a consistent predictor variable between the training and testing data sets. Aspect.cat with eight categories explained significantly more variation than aspect.cat1.

Variable	Data type	Description
fire	continuous	stand origin date based on Park Stand origin map
firecat	categorical	Six stand origin categories of 75-year intervals; present day-1926, 1925-1851, 1850-1776, 1775-1701, 1700-1626, **1625 -all earlier fire origins***
fire.old	binary	stand origin date of either before or after 1850AD
elev	continuous	elevation in meters above sea level from the Park Digital Elevation Model
slope	continuous	slope in degrees from the Park Digital Elevation Model
aspect.cat	categorical	Eight aspect categories of 45 degree intervals: **North***, Northeast, East, Southeast, South, Southwest, West, and Northwest
aspect.cat1	binary	South and Southwest aspect (157.6-247.5 degrees azimuth) versus any other aspect
closure	binary	Closed forest versus open based on Holland and Coen (1983). Open stands include meadow, shrub, alpine and deciduous coded sites

***reference categories for each categorical variable**

Table 2.2: Definitions of independent variables that were included in the top ten fine scale selection models.

Variable	Data type	Description
cladonia.cov	continuous	average percent *Cladonia* cover (from 5 quadrats per sample locations)
#saplings	count	number of saplings
all.lichen.cov	continuous	average percent cover of lichens (from 5 quadrats per sample locations)
#logs	count	number of logs from line intersect count
%notPl.Se.Fa	continuous	percent of trees in plot that are not pine, spruce or fir
max.core	continuous	highest tree age (ring count from increment core) in plot
litter&moss	continuous	average depth in cm of litter and moss (5 measures per sample location)
#class1trees	count	number of arboreal lichen class 1 trees in a plot
basal.area	continuous	basal area of all trees in a plot calculated from dbh measurements from each tree
SorSW.aspect	binomial	South and Southwest aspect (157.6-247.5 degrees azimuth) versus any other aspect
%fir	continuous	percent of trees in plot that are subalpine fir

Table 2.3: The top ten candidate coarse scale habitat selection models for caribou. Differences in AIC values from the best model (ΔAIC) and Akaike weights (AICwi; Burnham and Anderson 1998) were calculated to determine model rankings.

model name	model structure	K	ΔAIC	AICw$_i$	rank
full1	firecat - slope + elev + aspect.cat +closure	16	0	1E+00	1
full1a	firecat - slope + elev + aspect.cat1 +closure	10	14	8E-04	2
drop1	firecat - slope + elev + aspect.cat	15	17	2E-04	3
drop1a	firecat - slope + elev + aspect.cat1	9	33	6E-08	4
drop2	firecat + elev + aspect.cat	14	83	1E-18	5
drop2a	firecat2 + elev + aspect.cat1	8	93	7E-21	6
full2	fire.old - slope + elev + aspect.cat +closure	12	111	8E-25	7
full2a	fire.old - slope + elev + aspect.cat1 +closure	6	126	5E-28	8
full3	fire - slope + elev + aspect.cat + closure	12	150	3E-33	9
full3a	fire - slope + elev + aspect.cat1 + closure	6	163	3E-36	10

Table 2.4: Coefficients and significances of coarse scale model (*full1*). The reference category firecat (stand origin categories) is 1300AD-1625AD and the reference category for aspectcat (Aspect categories) is North (337.6 degrees-22.5 degrees azimuth). Beta coefficients and 95% confidence intervals are from a combined data set of all three years of caribou data (2001-2004). The portion of variation explained by each parameter is included.

Variable	β	SE	CI upper	CI lower	t value	Percent of model variation explained
elev	0.007	0.0001	0.0072	0.0068	55.49	74%
slope	-0.054	0.0025	-0.049	-0.0590	-21.82	11%
closure	0.375	0.047	0.4690	0.2810	7.99	2%
firecat1626-1700	-0.195	0.0531	-0.0888	-0.3012	-4.72	
firecat1701-1775	0.148	0.0221	0.1922	0.1038	8.65	
firecat1776-1850	-0.052	0.0275	0.0030	-0.1070	-2.58	
firecat1851-1925	0.052	0.0134	0.0788	0.0252	5.57	
firecat1926-2000	-0.071	0.0333	-0.0044	-0.1376	-2.49	Total= 4%
aspectcatNE	0.009	0.0348	0.0786	-0.0606	0.24	
aspectcatE	0.001	0.0196	0.0402	-0.0382	0.07	
aspectcatSE	-0.086	0.0163	-0.0534	-0.1186	-5.28	
aspectcatS	-0.235	0.0174	-0.2002	-0.2698	-13.5	
aspectcatSW	-0.067	0.0093	-0.0484	-0.0856	-7.27	
aspectcatW	0.055	0.0078	0.0706	0.0394	7.09	Total= 8%
aspectcatNW	0.029	0.0073	0.0436	0.0144	4.00	

Table 2.5: Validation performance of coarse scale model *full1* on independent data sets from JNP season 2003/2004 and BNP season 2003/2004 with Spearman's rho value (r_s) and its two-tailed probability value. The calculated area under the receiver operating characteristic curve (ROC) and its interpretation are also displayed. The model was trained on use location data from the winters of 2001/2002 and 2002/2003 from Jasper National Park and tested on winter data from 2003/2004 from both Jasper and Banff National Parks.

Data set	r_s	P*	ROC	ROC discrimination**
BNP04	0.983	<0.001	0.795	Acceptable
JNP04	0.950	<0.001	0.859	Excellent

*** Zar 1999**
****Hosmer and Lemeshow 2000**

Table 2.6: Multiple comparisons of fire categories in the coarse selection model *full1* using the Sidak method simultaneous multiple comparison test with 95% confidence intervals. The β estimate is the estimated change to the model by substituting one category for another. The most preferred category of stand origin was 1701AD-1775AD, followed by 1851AD-1925AD. The most avoided categories were 1626 AD -1700 AD, 1776 AD -1850 AD, and 1926 AD -2000 AD. Multiple comparison tests were performed in S-PLUS v.6.2 (Venables and Ripley 1999).

Firecat(egories)	comparison	β estimate	SE	95%CI lower	95%CI upper	Preferred category	Avoided category
1 -> pre-1625 (reference)	1-2	0.39	0.08	0.17	0.62	1	2
2 -> 1626-1700	1-3	-0.25	0.07	-0.46	-0.04	3	1
3 -> 1701-1775	1-4	0.25	0.10	-0.03	0.53	ns	ns
4 -> 1776-1850	1-5	-0.16	0.07	-0.38	0.06	ns	ns
5 -> 1851-1925	1-6	0.47	0.17	-0.03	0.97	ns	ns
6 -> 1926-2000	2-3	-0.64	0.05	-0.78	-0.50	3	2
	2-4	-0.14	0.08	-0.37	0.10	ns	ns
	2-5	-0.55	0.05	-0.71	-0.40	5	2
	2-6	0.08	0.16	-0.39	0.55	ns	ns
	3-4	0.50	0.07	0.29	0.72	3	4
	3-5	0.09	0.04	-0.04	0.21	ns	ns
	3-6	0.72	0.16	0.26	1.19	3	6
	4-5	-0.42	0.08	-0.64	-0.19	5	4
	4-6	0.22	0.17	-0.28	0.72	ns	ns
	5-6	0.63	0.16	0.17	1.10	5	6

Table 2.7: Multiple comparisons of aspect categories in the coarse selection model full1 using the Sidak method simultaneous multiple comparison test with 95% confidence intervals. The β estimate is the estimated change to the model by substituting one category for another. The most avoided aspects were south and southwest. Multiple comparison tests were performed in S-PLUS v.6.2 (Venables and Ripley 1999).

Aspectcat(egories)	**Comp-arison**	**β estimate**	**95%CI lower**	**95%CI upper**	**Preferred category**	**Avoided Category**
1 -> N (reference)	N-NE	-0.03	-0.24	0.17	**ns**	**ns**
2 -> NE	N-E	-0.03	-0.24	0.19	**ns**	**ns**
3 -> E	N-SE	0.28	0.04	0.52	**N**	**SE**
4 -> SE	N-S	1.08	0.79	1.38	**N**	**S**
5 -> S	N-SW	0.49	0.27	0.71	**N**	**SW**
6 -> SW	N-W	-0.09	-0.31	0.13	**ns**	**ns**
7 -> W	N-NW	0.04	-0.19	0.26	**ns**	**ns**
8 -> NW	NE-E	0.01	-0.18	0.20	**ns**	**ns**
	NE-SE	0.31	0.10	0.53	**NE**	**SE**
	NE-S	1.12	0.84	1.39	**NE**	**S**
	NE-SW	0.52	0.33	0.72	**NE**	**SW**
	NE-W	-0.06	-0.25	0.13	**ns**	**ns**
	NE-NW	0.07	-0.14	0.28	**ns**	**ns**
	E-SE	0.30	0.08	0.53	**E**	**SE**
	E-S	1.11	0.83	1.39	**E**	**S**
	E=SW	0.52	0.31	0.72	**E**	**SW**
	E-W	-0.07	-0.27	0.14	**ns**	**ns**
	E-NW	0.06	-0.15	0.27	**ns**	**ns**
	SE-S	0.80	0.51	1.10	**SE**	**S**
	SE-SW	0.21	-0.01	0.44	**ns**	**ns**
	SE-W	-0.37	-0.59	-0.15	**W**	**SE**
	SE-NW	-0.24	-0.48	-0.01	**NW**	**SE**
	S-SW	-0.59	-0.87	-0.32	**SW**	**S**
	S-W	-1.17	-1.45	-0.89	**W**	**S**
	S-NW	-1.05	-1.34	-0.76	**NW**	**S**
	SW-W	-0.58	-0.78	-0.38	**W**	**SW**
	SW-NW	-0.45	-0.67	-0.24	**NW**	**SW**
	W-NW	0.13	-0.09	0.34	**ns**	**ns**

Table 2.8: The top ten candidate models used in fine scale habitat selection modeling. Models were compared using AIC corrected for small sample sizes. Difference of AICc from the best model (ΔAICc) and Akaike weights (AICc w_i; Burnham and Anderson 1998) were used to determine model rankings.

model name	model structure	ΔAICc	AICc w_i	rank
drop6	cladonia.cov+#saplings+all.lichen.cov-#class1trees -#logs+ max.core-litter&moss-%not.Pl.Se.Fa	0.00	0.237	1
drop5	cladonia.cov+#saplings+all.lichen.cov-#class1trees -#logs+max.core-litter&moss-%not.Pl.Se.Fa- SorSW.aspect	0.83	0.157	2
add9	cladonia.cov-basal.area+#saplings+ all.lichen.cov -#logs-%not.Pl.Se.Fa+max.core-litter&moss-#class1trees	1.44	0.116	3
add8	cladonia.cov-basal.area+#saplings+ all.lichen.cov -#logs-%not.Pl.Se.Fa+max.core-litter&moss	1.51	0.112	4
drop4	cladonia.cov+#saplings+all.lichen.cov-#class1trees -#logs+max.core-litter&moss-%not.Pl.Se.Fa -SorSW.aspect+%fir	1.84	0.094	5
add10	cladonia.cov-basal.area+#saplings+ all.lichen.cov -#logs-%not.Pl.Se.Fa+max.core-litter&moss-#class1trees-SorSW.aspect	2.93	0.055	6
add7	cladonia.cov-basal.area-#saplings+ all.lichen.cov -#logs-%not.Pl.Se.Fa+max.core	3.17	0.049	7
add11	cladonia.cov-basal.area+#saplings+ all.lichen.cov -#logs-%not.Pl.Se.Fa+max.core-litter&moss-#class1trees-SorSW.aspect-%fir	3.75	0.036	8
drop3	cladonia.cov+#saplings+all.lichen.cov-#class1trees -#logs+max.core-litter&moss -%not.Pl.Se.Fa-SorSW.aspect-%fir-basal.area	3.75	0.036	8
add6	cladonia.cov-basal.area+#saplings+all.lichen.cov -#logs-%not.Pl.Se.Fa	3.91	0.034	9
drop7	cladonia.cov+#saplings+all.lichen.cov-#class1trees-#logs+max.core-litter&moss	5.50	0.015	10

Table 2.9: Coefficients and 95% confidence intervals of variables included in the best fine scale model (*drop6*). Data were from all 192 plots sampled.

Variable	β	SE	CI upper	CI lower	t value
cladonia.cov	0.129	0.049	0.226	0.032	2.65
#saplings	0.118	0.054	0.227	0.009	2.18
all.lichen.cov	0.054	0.025	0.103	0.005	2.22
#class1trees	-0.037	0.014	-0.010	-0.064	-2.72
#logs	-0.147	0.060	-0.028	-0.266	-2.46
max.core	0.008	0.003	0.014	0.002	2.42
litter&moss	-0.226	0.096	-0.034	-0.418	-2.36
%not.Pl.Se.Fa	-4.392	2.036	-0.321	-8.463	-2.16

Table 2.10: Cross-validated Spearman rank coefficients (Spearman's rho values r_s) from model validation of the best fine scale model, *drop6*. Each k-fold was a random draw of 80 percent (154 plots) of the data for model training and testing was on the remaining 20 percent (38 plots) using six probability bins for the Spearman rank correlation test with bin ranges 0.00-0.25, 0.26-0.50, 0.51-0.70, 0.71-0.85, 0.85-0.95, and 0.96-1.00.

K-fold run	r_s	P*	ROC	discrimination**
1	0.943	0.02	0.872	excellent
2	1.000	0.005	0.862	excellent
3	0.771	$0.10<P<0.200$	0.961	outstanding
4	0.943	0.02	0.830	excellent
5	1.000	0.005	0.941	outstanding
6	0.886	0.05	0.860	excellent
7	1.000	0.005	0.850	excellent
8	0.943	0.02	0.857	excellent
9	0.743	$0.10<P<0.200$	0.875	excellent
10	0.979	$0.01<P<0.02$	0.881	excellent
average	**0.921**	**$0.02<P<0.05$**	**0.897**	**excellent**

*** Zar 1999**

****Hosmer and Lemeshow 2000**

Table 2.11: Akaike weights and ranking of fine scale habitat selection variables. AIC values were corrected for small sample sizes (AICc; Burnham and Anderson 1998).

variable	AICc w_i	rank
cladonia.cov	1.000	1
#saplings	1.000	1
all.lichen.cov	1.000	1
#logs	0.996	2
%notPl.Se.Fa	0.957	3
max.core	0.947	4
litter&moss	0.889	5
#class1trees	0.799	6
basal.area	0.474	7
SorSW.aspect	0.409	8
%fir	0.198	9
%blackspruce	0.030	10

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Chapter 3: Modeling Lichen Occurrence and Abundance in Relation to Fire in Jasper and Banff National Parks

Introduction

Woodland caribou (*Rangifer tarandus caribou*) in Alberta, Canada are listed federally and provincially as a threatened species (Alberta Wildlife Act 2002, COSEWIC 2003). Direct disturbance from human activities, increased predation due to predator access along anthropogenic linear features and alternate prey population increases in recently cleared forest, in conjunction with habitat loss associated with industrial activity, have been identified as the most likely reasons for population decline (Emonds 1988, Seip 1992, James and Stuart-Smith 2000, Oberg 2001, Kuzyk, 2002, Thomas and Gray 2002, McLoughlin et al. 2003, Wittmer et al. 2005). Jasper and Banff National Parks (JNP and BNP) contain the most southerly distribution of woodland caribou in Alberta. Canada's recent Species at Risk legislation and Parks Canada's management plans identify population recovery of threatened species as a priority (Parks Canada 2000, COSEWIC 2003). Despite protection from industrial development, the south JNP population is in serious decline, while the north BNP population is considered functionally extirpated (Flannigan and Rasheed 2002, Mercer 2002).

Within caribou range in the national parks, Parks Canada suspects declines are partly related to habitat deterioration from human use infrastructure (primarily hotels, campgrounds, roads and trails; Parks Canada 2000) or from a lack of recent fire events (Thomas and Armbruster 1996, D. Smith pers. comm.). JNP has experienced few fires over the past century compared to the later part of the 19th century (Tande 1979, Achuff et al. 1996, Rhemtulla et al. 2002), and it is possible that successional processes in these older stands have been detrimental for forage resources for caribou (Klein 1982, Schaefer and Pruitt 1991, Payette et al. 2000, Coxson and Marsh 2001). My research focused on the effect of natural disturbances to caribou forage lichens.

