Close encounters of the burned kind: Spatiotemporal effects of fire on habitat selection strategies of woodland caribou (*Rangifer tarandus caribou*) during winter

by

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ABSTRACT

Forest fire is the primary natural disturbance process influencing the distribution and abundance of terrestrial lichens across ranges of woodland caribou (*Rangifer tarandus caribou*), including the Klaza Caribou Herd in west-central Yukon. I used stand and understory data to understand variation in the abundance of lichens in burns of various ages. Focusing on the distribution of individual caribou, I used a dataset of GPS collar locations to examine resource selection on the winter range and within burns. Results suggested that burns provided suboptimal habitat for the KCH until 50 years post-fire; however, analyses focused on the use of burned habitat indicated that they regularly encountered burns and opportunistically used remnant lichen within the burn perimeter. The relationship between caribou and burned landscapes is complex and non-linear indicating that wildlife managers should look beyond burn age to account for the effects of fire on the availability and quality of caribou habitat.

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CHAPTER ONE: THESIS INTRODUCTION

Populations of woodland caribou (*Rangifer tarandus caribou*) are of increasing conservation concern. Habitat loss and alteration, natural and anthropogenic disturbance, and predation are believed to have contributed to population declines across much of their distribution (Dyer et al. 2002; Vors et al. 2007; Festa-Bianchet et al. 2011; Environment Canada 2012). In the Yukon, the Northern Mountain (NM) population (i.e., Designatable Unit; DU) of woodland caribou is currently assessed as Special Concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2014). Within this population, each herd is subject to a unique suite of threats that act cumulatively to influence population dynamics.

Caribou in the NM population in the Yukon are distributed throughout mountainous and valley habitats, generally south of 65 degrees latitude (COSEWIC 2014). These herds are believed to have one of two wintering strategies: alpine or forest-dwelling, depending on snow conditions within their range (Kuzyk et al. 1999). During the winter, these caribou forage primarily on terrestrial lichens from the *Cladina, Cetraria*, and *Cladonia* genera (henceforth referred to as forage lichens), which are found in spruce-pine forests or wind-swept alpine or subalpine slopes (Heard and Vagt 1998; Johnson et al. 2004a; Jones et al. 2007). Forest fires in wintering areas can reduce the availability of slow-growing lichens, resulting in changes to the distribution of caribou (Scotter 1970; Thomas et al. 1996; Environment Canada 2012; Anderson and Johnson 2014).

The effects of forest fire on caribou winter range have been studied extensively. Previous research suggested that, in the short-term, forest fire decreases the overall availability of slow-growing forage lichens (largely from the *Cladina* genus). Additionally, the energy costs of movement and foraging increase due to higher amounts of downed woody debris and greater snow depths resulting from reduced canopy interception (Schaefer and Pruitt 1991). In the long-term, however, fire may play an important role in maintaining the diversity and abundance of lichen forage (Klein 1982; Schaefer and Pruitt 1991).

Klein (1982) stressed the importance of differentiating between short- and long-term effects of forest fires on caribou habitat, suggesting that fire may reduce an ecosystem's potential to support caribou for approximately 50 years, but over the long-term, it likely benefits caribou habitat by resetting forest succession (Coxson and Marsh 2001). Similarly, Skoog (1968) suggested that although forest fires can destroy large tracts of winter habitat, theoretically reducing the potential carrying capacity of the overall range, caribou populations occur at much lower densities than the maximum determined by the abundance of forage lichens. Thus, the abundance of forage is not always a primary cause of population declines. However, more recent research has suggested that with the onset of global climate change, forest fire intervals may become shorter, further decreasing the area of mature spruce–lichen forest and the availability of terrestrial lichens (Stocks et al. 1998; Rupp et al. 2006).

The question of when a burn is no longer a 'burn' to caribou is especially important when assessing the availability of habitat across a herd's range (Francis et al. 2013). The consensus is that 50 years is an appropriate benchmark for this relationship (Joly et al. 2003; Dalerum et al. 2007; Sorensen et al. 2008). In 2008, Environment Canada published its Scientific Review for the Identification of Critical Habitat for Woodland Caribou (*Rangifer tarandus caribou*), Boreal Population, in Canada. In that report, a herd's total range disturbance was calculated as the area recently burned (in the last 50 years) plus the area of anthropogenic (human-caused) disturbance (Environment Canada 2008). In 2011, the area considered to be 'recently burned' was changed to any burn that was 40 years or younger; however, this was not a result of new information regarding habitat suitability, rather it was a constraint imposed by mapping limitations across jurisdictions (Environment Canada 2011).

Environment Canada (2011) developed a quantitative relationship between total range disturbance and the probability of persistence of a population of boreal caribou (e.g., 35% total range disturbance = 60% probability of persistence). Although their report was focused on boreal caribou, the method of linking a herd's persistence to range disturbance has been applied to other populations (e.g., Reid et al. 2013; Environment Canada 2014), and as suggested by Francis et al. (2013), it is important to better understand these dynamics as they relate to specific herds and other ecotypes of caribou.

When considering long-term range conservation and management for caribou, it is important to quantify and qualify the cumulative change in habitat resulting from natural disturbance, such as forest fires, and human activities. When considering forest fires, habitat loss and recovery can be quantified by determining the time and conditions required for forage lichens to recover post-fire. The magnitude of the effect of forest fires can be qualified by exploring the suite of behavioural responses caribou display when they encounter burns within their range. This information can then be related to the predicted effects of environmental change, proposed resource development, or other anthropogenic disturbances.

Research objectives

The Klaza Caribou Herd (KCH) in west-central Yukon is an example of a NM herd that has increasingly been subjected to anthropogenic and natural disturbance. My thesis is focused on this herd, and is part of a larger initiative by Environment Yukon to conduct a range-wide assessment of the KCH "…to assess risk to population viability, define management objectives, and identify actions to meet the objectives for focal wildlife species" (Francis et al. 2013, p. vii). Francis et al. (2013) identified forest fire as a natural factor that can cumulatively influence caribou habitat, and recommended the development of a quantitative threshold for 'recently burned habitat' specific to the winter range of the KCH.

The overall goal of this research is to understand the contribution of forest fires to cumulative habitat change across the winter range of woodland caribou. Although it is relatively simple to quantify total area burned, there is considerable uncertainty in our understanding of the ecological conditions that allow caribou to use or re-occupy habitats that have been changed by fire. I integrated field vegetation data collected in the summer of 2014 with global positioning system (GPS) collar data for caribou to investigate the relationship between habitat selection and burns during the early and late winter seasons. Specifically, I addressed the following research objectives:

1. Examine the environmental characteristics that influence the variability of lichen abundance within burns.

2. Examine range-wide habitat selection strategies during the early and late winter as well as those strategies employed by caribou that occupied recent burns.

Study area

The study area is focused on the annual range of the KCH (Environment Yukon 2014) in west-central Yukon. The range encompasses approximately 11,095 km^2 and is roughly bounded by the Yukon River to the north and east, the White River to the west, and the Nisling River to the south (Figure 1). This area lies primarily within the Klondike Plateau Ecoregion, and to a lesser extent, the Yukon Plateau-Central Ecoregion (Yukon Ecoregions Working Group [YEWG] 2004; Soil Landscapes of Canada Working Group 2013). The area is characterised by smooth, rolling hills often with ridges and tors protruding from ridge tops, and narrow, V-shaped valleys (YEWG 2004). Due to the region's fluvial origin and absence of glacial scouring, there are very few lakes (YEWG 2004). The Klondike Plateau is also within a zone of extensive discontinuous permafrost, with 50 to 90% of the soils containing permafrost (McKillop 2013), especially in valley bottom sediment deposits and upland slopes (YEWG 2013). Elevations range from 300 m at the Yukon River to approximately 2,000 m at Apex Mountain, which is located roughly in the centre of the KCH annual range.

The climate within the KCH range is largely continental, with very cold winters and warm summers (YEWG 2013). Forests of the Klondike Plateau are dominated by white (*Picea glauca*) and black spruce (*P. mariana*) stands, either unmixed or mixed with balsam poplar (*Populus balsamifera*; typical of floodplains), paper birch (*Betula papyrifera*), or trembling aspen (*Populus tremuloides*; YEWG 2013). Unlike habitats typical of woodland caribou herds in the southern Yukon, lodgepole pine (*Pinus contorta*) are largely absent from the area, except near the Yukon River.

The study area also hosts a number of existing and potential human activities, including placer mining, mineral exploration, a proposed hard rock mine using existing and new access roads, existing resource access roads in the north (via the Yukon River) and southeast parts of the range, hunting, trapping, and year-round motorized recreation.

Klaza caribou

The KCH are part of the NM DU of woodland caribou (COSEWIC 2011), which were assessed as Special Concern by COSEWIC in 2002 and again in 2014, and federally listed on Schedule I of the Species at Risk Act in 2005. NM caribou are generally distinguished from other DUs by seasonal altitudinal migrations and a diet composed primarily of terrestrial lichens (Heard and Vagt 1998; Environment Canada 2012). During winter, NM caribou access terrestrial lichens by cratering through snow with their hooves. NM caribou generally spend the winter season at low elevations in mature lodgepole pine or black spruce stands or on windswept slopes, and move to higher elevations for spring and summer (COSEWIC 2011). Klaza caribou winter primarily in the alpine and subalpine, with the herd's winter range characterized as a relatively low-snow area due to its location in the snow-shadow of the St. Elias mountain range (Farnell et al. 1991; Kuzyk et al. 1999).

Study of the KCH, formerly known as the Klotassin herd (Jingfors 1989), began in the mid-1980s when the Casino Trail was being constructed to access the Casino Mine (Farnell et al. 1991). Between 1987 and 1990, 17 very high frequency (VHF) collars were deployed on female caribou in the herd (Farnell et al. 1991), with additional collars deployed and active until 2000 as part of a study on the neighbouring Aishihik caribou herd. The Aishihik herd's range overlaps the southern portion of the KCH range, near the Nisling River (Hayes et al. 2003). With a restored interest in the development of the Casino Mine project, Environment Yukon deployed 45 GPS radio collars on Klaza caribou from 2012 to 2015 (Hegel 2013).

Population estimates were conducted for the KCH from 1989 to 2012, although survey methods and study areas changed over the years making population estimates difficult to compare (Hegel 2013). During a 2012 mark-resight survey, the herd was estimated at 1,179 caribou (95% CI = 952–1,461) (Hegel 2013). Although this is higher than previous estimates, it is not possible to determine a population trend as previous survey areas and methods are incomparable (Hegel 2013).

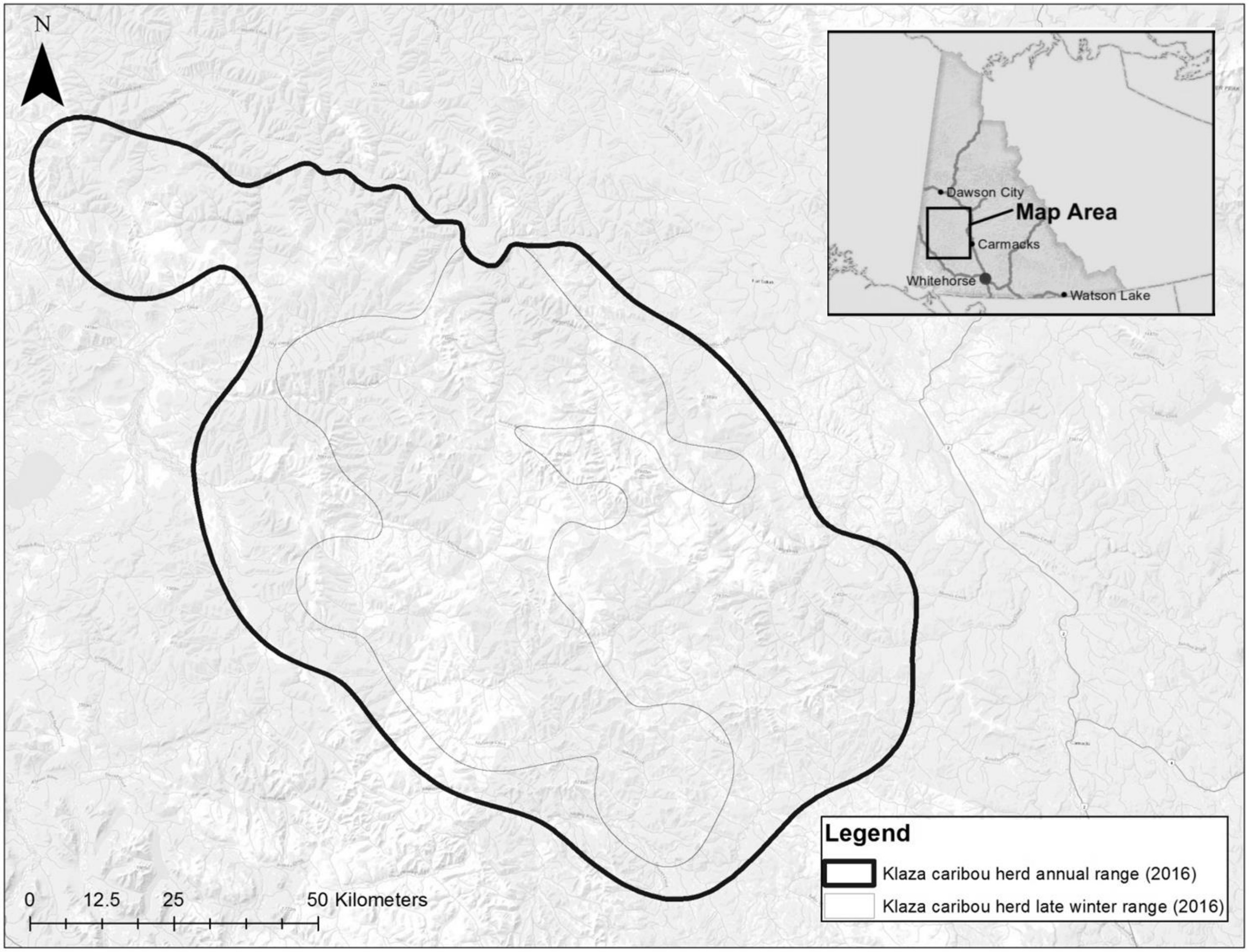

Figure 1. The study area, located within the annual range of the Klaza caribou herd, west-central Yukon.

Forest fire history

Forest fires are considered frequent in the Klondike Plateau, known as the ‘fire belt’ of the Yukon, with fires regularly occurring every 50 to 200 years (Yukon Government 2010); however, fire cycles in the broader boreal forest region are often estimated to be between 50 to 100 years (Rowe 1983; Payette 1992). As of 2015, approximately 20% of the KCH’s annual range was burned in the last 50 years (2,213 km^2 of 11,095 km^2; Figure 2), with the majority of mapped burns (40 out of 59 burns) having occurred in the last 20 years (Figure 2). During the study period (2011–2015), recent burns comprised an average of 19.3 and 23.3% of the annual and late winter ranges, respectively (Table 1). Most burns are located closer to the edge of the herd’s range, with a large area of higher elevation habitat in the centre of the range remaining unburned in recent years (Figure 3).

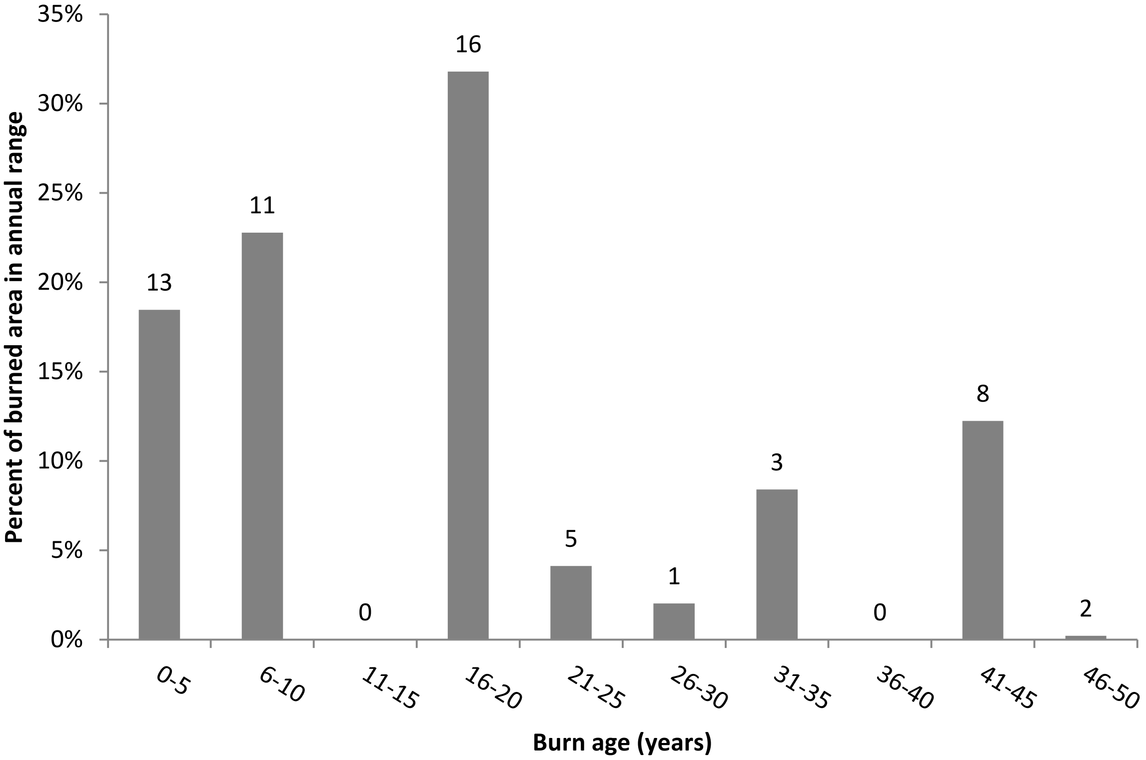

Figure 2. Percent of area burned by burn age in the annual range of the Klaza caribou herd, as of 2015. The numbers above the bars represent the number of burns within each burn age category (Yukon Fire History database 2016).

Table 1. Total area of recent burns (≤50 years) in the Klaza caribou herd's annual and late winter range (Environment Yukon 2016), during the study period, 2011–2015.

Year	Annual range		Late winter range	
	Area burned[1] (ha)	**Total area (ha) of recent burns[2] (% of range)**	**Area burned[1] (ha)**	**Total area (ha) of recent burns[2] (% of range)**
2011	1,802	206,809 (19.1)	1,733	100,059 (23.2)
2012	156	206,964 (19.1)	0	100,059 (23.2)
2013	924	207,888 (19.2)	914	100,973 (23.4)
2014	0	207,888 (19.2)	0	100,973 (23.4)
2015	9,960	217,847 (20.1)	410	101,383 (23.5)

[1] Area burned refers to new burns that had occurred by the end of each calendar year.

[2] Total area of recent burns refers to burns that occurred in the last 50 years.