Caribou use both fruticose or foliose terrestrial lichens, hereafter referred to as terrestrial lichens (*Cladonia* spp., *Cladina* spp., *Stereocaulon* spp., *Cetraria* spp., *Flavocetraria* spp., and *Peltigera* spp.; Thomas and Hervieux 1994 , Thomas and Armbruster 1996, Thomas et al. 1996b, Terry et al. 2000), and fruticose arboreal lichens (*Alectoria spp., Bryoria spp.,* and *Usnea spp.*; Edwards et al. 1960, Van Daele and Johnson 1983, Thomas et al. 1996b, Mosnier et al. 2003), hereafter called arboreal lichens, for their primary winter forage. Efforts to understand the relationship between past fire and terrestrial lichen abundance are complicated by the long periods needed for lichen recovery and the confounding effects of forest succession. Some researchers have argued that, in the long term, fire is necessary to maintain terrestrial lichen cover for caribou because succession in the absence of fire can ultimately lead to high competing cover of feathermosses and forest litter, which may eventually overtop lichen (Klein 1982, Schaefer and Pruitt 1991, Payette et al. 2000, Coxson and Marsh 2001). In contrast, other research suggests that for caribou, terrestrial lichens do not benefit from fire events because of the long recovery period (often centuries) for preferred forage-lichen species to reach ideal abundance levels (Thomas and Armbruster 1996, Thomas et al. 1996a, Arsenault et al. 1997, Joly et al. 2003). One study in the Alberta Foothills found that two of the main terrestrial lichens for caribou forage (*Cladina* spp. and *Cetraria* spp.) were only present in old forest (>100 yrs; Snyder and Woodard 1992) and another reported that the main caribou forage species require 150-250 years to reach peak abundance in the western boreal forests of northern Canada (Thomas et al. 1996a). Further, arboreal lichen is generally considered to have significant abundance only in older forests (Edwards et al. 1960, Arseneau et al. 1997, Sillet and Goslin 1999, Terry et al. 2000, Apps et al. 2001). Since terrestrial and arboreal lichen may differ in peak abundance relative to time since fire, it is important to examine terrestrial and arboreal lichen abundance separately.

Terrestrial lichen provides the main forage for caribou in JNP and BNP (Thomas et al. 1996b). In northeastern British Columbia, researchers found that caribou select whichever lichen is present in the greatest abundance (Poole et al. 2000, Johnson et al. 2001). Saher's (2005) findings in a recent study of mountain caribou in west-central Alberta support this result. She found the most abundant lichens (*Cladina mitis* and *Stereocaulon* spp.) were a significant predictor of caribou foraging preference. A recent study in JNP determined that caribou were selecting *Cladonia* spp. (see Chapter 2). *Cladonia* spp. is the most common of the terrestrial lichen forage genera in JNP, and establishes much faster than *Cladina* spp. following fires (Thomas and Armbruster 1996). Thomas et al. (1995) estimated peak abundance of this lichen to occur 40-60 years post fire in the northwestern boreal forest of Canada, while Yarranton (1975) reported *Cladonia* appearance in northern Ontario 25 years after burning, with rapid increases soon after establishment. Following large fires in 1988 in Yellowstone National Park in Wyoming, Eversman and Horton (2004) found that *Cladonia* was the primary colonizing lichen genus, appearing just 13 years after the fires. Thomas and Armbruster (1996) similarly report that *Cladonia* spp. establishes first (relative to other lichens) in JNP, appearing around 20 years post-fire. Based on this research, and my findings that caribou were selecting *Cladonia* spp. in JNP (Chapter 2), I selected *Cladonia* spp. occurrence as the dependent variable for my terrestrial lichen probability modeling.

For examining arboreal lichen in relation to past fire events, I did not differentiate by species, and chose instead to look at overall arboreal lichen abundance and probability of occurrence. Previously, I found that arboreal lichen abundance was not a significant predictor of caribou habitat selection in JNP (Chapter 2). Thomas et al. (1996) also found that arboreal lichen made up only one percent of a caribou's diet in west-central Alberta. However, in most of British Columbia, arboreal lichen, rather than terrestrial lichen, is the primary food source for mountain caribou (Edwards et al. 1960, Klein 1982, Daele and Johnson 1983, Servheen and Lyon 1989, Apps et al. 2001). Nevertheless, even in British Columbia, where it provides the majority of a caribou's diet, researchers found that arboreal lichen abundance did not provide a good indication of caribou habitat preference because a small caribou population size made it a non-limiting resource (Servheen and Lyon 1989). In areas that typically have drier climates and lower snow cover (e.g. east of the continental divide), arboreal lichen is considered a critical food source when snow depth or hardness prevents caribou from readily accessing terrestrial lichen (Thomas et al. 1996b, Johnson et al. 2001, Szkorupa 2002).

Edwards et al. (1960) found that forests younger than 50 years in Wells Gray Provincial Park in central British Columbia did not have significant amounts of arboreal lichen.

They also found that the greatest arboreal lichen abundance was in older, high elevation forests (especially near treeline) that did not include pine trees (*Pinus contorta* var. *latifolia* Engelm.). Conversely, Arseneau et al. (1996) found that arboreal lichen loads decreased with increasing elevation in boreal forest in Quebec, and that tree diameter along with elevation were the best predictors of arboreal lichen abundance. Campbell and Coxson (2001) found that lichen abundance in the northern Cariboo Mountains of British Columbia was related to tree dispersion, where clumped patches of trees had greater loads of lichen than solitary trees. Interestingly, Coxson et al. (2003) and Rominger et al. (1994) reported that arboreal lichen loads in the lower canopy of trees (where they are accessible by caribou) were not initially affected by reductions in stand density from mechanical thinning. Shifts in microclimate however, most dramatically the reduction of moisture on southerly aspected sites, would have a negative impact on lichen growth over an extended period of time (Coxson et al. 2003).

In summary, both terrestrial and arboreal lichen presence and abundance have been related to time since fire, topography and forest composition in numerous studies (Edwards et al. 1960, Daele and Johnson 1983, Servheen and Lyon 1989, Rominger et al. 1994, Arseneau et al. 1997, Arseneault et al. 1997, Pharo et al. 1999, Dettki et al. 2000, Arseneault 2001, Campbell and Coxson 2001, Cornelissen et al. 2001, Coxson and Marsh 2001). I modelled the effect of time since fire on the prescence of terrestrial and arboreal lichens using fine-scale vegetation data collected in caribou use areas in BNP and JNP. These models were then used to explore how Parks Canada could use fire management within caribou range to improve or maintain lichen forage opportunities for caribou.

Materials and Methods

Study Area

I conducted my study in the southern half of JNP (North 52 deg 59 min, West 118 deg 03 min) and the northern portion of BNP (North 51 deg 32 min, West 116 deg 02 min) (Figure 3.1), in the Rocky Mountains of Alberta, Canada. Both areas lie immediately east of the continental divide and include wide, U-shaped, intersecting glacier-carved valley systems. In JNP, a large portion of the park area is rock and glacial ice (19%; Holland and Coen 1983). Forested areas included the montane (7%), lower subalpine (30%), and upper subalpine (37 %) ecological regions, which are classified by vegetation and elevation (Holland and Coen 1983). The BNP valley systems for this study were all higher elevation valleys and did not include any montane zones. In the vegetated portion of the BNP study area, 44% was alpine, 30% was upper subalpine, and 25% was lower subalpine (Holland and Coen 1983). Montane forest is primarily composed of dominant and mixed stands of lodgepole pine(*Pinus contorta* var. *latifolia* Engelm.), white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana (*Mill.)B.S.P.), Douglas-fir, and trembling aspen (*Populus tremuloides* Michx.). Subalpine forests include lodgepole pine, subalpine fir, Engelmann spruce, black spruce, whitebark pine (*Pinus albicaulus* Engelm.), and subalpine larch (*Larix lyallii* Parl. -BNP only). Stand boundaries in both study areas result primarily from stand initiating fire events (Tande 1979, Achuff et al. 1996). In the study area in JNP, stand origin dates ranged from 1600 to 2000 (Tande 1979, Parks Canada file data); in the BNP study area, stands were generally older, ranging from 1390 to 1936 (Van Wagner 1995, Rogeau 1996, Parks Canada file data).

Elevations of sample locations ranged from 1019m to 2393m a.s.l. in JNP and 1494m to 2589m a.s.l. in BNP.

Study Design

To build models of lichen occurrence and abundance, I used data on stand structure and composition collected during sampling for the Resource Selection modeling (Chapter 2; n=192 plots) along with additional data from stratified random sampling within the boundaries of historic burns that had occurred since 1900_{AD} in the southern portion of JNP (n=137 plots). I conducted sampling below treeline in subalpine or montane forest zones. Locations for sampling were selected using random generation of sample points within stand origin polygons (Tande 1979, Parks Canada File Data) using Arc^{TM} GIS (ESRI GIS Systems). I assumed significant inherent variability in fire behavior within fires (La Roi and Hnatiuk 1980), and therefore obtained multiple random samples from many of the large burns. I assumed that the samples from the RSF plots would provide sufficient numbers of plots in older-aged forest (i.e. pre-1900_{AD}). Therefore I focused on additional locations such that I would have samples from a continuous range of stand ages. I did this to examine different stages of lichen abundance reported to be related to changes in forest structure and composition during the first century of forest succession following stand-replacing fire (Thomas et al. 1996a, Coxson and Marsh 2001).

To determine vegetation plot locations for my RSF sampling in 2003, I used a random draw of 38 locations from 787 treed relocations from two collared caribou. In 2004, I chose 90 use sites from 3505 treed caribou locations by random selection of ten locations from each of a total of nine caribou collared in 2002 and 2003. In conjunction with these use locations, I also randomly generated 64 sample point locations in forested areas within valleys that contained caribou use locations. Valleys were delimited by surrounding mountain ranges, and defined as the continuous forest cover on either side of a valley bottom river or stream.

Data Collection

I conducted vegetation sampling from June to the end of August in 2003 and 2004. I used two diagonally-adjacent 10m by 10m fixed area plots laid out on a north-south by east-west grid (Figure 3.2). For each tree (defined as minimum 5cm diameter at 130cm above ground) within the total 200 m^2 area, I recorded species, diameter at 1.3m height, and arboreal lichen abundance class (as per Stevenson et al. 1998). Class 1 trees have less than 5 grams of arboreal lichen, Class 2 have 5-50 grams, and Class 3 trees, which were the highest abundance class found in JNP or BNP, have over 50 grams of arboreal lichen. The abundance estimate was made for the first 2.5m of tree branches above ground, which I assumed was the average height a caribou could reach given an average 0.50-meter snowpack (Wesbrook pers. comm.). From the diameter measurements basal area was calculated. The percent of trees that were pine, spruce, fir, black spruce or other was also calculated. From the dominant canopy layer, I selected three trees for which I measured height and took cores for aging and measurement of sapwood width. From the three tree cores taken at breast height from each plot, I used the maximum core value as a conservative measure of minimum number of years since stand replacing fire.

I estimated percent cover for understory herbaceous plants (to species), terrestrial lichens (to genus), shrubs <10cm tall (to species), and litter using five, 240cm^2 quadrats in fixed corner locations of the two 10m by 10m squares. Cover estimates were to the nearest percent for terrestrial lichens and to the nearest five percent for all other species. Cover of lichens relates directly to the biomass of lichens present (Thomas et al. 1996a). I combined all grass species and made a single cover estimate; cover of moss was estimated as either feathermoss (*Pleurozium* spp. or *Ptilium* spp.) or other moss spp. (all other moss genera). All quadrat cover estimations used in analyses are the average obtained from the five quadrats within a plot. I maintained cover estimation consistency in quadrats by using standardized cover cards and conducted periodic consistency checks among my four field personnel. I also estimated canopy cover at each of the five quadrats using a convex spherical densiometer (Lemmon, Model A Forest Densiometers), and recorded litter depth, moss depth, and depth from litter or moss surface to mineral soil. Depths used in analysis are the average of the five measures taken within each plot. I used the east-west line as a 20m line intersect sample to count number of downed logs, and had a 2m by 2m square microplot off the plot center in which I recorded the number and species of saplings (<5cm diameter at 130m height above ground). I visually estimated percent cover of all tall shrub species (>10cm) recorded to species, to the nearest five percent, in the south 10m X 10m square. I also subjectively classified each site by fuel type category according to the standardized fuel categories for the Canadian Forest Fire Danger Rating System and Fire Behavior Prediction (Hirsch 1996).

To obtain stand origin date, elevation, slope, and aspect for all data points, I used JNP's and BNP's respective stand origin map layers (Tande 1979, Park File data) and their Digital Elevation Models (20m resolution). I generated this location-based data using 'Gridspot' and 'Identity' commands in Arc^{TM} GIS (ESRI GIS Systems). I also included a binary stand origin category that distinguished between stands that originated in the most recent 75 years (15% of plots) and those established before 1925$_{AD}$. This division was based on prior knowledge of caribou lichen forage ecology in JNP (Thomas and Armbruster 1996). Recent research on stand origin dependencies of different lichen species in west-central Alberta and northern British Columbia also indicated that forage lichen abundance was highest in open pine stands after 75 years (Coxson and Marsh 2001, Szkorupa 2002). Plot aspect was parameterized in two different ways. I created a binary variable that classified the plot as having a south or southwest aspect (157.6 degrees to 247.5 degrees) versus all other aspects. I also included a measure called SW.aspect that was the absolute number of degrees away from 225 degrees azimuth. I chose the southwest to be the reference aspect because it is considered the sunniest and driest aspect at JNP and BNP's latitude (Holland and Coen 1983). Geographic location was quantified by UTM Easting and Northing, recorded from Global Positioning System (GPS) locations taken on site using a minimum of 25 satellite relocations. The full set of variables I evaluated are listed and described in Table 3.1.

Data Analysis

Cladonia Abundance

Logistic regression models were created in S-PLUS v.6.2 (Venables and Ripley 1999) using Generalized Linear Models (GLMs), with *Cladonia* spp. presence/absence as the dependent variable. I used a cut-off value of five percent *Cladonia* spp. cover as the lower threshold for presence. Five percent approximates the lower limit of the 95% confidence interval of the mean *Cladonia* spp. cover in all the caribou locations sampled. Each candidate variable (Table 3.1) was first evaluated in a univariate analysis and retained for possible model selection if $p < 0.20$ for individual significance. I selected candidate models from a series of both forward and reverse stepwise selection. No two variables retained for modeling had Pearson correlation coefficients greater than 0.4. The most parsimonious model was selected from among the set of candidate models using the Akaike Information Criterion (AIC) corrected for small sample sizes (AICc; Burnham and Anderson 1998). Candidate models were developed and compared using the total data set (summary statistics from the top ten evaluated variables are listed in Appendix B). I then evaluated the best model using a K-fold cross validation technique (Boyce et al. 2002), with a series of ten random draws of 80 percent of the full data set for model training (263 plots), and tested the model on each remaining 20 percent (66 plots). To determine model performance, I calculated the area under the Receiver Operating Characteristic Curve (ROC; Hosmer and Lemeshow 2000) for each of the ten K-fold validation data sets. The ROC value provides a measure of each training model's ability to distinguish between presence/absence locations using calculated probabilities and the actual presence or absence of lichen for each test data set (Hosmer and Lemeshow 2000). To evaluate whether inclusion of RSF plots biased *Cladonia* model parameter selection, I conducted an additional validation run using all non-use plots to construct a model (183 plots), and then tested this model on the caribou use plots (146 plots). I also compared the coefficients from a model using all data (329 plots) to the coefficients of a model with caribou use locations excluded (183 plots) using a Wilcoxon signed ranks test.

Arboreal Lichen Abundance

A large number of plots contained no Class 3 arboreal lichen trees (Figure 3.3), suggesting the potential that one set of factors determines Class 3 occurrence, and a different set of factors determines frequency. There are two types of models which can simultaneously account for the factors influencing presence/absence versus those influencing abundance: Zero-inflated Poisson (ZIP) models and Zero-inflated Negative Binomial (ZINB) models (Lambert 1992). A two-staged model appeared to be the most biologically appropriate for determining conditions necessary to determine the presence, and also abundance of Class 3 arboreal-lichen bearing trees (Nielson et al. 2005). For my data, 200 of the 329 plots (61%) had a count of zero, and the rest of the plots had between one and 22 Class 3 arboreal lichen trees.