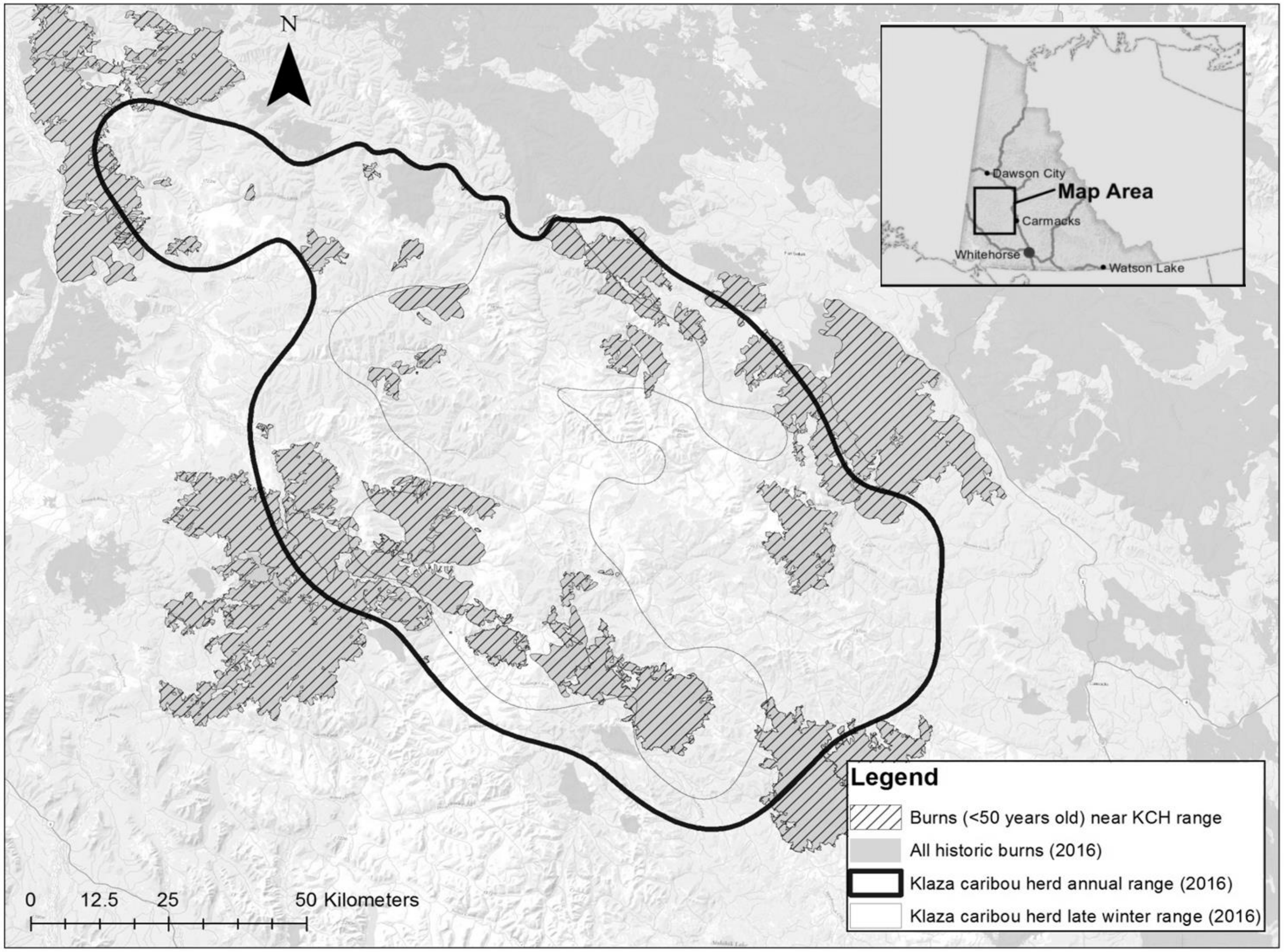

Figure 3. Recent burns near the study area, located within the annual and late winter range of the Klaza caribou herd, west-central Yukon (range polygons developed by Environment Yukon, 2016).

CHAPTER TWO: POST-FIRE DYNAMICS OF FORAGE LICHENS ON THE KLAZA CARIBOU HERD RANGE

Introduction

Forest fire is the primary natural disturbance process that influences the distribution and abundance of terrestrial lichens across most boreal and sub-boreal ecosystems (Coxson and Marsh 2001; Skatter et al. 2014). Lichens are the main food source for caribou, particularly during winter (Klein 1982; Thomas et al. 1996; Johnson et al. 2001; Bergerud et al. 2008), thus, a better understanding of the spatiotemporal succession of lichens can provide guidance for the conservation and management of caribou habitat. The length of time required for lichens to return to fire-affected areas in sufficient abundance to support the forage requirements of caribou is thought to be 50–60 years (Thomas et al. 1996; Joly et al. 2003, 2007; Dalerum et al. 2007; Sorensen et al. 2008; Collins et al. 2011). However, the characteristics of the fire history (fire intervals, intensity, severity, etc.) and the biophysical attributes of the ecosystem (landforms and vegetation) can influence the time and conditions needed for the reestablishment of forage lichens. At the landscape scale, the time since burn may provide a sufficient gauge of relative abundance (cover, volume, and/or biomass) of forage, but at the scale of an individual burn, this relationship can be complicated by site variability.

In forests, lichen productivity is typically highest on sites with coarse, well-drained, nutrient-poor soils, and a canopy dominated by coniferous trees (Carroll and Bliss 1982; Coxson and Marsh 2001; Coxson 2015; Haughian and Burton 2015). The sequence of lichen succession typical of severe burns in the boreal forest generally includes a period of early succession (10–30 years post-fire) dominated by *Cladonia* spp., followed by a mid-succession stage (30–80 years post-fire) dominated by ‘reindeer lichens’ (*Cladina mitis/arbuscula, C. rangiferina,* and *Cladonia uncialis*), and finally, a late succession stage (>80 years post-fire) that is dominated by *Cladina stellaris* (Rowe and Scotter 1973; Thomas and Kiliaan 1998; Coxson and Marsh 2001; Cichowski and Haeussler 2013; Haughian and Burton 2015). The richness of lichen species may peak around 30 years post-fire and then decrease, as some lichen species, predominantly from the *Cladina* genus, exclude others (Holt et al. 2008).

The dynamics of lichen succession are likely variable throughout the range of woodland caribou, with factors such as latitude, soil texture, moisture regime, and local climate affecting reestablishment and growth rates (Coxson and Marsh 2001; Coxson 2015; Haughian and Burton 2015; Girard et al. 2017). At a finer, stand-level scale, lichen distribution and abundance is patchy and largely influenced by changes in canopy cover (Sulyma and Coxson 2001). Haughian and Burton (2015) reported that this patchiness is influenced more by niche processes, such as environmental micro-habitats, than neutral processes (e.g., random post-fire colonization), suggesting that management efforts should focus on understanding the stand characteristics that support these productive lichen patches. The amount of light reaching the forest floor is considered a significant factor in lichen growth, with fires promoting a more open canopy (Nelson et al. 2013), resulting in periods of desiccation that prevent competitors, such as mosses, from establishing in a stand (Cichowski and Haeussler 2013).

Even if fire-lichen dynamics could be accurately predicted to determine quality and quantity of forage lichens, other factors influence lichen availability, and ultimately, the selection strategies of caribou. Access to terrestrial lichens during winter can be limited by snow depth, hardness, and density (Collins and Smith 1991; Johnson et al. 2001, 2002). Not only does deep, hard snow restrict movement, but it can also hinder the accessibility and detection of lichen (Collins and Smith 1991; Johnson et al. 2000, 2001). To reduce predation risk, caribou avoid wolves and their primary prey, moose (*Alces alces*; Bergerud et al. 1984; Seip 1992; Johnson et al. 2001; James et al. 2004). Fire is believed to affect this spatial separation by increasing the overlap between caribou, moose, and wolves, potentially resulting in higher predation rates (Wittmer et al. 2005; Robinson et al. 2012).

Despite a number of studies that have explored fire-lichen dynamics, there is still uncertainty in our understanding of the successional patterns of forage lichens, primarily as they relate to the quantity and quality of caribou habitat. Many studies exploring caribou-fire relationships have focused on the boreal or barren-ground ecotypes of caribou (e.g., Schaefer and Pruitt 1991; Anderson and Johnson 2014). Thus, it is convenient to extrapolate those results and associated conservation guidance to all ecotypes of *Rangifer*. Environment Canada's (2011) guidance on habitat disturbance, considers burns ≤50 years old as 'disturbed' habitat. However, forest communities across the range of woodland caribou may have different fire-lichen dynamics that influence the recovery or succession of habitat. For example, lodgepole pine (*Pinus contorta*) forests typical of some NM caribou winter ranges may not reach peak lichen productivity until 80–120 years post-fire (Coxson and Marsh 2001).

Accurately predicting the burn-specific succession sequence of forage lichens is difficult due to local variation in environmental conditions, including fire history (Skoog 1968; Rowe 1983; Payette 1992). However, this is an important consideration when assessing the ability of winter range to support populations of woodland caribou. Thus, I used plot-level data to identify environmental factors that influenced the variability in lichen abundance within burns. I focused on the winter range of a population of NM caribou – the KCH – found across a northern semi-arid ecosystem in west-central Yukon with a frequent fire-return interval. I quantified the biomass and cover of forage lichens in burns of a given age. I then investigated the reputed influence of the time since burn on lichen abundance, in addition to other ecologically plausible factors that may influence the establishment and succession of terrestrial lichens that serve as forage for woodland caribou.