Inspection of the data indicated that a ZINB distribution was more appropriate than a ZIP distribution (Long and Freese 2003). Including tree counts of zero, the mean value for 329 plots was 2.100 with a variance of 14.371; and even excluding plots with zero counts, the mean was 5.357 and variance was 19.247 for 129 plots. These inflated variance values compared to the mean strongly suggests overdispersion of the data. Comparing a ZIP model and ZINB model, I found reduced deviance and lower standard errors using a ZINB model. Because of the evidence of overdispersion, the variance reduction when applying the ZINB distribution model, and the likelihood that there were important unmeasured sources of heterogeneity (e.g. fire severity, lichen autecology) I concluded that a ZINB model would be more appropriate than a ZIP model (Long and Freese 2003).

I created ZINB distribution models using the Zicounts package extension (Mwalili 2005, v. 1.1.4) in the freeware statistical package "R" (Ihaka and Gentleman 1996). Starting with a global model that included all measured variables (see Table 3.1 for the complete list of variables), I created a series of ZINB candidate models by eliminating variables in a reverse stepwise selection process, removing variables with the lowest z-probability score in a sequential fashion. I compared candidate models based on AICc weights; variables in the selected best model all had significant beta coefficients ($p<0.05$; summary statistics for the highest AIC weighted variables used for presence/absence evaluation are listed in Appendix B).

To test the ZINB model performance, I created K-fold cross validation data sets (Boyce et al. 2002) with a series of five random draws of 80 percent of my data for model training (262 plots) and tested each of these models on the remaining 20 percent (67 plots), as with the terrestrial lichen abundance. I generated predicted occurrence and count values for the presence/absence and abundance of Class 3 trees using the Zicounts package extension (Mwalili 2005, v. 1.1.4) in the freeware statistical package “R” (Ihaka and Gentleman 1996). The upper cut-off value specified for the predicted count of Class 3 trees at each plot location was the total number of trees. I assessed model performance using several methods. To evaluate how well the model distinguished between sites with Class 3 trees and those without, I converted predicted counts to probabilities, by dividing the predicted value for each plot within a data set by the maximum count predicted in that set. This resulted in the plot with the highest predicted count having the highest probability, while the lowest probability went to the plot with the lowest predicted count. I then converted the actual count of Class 3 trees to a binary variable with all plots with zero counts coded as “0” and all sites with one or more Class 3 trees present as “1”. These converted variables allowed me to calculate the ROC for each model’s performance for each test data set (Hosmer and Lemeshow 2000). I used two indirect methods to compare predicted to actual counts. I first calculated the Chi-squared values comparing predicted to actual counts to see if they were significantly different. I then used Pearson correlations and simple linear regression to assess the similarity of actual and predicted counts. I performed these tests using S-PLUS v.6.2 (Venables and Ripley 1999).

Results

Cladonia Occurrence

Evaluated by AICc values, the most parsimonious model explaining *Cladonia* spp. occurrence (>5% cover) in a plot, in which all variables were significant ($p < 0.05$), was the model CLAD10 (Table 3.2). AICc weights of individual variables are displayed in Table 3.3. The best model showed increasing probability of occurrence of *Cladonia* spp. in sites that had higher elevations, steeper slopes, a greater diversity of vascular species, were located further south, occurred in stands that burned before 1925, and had higher litter cover. While the binary designation of stands older or younger than 1925_{AD} was a significant predictor of Cladonia occurrence, the linear form of stand origin date was not. The final model was therefore:

$$\mathbf{\log(p/1\text{-}p) = \beta_0 + \beta_1 (elev) + \beta_2(slope) + \beta_3(Number.vascular) - \beta_4 (UTM.Northing) + \beta_5(fire.category) + \beta_6(litter.cover)}$$

where **p** equals the probability of presence of *Cladonia* spp.. All model components and parameter significances are displayed in Table 3.4. In each K-fold run, the model performed very well, with an average ROC value of 0.859, considered excellent discrimination by Hosmer and Lemeshow (2000; Table 3.5). Validation using non-caribou locations as training data and caribou use points as testing data also resulted in good model performance (ROC = 0.702, acceptable discrimination; Hosmer and Lemeshow 2000). When I compared the coefficients from the model using all data, to the coefficients of a model with caribou use locations excluded, I found no significant difference between coefficients of the two models (Paired Wilcoxon signed rank test;

p=0.3125). These results suggest that my *Cladonia* model coefficient values were not unduly biased by inclusion of caribou use locations.

Arboreal Lichen Occurrence and Abundance

ZINB models predicting occurrence and abundance of Class 3 lichen-bearing trees are listed in Table 3.6. The two top models, which are equally parsimonious based on AICc, predict increasing numbers of Class 3 trees in areas with increasing elevation, greater depth of moss and litter, increasing tall shrub cover (>10cm height), higher tree density, lower proportion of pine, and areas either found further north, or found further west. Probability of at least one Class 3 tree occurring at a site increased with higher elevations, increasing canopy cover and time since fire, on aspects closer to 225 degrees azimuth, with fewer downed logs present, on lower angled slopes, and with a higher percentage of spruce in the forest canopy. The negative binomial portion of the best AICc model is:

$$\log(\lambda) = -\beta0 + \beta1\ (\text{telev}) + \beta2(\text{litter\&moss.depth}) + \beta3(\text{shrubcov}) + \beta4(\text{trees.per.plot}) - \beta5(\text{\%pine}) - \beta6(\text{UTM.Easting})\ [\text{or } + \beta6(\text{UTM.Northing})]$$

where λ = the predicted count, with a Zero-inflated portion described by:

$$\log(p/1-p) = \beta0 - \beta1\ (\text{telev}) - \beta2(\text{canopycov}) - \beta3(\text{max.core}) + \beta4(\text{SW.aspect}) + \beta5(\text{\#logs}) + \beta6(\text{slope}) - \beta7(\text{\%spruce}) + \beta8(\log(\text{tau}))$$

where **p** = the predicted probability of absence of Class 3 arboreal lichen trees and **tau** is an error term. This model is displayed with the UTM.Easting parameter in Table 3.7. It is important to note that the Zero-inflated portion of the model predicts the likelihood of being in the zero count, or "no Class 3 trees" state, so the beta coefficient signs are interpreted in the reverse from standard logistic regression models that predict probability of occurrence (Long and Freese 2003). In five K-fold runs, this model performed quite well. Evaluated as a logistic function, the model had consistent and overall "outstanding" ability (Hosmer and Lemeshow 2000) to distinguish between sites with or without Class 3 trees (minimum ROC = 0.917; Table 3.8). Using a Chi square test, the predicted counts were not significantly different from the actual (or observed) counts (minimum chi squared probability = 0.157, average = 0.326). Additionally, the correlation and multiple regression coefficients between the actual counts and predicted values were also quite high, with average values of 0.924 and 0.857 respectively.

Discussion

Forests that were most likely to have *Cladonia* spp. present were older, at high elevations, on steeper slopes, and in the southern portion of the park. They tended to have greater litter cover, and a higher diversity of vascular plant ground-cover (forbs, grasses, dwarf shrubs). Locations with at least one tree with abundant arboreal lichen were also most likely to occur at higher elevations, but on flatter slopes, and on south or southwest aspects. At the stand level, associated characteristics included higher proportions of spruce in the canopy and higher canopy cover. The immediate area would tend to have at least one older tree present, and there would likely be few downed logs on the forest floor. Increasing numbers of Class 3 trees tended to occur at higher elevations and further west in JNP and BNP. A lower proportion of lodgepole pine, higher tree density, deeper organic layers on the forest floor, and higher shrub cover were also characteristic of sites with more Class 3 trees.

Relationship of *Cladonia* lichen presence to stand characteristics, and stand origin

Cladonia was more likely to occur at higher elevations, and on steeper slopes. These locations tend to have distinct soil and moisture properties from lower elevation and flatter sites (La Roi and Hnatiuk 1980, Holland and Coen 1983, Achuff et al. 1996). Due to this, the effect of slope and elevation may simply be regulation of forest structure that in turn influences *Cladonia* presence. Possibly, as speculated by Snyder and Woodard (1992), steeper slopes at high elevation may allow for greater lichen cover because they are more nutrient impoverished, making terrestrial lichen, which relies solely on the atmosphere for nutrient uptake, at advantage over plants with true root systems. Alternatively, elevation and slope relationships may be explained by historical fire occurrences. High elevation forests tend to have older stands than at lower elevation sites in JNP and BNP (Tande 1979, Van Wagner 1995, Achuff et al. 1996 , Rogeau 1996). This fire relationship is reinforced by the observed increased probability of *Cladonia* occurrence in older forests, those originating before 1925. When fire does occur at higher elevations, it is during periods of prolonged drought and high winds (Johnson and Wowchuk 1993, Bessie and Johnson 1995, Schoennagel et al. 2004). These weather conditions typically result in very intense and severe fires (Schoennagel et al. 2004). Increasing slope can also be associated with more intense fires (Gray et al. 2002, Gavin et al. 2003), due to the effect of preheating of upslope fuels from increased convective heating and more direct radiated heat transfer from tilted flame direction (Alexander 1982, Hirsch 1996). Since *Cladonia* occurrence was also positively associated with steeper slopes, it is possible there has been an influence of past fire severity. Inferring relationships to fire severity is highly speculative however, since direct, historical evidence was not available for this study.

Some of my model results stand in contrast to other related research. I found that *Cladonia* was more likely to occur (>5% cover) 75 years post-fire while other research has indicated faster *Cladonia* establishment (< 30 years post-fire; Yarranton 1975, Snyder and Woodard 1992, Thomas et al. 1996b, Eversman and Horton 2004; but see Brulisauer et al. 1996) with rapid cover increases soon after initial colonization (Yarranton 1975). Like La Roi and Hnatiuk (1980), I found a significant correlation between *Cladonia* presence and increasing cover of litter, but this was contrary to Coxson and Marsh (2001) who found that increasing litter cover inhibited terrestrial lichen in northeastern British Columbia. My models had a significant latitude effect where, regionally, locations further south had an increased probability of having *Cladonia* and this differs from Cornelissen et al. (2001) who found locations further south in Europe were less likely to sustain lichen cover. A possible explanation for timing differences in *Cladonia* establishment could be that other caribou-oriented conservation studies are reporting initial appearance of *Cladonia* (Yarranton 1975, Snyder and Woodard 1992, Thomas et al. 1996b, Eversman and Horton 2004), while I recorded occurrence as greater than five percent cover. Differences in litter cover relationships may relate to overstory canopy differences. Coxson and Marsh (2001) examined lodgepole pine forest while high elevation sites in JNP and BNP were dominated by Engelmann spruce and subalpine fire (La Roi and Hnatiuk 1980, Holland and Coen 1983). The broader geographic trend reported by Cornelissen et al. (2001) is likely not applicable at the regional scale of my study where there were confounding local differences in topography in the south and north portions of JNP and BNP (eg. terrain configuration, elevation differences).

While vascular plant cover did not have a direct relationship to probability of *Cladonia* occurrence, there was a positive association between the number of different vascular plant species and *Cladonia* presence. Halpern (1988, 1989) found that understory composition was related to disturbance intensity and that ultimate understory structure would be shaped by both the initial stochastic influence, as well as deterministic processes like succession. Low intensity fire could lead to understory communities dominated by a small number of dominant species (Schimmel and Granstrom 1996). De Grandpre et al. (1993), for a similar scale of examination as my study ($100m^2$; De Grandpre et al. (1993) vs. $200m^2$; this study), found there was a decline in understory species diversity with increasing time since fire in the southern boreal forest. When the forest experienced partial disturbances that removed portions of the canopy however, this trend was reversed, resulting in an increase in understory plant diversity (De Grandpre et al. 1993). Coxson and Marsh (2001), Thomas and Armbruster (1996), and Lar Roi and Hnatiuk (1980) all report that more open, older forests promoted the most terrestrial lichen. If, as speculated by De Grandpre et al. (1993), these forest openings are also allowing early successional species to again re-establish, this could account for the positive relationship between number of different vascular species and *Cladonia* occurrence in these older forests.

Relationship of arboreal lichen presence to stand characteristics, stand origin, and fire severity

The probability that at least one Class 3 arboreal lichen tree was present at a sampling location depended on several interrelated factors. Several of these suggested a positive effect of forest age, which is in agreement with prior studies. Indeed, some researchers refer to these arboreal lichens as old growth dependent (Sillet and Goslin 1999, Coxson et al. 2003) or as late successional lichens (Arseneau et al. 1997). Firstly, presence of Class 3 trees was more likely at higher elevations, and this is well supported by other studies (Edwards et al. 1960, Stevenson and Enns 1992, Terry et al. 2000). As mentioned for *Cladonia*, the influence of elevation could be related to forest age, as older forests in JNP and BNP tend to be found at higher elevations (Tande 1979, Achuff 1996, Rogeau 1996). That older forests, or those with at least some older trees present, are more likely to have Class 3 lichen trees was shown by the inclusion of tree age in the model. Summary statistics show that trees cored in sites that supported at least one Class 3 tree averaged 175 years (+/- 15 years for 95% confidence interval; Appendix B). This suggests that arboreal lichen requires a long time to establish or that younger stands need some old trees to provide a source population for arboreal lichen redevelopment in regenerating forest. Younger forests will have higher arboreal lichen abundance in locations where the stand includes some older trees (e.g. unburnt trees remaining after a less intense or severe fire; Thomas and Armbruster 1996, Sillet and Goslin 1999, Detki et al. 2000, Coxson et al. 2003). Surviving trees serve as a source to "seed" younger trees with arboreal lichen (Stevenson and Enns 1992).

Increasing canopy cover also favoured the presence of Class 3 trees and this likely relates to moisture requirements for arboreal lichen or lichen propagule distribution. Increasing canopy closure promotes a moister microclimate below the canopy (Stevenson and Enns 1992, Campbell and Coxson 2001, Coxson et al. 2003) and since lichens must be moist to photosynthesize (Campbell and Coxson 2001), a closed canopy would promote better lichen growth. Greater canopy closure could also better facilitate lichen colonization of new trees by decreasing the physical distance for propagule spread (Stevenson and Enns 1992, Sillet and Goslin 1999). Closed canopy forest may also be reflective of forest age. Forests in subalpine areas tend to have open canopies for the first 25 years following a stand replacing fire event, and subsequently become more continuous (Bessie and Johnson 1995, Coxson and Marsh 2001).

The probability of presence of Class 3 trees was also positively associated with the amount of Engelmann spruce in the canopy. Edwards et al. (1960) and Stevenson and Enns (1992) hypothesized that the positive association between arboreal lichens and Engelmann spruce mainly depended on the growth form of spruce, which tends to be conical, and has longer, thick, lower branches with high needle density. These provide ideal anchoring locations for lichen establishment. Having more places for attachment of lichen fragments greatly speeds up lichen colonization of trees (Stevenson and Enns 1992). Engelmann spruce is also found in greater proportion in older forests in JNP and BNP (La Roi and Hnatiuk 1980, Achuff et al. 1996). This occurs when forests are either: (1) old with the shorter-lived lodgepole pine having died out of the canopy, or, (2) were old before they had a stand initiating fire event [i.e. old enough that lodgepole pine previously present would have thinned out of the stand, and would therefore not able to re-seed post fire (Johnson and Fryer 1989, Antos and Parish 2002)]. The former reinforces the hypotheses that older forests are more likely to have Class 3 trees, with lichens having developed over many years. In the latter case, spruce forests would not necessarily be older but the importance of maximum tree age in our model supports the 'remnant tree hypothesis'; i.e., that old trees surviving a fire provide a propagule source for lichen redevelopment in the new stand (Stevenson and Enns 1992, Sillet and Goslin 1999, Dettki et al. 2000). Further, Stevenson and Enns (1992) and Dettki et al. (2000) found that arboreal lichen presence (and abundance) was directly related to the distance from surviving old growth trees or old forest edge. Overall, it is likely that a less severe fire that left behind more surviving older trees, would provide better lichen colonization of the new stand (Stevenson and Enns 1992, Sillet and Goslin 1999, Dettki et al. 2000).

The probability of presence of Class 3 trees declined with increasing slope. As mentioned above, slope affects soils and light availability (and subsequently forest composition) but steeper slopes may also experience more intense fires. Since higher elevation sites tend to see infrequent, large, and severe fires, this could indicate that Class 3 trees are more likely to occur in these slope-related "refugia" (i.e. flatter locations that may see less intense fire behavior; Rothermal 1972 in Bessie and Johnson 1995). There was also a higher probability of a Class 3 trees occurring on aspects closer to 225 degrees azimuth (due southwest); unlike other parameters, this is usually contraindicative of older forests. southwest aspects, because of their greater sun exposure, tend to have more frequent fire events than other aspects (Tande 1979, Rogeau 1996, Gavin et al. 2003). However, the aspect relationship likely reflects the need for greater sun exposure at the base of trees (2.5m above ground) for lichen photosynthesis, and thus growth (Stevenson and Enns 1992). Stevenson and Enns (1992) found the greatest abundance of arboreal lichen on southerly facing slopes at higher elevations in the south-coastal forests of British Columbia, and reasoned this was due to greater sun exposure. Coxson et al. (2003) also hypothesized that light might be a limited resource for lichens in lower tree branches of denser stands.

The relationship of decreasing number of logs to Class 3 tree occurrence does not have a clear link to site conditions or past fire occurrences. Possibly, fewer downed logs are the result of longer time since fire and diminished self-thinning of the stand. Reduced self-thinning, regardless of time-since-fire, would promote stands containing more trees with more bushy, basal branches (capable of supporting more arboreal lichen; Edwards et al. 1960, Stevenson and Enns 1992), as increased falling trees would remove more branches from neighboring stems.

Relationship of arboreal lichen abundance to stand characteristics, stand origin, and fire severity

For the prediction of abundance (negative binomial) portion of the model, the independent variables were consistent in suggesting a reliance on either older forest, or sites that would promote higher moisture availability. As for presence of Class 3 arboreal lichen trees, their abundance was also greater at higher elevations. As mentioned above, this may suggest a dependency on older forest, and may also relate to the growth form of

Engelmann spruce trees (Edwards et al. 1960) which are increasingly dominant at higher elevations (Holland and Coen 1983). Since trees near treeline tend to be shorter and somewhat shrub-like, anchoring structures for the arboreal lichen (i.e. branches and needles) would be more plentiful in the lower 2.5 meters of the tree at these higher elevations. In treeline areas, subalpine fir and Engelmann spruce also tend to have a more clumped distribution pattern (Shea 1985, MacKinnon et al. 1992). Having more abundant arboreal lichen in these treeline areas with patchy tree distribution is supported by Campbell and Coxson (2001) who found that trees located within clumps carried greater amounts of arboreal lichen than solitary trees. My model reinforces this, showing that higher tree density was associated with a greater abundance of Class 3 trees. Coxson et al. (2003) speculated that higher tree density would be beneficial for arboreal lichen in areas that might be more moisture limited. As described above, presence of at least one Class 3 tree was more likely on southwest aspects; in turn, trees on these drier, sunnier aspects would more likely need to conserve moisture.

Abundance of Class 3 trees was negatively related to the abundance of lodgepole pine. This is complementary to the positive influence of spruce abundance on the presence of a Class 3 trees and, as described above likely relates to tree growth form., Lodgepole pine does not having many basal branches for attachment of arboreal lichens, especially as compared to Engelmann spruce (Edwards et al. 1960). Lodgepole pine forests in JNP and BNP are also generally younger (La Roi and Hnatiuk 1980, Achuff et al. 1996) so this may reinforce needing more time for arboreal lichen to develop. The positive correlation of Class 3 tree abundance with areas that are further west is also likely related to moisture. Western sites, or locations closer to the continental divide in JNP and BNP, have longer fire return intervals (Rogeau 1996) and tend to be moister. This is because proximity to the continental divide results in greater moisture from increased precipitation which is associated with orographic lifting, as weather systems move across the Rocky Mountains (Schroeder and Buck 1970). Growth of arboreal lichens is increased by greater moisture availability since photosynthesis only occurs when the lichen thallus is wet (Campbell and Coxson 2001), and therefore wetter, western locations would be expected to have higher abundance from growth as well as benefiting from a longer period of accumulation between fire events.

The positive relationship between abundance of Class 3 trees and litter and moss depth, and shrub cover, is likely reflective of complementary site characteristics rather than a causative relationship. Litter and moss may accumulate in sites that have poor nutrient cycling, high needle fall, acidic needle litter, cooler annual temperatures, or simply from specific growth characteristics of a moss type (Armson 1977, Payette et al. 2000). Shrub cover can be negatively correlated with canopy cover (Hamer 1996), and may be influenced by site conditions (Arseneault and Payette 1992, Bessie and Johnson 1995) or species autecology (De Grandpre et al. 1993, Schimmel and Granstrom 1996). However, both duff accumulation (Coxson and Marsh 2001), and cover of shrubs (Brulisauer et al. 1996) could also be indicators either of longer times since severe fires or low severity fires. Fire severity is defined as the measure of the depth of burn (Sirois 1993, Schimmel and Granstrom 1996), and Coxson and Marsh (2001) and Payette et al. (2000) found that litter and moss cover increased with time since fire. In relation to shrub cover, Wang and

Kemball (2005) reported that woody stemmed plant cover was only a significant post-fire component of light-severity (or scorched only) burn areas immediately following burning. With greater time since fire (1- 300 years post-fire), Brulisauer et al. (1996) found that shrub cover continually increased in mesic lodgepole pine sites, as stand age increased. This understory cover would not be expected to change much with succession from lodgepole pine to spruce/fir dominated canopy (La Roi and Hnatiuk 1980).

Overall, both presence and abundance of arboreal lichens seems to depend on old forest characteristics, and moisture. With the exception of aspect, which likely relates to photosynthetic requirements for lichen near the tree base, the model parameters are consistent in predicting Class 3 trees in sites that likely experience less frequent fires, or fires of low severity and intensity.

Conclusions

The goal of my research was to determine how preferred lichen forage genera in JNP and BNP were affected by fire-related forest conditions (primarily forest age, structure, location, and composition), and to use this information to inform fire management activities in caribou range. Both *Cladonia* spp. and Class 3 arboreal lichen trees require a significant length of time post-fire to establish, so prescribed burns could be used for future habitat creation, but not for current habitat enhancement. *Cladonia* and Class 3 trees are both more likely to be found at higher elevations, but *Cladonia* favoured steeper slopes, while Class 3 trees tended to be found in flatter locations. *Cladonia* did not occur preferentially on a specific aspect, but Class 3 trees were positively associated with southwest aspects. Class 3 trees were more likely to occur in forests with a higher spruce component while the probability of *Cladonia* occurrence did not respond to canopy composition. Finally, Class 3 tree presence and abundance was characterized by site characteristics that reflect less severe fires, or old forest, while Cladonia occurrence was simply associated with older forest. Together, these results suggest there is some spatial separation between areas that have Class 3 trees, and those that have *Cladonia* present. Specific fire prescriptions could be applied that assist long-term future arboreal or terrestrial lichen growth by trying to create forest conditions that would achieve future lichen abundance. This may be particularly important for JNP and BNP since they have a low lichen abundance relative to other caribou ranges in Canada (Thomas and Armbruster 1996, Thomas et al. 1996a, 1996b). The dominant canopy cover could also be used to help select areas to receive a planned low fire severity treatment. Lodgepole pine forests, since they would likely initially re-seed to lodgepole pine, would not be good candidates to burn for future Class 3 tree creation. Since Class 3 trees are more likely in spruce dominated forests with older trees present, lower intensity and lower severity fires that don't kill or remove larger, older, trees would be preferable in terms of ensuring future abundance of Class 3 trees.

Ultimately, it is important to determine whether caribou conservation efforts need to focus on current habitat protection, future habitat creation, or some combination of the two. For the benefit of caribou forage opportunities now, land managers need to protect areas that have abundant lichen forage, or lichen forage potential. For all areas within or near caribou range, burning for other land management objectives should focus on areas that do not currently have characteristics that support either terrestrial or arboreal lichens. To have the least negative impact on future caribou forage opportunities, these burns should have fire prescriptions that promote future lichen growth. For arboreal lichens, this would be lower severity burns in Engelmann spruce forests that leave part of the forest canopy intact. They would primarily be burns on more southwesterly aspects on flatter terrain. Burns to encourage *Cladonia* development would be on steeper slopes and likely do not depend on forest type or aspect.

There are many competing interests for fire management objectives, and this may limit a land manager's ability to conduct burns that will always favour caribou. To achieve other fire management goals that may conflict with caribou needs, burning in areas that will always be less favourable for either arboreal or terrestrial lichen would have the least impact. In JNP and BNP for arboreal lichen, sites further east would be less important; for terrestrial lichen, sites further north appear to be less favourable for *Cladonia*. For both lichen types, burning in lower elevations sites would have the least impact on future lichen availability to caribou.

The lichen models I developed can be used to help plan prescribed burns within the area presently considered caribou home range, as well as in potential caribou habitat identified through habitat selection (RSF) models. In JNP and BNP, these models, along with considerations of fire impacts on predator and prey distributions, could serve as part of the prescribed fire assessment process that would help Parks Canada achieve other fire management objectives while still protecting caribou habitat.

Tables and Figures

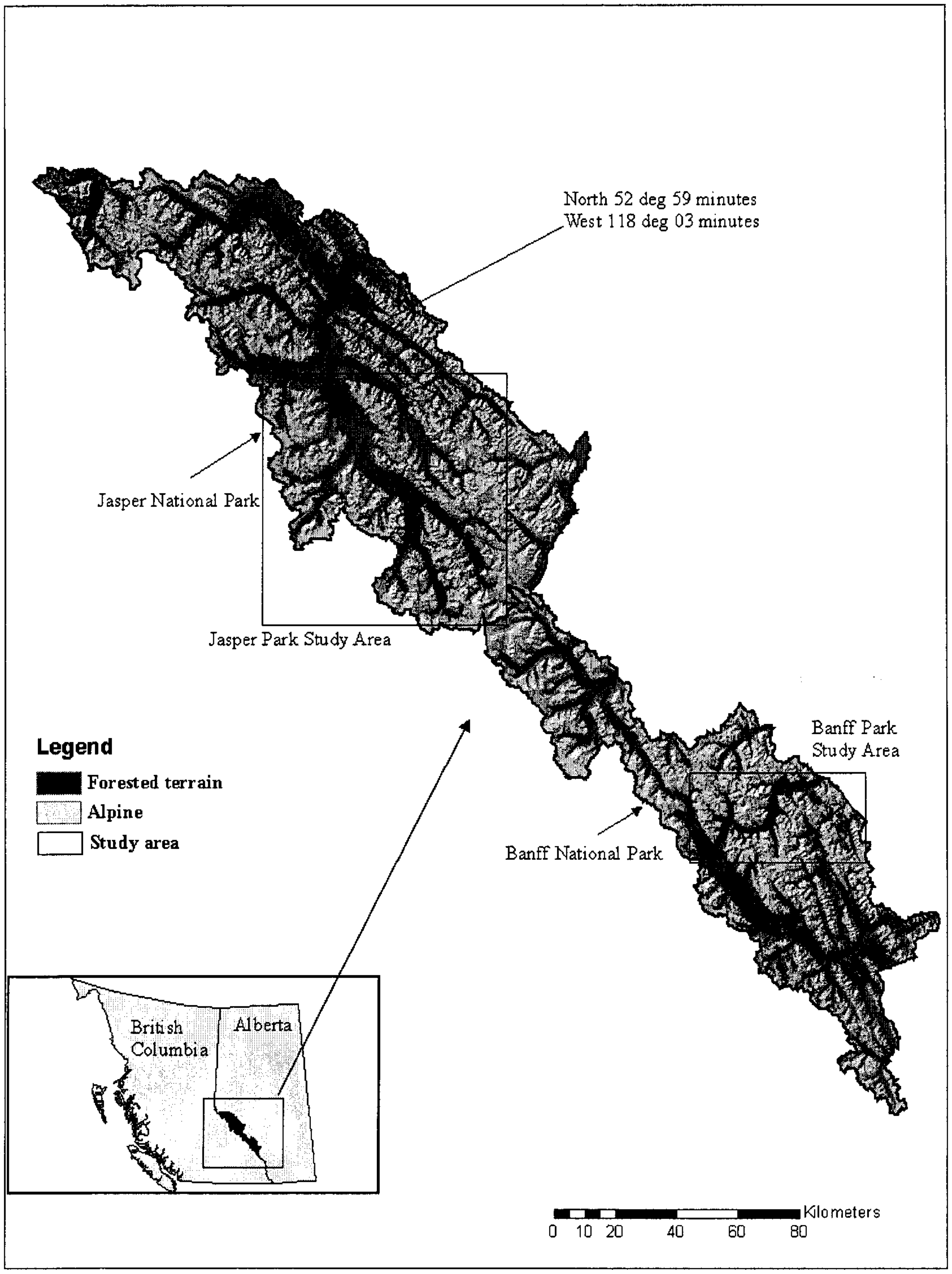

Figure 3.1: Jasper and Banff National Parks in relation to British Columbia and Alberta. Both parks are within the Rocky Mountain range on the East side of the Continental Divide.

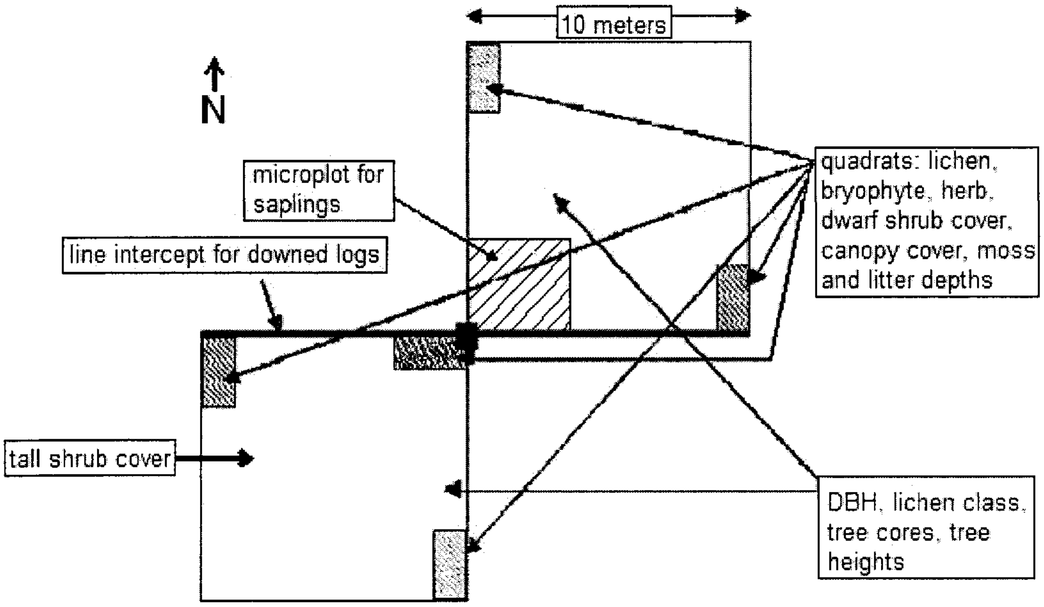

Figure 3.2: Plot layout for stand structure sample plots. Plot was a fixed area design with five nested 240cm^2 quadrats for measuring cover of lichens, bryophytes, herbaceous vascular plants and shrubs shorter than 10cm. Tree density by species, tree heights and DBH, increment cores, and arboreal lichen abundance per tree were measured in the two 10 meter by 10 meter squares. The 20m east/west line was used as a line intercept for counting downed logs, and a 2 m by 2 m microplot was used to count number of saplings. Trees were differentiated from saplings based on a diameter greater than 5cm at 130cm above ground. Tall shrub species cover was estimated for the south 10m by 10m square.

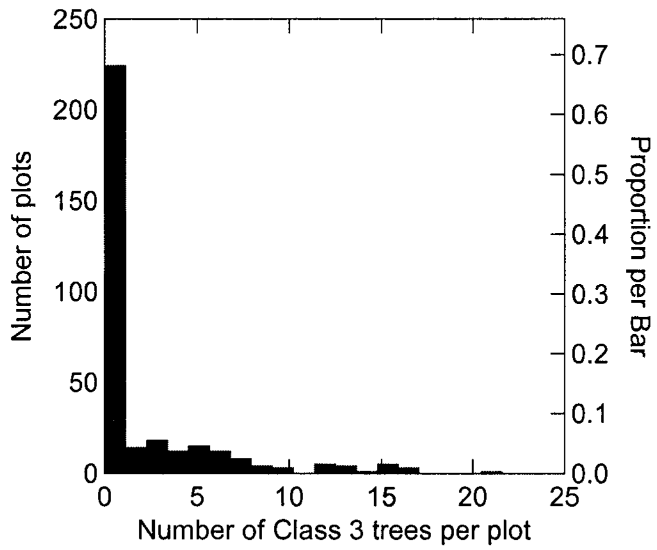

Figure 3.3: Histogram of abundance of Class 3 arboreal lichen bearing trees. Class 3 indicates greater than 50 grams dry-weight of lichen in the lower 2.5m of the tree's branches (as per Stevenson et al. 1998). Inflated zero count indicates need to use a zero-inflated distribution for our models.