Methods

Site selection and plot layout

Field sites were selected from existing burns located within the KCH annual range. The annual range was considered to be representative of the maximum boundary of current and future winter range. Forest fires in proximity to the KCH annual range were mapped as polygons in the 2013 Yukon Fire History database and were available from Wildland Fire Management (database updated 18 February 2014). I randomly selected 51 burn polygons, ranging in age from 1 to 63 years old (burned between 1951 and 2013), and in size from 1 to 97,665 ha. Polygons intersected or were within the buffered (10 km) annual range of the KCH estimated for 2014. Burn polygons were then separated into four pre-determined burn age classes (1–10, 11–30, 31–50, and 51–70 years post-fire). Due to the challenging access (all sites helicopter accessible only), unburned sites were typically located adjacent to burn plots; however, I ensured that unburned plots were located well outside of burns. Some unburned plots were randomly selected where landing sites were accessible.

Sample plots were selected according to a random distance and bearing from the edge of the burn. To avoid edge effects, all plots were located at least 100 m into the burn interior which was based on an in-field assessment of stand characteristics (e.g., no apparent transition from burned to unburned forest). Plots were also located at least 100 m from each other. To sample across potential patches of lichen (Haughian and Burton 2015) and avoid sampling bias involved with randomly encountered linear terrain features, each plot was composed of five parallel 20-m transects, spaced 5 m apart (Figure 4), and oriented in a random direction.

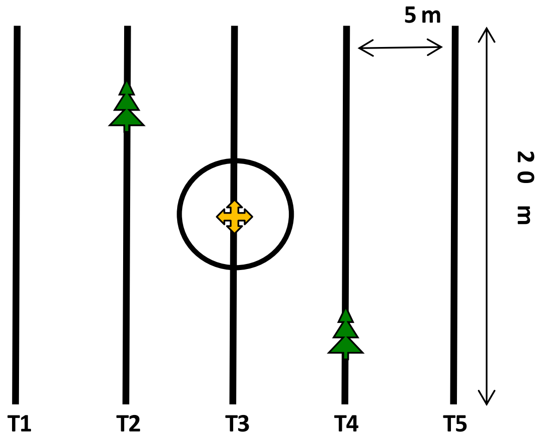

Figure 4. Schematic diagram of the plot layout for vegetation sampling, with the quad arrow representing plot centre, trees representing the location of canopy openness measurements, and the central circle representing the area measured for tall shrub cover.

Sampling design

Field sampling was conducted in July and August of 2014. At each sample plot I described the site, including dominant species of tree, tall shrub, and understory; soil moisture regime; burn description (presence of burned snags or soil); and indications of the presence of foraging by caribou (e.g., foraged/disturbed lichen or pellet groups). Soil moisture regime was a subjective classification based on general environmental factors, soil properties, and indicator plants (B.C. Ministry of Forests and Range and B.C. Ministry of Environment 2010). Additionally, I recorded topographic characteristics for the plot, including elevation (m), aspect (degrees), and slope (percent) (Appendix A: Table 17).

I used a marked boot/step-point intercept method to measure percent ground cover of plant and lichen groups (National Applied Resource Sciences Center 1999). I recorded ground cover at 0.5-m intervals/steps per 20-m transect (200 total points/plot), with the dominant species recorded per step. Species percent cover estimates were derived by taking the average from these 200 points. Lichens were identified to species when possible; otherwise they were grouped by genus (e.g., *Cladonia* spp., *Peltigera* spp.). I recorded heights, measured as the portion of intact, living thallus (Moen et al. 2007), of all fruticose lichens (i.e., *Cladina* spp., *Cladonia* spp., and *Stereocaulon* spp.) to the nearest 0.5 cm each time a dominant lichen was intercepted along a transect. I considered *Cladina arbuscula/mitis* (referred to as *C. mitis* henceforth), *C. rangiferina/stygia* (referred to as *C. rangiferina* henceforth), *Cladina stellaris*, *Cetraria cucullata*, *Cet. ericetorum/islandica* (grouped as *Cet. ericetorum/islandica*), and *Cet. nivalis* to be primary forage species (henceforth referred to as ‘forage lichens’). *Cladonia uncialis* was not differentiated from *Cladonia* spp. at all sites, thus it was excluded from the forage lichen group for analyses. Non-lichen ground cover was classified into discrete groups: graminoids, forbs, bryophytes, dwarf shrubs (<50 cm tall), mushrooms, litter, soil, and rock (Appendix A: Table 19; Barrier 2011). At the plot centre I conducted a visual estimate of tall shrub cover (>50 cm tall) in a 5.64 m^2 (0.01 ha) fixed-area plot and identified the top three most frequent shrub species.

I used a rod relascope to determine stand basal area (m^2/ha) in each plot. Canopy openness was recorded with a levelled fisheye lens camera where I took two hemispherical photos of the canopy. I used Gap Light Analyzer (V. 2.0) software (GLA 2.0; Frazer et al. 1999) to calculate average percent canopy openness. The time since burn was determined based on the mapped burn age and/or by using an increment borer to core five of the most representative conifer trees (if present) within the plot. The cores were dated at the University of Northern British Columbia's Enhanced Forestry Lab. The height of each cored tree was measured using a Vertex hypsometer (Haglöf, Sweden).

Results from the tree core samples suggested that the stand age of some of the plots (primarily older burns) did not reflect the stand age determined using burn mapping (i.e., the date at which the most recent burn occurred). Of the plots that were inconsistent with burn mapping, the aged tree cores generally were older than the mapped burn. Of the 78 plots for which trees were cored, 28 had tree age differences that were equal to or greater than 50 years apart, and of the plots (n = 48) that were within a mapped burn boundary, 21 had a minimum tree age that was older than the mapped burn age. To maintain consistency for determining the plot age class, I developed a protocol to determine time since burn for vegetation plot age classes (Appendix A: Table 18). Plots were considered equal to the mapped burn age, minimum core age, median core age, or maximum core age depending on their location inside or outside of a mapped burn and the difference between mapped burn age and tree core results.

Although I attempted to measure key mechanistic parameters that may influence lichen recovery and growth following fire, field logistics (e.g. helicopter time and site accessibility) prevented the testing of all factors known to influence the abundance of terrestrial lichens. In an effort to assess a large number of sites, at the expense of an intensive assessment of a few sites, I did not measure variables that required substantial time and/or complex field equipment (e.g., soil classification, permafrost).

Data analyses

Examining lichen abundance by burn age

I categorized stand age into 15-year intervals, allowing for statistical comparison of age classes representing the time since last major fire (Skatter et al. 2014). Lichen volume and biomass were estimated using methods outlined by Fleischman (1990). Volume was calculated by multiplying percent cover (% = dm^2/m^2) by height (dm). Lichen volume is highly correlated with biomass (Fleischman 1990; Kumpula et al. 2000; Moen et al. 2007), thus biomass estimates were derived for each species by multiplying Fleischman's (1990) ratio functions (lichen species weight to volume) by volume (dm^3/m^2). The ratios of weight to volume ranged from 9.6 to 20.3, depending on the species. These values for biomass must be considered cautiously, as no lichen samples were taken to develop site-specific correction factors for this area. The volume estimates of *Cladina* spp. and *Cetraria* spp. were summed into a final volume estimate for each plot. Stand age (i.e., time since burn) was considered to be the time at which the ground burned, and did not account for the lag time between fire and seedling emergence. I used a non-parametric pairwise comparison test, with Tukey's method of adjustment for multiple comparisons, to test for differences in lichen volume among stand age groups (Tukey 1953). All statistical analyses were completed using Stata/IC (Version 12.1; StataCorp 2011) statistical software.

Statistical model selection and assessment

I used zero-inflated count models (Martin et al. 2005) to investigate ecological factors hypothesised to explain measured variation in lichen volume. Although the lichen data collected in this study were not discrete integers, as one observes with counts, these data were non-negative, overdispersed (i.e., the sample variance is greater than the mean), and had an excess of zeros (i.e., no lichens present) (Martin et al. 2005; Richards 2008; Zuur et al. 2007, 2009, 2010). To conform to count distributions, I rounded all volume estimates to the nearest whole number.

Count models were constructed using either Poisson or negative binomial distributions. Considering the prevalence of zeros in the data (20%), I used a Vuong test to determine if a zero-inflated model was appropriate (Vuong 1989; Long and Freese 2001). In preparation for data analysis, lichen data were summarized for each plot into a single value representing the total forage lichen group (all *Cladina* spp. and *Cetraria* spp.). I used the terrain and environmental variables collected during field studies to construct candidate models to explain observed variation in lichen volume (Appendix A: Table 17; Table 2), with a focus on more mechanistic predictors that allowed a test of ecological hypotheses (Wiersma et al. 2011). I used quadratic terms to allow for a non-linear representation of the independent variables where necessary (e.g., tree height; Long and Freese 2001).

Zero-inflated models may be more informative if the same predictors are believed to influence both the false (undetected because of sampling error) and true zeros (low frequency of occurrence due to demographics, competition, or habitat quality), or if there is no clear evidence that distinguishes between the mechanisms affecting species distribution (e.g., presence/absence) and abundance (Martin et al. 2005). Thus, I used a consistent set of variables to represent the hypothesized ecological processes influencing lichen distribution (presence/absence) and abundance (volume counts).

I used fractional logit models (generalized linear models with binomial family and logit link; Papke and Wooldridge 1996) to investigate ecological factors hypothesised to explain variation in the percent cover of lichen. This allowed me to determine if a consistent set of predictor variables influenced the volume and percentage cover of forage lichens. Percent cover is a common and more rapid measure of lichen abundance.