Table 3.1: Independent variables evaluated in the *Cladonia* probability and Zero Inflated Negative Binomial models.

Variable abbreviation	Data type	Description
elev	continuous	elevation above sea level in meters
telev	continuous	elevation above sea level in meters, divided by 1000
slope	continuous	slope in degrees
Number.vascular	continuous	number of different vascular plants species found at a plot in all 5 quadrats
#saplings	count	number of saplings from microplot
shrubcov	continuous	estimated percent tall shrub cover (>10cm height) in plot
canopycov	continuous	average % canopy cover estimated by densiometer from 5 quadrat locations
#logs	count	number of logs from line intersect count
max.core	continuous	highest increment core tree ring count from plot
fire	continuous	Stand origin date in year AD
fire.category	binomial	Stands originating either before or after 1925AD
litter.cover	continuous	average percent cover of forest floor litter from 5 plot quadrats
avglittermoss	continuous	average depth in cm of litter and moss from 5 quadrat locations in a plot
treesperplot	continuous	Number of trees in each sample plot
SorSW.aspect	binomial	South&Southwest aspects (157.6-247.5 degrees azimuth) versus all others
SW.aspect	continuous	Absolute number of degrees away from 225 degrees azimuth
UTM.Easting	continuous	NAD 83 Easting position from UTM grid reference
UTM.Northing	continuous	NAD 83 Northing position from UTM grid reference
tUTM.North/Easting	continuous	NAD 83 reference in scientific notation: (Northing/1000000; Easting/100000)
%pine	continuous	percent of trees in plot that are lodgepole pine
%spruce	continuous	percent of trees in plot that are Engelmann or White spruce
%fir	continuous	percent of trees in plot that are subalpine fir
%notPl.Se.Fa	continuous	percent of trees in plot that are not pine, spruce or fir
FBP	categorical	Fuel categories from Canadian Forest Fire Danger Rating System
basal.area	continuous	basal area of all trees in a plot in meters squared
avglitter	continuous	average depth of litter from 5 quadrats in plot
avgmoss	continuous	average depth of moss from 5 quadrats in plot
avgmineral	continuous	average depth of moss & litter/ferric/humic soil layer from 5 quadrats in plot
avgfeathermosscov	continuous	average percent cover of feathermosses from 5 plot quadrats
avgmosscov	continuous	average percent cover of moss (not feathermoss) from 5 plot quadrats
%blackspruce	continuous	percent of trees in plot that are black spruce
vasc.cover	continuous	average percent cover of forest floor litter from 5 plot quadrats

Table 3.2: Top ten candidate models for probability of *Cladonia* cover greater than 5%. Change in Akaike values (corrected for small sample sizes AICc) and AICc weight (AICc w_i) calculated from Burnham and Anderson (1998). Variable abbreviations are as in Table 3.1.

model name	model structure	AICc	ΔAICc	AICc w_i
CLAD10	elev+slope+Number.vascular-UTM.Northing+fire.young+litter.cover	347.4	0	0.223
CLAD9	elev+slope+Number.vascular-UTM.Northing+fire.young+litter.cover+max.core	347.7	0.3	0.189
CLAD7	elev+slope+Number.vascular-UTM.Northing+fire.young+litter.cover+max.core-%fir+saplings	348.0	0.6	0.162
CLAD11	elev+slope+Number.vascular-UTM.Northing+fire.young	348.4	1.0	0.134
CLAD6	elev+slope+Number.vascular-UTM.Northing+fire.young+litter.cover+max.core-%fir+saplings-UTM.Easting	348.4	1.1	0.131
CLAD8	elev+slope+Number.vascular-UTM.Northing+fire.young+litter.cover+max.core-%fir	349.4	2.0	0.082
CLAD12	elev+slope+Number.vascular-UTM.Northing	351.1	3.7	0.034
CLAD5	elev+slope+Number.vascular-UTM.Northing+fire.young+litter.cover+max.core-%fir+saplings-UTM.Easting-avglittermoss	351.3	3.9	0.031
CLAD4	elev+slope+Number.vascular-UTM.Northing+fire.young+litter.cover+max.core-%fir+saplings -UTM.Easting-avglittermoss-%Not.Pl.Se.Fa	353.4	6.0	0.011
CLAD3	elev+slope+Number.vascular-UTM.Northing+fire.young+litter.cover+max.core-%fir+saplings -UTM.Easting-avglittermoss-%Not.Pl.Se.Fa+fire	357.2	9.8	0.002

Table 3.3: Akaike (corrected for small sample sizes; AICc) weights and ranking of the top ten weighted variables for all *Cladonia* cover probability candidate models. Variable abbreviations are as in Table 3.1.

variable	**AICc weight**	**rank**
elev	1.00	1
slope	1.00	2
Number.vascular	1.00	3
UTM.Northing	1.00	4
fire.category	0.96	5
litter.cover	0.83	6
%fir	0.61	7
#saplings	0.42	8
max.core	0.34	9
UTM.Easting	0.18	10
%Not.Pl.Se.Fa	0.04	11
litter&moss	0.01	12

Table 3.4: Coefficient and 95% confidence intervals for variables included in the best predictive *Cladonia* model (CLAD10). Variable abbreviations are as in Table 3.1.

Variable	β	SE	CI upper	CI lower	t value	% of explained variation
elev	0.003	0.001	0.004	0.002	5.09	34.8
slope	0.078	0.016	0.110	0.045	4.70	29.8
UTM.Northing	-1.2E-05	4.5E-06	-3.1E-06	-2.1E-05	-2.69	9.8
Number.vascular	0.217	0.081	0.380	0.055	2.67	9.6
fire.category	1.135	0.442	2.019	0.251	2.66	9.5
litter.cover	0.012	0.006	0.023	0.001	2.19	6.5

Table 3.5: Receiver Operating Characteristic curve (ROC*) values from K-fold model validation runs of best predictive *Cladonia* model (CLAD10), using an 80% random draw from the total data set for model creation and the remaining 20% for model validation runs.

K-fold run	ROC value	ROC discrimination*
1	0.816	excellent
2	0.894	excellent
3	0.908	outstanding
4	0.798	acceptable
5	0.894	excellent
6	0.875	excellent
7	0.911	outstanding
8	0.813	excellent
9	0.853	excellent
10	0.828	excellent
average	**0.859**	**excellent**

*Hosmer and Lemeshow 2000 (p162)

Table 3.6: Candidate models in order based on AICc values and AICc weights (w_i) for Zero-inflated Negative Binomial models of Class 3 lichen bearing trees. The Negative binomial (Neg.Bin.) portion predicts counts of Class 3 trees, the Z-inflated portion predicts probability of a zero count (i.e., absence of any Class 3 trees). Change in AICc and AIC weight (AICc w_i) calculated from Burnham and Anderson (1998). Variable abbreviations are as in Table 3.1.

Portion	model structure	ΔAICc	AICc w_i
Neg.Bin.	telev+avglittermoss+shrubcov+treesperplot-%pine-UTM.Easting	0.00	0.27
Z-inflated	-telev-canopycov-max.core-SW.aspect+#logs+slope-spruce		
Neg.Bin.	telev+avglittermoss+shrubcov+treesperplot-%pine+ UTM.Northing	0.00	0.27
Z-inflated	-telev-canopycov-max.core -SW.aspect+#logs+slope–spruce		
Neg.Bin.	telev+avglittermoss+shrubcov+treesperplot-%pine +UTM.Northing	2.28	0.09
Z-inflated	-telev-canopycov-max.core -SW.aspect+#logs+slope		
Neg.Bin.	telev+avglittermoss+shrubcov+treesperplot-%pine-UTM.Easting	2.30	0.09
Z-inflated	-telev-canopycov-max.core-SW.aspect+#logs+slope		
Neg.Bin.	telev+avglittermoss+shrubcov+treesperplot-%pine	2.53	0.08
Z-inflated	-telev-canopycov-max.core -SW.aspect+#logs+slope		
Neg.Bin.	telev+avglittermoss+shrubcov+treesperplot-%pine +UTM.Northing	2.60	0.07
Z-inflated	-telev-canopycov-max.core-SW.aspect+#logs+slope +fire.category		
Neg.Bin.	telev+avglittermoss+shrubcov+treesperplot-%pine -UTM.Easting	3.00	0.06
Z-inflated	-telev-canopycov-max.core -SW.aspect+#logs+slope +fire.category		
Neg.Bin.	telev+avglittermoss+shrubcov+treesperplot-%pine -UTM.Easting	3.93	0.04
Z-inflated	-telev-canopycov-max.core-SW.aspect+#logs+slope-%spruce+ SorSW.aspect		
Neg.Bin.	telev+avglittermoss+treesperplot-%pine	4.23	0.03
Z-inflated	-telev-canopycov-max.core-SW.aspect+#logs+slope		
Neg.Bin.	telev+avglittermoss+shrubcov+treesperplot-%pine+UTM.Northing-%fir	4.80	0.02
Z-inflated	-telev-canopycov-max.core-SW.aspect+slope		

Table 3.7: Coefficients, 95 percent confidence intervals, and significances for variables included in the best predictive ZINB model. The Negative Binomial portion predicts counts of Class 3 trees, the Z-inflated portion predicts probability of a zero count (i.e., absence of any Class 3 trees); log(tau) is an error term.Variable abbreviations are as in Table 3.1.

Variable	β	SE	CI upper	CI lower	Z value	Pr(>|z|)
Negative Binomial Portion						
telev	3.053	0.489	2.094	4.011	6.244	0.000
avglittermoss	0.011	0.004	0.003	0.019	3.032	0.002
shrubcov	0.011	0.004	0.003	0.019	2.627	0.009
treesperplot	0.013	0.005	0.004	0.023	2.673	0.008
%pine	-0.905	0.296	-1.485	-0.325	3.060	0.002
tUTM.Easting	-0.050	0.023	-0.095	-0.004	-2.148	0.032
Zero-inflated Portion						
telev	-7.624	3.006	-13.520	-1.732	-2.536	0.011
canopycov	-0.148	0.054	-0.254	-0.042	-2.726	0.006
max.core	-0.065	0.024	-0.111	-0.019	-2.746	0.006
SW.aspect	-0.027	0.012	-0.051	-0.004	-2.335	0.020
#logs	0.289	0.141	0.014	0.565	2.058	0.040
slope	0.190	0.085	0.024	0.357	2.236	0.025
%spruce	-3.987	1.976	-7.860	-0.113	-2.017	0.044
log(tau)	0.160	0.189	-0.210	0.530	0.849	0.396

Table 3.8: Zero Inflated Negative Binomial Model Validation results with five K-fold validation runs. Each training set is a random draw of 80% of data (262 plots); validation sets are the remaining 20% (67 plots). Receiver Operating Characteristic Curve (ROC) values were calculated by creating probability values from predicted count values: firstly by dividing all predicted counts by the maximum predicted count for each validation data set, and secondly, designating plots as having at least one Class 3 tree (1) or not (0). The Chi Squared significance, Pearson correlation, and regression coefficient (R^2) are for the observed Class 3 tree counts versus the predicted counts.

K-fold run	ROC value	ROC discrimination*	Chi Squared significance	Pearson Correlation	Multiple R^2
1	0.993	outstanding	0.385	0.949	0.901
2	0.917	outstanding	0.443	0.966	0.934
3	0.974	outstanding	0.157	0.846	0.716
4	0.958	outstanding	0.276	0.886	0.786
5	0.970	outstanding	0.371	0.974	0.949
average	**0.962**	**outstanding**	**0.326**	**0.924**	**0.857**

*Hosmer and Lemeshow 2000 (p162)

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Chapter 4: Thesis Conclusions

Since the early 1900's, both Jasper (JNP) and Banff National Parks (BNP) have experienced a decline in area burnt by wildfires, as compared to previous centuries (Tande 1979, Van Wagner 1995, Achuff et al. 1996, Rhemtulla et al. 2002). Some research has suggested that long periods without fire may cause habitat deterioration for woodland caribou (*Rangifer tarandus caribou;* hereafter caribou; Klein 1982, Schaefer and Pruitt 1991, Coxson and Marsh 2001). This is thought to relate primarily to feathermoss or litter accumulation over terrestrial fruticose lichens (Payette et al. 2000, Coxson and Marsh 2001), the main food source for caribou in JNP and BNP (Thomas and Armbruster 1996, Thomas et al. 1996a). I examined caribou habitat selection and lichen abundance in relation to topography, and forest age, structure and composition in an attempt to determine whether the recent lack of fire was limiting caribou selection of preferred habitat or negatively affecting lichen abundance. In contrast to previous suggestions, I found no evidence that caribou avoided older forest. My research suggests that during winter, when caribou occupy sites below treeline, they avoid young fire-generated stands (originating since 1925_{AD}) in JNP and BNP while preferring areas with forest 75-150 or 225-300 years old. Furthermore, I conclude that neither terrestrial nor arboreal lichens are likely to benefit from wildfire or a prescribed burning program for at least 75 years.

General Findings

I examined caribou habitat selection from mid-October to mid-April, in 2003 and 2004, at both coarse and fine scales. At a coarse scale, I found caribou preferred gentler slopes, higher elevations, and avoided south and southwest aspects. They selected closed-canopy and older forest, showing the greatest preference for stands that originated between 1701-1775_{AD} and $1851\text{-}1925_{AD}$. Caribou were least likely to select the youngest stands (originating since 1925_{AD}), and older stands from the intervals $1626\text{-}1700_{AD}$ or 1776-1850_{AD}. At a fine scale, caribou appeared to be most responsive to forage opportunities, as reflected by lichen abundance, but also selected sites with specific stand structures. Caribou selected sites with high fruticose terrestrial lichen cover, primarily *Cladonia* spp., and which had older trees and more saplings. Caribou avoided areas with deeper duff, more downed logs, and higher densities of trees that had low arboreal lichen abundance (Class 1 trees; Stevenson et al. 1998), and sites that had Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco), black spruce (*Picea mariana (*Mill.) B.S.P.), or deciduous trees in the canopy. In summary, caribou selected habitat at a coarse scale primarily based on topography and stand age, and at a fine scale based on terrestrial lichen cover and forest structure.

I created models to predict *Cladonia* spp. occurrence and to predict the occurrence and abundance of trees with over 50 grams of fruticose arboreal lichen 2.5m up the tree (Class 3 trees; Stevenson et al. 1998). Forests most likely to have *Cladonia* spp. present were older (>75 years) and *Cladonia* was increasingly likely to occur at higher elevations and on steeper slopes. Sites at which *Cladonia* was found tended to have higher litter cover, and a higher richness of understory vascular plants. Trees with high loads of fruticose arboreal lichen (Class 3 trees) were most likely to occur in forests at higher elevations, on flatter slopes, and on south or southwest aspects. These forests were older (originated before 1925$_{AD}$), and had higher proportions of spruce in the canopy and higher canopy cover. The immediate sample area had older trees, or at least one older tree present, and there were fewer downed logs on the forest floor. Abundance of Class 3 trees increased with elevation and in forests that were further west within the study area. Sites with more Class 3 trees had higher tall shrub cover (>10cm height), deeper duff, higher tree density, and a lower proportion of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) in the canopy.

In general, caribou and their preferred forage were likely to be found in similar locations in JNP and BNP. In the winter, caribou selected high elevation, older, closed forests. In these stands they focused on sites with higher abundance of terrestrial lichen. These selection patterns closely match the ecology of preferred forage lichens, which occurred at higher elevation sites in older, closed spruce forest.

Management Recommendations

Parks Canada's fire management objectives include using prescribed fire to restore habitat for fire-dependent species, reduce the risk of insect infestation, and for facility protection (Van Wagner and Methven 1980, Achuff et al. 1996, D. MacDonald pers. comm.). In this section, I recommend fire management actions designed to promote habitat elements selected by caribou, including forage lichens. Additional reccomendations are coupled with suggested areas of research that should be supported by Parks Canada to more fully understand direct and indirect fire effects on caribou in JNP and BNP.

Recommendation 1: Manage fire to protect caribou range and caribou forage

To ensure maintenance of foraging opportunities for caribou, their range should be protected from wildfires and not subjected to prescribed fires. I found that both caribou and lichens are more likely to be found at high elevations and in older forests in JNP and BNP. Both *Cladonia* spp. and Class 3 trees require a significant length of time post-fire to establish in JNP and BNP. My results suggest that carefully designed prescribed burns could be used for creation of future caribou habitat, but not for current habitat enhancement (i.e. minimum 75 years). Similarly, wildfires in caribou range will reduce current lichen-forage opportunites for caribou.

The caribou populations in both JNP and BNP are at low numbers and currently in decline (Flannigan and Rasheed 2002, Mercer et al. 2004). The primary forage for caribou in JNP and BNP is fruticose terrestrial lichens (Thomas and Armbruster 1996, Thomas et al. 1996a), but arboreal lichens become a critical food resource as snow depth and/or hardness increases in late winter (Thomas et al. 1996a). Caribou dependence on lichens is greatest during the winter (Thomas et al. 1996a, 1996b); during this time, caribou remain primarily below treeline. Prescribed burns in caribou range would therefore affect forage availability in habitats utilized during the most food-limited time of year. Consistent with Parks Canada policy and Species at Risk legislation (protection of critical habitat and caribou population recovery; Parks Canada 2001, Species at Risk Act 2004), fire management activities in JNP and BNP must not jeopardize terrestrial and arboreal lichen forage opportunities for caribou.

Parks Canada manages fire with the objective of maintaining or restoring the distribution and abundance of forest stand ages within the historic range of variability for the landscape (Achuff et al. 1996). For the subalpine, fires have historically been rare, large, and coincident with extreme fire weather (Bessie and Johnson 1995, Buechling and Baker 2004). Prescribed fires for these subalpine areas would therefore ideally be large and severe. However, planning for conservation of a threatened species requires a species-specific, fine-filter approach (Armstrong et al. 2003) that may conflict with plans to restore historical fires in some subalpine forests. Fortunately, longer fire cycles in high elevation areas in JNP and BNP reduce the urgency for fire restoration in the subalpine. To achieve other fire management goals that may conflict with caribou needs, Parks Canada could conduct burns in areas less favourable to either arboreal or terrestrial lichen. For example, burning in lower elevations sites would have less impact on future abundance of both types of lichen than would higher elevation burns, as decreasing elevation reduces the likelihood of lichen occurrence. Furthermore, caribou tend to avoid lower elevation terrain in JNP and BNP.

Recommendation 2: Create a fire management map for caribou recovery based on my research and other ongoing research in JNP and BNP.

This map should identify: 1) areas where fire is unlikely to affect caribou habitat; 2) areas where fire should be excluded to protect high quality caribou habitat; and 3) areas where small-scale burns could be applied within caribou range to achieve other ecological objectives and potentially enhance caribou habitat over the long-term. To achieve this, Parks Canada will need to incorporate a combination of stand age, topography, forage availability, stand structure, habitat security, and predation risk into empirical models to identify important habitat for caribou in JNP and BNP. I created resource selection function (RSF) models that predict caribou occurrence in JNP and BNP based on stand age, topography, forage, and stand structure parameters. However, these models do not account for habitat security parameters that also influence caribou habitat selection (e.g. distance to roads, trails; James and Stuart-Smith 2000, Oberg 2001, Whittington and Mercer 2004, Mercer et al. 2004), or predation risk factors (primarily wolf movement; Seip 1992, Kuzyk 2002, McLoughlin et al. 2003, Mercer et al. 2004, James et al. 2004). Ultimately, comprehensive models should be used for fire management planning. Ongoing research in JNP and BNP will provide complementary information to this end.

Recommendation 3: Create fireguards in strategic locations throughout caribou range to allow for control of future wildfires.

Wildfires in the subalpine tend to be large and coincide with extreme fire weather (Bessie and Johnson 1995, Buechling and Baker 2004). Restricting fire spread during extreme fire events is a difficult fire suppression challenge. To be successful at limiting fire extent under extreme burning conditions, Parks Canada could create fireguards in strategic locations throughout caribou range in JNP and BNP (Kubian pers. comm., MacDonald pers. comm.). These fire guards could be used to aid fire suppression operations, serving as anchor points to build blackline, burn off, or conduct backfiring (three methods in which fire is used to deprive an advancing fire of fuel; Parks Canada 2000a). To minimize negative impacts on caribou, such guards should have low forage quality for alternate prey. This is necessary to ensure the guards do not attract other ungulates, and thus more predators, into caribou range (Seip 1992, Kuzyk 2002, McLoughlin et al. 2003, James et al. 2004). Burns used to augment guards should be small and isolated, as a series of smaller, clumped, fires might attract elk in a manner similar to a single large fire (Turner et al. 1994). Enhancing natural fuel breaks on the landscape (e.g. rockslides, cliffs, streambeds, avalanche paths, mass wasting deposits, current vegetation breaks, wetlands etc.) through fuel reduction, combined with small, isolated burns, would likely meet these requirements.

Recommendation 4: Use prescribed fire to promote forage lichens.

Prescribed fires that do occur in higher elevation forests (but not in areas considered current caribou range) should attempt to promote terrestrial or arboreal lichens where terrain and vegetation allow. Fires for future *Cladonia* spp. establishment and growth (75 years after burning) are likely to be most successful at higher elevations, on steeper slopes, and if they occur in the southern portions of JNP.

To permit recruitment of Class 3 trees, fires should be low severity in Engelmann spruce forest, to leave all, or patches, of the canopy intact. Burns planned on flatter sites with south or southwest aspects in more western locations in JNP and BNP are likely to have the most arboreal lichen in the future. To help select areas for low severity fire treatment, the Ecological Land Classification (Holland and Coen 1983) could be used to generally identify the dominant forest canopy. Class 3 trees are more likely to occur in spruce dominated forests with older trees present. Arboreal lichens require the presence of old, lichen-bearing trees as a propagule sources for "seeding" new trees (Sillet and Goslin

1999, Dettki et al. 2000, Coxson et al. 2003). Lodgepole pine forests, which initially re-seed to lodgepole pine after a fire, are not likely to promote future Class 3 trees.

Even severe wildfires may not remove all arboreal lichen producing trees. Within large, stand-replacing fires (the landscape-level norm for higher elevation subalpine areas; Bessie and Johnson 1995, Buechling and Baker 2004), residual old forest patches and surviving single trees are common (Camp et al. 1997, DeLong and Kessler 2000, Bonar et al. 2003). These older forest remnants may still provide areas with high arboreal lichen abundance within a larger wildfire. Prescribed fires should identify specific measures to ensure conditions for arboreal lichen persistence and future abundance in caribou range are maintained or promoted.

Future Research

Future research on the effect of fire and fire management on caribou habitat should focus on alternate prey and wolf response to fires in proximity to caribou habitat. There is abundant evidence to suggest that recently burned areas attract alternate prey (Gasaway et al. 1989, MacCracken and Viereck 1990, Peck and Peek 1991, Turner et al. 1994, Pearson et al. 1995, Fuller and DeStefano 2003), and subsequently their predators (Seip 1992, Ballard et al. 2000, Rettie and Messier 2000, Kuzyk 2002, McLoughlin et al. 2003, James et al. 2004). In JNP and BNP, the primary alternate prey species that influences distribution and abundance of wolves, is elk (*cervus elaphus*; Parks Canada 2000b, Hebblewhite and Pletscher 2002, Hebblewhite et al. 2002, Hebblewhite et al. 2005).

Creating large fires, or aggregations of smaller fires (same response by elk; Turner et al. 1994) that attract significant numbers of elk (i.e. minimum herd size that will attract wolves; Hebblewhite and Pletscher 2002) are likely to cause further caribou population decline. An important question for Parks Canada is whether burns at the entrance to valley systems will impede or facilitate access to caribou by predators (M. Bradley pers. comm., C. White pers. comm.). Using an experimental approach, Parks Canada could explore whether prescribed burns intended to intercept or concentrate alternate prey away from caribou will result in reduced predator abundance in caribou habitat. Determining the size at which fires attract alternate prey in sufficient numbers to attract wolves (Hebblewhite and Pletscher 2002) is also an important research objective, with application for determining the size of prescribed burn that could occur in caribou habitat. This would also inform fire use in caribou ranges for whitebark pine restoration and fireguard construction burning.

Future research related to caribou forage should focus on the time periods when forage is potentially limiting (e.g. deep or hard snow periods) and how non-lichen forage species that are used by caribou (e.g. certain forb and graminoid species; Thomas et al. 1996a) respond to fire. The relative importance of these forage species to caribou could be determined by additional fine-scale RSF sampling. A sampling focus on late winter selection patterns would represent the time when caribou are most food-limited, but calving and post-parturition periods are also important. In these models, highly specific, late winter conditions could be identified through snow depth and snow density data collected by Parks Canada's avalanche forecasting staff.

During my research, I identified serious errors in JNP's current stand origin map (Tande 1979, Parks Canada file data). The portion of the stand origin map near Jasper townsite is quite detailed, but the majority of JNP was not mapped to this standard (R. Kubian pers. comm.). I found that stand origin-defined map boundaries often did not match the apparent age of forest on the ground. Using a simple paired correlation between the oldest tree core increment at a sample site and the stand origin date for that site (329 samples) I found no correlation between the age of the oldest tree at the site site and the stand origin age from JNP's stand origin map (the Pearson correlation coefficient was -0.523). Recent fires also were not mapped accurately; for example, the mapped location of a 1996 fire was five kilometers away from its actual location. Further, the mapped boundary of the 2003 Syncline Ridge fire, which had daily helicopter Global Positioning System (GPS) mapping updates, does not include any of the large, unburnt islands within the larger fire perimeter. I used broad stand origin categories, which I deemed suitable for coarse scale analysis. However, a more accurate stand origin map layer is necessary to increase confidence at finer scales.

The general goal for Parks Canada's fire management program is to burn 50% of the calculated long-term fire cycle within the forested landscapes of JNP and BNP (Parks Canada 2005), and this has generated significant pressure to conduct burns within large landscape units that contain caribou (A. Dibb pers. comm., D. Smith pers. comm.). Recent studies in BNP have begun to re-examine historical fire frequency and distribution (White et al. 2000), but this has not yet occurred in JNP, despite more recent information about historical fire events becoming available (Schindler et al. 2000, Rhemtulla et al. 2002). Fire cycles calculated for JNP are based on the stand origin map described above, and have not incorporated recently developed analytical techniques (e.g. Armstrong 1999, Baker and Ehle 2001, Reed and Johnson 2004), or historical fire evidence from lake core sampling (Schindler et al. 2000). A recalculation of fire cycles for JNP, incorporating recent evidence of historical range of variation (Schindler et al. 2000), would affect JNP's annual targets for area to be burnt. Furthermore, as recommended by Rhemtulla et al. (2002), a clear set of fire restoration goals needs to be articulated for JNP and these goals should support the recovery of threatened and endangered species. Together, these measures should reduce the pressure to burn in areas that would negatively affect caribou and could emphasize measures likely to aid in caribou recovery.

My research can be used to help plan prescribed burns that will be less likely to negatively affect caribou, and which could promote maintenance and development of lichen resources. In JNP and BNP, this research, along with considerations of fire impacts on predator and prey distributions, could inform the prescribed fire assessment process to help Parks Canada achieve other fire management objectives while still protecting caribou habitat.

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Appendix A

Summary Statistics for all Coarse Scale locations from JNP and BNP from October 15 to April 15 (2001-2004) grouped by 75 year interval fire categories

Firecategory: 1625 and Earlier

```
                 fire     slope        elev
     Min: 1390.000000  0.000000  1452.000000
 1st Qu.: 1600.000000 10.000000  1914.000000
    Mean: 1594.523477 15.598402  2005.115884
  Median: 1600.000000 15.000000  2006.000000
 3rd Qu.: 1600.000000 21.000000  2100.000000
     Max: 1620.000000 46.000000  2317.000000
Variance:  435.521698 65.138557 19275.222557
Std Dev.:   20.869157  8.070846   138.835235
 SE Mean:    0.659611  0.255095     4.388162
LCL Mean: 1593.229096 15.097819  1996.504822
UCL Mean: 1595.817857 16.098985  2013.726946
-----------------------------------------------------------------------
```

Firecategory: 1626-1700

```
                  fire      slope        elev
     Min: 1626.0000000  0.0000000  1443.00000
 1st Qu.: 1645.0000000  9.0000000  1880.00000
    Mean: 1668.0827685 15.0934713  1975.78737
  Median: 1680.0000000 14.0000000  2000.00000
 3rd Qu.: 1680.0000000 20.0000000  2090.00000
     Max: 1700.0000000 49.0000000  2558.00000
Variance:  530.0259806 67.4330873 23577.28882
Std Dev.:   23.0222931  8.2117652   153.54898
 SE Mean:    0.4348476  0.1551047     2.90025
LCL Mean: 1667.2301146 14.7893403  1970.10053
UCL Mean: 1668.9354223 15.3976023  1981.47421
-----------------------------------------------------------------------
```

Firecategory: 1701-1775

```
                  fire      slope         elev
     Min: 1704.0000000  0.0000000  1020.000000
 1st Qu.: 1737.0000000 10.0000000  1791.000000
    Mean: 1743.5468652 15.6548589  1880.065361
  Median: 1747.0000000 15.0000000  1941.000000
 3rd Qu.: 1749.0000000 21.0000000  2036.000000
     Max: 1775.0000000 58.0000000  2369.000000
Variance:  155.4339218 71.6908605 56298.026610
Std Dev.:   12.4673141  8.4670456   237.272052
 SE Mean:    0.1560855  0.1060038     2.970546
LCL Mean: 1743.2408852 15.4470558  1874.242093
UCL Mean: 1743.8528452 15.8626621  1885.888628
--------------------------------------------------------------------
```

Firecategory: 1776-1850

```
                  fire      slope          elev
     Min: 1776.0000000  0.0000000   1016.000000
 1st Qu.: 1802.0000000  8.0000000   1420.500000
    Mean: 1822.8979592 14.1013605   1702.997959
```

```
  Median: 1834.0000000 13.0000000   1779.500000
 3rd Qu.: 1847.0000000 20.0000000   1994.750000
     Max: 1849.0000000 46.0000000   2568.000000
Variance:  642.4170823 68.2953691 123759.859084
Std Dev.:   25.3459480  8.2641012   351.795195
 SE Mean:    0.6610737  0.2155445     9.175532
LCL Mean: 1821.6012101 13.6785527   1684.999418
UCL Mean: 1824.1947082 14.5241684   1720.996500
------------------------------------------------------------------
```

Firecategory: 1851-1925

```
                fire      slope         elev
     Min: 1853.0000000  0.0000000   1020.000000
 1st Qu.: 1889.0000000  7.0000000   1340.000000
    Mean: 1892.5507807 14.3532630   1637.508875
  Median: 1889.0000000 13.0000000   1668.000000
 3rd Qu.: 1892.0000000 20.0000000   1909.000000
     Max: 1925.0000000 53.0000000   2481.000000
Variance:  143.8056498 79.8817289 100092.149314
Std Dev.:   11.9918993  8.9376579   316.373433
 SE Mean:    0.1385352  0.1032514     3.654872
LCL Mean: 1892.2792129 14.1508614   1630.344301
UCL Mean: 1892.8223486 14.5556647   1644.673449
----------------------------------------------------------------------
```

Firecategory: 1926-2000

```
                fire      slope        elev
     Min: 1926.0000000  0.0000000  1250.00000
 1st Qu.: 1926.0000000  6.0000000  1409.00000
    Mean: 1934.7553957 14.4460432  1657.50600
  Median: 1926.0000000 13.0000000  1616.00000
 3rd Qu.: 1937.0000000 21.0000000  1888.00000
     Max: 1971.0000000 44.0000000  2291.00000
Variance:  162.0938711 96.6322980 66696.15922
Std Dev.:   12.7316091  9.8301728   258.25600
 SE Mean:    0.6234696  0.4813856    12.64685
LCL Mean: 1933.5298522 13.4997917  1632.64630
UCL Mean: 1935.9809392 15.3922947  1682.36569
```