To control for a lack of sample independence across plots, all models were clustered by site ID (i.e., the same mapped burn) allowing for the estimate of robust standard errors (Long and Freese 2001). I used tolerance scores and a threshold of ≤2 to test predictor variables for collinearity (Menard 2002). Using deviation coding, I generated a design matrix of dummy variables to represent contrasts between classes of categorical predictor variables (Hendrickx 1999).

Table 2. Variables used in count models of volume of forage lichens in burns surveyed on the Klaza caribou range, west-central Yukon, 2014.

Parameter	Abbreviation	Description
Aspect	North+East	Northness (cosine of aspect) and eastness (sine of aspect)
Elevation	Elev	Elevation above sea level (m)
Canopy openness	CO	Percent canopy openness (expressed as a proportion)
Cover type	CT	Dominant cover type in plot (e.g., coniferous, deciduous, open)
Slope angle	S	Percent slope (expressed as a proportion)
Soil moisture regime	SMR	Categorical soil moisture regime (dry, moist, wet)
Stand basal area	SBA	Cross-sectional area of trees in the stand (m^2)
Tall shrub cover	TSC	Percent of tall shrub (>0.50 m) cover (expressed as a proportion)
Time since burn	TSB	Number of years since the site burned, estimated using burn mapping and/or tree core aging
Tree height	TH	Average tree height (m)

I used Akaike's Information Criterion (Akaike 1973) adjusted for small sample sizes (AIC_c) to select the most parsimonious model(s) (i.e., the fewest predictor variables to explain the greatest variation in the data). I used cross-validation to test the predictive ability of the most parsimonious models. Using a jackknifing procedure, I sequentially withheld the data from each plot during the model-fitting process; the resulting model (N-1, where N = number of sample plots) and the withheld record were then used to generate an independent prediction (Bridger et al. 2016). I regressed the predicted versus observed values and used the coefficient of determination (R^2) to measure the variation explained by each model. Also, I used Wilcoxon sign-rank equality tests for matched pairs to statistically compare the differences in the predicted and observed lichen values.

Results

General plot characteristics

A total of 100 plots were sampled in 18 different burns and 13 different unburned sites (Table 3; Figure 5), with plots ranging in age from 1 to 271 years post-fire. Over one third of all mapped burns in the KCH were sampled; 29% of which were recent burns (<50 years old). Age class 1 (1–10 year old burns) sites were sampled with the lowest intensity, while sites in age classes 3 to 5 were sampled more frequently to focus efforts on age classes that were more likely to support forage lichens (Rowe and Scotter 1973; Thomas and Kiliaan 1998; Coxson and Marsh 2001; Cichowski and Haeussler 2013). Despite being a high priority for sampling, burns in age class 4 (51–70 years old) were uncommon within the KCH's annual range, and sampling efforts were expanded to a burn on the northeast side of the Yukon River (Figure 5).

Table 3. Vegetation sampling in burns by age class (based on both tree core results and existing burn mapping), on the Klaza caribou range, west-central Yukon, 2014.

Age class (years)	Number of unique burns/sites	Number of sample plots
1 (1–10)	2	3
2 (11–30)	7	16
3 (31–50)	6	21
4 (51–70)	3	18
5 (>70/unburned)	13	42
TOTAL	**31**	**100**

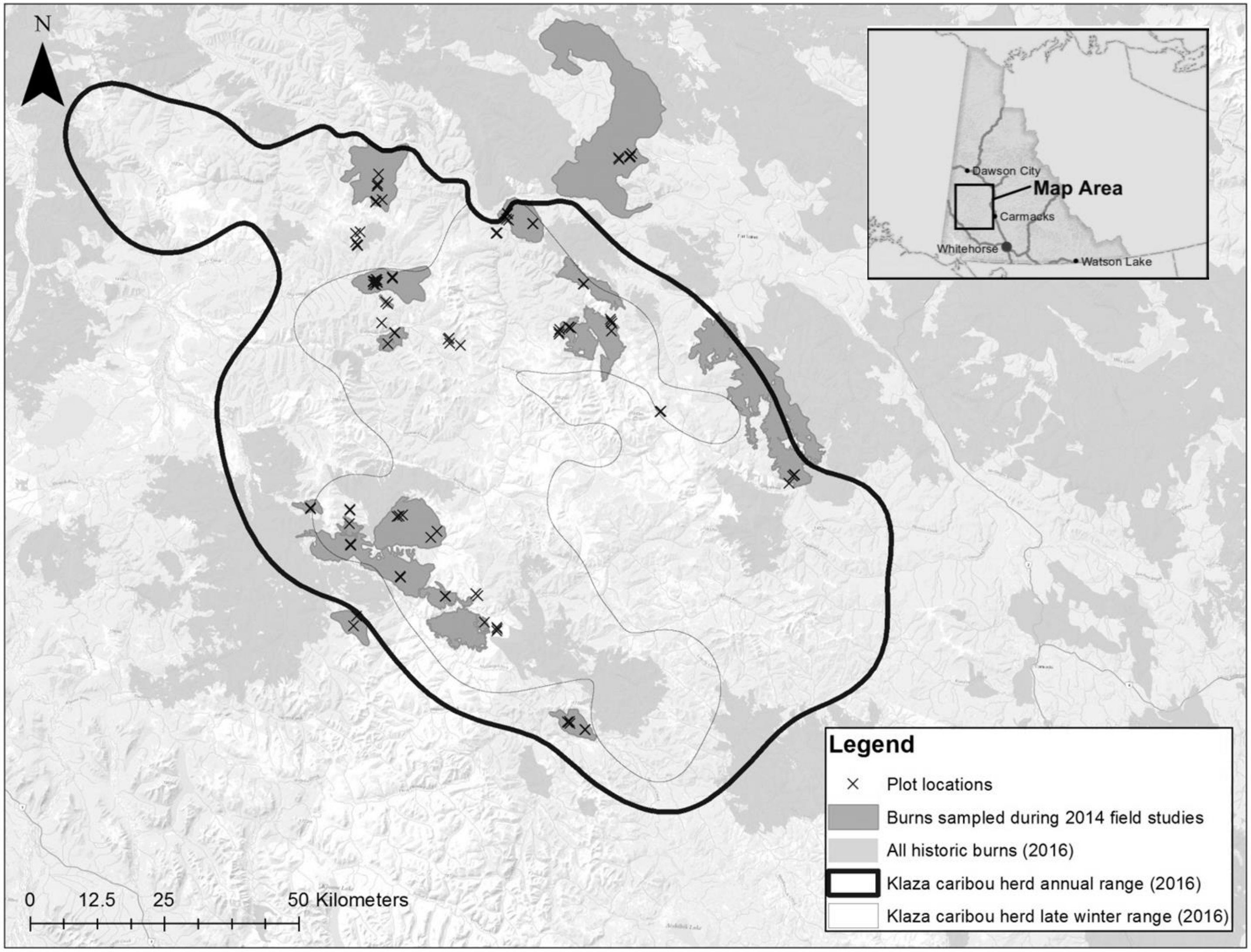

Figure 5. Burns and vegetation plots sampled in summer 2014 within the Klaza caribou range, west-central Yukon.

Patterns in the abundance of forage lichens post-fire

The succession sequence of lichens began with *Cladonia* spp. dominating post-fire, followed by *Cladina mitis* and *C. rangiferina* dominating both mid and late successional stages (Figure 6). The percent cover of forage lichens (*Cladina* spp. and *Cetraria* spp.) increased 40 years post-fire, peaked at 85–99 years, and then decreased in plots that were >99 years old (Table 4). Similar patterns were observed for both lichen volume and biomass (Table 4). Lichen volume in 25–39 year old burns was significantly less than all older age groups ($P < 0.05$), with the exception of the 55–69 and 100–149 year age groups ($P = 0.98$ and 0.32, respectively; Table 5). Conversely, the volume of lichen in 40–54 year old burns was not significantly different than all older age groups ($P > 0.05$; Table 5).

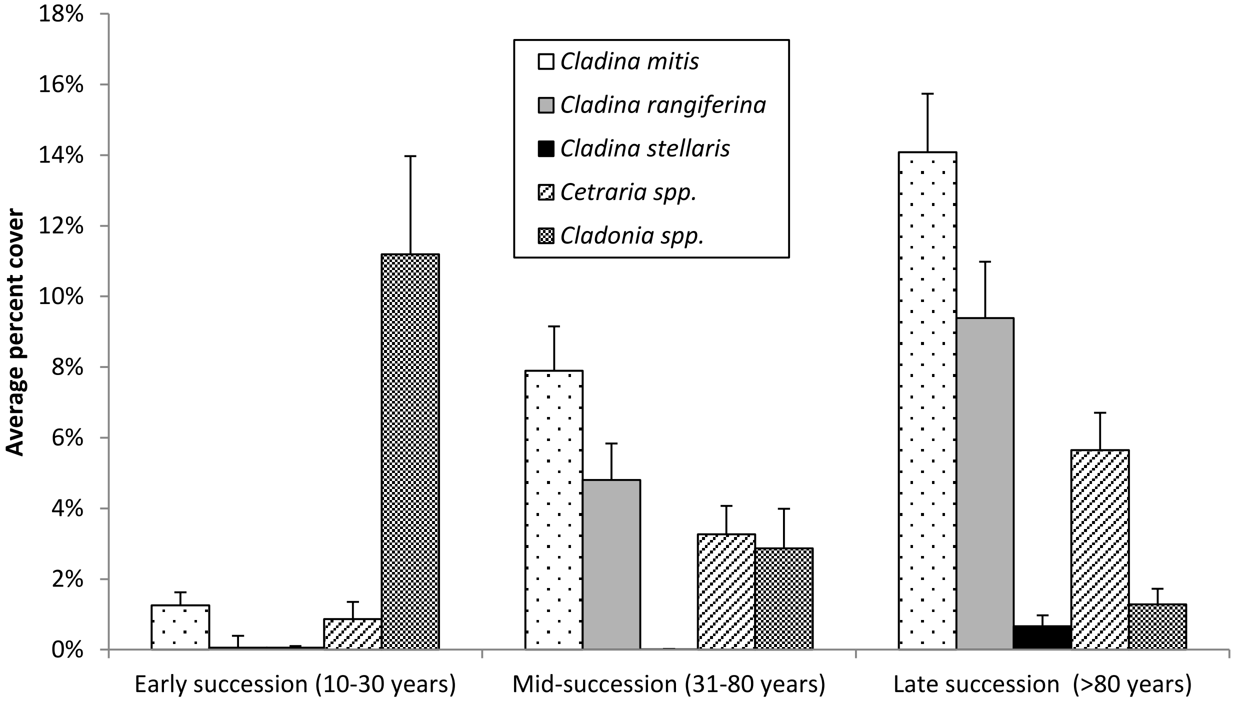

Figure 6. Sequence of post-fire lichen succession observed in the Klaza caribou range, west-central Yukon, summer 2014.