Summary Statistics for all Coarse Scale locations from JNP and BNP from October 15 to April 15 (2001-2004)

```
                   fire         slope         elev
     Min:  1390.0000000 0.000000e+000  1016.000000
 1st Qu.:  1730.0000000 8.000000e+000  1614.000000
    Mean:  1792.2162646 1.493054e+001  1789.230781
  Median:  1758.0000000 1.400000e+001  1883.000000
 3rd Qu.:  1889.0000000 2.100000e+001  2014.000000
     Max:  1971.0000000 5.800000e+001  2568.000000
 Total N: 19564.0000000 1.956400e+004 19564.000000
Variance:  9595.3934460 7.452204e+001 91570.965242
Std Dev.:    97.9560792 8.632615e+000   302.606948
 SE Mean:     0.7003297 6.171824e-002     2.163466
LCL Mean:  1790.8435586 1.480956e+001  1784.990203
UCL Mean:  1793.5889706 1.505151e+001  1793.471359
```

Summary Statistics for all Coarse Scale locations from JNP and BNP from October 15 to April 15, (2001-2004) grouped by use or available

Available location

```
                 fire       slope         elev
     Min: 1390.000000  0.00000000  1016.000000
 1st Qu.: 1730.000000  8.00000000  1414.000000
    Mean: 1807.006588 14.96588503  1680.375422
  Median: 1847.000000 14.00000000  1733.000000
 3rd Qu.: 1889.000000 21.00000000  1932.000000
     Max: 1971.000000 58.00000000  2568.000000
Variance: 9239.214388 88.16126745 97805.194812
Std Dev.:   96.120832  9.38942317   312.738221
 SE Mean:    0.851227  0.08315087     2.769548
LCL Mean: 1805.338055 14.80289685  1674.946693
UCL Mean: 1808.675120 15.12887321  1685.804150
------------------------------------------------------------------------
```

Use location

```
                 fire      slope         elev
     Min: 1550.000000  0.0000000  1439.000000
 1st Qu.: 1693.000000 10.0000000  1929.000000
    Mean: 1764.535153 14.8643769  1992.961104
  Median: 1747.000000 14.0000000  2000.000000
 3rd Qu.: 1889.000000 19.0000000  2080.000000
     Max: 1937.000000 39.0000000  2347.000000
Variance: 9087.632242 48.9977517 16223.288416
Std Dev.:   95.329073  6.9998394   127.370673
 SE Mean:    1.154931  0.0848045     1.543122
LCL Mean: 1762.271127 14.6981336  1989.936103
UCL Mean: 1766.799180 15.0306202  1995.986105
```

Summary Statistics for all Fine Scale locations from JNP grouped by use versus available

available

```
           avglittermoss  #saplings   shrub.cov treesperplot     #logs
     Min:      0.0000000  0.0000000    0.000000     0.000000  0.0000000
  1st Qu.:     2.0000000  0.0000000    6.000000    15.000000  1.0000000
     Mean:     4.1202186  2.9453552   23.103825    33.486339  5.7540984
   Median:     4.0000000  1.0000000   18.000000    26.000000  3.0000000
  3rd Qu.:     5.0000000  2.5000000   33.000000    44.000000  8.0000000
      Max:    32.0000000 44.0000000  114.000000   132.000000 44.0000000
 Variance:     9.4909626 44.2387558  517.071579   738.118097 48.0326067
 Std Dev.:     3.0807406  6.6512221   22.739208    27.168329  6.9305560
  SE Mean:     0.2277349  0.4916725    1.680931     2.008341  0.5123214
 LCL Mean:     3.6708785  1.9752440   19.787208    29.523714  4.7432451
 UCL Mean:     4.5695587  3.9154663   26.420443    37.448964  6.7649516
-----------------------------------------------------------------------
```

use

```
           avglittermoss  #saplings   shrub.cov treesperplot     #logs
     Min:      0.0000000   0.000000    0.000000     0.000000  0.0000000
  1st Qu.:     2.0000000   1.000000    0.000000    14.250000  0.0000000
     Mean:     3.5753425   8.438356   14.171233    26.559817  2.9041096
   Median:     3.0000000   3.000000    5.000000    23.000000  2.0000000
  3rd Qu.:     4.0000000  10.000000   20.000000    32.000000  4.0000000
      Max:    15.0000000 114.000000   89.000000   132.000000 22.0000000
 Variance:     5.4735947 235.075484  391.811856   384.206313 14.5010864
 Std Dev.:     2.3395715  15.332172   19.794238    19.601181  3.8080292
  SE Mean:     0.1936243   1.268900    1.638183     1.622205  0.3151547
 LCL Mean:     3.1926518   5.930428   10.933431    23.353594  2.2812190
 UCL Mean:     3.9580331  10.946285   17.409035    29.766041  3.5270002
```

available

```
             max.core       fire  avg.lichen #class3trees #class1trees
     Min:    0.000000 1550.00000   0.0000000    0.0000000     0.000000
  1st Qu.:  63.000000 1847.00000   1.0000000    0.0000000     3.000000
     Mean:  98.136612 1867.50820  12.4596669    1.1092896    14.936248
   Median:  88.000000 1892.00000   9.0000000    0.0000000     9.000000
  3rd Qu.: 113.500000 1915.00000  21.0000000    0.0000000    18.333333
      Max: 445.000000 2000.00000  56.6000000   26.0000000   184.000000
 Variance: 5199.085630 8357.81175 150.2364414   9.4324346   465.036817
 Std Dev.:  72.104685   91.42107  12.2570976    3.0712269    21.564712
  SE Mean:   5.330132    6.75804   0.9060707    0.2270316     1.594109
 LCL Mean:  87.619814 1854.17402  10.6719132    0.6613371    11.790936
 UCL Mean: 108.653410 1880.84238  14.2474206    1.5572421    18.081560
-----------------------------------------------------------------------
```

use

```
             max.core         fire  avg.lichen #class3trees #class1trees
     Min:    0.000000  1600.000000   0.0000000    0.0000000     0.000000
  1st Qu.:  83.000000  1699.750000   2.8500000    0.0000000     2.000000
     Mean: 156.938356  1790.767123  13.3135029    3.9977169    12.037900
   Median: 127.500000  1753.500000  10.4000000    2.0000000     8.000000
  3rd Qu.: 230.000000  1889.000000  21.5000000    6.0000000    20.000000
      Max: 430.000000  1937.000000  49.4000000   32.0000000    70.000000
 Variance: 9058.775484 10260.800567 141.8912090  30.0145541   170.747029
 Std Dev.:  95.177600   101.295610  11.9118096    5.4785540    13.067021
  SE Mean:   7.876954     8.383284   0.9858284    0.4534084     1.081434
 LCL Mean: 141.369875  1774.197901  11.3650530    3.1015736     9.900488
 UCL Mean: 172.506838  1807.336346  15.2619529    4.8938602    14.175311
```

available

```
         litter.cover  basalarea  avgfeathermosscov avgcladina avgcladonia
     Min:    0.000000   0.000000     0.000000  0.0000000   0.0000000
  1st Qu.:   4.142857  15.221889     0.000000  0.0000000   0.0000000
    Mean:   23.505256  25.648480    30.967161  0.5807963   4.8607858
  Median:   18.000000  25.707554    21.000000  0.0000000   0.6000000
  3rd Qu.:  35.500000  34.298213    58.000000  0.0000000   7.3000000
     Max:   92.000000  76.321075   100.000000 24.0000000  42.0000000
 Variance:  512.221053 196.023351 1031.307740  5.0784137  57.1525072
 Std Dev.:   22.632301  14.000834    32.113980  2.2535336   7.5599277
  SE Mean:    1.673028   1.034971     2.373934  0.1665860   0.5588459
 LCL Mean:   20.204232  23.606394    26.283190  0.2521081   3.7581358
 UCL Mean:   26.806281  27.690565    35.651132  0.9094844   5.9634359
--------------------------------------------------------------------------
```

use

```
         litter.cover basalarea avgfeathermosscov avgcladina avgcladonia
     Min:    0.000000   0.00000   0.000000  0.0000000   0.0000000
  1st Qu.:  11.000000  10.18188   0.000000  0.0000000   2.6000000
    Mean:   34.821885  20.38658  22.019667  3.7678082   8.4313438
  Median:   33.000000  20.76207   9.000000  0.4000000   6.4000000
  3rd Qu.:  55.500000  28.34501  33.178571  5.0000000  13.4000000
     Max:   91.000000  59.72835 100.000000 25.4000000  36.0000000
 Variance:  664.639332 160.94967 789.191267 36.8155006  57.7948680
 Std Dev.:   25.780600  12.68659  28.092548  6.0675778   7.6022936
  SE Mean:    2.133618   1.04995   2.324956  0.5021563   0.6291703
 LCL Mean:   30.604876  18.31140  17.424486  2.7753166   7.1878141
 UCL Mean:   39.038894  22.46177  26.614849  4.7602999   9.6748734
```

available

```
         Peltigera Stereocaulon canopycov #vascular vasc.cover
     Min:  0.000000 0.00000000   0.00000  2.0000000 11.0000000
  1st Qu.: 0.000000 0.00000000  31.20000  7.0000000 17.0000000
    Mean:  3.410435 0.11584699  39.92842  8.0601093 20.4480874
  Median:  1.000000 0.00000000  42.60000  8.0000000 20.0000000
  3rd Qu.: 4.600000 0.00000000  52.90000  9.0000000 23.0000000
     Max: 32.000000 5.00000000  79.70000 15.0000000 50.0000000
 Variance: 27.022131 0.23046178 409.55672  3.4853780 25.2376749
 Std Dev.:  5.198282 0.48006435  20.23751  1.8669167  5.0237113
  SE Mean:  0.384268 0.03548738   1.49600  0.1380065  0.3713634
 LCL Mean:  2.652241 0.04582741  36.97668  7.7878110 19.7153562
 UCL Mean:  4.168628 0.18586657  42.88015  8.3324076 21.1808187
--------------------------------------------------------------------------
```

use

```
          Peltigera  Stereocaulon canopycov #vascular vasc.cover
     Min:  0.0000000  0.0000000   0.000000  1.0000000  0.0000000
  1st Qu.: 0.4000000  0.0000000  24.400000  7.0000000 16.0000000
    Mean:  4.5595890  0.5890085  34.328425  8.6369863 19.2671233
  Median:  2.4000000  0.0000000  34.300000  9.0000000 20.0000000
  3rd Qu.: 6.6666667  0.0000000  43.400000 10.0000000 22.0000000
     Max: 25.6000000 24.1666667  77.300000 14.0000000 36.0000000
 Variance: 31.1659036  5.7977898 262.434238  3.5569674 22.5695324
 Std Dev.:  5.5826431  2.4078600  16.199822  1.8859924  4.7507402
  SE Mean:  0.4620228  0.1992759   1.340707  0.1560858  0.3931741
 LCL Mean:  3.6464196  0.1951477  31.678572  8.3284889 18.4900307
 UCL Mean:  5.4727585  0.9828693  36.978277  8.9454837 20.0442159
```

available

```
             %pine    %spruce        %fir %blkspruce %notPl.Se.Fa
     Min: 0.00000000 0.00000000 0.00000000  0.00000000 0.00000000
  1st Qu.: 0.02565789 0.00000000 0.00000000  0.00000000 0.00000000
     Mean: 0.51235738 0.21124059 0.11100982  0.04623204 0.10289617
   Median: 0.54545455 0.05454546 0.00000000  0.00000000 0.00000000
  3rd Qu.: 1.00000000 0.32051282 0.04761905  0.00000000 0.04000000
      Max: 1.00000000 1.00000000 1.00000000  0.89285714 1.00000000
 Variance: 0.17856589 0.08426214 0.05597128  0.02170144 0.05517124
 Std Dev.: 0.42257057 0.29027942 0.23658251  0.14731409 0.23488558
  SE Mean: 0.03123732 0.02145807 0.01748868  0.01088977 0.01736324
 LCL Mean: 0.45072353 0.16890201 0.07650318  0.02474560 0.06863704
 UCL Mean: 0.57399123 0.25357917 0.14551646  0.06771847 0.13715531
---------------------------------------------------------------------
```

use

```
             %pine    %spruce        %fir  %blkspruce    %notPl.Se.Fa
     Min: 0.00000000 0.00000000 0.00000000 0.0000000000  0.000000000
  1st Qu.: 0.00000000 0.07095491 0.00000000 0.0000000000  0.000000000
     Mean: 0.28769719 0.32384181 0.33734857 0.0103931208  0.004178082
   Median: 0.09545455 0.26120858 0.22222222 0.0000000000  0.000000000
  3rd Qu.: 0.57854406 0.50000000 0.69085678 0.0000000000  0.000000000
      Max: 1.00000000 1.00000000 1.00000000 0.4857142860  0.550000000
 Variance: 0.12941103 0.08562280 0.11720743 0.0039578516  0.002081044
 Std Dev.: 0.35973744 0.29261374 0.34235570 0.0629114586  0.045618460
  SE Mean: 0.02977208 0.02421689 0.02833356 0.0052065894  0.003775411
 LCL Mean: 0.22885387 0.27597812 0.28134843 0.0001025074 -0.003283864
 UCL Mean: 0.34654051 0.37170551 0.39334870 0.0206837341  0.011640029
```

Summary Statistics for all Fine Scale locations from JNP grouped by stand origin before or after 1925$_{AD}$

Pre 1925$_{AD}$

```
          avglittermoss    #saplings   shrub.cov treesperplot    #logs
     Min:     0.0000000    0.0000000    0.000000     0.000000 0.0000000
  1st Qu.:     2.0000000    0.0000000    2.000000    14.000000 0.0000000
     Mean:     3.9537367    5.8683274   18.903915    28.808066 3.6868327
   Median:     3.0000000    2.0000000   10.000000    24.000000 2.0000000
  3rd Qu.:     5.0000000    6.0000000   30.000000    37.000000 5.0000000
      Max:    32.0000000  114.0000000  114.000000   132.000000 44.0000000
 Variance:     8.0728521  152.0218861  504.022877   495.986220 27.2015760
 Std Dev.:     2.8412765   12.3297156   22.450454    22.270748 5.2155130
  SE Mean:     0.1694963    0.7355292    1.339282     1.328561 0.3111314
 LCL Mean:     3.6200878    4.4204585   16.267575    26.192830 3.0743791
 UCL Mean:     4.2873855    7.3161963   21.540254    31.423303 4.2992864
---------------------------------------------------------------------
```

Post 1925$_{AD}$

```
          avglittermoss   #saplings   shrub.cov treesperplot   #logs
     Min:     0.0000000   0.0000000    0.000000     0.000000  0.000000
  1st Qu.:     2.0000000   0.0000000    9.250000    16.000000  2.750000
     Mean:     3.4375000   2.5416667   20.520833    39.805556  9.187500
   Median:     3.0000000   1.0000000   15.000000    29.500000  8.500000
  3rd Qu.:     4.0000000   2.0000000   24.500000    55.000000 15.000000
      Max:    13.0000000  33.0000000   80.000000   132.000000 28.000000
 Variance:     5.8257979  33.3599291  343.957004  1066.150512 56.325798
 Std Dev.:     2.4136690   5.7758055   18.546078    32.651960  7.505051
  SE Mean:     0.3483831   0.8336657    2.676896     4.712905  1.083261
 LCL Mean:     2.7366436   0.8645476   15.135614    30.324415  7.008260
 UCL Mean:     4.1383564   4.2187858   25.906053    49.286697 11.366740
```

Pre 1925$_{AD}$

```
             max.core         fire   avg.lichen #class3trees  #class1trees
     Min:    0.000000 1550.000000    0.0000000  0.000000    0.0000000
 1st Qu.:   83.000000 1739.000000    1.2000000  0.000000    2.0000000
    Mean:  135.377224 1813.637011   13.1092188  2.664294   13.7088968
  Median:  102.000000 1859.000000   10.2000000  0.000000    8.0000000
 3rd Qu.:  193.000000 1892.000000   21.8000000  4.000000   20.0000000
     Max:  445.000000 1918.000000   51.8000000 32.000000  100.0000000
Variance: 7717.328622 9683.417768  148.3270135 21.016661  273.2568452
Std Dev.:   87.848327   98.404358   12.1789578  4.584393   16.5304823
 SE Mean:    5.240592    5.870312    0.7265357  0.273482    0.9861259
LCL Mean:  125.061263 1802.081463   11.6790532  2.125952   11.7677351
UCL Mean:  145.693185 1825.192558   14.5393843  3.202636   15.6500585
---------------------------------------------------------------------------
```