Table 4. Mean (standard error, SE) cover, volume, and biomass of forage lichens in vegetation plots in burns by 15-year intervals, Klaza caribou range, west-central Yukon, summer 2014. Plots aged 100–149 and ≥150 years were grouped together rather than by 15-year intervals due to low sample sizes.

Age group (years)	***n***	**Lichen cover**		**Lichen volume**		**Lichen biomass**[1]	
		Mean (%)	**SE**	**Mean (dm^3/m^2)**	**SE**	**Mean (kg/ha)**	**SE**
<25	18	2.6	1.0	0.8	2.4	113	52
25–39	8	4.2	2.1	2.2	3.6	236	110
40–54	14	24.5	4.4	16.1	2.7	1,786	371
55–69	18	9.5	3.0	6.2	2.4	895	283
70–84	8	39.4	7.7	22.8	3.6	2,670	537
85–99	5	41.2	7.9	25.1	4.6	3,061	709
100–149	16	22.2	3.8	12.3	2.5	1,588	306
≥150	13	29.3	6.9	17.9	2.8	2,061	474

[1] Ratios of volume to biomass for each lichen species were derived from Fleischman (1990).

Table 5. Non-parametric pairwise comparison (using Tukey's method of adjustment for multiple comparisons) of lichen volume in different-aged vegetation plots in burns in the Klaza caribou range, west-central Yukon. *P* < 0.05 indicates a significant difference (in bold) between age groups.

Age group	*n*	Mean volume (dm^3/m^2)	±SE	Tukey test statistics	Age group (years)						
					25–39	**40–54**	**55–69**	**70–84**	**85–99**	**100–149**	**≥150**
<25 years	18	0.77	2.40	Contrast	1.45	15.33	5.38	21.98	24.37	11.48	17.10
				t-score	0.34	4.23	1.59	5.08	4.74	3.28	4.62
				P	1.00	**<0.001**	0.76	**<0.001**	**<0.001**	**0.03**	**<0.001**
25–39 years	8	2.22	3.60	Contrast		13.88	3.93	20.53	22.92	10.04	15.65
				t-score		3.08	0.91	4.04	3.95	2.28	3.42
				P		0.05	0.98	**<0.001**	**<0.001**	0.32	**0.02**
40–54 years	14	16.10	2.72	Contrast			-9.94	6.66	9.04	-3.84	1.77
				t-score			-2.74	1.48	1.71	-1.03	0.45
				P			0.12	0.82	0.68	0.97	1.00
55–69 years	18	6.15	2.40	Contrast				16.60	18.99	6.10	11.71
				t-score				3.84	3.69	1.75	3.16
				P				**0.01**	**0.01**	0.66	**0.04**
70–84 years	8	22.75	3.60	Contrast					2.39	-10.50	-4.89
				t-score					0.41	-2.38	-1.07
				P					1.00	0.26	0.96
85–99 years	5	25.14	4.55	Contrast						-12.88	-7.27
				t-score						-2.47	-1.36
				P						0.22	0.87
100–149 years	16	12.26	2.54	Contrast							5.61
				t-score							1.48
				P							0.82
≥150 years	13	17.87	2.82	Contrast							-
				t-score							-
				P							-

Statistical models

Model selection

I used data from 100 field sites within the KCH annual range to generate statistical count models. The alpha parameter was significantly different from zero in all model sets and Vuong z-tests for each model set were significant ($P < 0.05$) indicating that a zero-inflated negative binomial distribution was most supported; however, during the cross-validation process, the zero-inflated negative binomial (ZINB) models would not converge, and the models were run using a zero-inflated Poisson (ZIP) model. Although the coefficient estimates differed, the same top-ranked candidate models were identified during the model selection process using both distributions.

The most parsimonious model for lichen volume included covariates for time since burn, canopy openness, stand basal area, tree height, and cover type (Table 6). The top-ranked model had a large AIC_c weight ($AIC_c w_i = 0.95$; Table 6). For lichen cover, there were seven top-ranked models (Δ_i $AIC_c \leq 2.00$) accounting for 79% of the AIC_c weight (Table 6).

Table 6. Summary of model selection statistics for the most parsimonious models (Δ_i AIC$_c$ ≤2) of volume and cover of forage lichens in the Klaza caribou range, west-central Yukon. Parameters are defined in Table 2.

Rank	**Model parameters**	**AIC$_{ci}$**	**AIC$_c$ w_i**	**Δ_i AIC$_c$**
	Volume models			
1	Time since burn+Canopy openness+Stand basal area+Tree height+Tree height^2+Cover type	782.58	0.95	0.00
	Cover models			
1	Canopy openness +Stand basal area+Tree height+Tree height^2	71.37	0.17	0.00
2	Canopy openness +Tree height+Tree height^2	71.43	0.16	0.06
3	Tree height+Tree height^2+Cover type	71.79	0.13	0.42
4	Time since burn+Canopy openness +Tree height+Tree height^2	72.07	0.12	0.70
5	Time since burn+Canopy openness +Stand basal area+Tree height+Tree height^2	72.96	0.08	1.59
6	Time since burn+Tree height+Tree height^2	73.02	0.07	1.65
7	Canopy openness +Tree height+Tree height^2+Tall shrub cover	73.36	0.06	1.99

Forage lichen volume

Stand basal area, tree height, and cover type were significant predictors of the volume of forage lichens in the top-ranked ZIP model (Figure 7, Appendix B: Table 20). Lichen volume increased with stand basal area and the negative quadratic term for tree height (tree height^2) indicated a positive non-linear influence on volume (Appendix B: Table 22). Deciduous and open cover types had a negative influence on lichen volume when compared to coniferous cover types (Appendix B: Table 22). The covariate for time since burn had only a small effect and was not statistically significant.

For the binary part of the ZIP model, canopy openness, stand basal area, and cover type were all significant predictors of lichen presence/absence (Figure 8, Appendix B: Table 22). For every unit increase in canopy openness (%) and stand basal area (m^2/ha), the probability of lichen absence decreased (Appendix B: Table 22). The negative quadratic term for tree height (tree height^2) indicated a positive non-linear influence on the probability of lichen absence (Appendix B: Table 22). Relative to coniferous cover types, deciduous cover types increased the probability of lichen absence, while open cover types decreased the probability of lichen absence (Appendix B: Table 22).

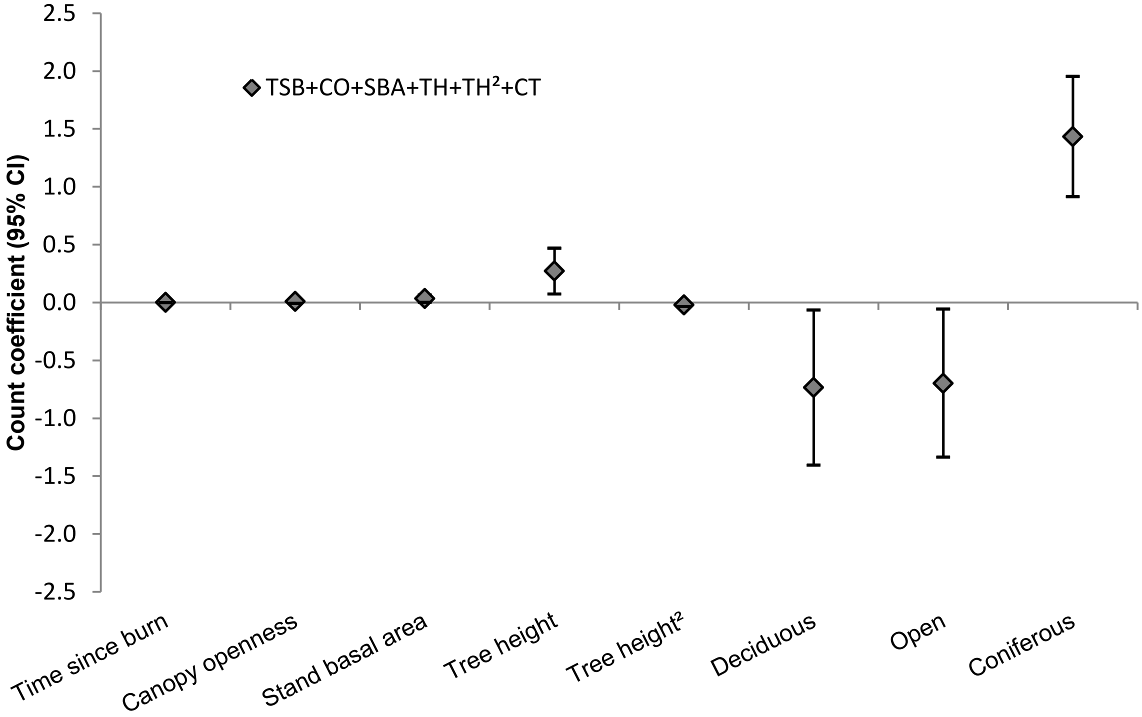

Figure 7. Coefficients for the count portion of the top-ranked zero-inflated Poisson model ($\Delta_i AIC_c \leq 2$) explaining lichen volume (counts) in the Klaza caribou range, west-central Yukon. All variables defined in Table 2.

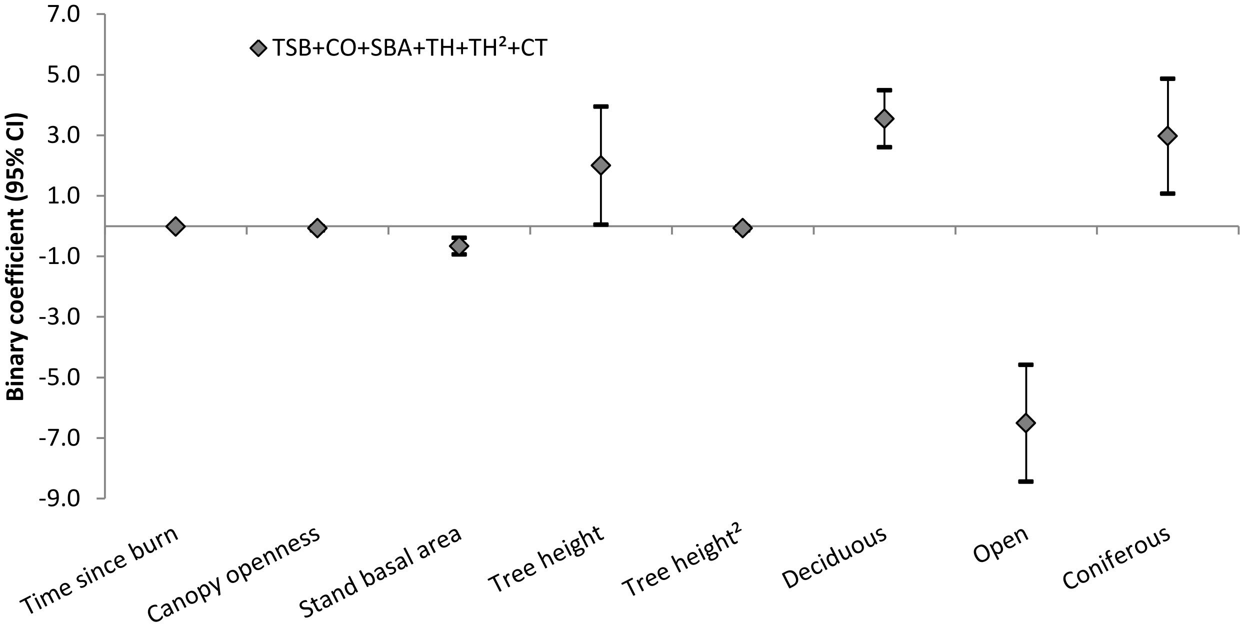

Figure 8. Coefficients for the binary portion of the top-ranked zero-inflated Poisson model ($\Delta_i AIC_c \leq 2$) representing influences on the probability of lichen absence in the Klaza caribou range, west-central Yukon. All variables defined in Table 2.

Forage lichen cover

The covariates included in the top-ranked models for percent cover of forage lichens were the same as those in the top volume model; however, there were fewer predictors in each candidate model (Appendix B: Table 21). Time since burn was included as a significant covariate in two of the seven top-ranked models (Appendix B: Table 23). Canopy openness was included in five of the top-ranked models (Appendix B: Table 23). Similarly, stand basal area was included in two top models and was a positive influence on cover in both (Appendix B: Table 23). Tree height was included in all top models (Appendix B: Table 23). The negative quadratic term for tree height (tree height^2) indicated a positive non-linear influence on lichen cover.

Model fit

The top-ranked ZIP model explained 54% of the observed variability in lichen volume (Table 7). For lichen cover, the top-ranked model explained 42% of the observed variability (Table 7). None of the top-ranked models for either lichen volume or cover showed a significant difference between observed and predicted values (Table 7). When plotted against the observed count values, the unstandardized residuals (predicted-observed lichen volume counts) revealed that the top ZIP model predicted well in the middle of the value range (10–25 dm^3/m^2), but over-predicted at lower volumes, and under-predicted at higher volumes (Appendix B: Figure 16). The same pattern was observed for most of the top-ranked cover models, with relatively good prediction between 10 and 40% cover; however the residuals of three of the top-ranked fractional logit models ($CO+TH+TH^2$, $TH+TH^2+CT$, and $CO+TH+TH^2+TSC$; defined in Table 2) did not show the same negative trend and were much closer to the observed values (Appendix B: Figure 17).

Table 7. R^2 values (observed versus predicted values) and test statistics from Wilcoxon sign-rank equality tests for matched pairs for the analysis of differences between observed and predicted lichen volume and cover values for the top-ranked (Δ_i AIC_c differed by ≤2 points) count and fractional models. The test revealed no statistically significant differences in the distribution of observed and predicted values when $P > 0.05$.

AIC_c rank	**Model**	**R^2**	**Wilcoxon sign-rank equality tests**	
			z-score	***P-value***
	Volume models			
1	Time since burn+Canopy openness+Stand basal area+Tree height+Tree height^2+Cover type	0.54	-0.85	0.40
	Cover models			
1	Canopy openness +Stand basal area+Tree height+Tree height^2	0.42	-0.89	0.37
2	Canopy openness +Tree height+Tree height^2	0.33	-0.65	0.52
3	Tree height+Tree height^2+Cover type	0.41	-0.29	0.77
4	Time since burn+Canopy openness +Tree height+Tree height^2	0.38	-0.53	0.60
5	Time since burn+Canopy openness +Stand basal area+Tree height+Tree height^2	0.44	-0.84	0.34
6	Time since burn+Tree height+Tree height^2	0.45	-0.29	0.78
7	Canopy openness +Tree height+Tree height^2+Tall shrub cover	0.33	-0.58	0.56

Discussion

Results from this study support previous research concluding that forage lichens require approximately 40–60 years to recover to levels that support caribou foraging (Schaefer and Pruitt 1991; Thomas et al. 1996; Joly et al. 2003, 2007, 2010; Collins et al. 2011). However, I observed that the average volume of forage lichens in burns that are 40–54 years post-fire is no different than in older burns (Table 5). These results also revealed that a suite of environmental factors may contribute to lichen recovery. Canopy openness, tree height, cover type, and stand basal area were consistently the best indicators of lichen volume and cover, but the time since burn did not have a significant influence on either metric (Table 6). Nonetheless, the time since burn was included in the top-ranked volume model, suggesting it is an important covariate relative to the other parameters in the model.

Lichen succession and abundance post-fire

The sequence of lichen succession was consistent with stand-replacing burns in the boreal forest (Rowe and Scotter 1973; Morneau and Payette 1989; Thomas and Kiliaan 1998; Coxson and Marsh 2001; Cichowski and Haeussler 2013; Skatter etal. 2014). Unlike other findings, however, *Cladina stellaris* did not dominate the late succession phase of the post-fire community; instead, *C. mitis* and *C. rangiferina* dominated the older age classes (Figure 6). *C. stellaris* may be rare in the KCH range because the fire frequency is too short to allow for the establishment of climax stands. Further, the majority of stands greater than 80 years old may be transitional, mid-seral stands and/or the majority of soils in the region may promote an earlier dominance of feather mosses, thus preventing *C. stellaris* from dominating.

My results suggest there was considerable variability in the abundance of lichen within a burn. For example, in plots that were 45 years post-fire, the average biomass was 1,786 kg/ha, but it ranged between 0 and 4,920 kg/ha. One possible explanation for the spatial variability in the biomass of forage lichens is the accuracy of burn mapping, especially older burns that were irregularly and/or poorly mapped, and which may not recognise large unburned patches within a burn perimeter (Yukon Government 2014). Additionally, although it is assumed most fires in the region are stand-replacing, some areas of a burn may have been of lower intensity and severity due to a lack of fuel (e.g., sparse spruce slopes, deciduous stands; Johnstone and Stuart-Chapin 2006). During site investigations it was apparent that there was considerable variability in burn intensity and typically the abundance of lichen was greater in low-intensity burns. For example, evidence of fire (e.g., burned soil or trees) often became less apparent on north or northeast-facing slopes with sparse tree cover, suggesting the lack of fuel (e.g., trees) resulted in less intense and severe burning. These slopes are also likely underlain by discontinuous permafrost, enabling lichen species to outcompete vascular plants that have difficulty establishing and growing in permafrost soils. In combination, these two factors may have resulted in relatively high levels of lichen abundance in some younger burns.