Post 1925$_{AD}$

```
            max.core        fire  avg.lichen   #class3trees  #class1trees
     Min:   0.00000 1926.000000    0.000000    0.0000000     0.000000
 1st Qu.:  29.75000 1933.000000    2.200000    0.0000000     3.000000
    Mean:  58.97917 1949.458333   11.254167    0.7916667    13.305556
  Median:  49.50000 1946.000000    7.800000    0.0000000     8.000000
 3rd Qu.:  74.25000 1960.000000   16.250000    0.0000000    17.000000
     Max: 250.00000 2000.000000   56.600000   26.0000000   184.000000
Variance:2987.51020  415.998227  134.123812   15.2748227   714.013396
Std Dev.:  54.65812   20.396035   11.581184    3.9083018    26.721029
 SE Mean:   7.88922    2.943914    1.671600    0.5641148     3.856848
LCL Mean:  43.10810 1943.535942    7.891342   -0.3431859     5.546578
UCL Mean:  74.85023 1955.380724   14.616992    1.9265192    21.064534
```

Pre 1925$_{AD}$

```
         litter.cover   basalarea  avgcladina  avgcladonia  avgfeathermosscov
     Min:    0.000000   0.0000000   0.0000000     0.000000     0.000000
 1st Qu.:    6.000000  13.9370134   0.0000000     0.000000     0.000000
    Mean:   29.042908  23.3021946   2.2867819     6.312100    26.825843
  Median:   25.000000  22.8611313   0.0000000     3.333333    14.000000
 3rd Qu.:   46.666667  32.4479790   1.6666667     9.800000    47.000000
     Max:   92.000000  59.8521152  25.4000000    42.000000   100.000000
Variance:  613.702879 174.5806285  24.6176684    61.105461   965.015867
Std Dev.:   24.773027  13.2128963   4.9616195     7.816998    31.064705
 SE Mean:    1.477835   0.7882153   0.2959854     0.466323     1.853165
LCL Mean:   26.133831  21.7506144   1.7041428     5.394156    23.177939
UCL Mean:   31.951985  24.8537747   2.8694210     7.230044    30.473747
---------------------------------------------------------------------------
```

Post 1925$_{AD}$

```
         litter.cover   basalarea  avgcladina  avgcladonia  avgfeathermosscov
     Min:     0.00000    0.000000 0.00000000    0.000000     0.000000
 1st Qu.:     4.00000   11.203683 0.00000000    0.000000     0.000000
    Mean:    25.50833   23.379086 0.28750000    7.225000    27.995833
  Median:    20.00000   19.765588 0.00000000    5.100000    19.500000
 3rd Qu.:    41.25000   29.908772 0.00000000   11.400000    48.250000
     Max:    91.00000   76.321075 3.40000000   31.000000    95.000000
Variance:   588.25865  263.396456 0.65005319   56.886170   816.417855
Std Dev.:    24.25404   16.229493 0.80625876    7.542292    28.573027
 SE Mean:     3.50077    2.342526 0.11637343    1.088636     4.124161
LCL Mean:    18.46569   18.666532 0.05338686    5.034947    19.699091
UCL Mean:    32.55097   28.091640 0.52161314    9.415053    36.292575
```

Pre 1925$_{AD}$

```
           Peltigera  canopycov     %pine    %spruce  %notPl.Se.Fa
     Min:  0.0000000   0.000000 0.0000000 0.00000000 -0.57692308
 1st Qu.:  0.0000000  27.400000 0.0000000 0.00000000  0.00000000
    Mean:  3.6434503  37.543416 0.3769148 0.27278466  0.05397472
  Median:  1.4000000  38.600000 0.2173913 0.19047619  0.00000000
 3rd Qu.:  5.0000000  49.300000 0.7777778 0.41666667  0.00000000
     Max: 26.0000000  79.700000 1.0000000 1.00000000  1.00000000
Variance: 25.8564566 353.514930 0.1547375 0.08632157  0.03436717
Std Dev.:  5.0849244  18.801993 0.3933668 0.29380533  0.18538383
 SE Mean:  0.3033412   1.121633 0.0234663 0.01752696  0.01105907
LCL Mean:  3.0463315  35.335513 0.3307220 0.23828332  0.03220524
UCL Mean:  4.2405690  39.751320 0.4231076 0.30728599  0.07574420
---------------------------------------------------------------------------
```

Post 1925$_{AD}$

```
           Peltigera  canopycov      %pine    %spruce %notPl.Se.Fa
     Min:  0.0000000   0.000000 0.00000000 0.00000000 0.00000000
 1st Qu.:  0.1500000  34.350000 0.00000000 0.00000000 0.00000000
    Mean:  5.5416667  36.857292 0.62191944 0.19344677 0.07467571
  Median:  2.9000000  41.900000 0.92307692 0.00000000 0.00000000
 3rd Qu.:  8.0500000  48.150000 1.00000000 0.25700090 0.00000000
     Max: 32.0000000  73.600000 1.00000000 0.95454545 0.75609756
Variance: 45.8892908 343.309254 0.20372344 0.09260813 0.04012633
Std Dev.:  6.7741635  18.528606 0.45135733 0.30431583 0.20031558
 SE Mean:  0.9777663   2.674374 0.06514782 0.04392421 0.02891306
LCL Mean:  3.5746546  31.477145 0.49085893 0.10508266 0.01651013
UCL Mean:  7.5086787  42.237438 0.75297995 0.28181088 0.13284129
```

Pre 1925$_{AD}$

```
          vasc.cover  #vascular Stereocaulon Flavocetraria Peltigera
     Min:  0.0000000  1.0000000  0.0000000     0.0000000  0.0000000
 1st Qu.: 16.0000000  7.0000000  0.0000000     0.0000000  0.0000000
    Mean: 20.0106762  8.2740214  0.3430436     0.5202678  3.6434503
  Median: 20.0000000  8.0000000  0.0000000     0.0000000  1.4000000
 3rd Qu.: 23.0000000 10.0000000  0.0000000     0.0000000  5.0000000
     Max: 50.0000000 15.0000000 24.1666667    24.1666667 26.0000000
Variance: 25.8463142  3.7425013  3.1066560     4.2726814 25.8564566
Std Dev.:  5.0839270  1.9345545  1.7625709     2.0670465  5.0849244
 SE Mean:  0.3032817  0.1154058  0.1051462     0.1233097  0.3033412
LCL Mean: 19.4136745  8.0468481  0.1360662     0.2775361  3.0463315
UCL Mean: 20.6076778  8.5011946  0.5500209     0.7629994  4.2405690
---------------------------------------------------------------------------
```

Post 1925$_{AD}$

```
          vasc.cover  #vascular Stereocaulon Flavocetraria  Peltigera
     Min: 12.0000000  5.0000000  0.000000000   0.000000000  0.0000000
 1st Qu.: 17.0000000  8.0000000  0.000000000   0.000000000  0.1500000
    Mean: 19.4166667  8.5625000  0.225000000   0.229166667  5.5416667
  Median: 19.0000000  9.0000000  0.000000000   0.000000000  2.9000000
 3rd Qu.: 22.0000000 10.0000000  0.000000000   0.000000000  8.0500000
     Max: 29.0000000 12.0000000  5.000000000   5.000000000 32.0000000
Variance: 15.4822695  2.6768617  0.646170213   0.645088652 45.8892908
Std Dev.:  3.9347515  1.6361118  0.803847133   0.803174111  6.7741635
 SE Mean:  0.5679325  0.2361524  0.116025340   0.115928197  0.9777663
LCL Mean: 18.2741339  8.0874227 -0.008412876  -0.004050785  3.5746546
UCL Mean: 20.5591994  9.0375773  0.458412876   0.462384118  7.5086787
```

Appendix B

Summary Statistics for top ten predictive *Cladonia* variables

Less than five percent Cladonia cover

```
           #vascular litter.cover      slope       elev       UTM.easting
     Min:  1.0000000    0.000000  0.0000000    978.2740      404499.000
 1st Qu.:  6.0000000    2.500000  5.0000000   1224.4750      428856.000
    Mean:  7.8342246   24.533639 12.3850267   1553.1423      442461.128
  Median:  8.0000000   18.000000 10.0000000   1544.3700      440549.000
 3rd Qu.:  9.0000000   42.000000 18.0000000   1879.1250      449632.000
     Max: 15.0000000   91.000000 38.0000000   2203.0300      575475.000
Variance:  4.2035536  596.342309 82.6251509 121943.1887 562777715.069
Std Dev.:  2.0502570   24.420121  9.0898378    349.2036       23722.936
 SE Mean:  0.1499296    1.785776  0.6647148     25.5363        1734.793
LCL Mean:  7.5384434   21.010660 11.0736774   1502.7643      439038.729
UCL Mean:  8.1300058   28.056618 13.6963761   1603.5203      445883.528
-----------------------------------------------------------------------
```

More than five percent Cladonia cover

```
           #vascular litter.cover      slope       elev     UTM.easting
     Min:  6.0000000    0.000000  2.0000000   998.52899 4.134790e+005
 1st Qu.:  8.0000000   14.250000 14.0000000  1761.83499 4.421923e+005
    Mean:  8.9507042   33.786385 19.1760563  1875.33055 4.587378e+005
  Median:  9.0000000   29.000000 20.0000000  1944.47498 4.533305e+005
 3rd Qu.: 10.0000000   49.750000 24.7500000  2046.38745 4.612628e+005
     Max: 14.0000000   92.000000 42.0000000  2262.58008 5.720960e+005
Variance:  2.0897513  582.748371 70.3446709 51898.94980 1.309257e+009
Std Dev.:  1.4455972   24.140182  8.3871730   227.81341 3.618366e+004
 SE Mean:  0.1213118    2.025799  0.7038359    19.11768 3.036465e+003
LCL Mean:  8.7108791   29.781519 17.7846209  1837.53621 4.527349e+005
UCL Mean:  9.1905294   37.791251 20.5674917  1913.12489 4.647407e+005
```

Less than five percent Cladonia cover

```
                %fir  #saplings   max.core UTM.northing     litter&moss
     Min: 0.00000000  0.0000000   0.000000  5711039.000       0.0000000
 1st Qu.: 0.00000000  0.0000000  72.500000  5834214.500       2.0000000
    Mean: 0.16783610  3.1390374 108.219251  5849114.021       4.1764706
  Median: 0.00000000  1.0000000  94.000000  5853362.000       4.0000000
 3rd Qu.: 0.22063492  3.0000000 135.000000  5860937.000       5.0000000
     Max: 1.00000000 44.0000000 405.000000  5912341.000      32.0000000
Variance: 0.08131164 36.4321776 5279.860273 888104435.387      9.6729918
Std Dev.: 0.28515196  6.0359074  72.662647    29801.081       3.1101434
 SE Mean: 0.02085238  0.4413893   5.313619     2179.271       0.2274362
LCL Mean: 0.12669853  2.2682647  97.736543  5844814.756       3.7277844
UCL Mean: 0.20897367  4.0098102 118.701960  5853413.287       4.6251568
-----------------------------------------------------------------
```

More than five percent Cladonia cover

```
                 %fir   #saplings max.core UTM.northing        litter&moss
     Min: 0.00000000   0.000000     0.000000 5.709314e+006       0.0000000
 1st Qu.: 0.00000000   0.000000    76.500000 5.814982e+006       2.0000000
    Mean: 0.26888970   8.338028   145.316901 5.827424e+006       3.4859155
  Median: 0.07692308   2.000000   102.000000 5.840457e+006       3.0000000
 3rd Qu.: 0.54166667   9.000000   230.000000 5.852262e+006       4.0000000
     Max: 1.00000000 114.000000   445.000000 5.914413e+006      13.0000000
Variance: 0.10917722 252.693437 10265.381131 1.707856e+009       5.0175307
Std Dev.: 0.33041976  15.896334   101.318217 4.132621e+004       2.2399845
 SE Mean: 0.02772821   1.333991     8.502436 3.468019e+003       0.1879753
LCL Mean: 0.21407292   5.700820   128.508168 5.820568e+006       3.1143012
UCL Mean: 0.32370647  10.975236   162.125635 5.834280e+006       3.8575298
```

Summary Statistics for top weighted variables predicting Class 3 tree occurrence

Class 3 trees absent

```
                slope         elev      #logs     max.core    %spruce
      Min:   0.000000    978.27399  0.0000000     0.000000 0.00000000
  1st Qu.:   6.000000   1243.27002  1.0000000    52.000000 0.00000000
     Mean:  15.364532   1584.89471  5.3743842    92.443350 0.18679598
   Median:  15.000000   1606.70996  3.0000000    84.000000 0.03030303
  3rd Qu.:  23.000000   1900.26001  7.0000000   104.000000 0.25462963
      Max:  42.000000   2262.58008 44.0000000   430.000000 1.00000000
 Variance: 103.183290 130053.95960 46.8789445  5109.416329 0.07796696
 Std Dev.:  10.157918    360.62995  6.8468200    71.480181 0.27922564
  SE Mean:   0.712946     25.31126  0.4805526     5.016925 0.01959780
 LCL Mean:  13.958761   1534.98654  4.4268416    82.551090 0.14815348
 UCL Mean:  16.770303   1634.80288  6.3219269   102.335609 0.22543847
-------------------------------------------------------------------------------
```

Class 3 trees present

```
                slope        elev      #logs    max.core    %spruce
      Min:  1.0000000  1182.66003  0.0000000    0.000000 0.00000000
  1st Qu.: 10.0000000  1761.67749  0.2500000   98.000000 0.13930976
     Mean: 15.2380952  1865.08667  3.0634921  175.444444 0.38109801
   Median: 15.0000000  1928.77502  2.0000000  165.000000 0.32575758
  3rd Qu.: 20.0000000  2026.46753  5.0000000  238.750000 0.56987578
      Max: 36.0000000  2188.00000 18.0000000  445.000000 1.00000000
 Variance: 65.3188571 48023.96196 12.9559365 7782.808889 0.08076988
 Std Dev.:  8.0820082   219.14370  3.5994356   88.220229 0.28420042
  SE Mean:  0.7200025    19.52287  0.3206632    7.859283 0.02531859
 LCL Mean: 13.8131209  1826.44848  2.4288598  159.889949 0.33098939
 UCL Mean: 16.6630696  1903.72486  3.6981243  190.998940 0.43120664
```

Class 3 trees absent

```
                 .fir      .pine  canopycov   basalarea       swasp
      Min: 0.00000000 0.00000000   0.000000   0.0000000    0.000000
  1st Qu.: 0.00000000 0.00000000  23.400000  13.3833100   19.000000
     Mean: 0.12574051 0.53375663  35.987685  24.0964974   70.719212
   Median: 0.00000000 0.61904762  39.800000  22.7036869   56.000000
  3rd Qu.: 0.04195804 1.00000000  49.100000  32.8713832  120.000000
      Max: 1.00000000 1.00000000  78.000000  76.3210752  180.000000
 Variance: 0.07256861 0.18308605 412.466778 201.6742948 2944.292055
 Std Dev.: 0.26938561 0.42788556  20.309278  14.2012075   54.261331
  SE Mean: 0.01890716 0.03003168   1.425432   0.9967294    3.808399
 LCL Mean: 0.08845980 0.47454085  33.177050  22.1311690   63.209897
 UCL Mean: 0.16302123 0.59297241  38.798319  26.0618259   78.228527
-------------------------------------------------------------------------------
```

Class 3 trees present

```
                 .fir      .pine  canopycov basalarea       swasp
      Min: 0.00000000 0.00000000   6.250000   0.00000    1.000000
  1st Qu.: 0.04599567 0.00000000  28.650000  13.54004   47.000000
     Mean: 0.34954257 0.21756027  39.788492  22.05178   99.738095
   Median: 0.26136364 0.07417582  36.800000  22.58849  111.500000
  3rd Qu.: 0.63625000 0.30844907  48.800000  29.84464  147.000000
      Max: 0.93939394 1.00000000  79.700000  59.85212  178.000000
 Variance: 0.10231422 0.08484895 245.580927 161.59362 2978.130857
 Std Dev.: 0.31986594 0.29128843  15.671022  12.71195   54.572254
  SE Mean: 0.02849592 0.02595004   1.396086   1.13247    4.861683
 LCL Mean: 0.29314560 0.16620193  37.025465  19.81048   90.116222
 UCL Mean: 0.40593954 0.26891861  42.551519  24.29308  109.359969
```