Skatter et al. (2014) observed a bi-modal pattern to lichen recovery in northern Saskatchewan, with higher lichen cover in stands ≤40 years old and >100 years old. Although my results do not show the same bi-modal pattern, they are similar in that lichen cover was substantially greater in 41–50 year old stands than 61–70 year old stands (25% versus 10%, respectively), increasing in stands from 70–110 years-post-fire (Table 4). This may indicate that the 41–50 year old plots in the KCH range are transitional, mid-seral stands (Haughian and Burton 2015). Holt et al. (2008) also reported that lichen cover, height, and species richness peaked at 30 years post-fire in northwestern Alaska. Similarly, Joly et al. (2010) highlighted the presence of relatively high lichen biomass in younger (<51 years old) plots in their Alaskan study area; however, they considered these to be ‘anomalous’ and not representative of the overall relationship of stand age and lichen abundance. Nelson et al. (2013) detected high levels of lichen cover in young burns (<25 years old), but they were exclusively located on alluvial terraces. These studies (Holt et al. 2008; Joly et al. 2010; Nelson et al. 2013; Skatter et al. 2014) support my results and are consistent with Haughian and Burton’s (2015) conclusion that the distribution of lichens is predominantly influenced by microsite characteristics that may change throughout the successional process.

Influence of stand characteristics on lichen volume

Past research suggests that lichens are most productive in open canopy forests with well-drained and nutrient poor soils (Coxson and Marsh 2001; Sulyma and Coxson 2001; Coxson 2015; Haughian and Burton 2015). Even though soil moisture regime (Appendix A: Table 17) was documented in my study, forest stand characteristics proved to be the most influential predictors of lichen volume (Table 6 and Figure 7). In addition, the time since burn, although not a significant predictor, did improve the performance of the top-ranked volume model (Table 6). The coefficient estimates from the ZIP models suggest that the same environmental parameters influence both the presence and amount (count) of lichen and that the mechanisms influencing the two processes do not differ (Appendix B: Table 22). The exception to this was canopy openness, which had a significant influence on the probability of lichen absence, but not on the volume counts. Results from the models for lichen cover were similar (Table 6), although there was relatively more model uncertainty in the cover models (i.e., 13 models made up 100% of the weight of evidence for cover versus two models for volume) and those models were less predictive. While the measured parameters were able to explain a considerable amount of the observed variability in lichen abundance, it is important to note that additional, unmeasured parameters, such as soil type and permafrost, might influence lichen recovery and growth following fire.

Cover type was a strong predictor of lichen volume (Figure 7), with coniferous types positively influencing abundance. According to Roturier et al. (2017), burned sites with remnant trees provide the best conditions for lichen establishment and growth. Open cover types were typically associated with younger burns (<45 years post-fire), whereas coniferous types were associated with older stands (minimum 34 years post-fire). Tree height was also an influential factor, which may be a result of its ability to broadly represent two mechanistic processes in a stand: site productivity and light interception. In combination with stand age, tree height has long been used to calculate site index – an estimate of site productivity for tree growth (Yukon Government 2006; Skovsgaard and Vanclay 2008). Additionally, tree height also may represent the amount of light reaching the forest floor, with taller trees decreasing canopy openness. Considering that lichens are generally poor competitors, but can thrive in nutrient-poor and dry sites (Haughian and Burton 2015), the negative coefficient for tree height^2 appears appropriate, and confirms findings by Lesmerises et al. (2011), who noted that a combination of landscape variables and stand age, density, and height best estimated both lichen occurrence and biomass.

A number of stand characteristics were important predictors of lichen abundance in the KCH range, yet model fit improved with the inclusion a measure of time since burn. This is consistent with the findings of other studies that reported stand age as influential, but not necessarily a significant predictor of lichen abundance (Arseneault et al 1997; Joly et al. 2010; Lesmerises et al. 2011). Some of the lack of explanatory power for stand age in the count models could be a product of relatively imprecise methods for identifying the boundaries of older burns (e.g., ~40–60 years old), and aging the stand, despite using two methods to determine stand age. Visually, the relationship between stand age and lichen abundance appears to be nonlinear and asymptotic; however, the quadratic term for stand age did not improve model performance. With the vast majority of sample plots being less than 150 years old, the scope of my field data may not have captured the complete successional pathway of terrestrial lichens across the range of the KCH.

Using biomass thresholds for changes in caribou selection strategies

Although lichen cover may be an adequate indication of the succession pattern of forage lichens following fire, biomass has more influence on caribou distribution and foraging behaviour (Klein 1982; Thomas et al. 1996; Joly et al. 2003, 2010; Collins et al. 2011). Some studies have estimated lichen cover at the landscape scale (Nelson et al. 2013; Caslys Consulting 2014), but fewer have provided estimates of biomass in burns of a range of ages (Joly et al. 2010; Collins et al. 2011; Lesmerises et al. 2011). Lichen biomass studies often are limited to landscapes with low canopy cover, unlike the majority of areas occupied by woodland caribou (Lesmerises et al. 2011).

Estimates from herds across the circumarctic suggest that the biomass of forage lichens typically found on the winter range of caribou is highly variable, but tends to be at least 500 kg/ha (Barrier 2011; Appendix C: Table 24). Thomas et al. (1996) observed a marked increase in the selection by caribou of older forest stands (41–60 versus 61–80 years post fire) and suggested that caribou may respond to a threshold in lichen biomass. At these sites, the average biomass of *Cetraria nivalis* increased from 30 to 72 kg/ha and *Cladina mitis* increased from 547 to 1,029 kg/ha (Thomas et al. 1996). This is similar to observed values of lichen biomass at sites avoided and selected by caribou in the Nelchina herd of Alaska, bordering the KCH range (Collins et al. 2011). During winter, Nelchina caribou selected stands that were more than 80 years post-fire, with >20% lichen cover, and more than 1,250 kg/ha of forage lichens. Nelchina caribou abandoned previously used winter range after grazing reduced the lichen biomass to approximately 400 kg/ha (Collins et al. 2011).

My estimates of lichen biomass (using ratios from Fleischman (1990) suggest that in the KCH range, some plots in 45-year old burns may have enough biomass to support foraging by caribou (Figure 9). While up to 23% of plots ≤50 years old could hypothetically be selected by Klaza caribou, no plots in burns less than 45 years old had lichen biomass levels above the Nelchina herd's observed selection threshold (Figure 9). The period of the greatest lichen productivity appears to occur between 80 and 110 years post-fire (Figure 9), which is consistent with findings from other studies (Coxson and Marsh 2001). Further, the amount of variability in lichen biomass observed beyond 45 years is notable (Figure 9), and highlights the importance of considering the influence of terrain and environmental variables on lichen biomass. Currently 20% of the annual and 24% of the late winter KCH range is comprised of burns that are less than 50 years old, regarded as disturbed habitat that results in a decline in boreal caribou (Environment Canada 2008; 2011), thus better understanding these relationships could have substantial implications for range assessment processes.

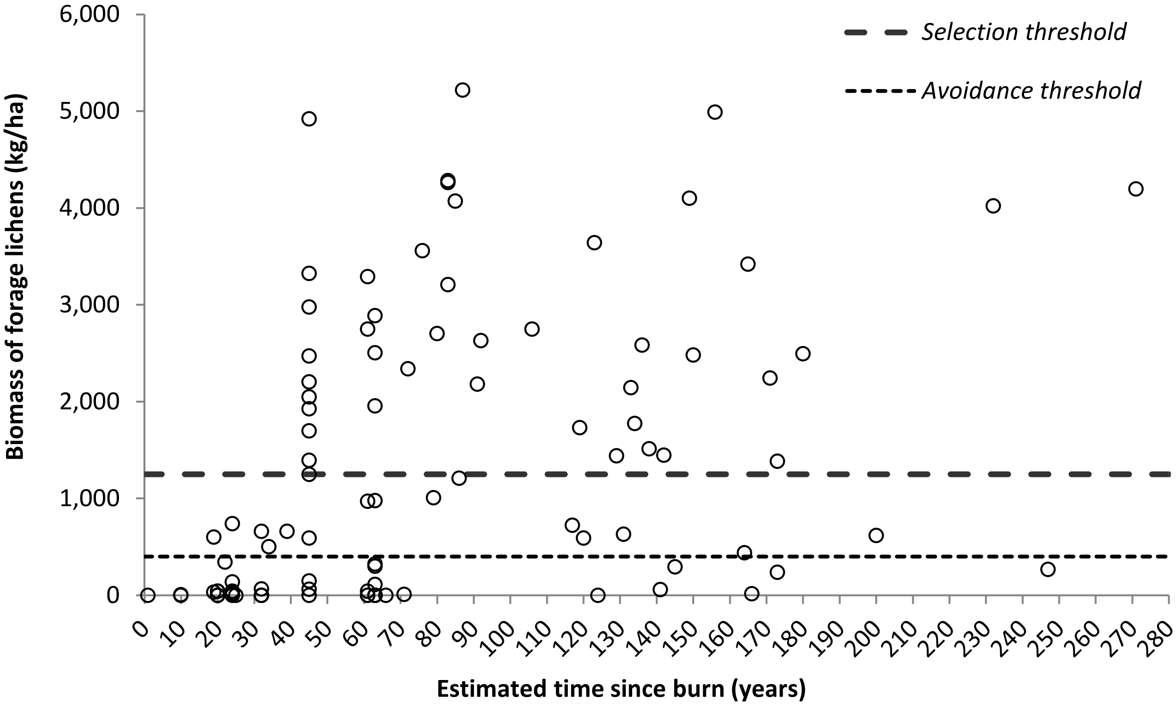

Figure 9. Biomass of forage lichens within different-aged stands throughout the Klaza caribou range, west-central Yukon. The two threshold values (selection = 1,250 kg/ha; avoidance = 400 kg/ha) represent biomass levels at sites avoided and selected by caribou in the neighbouring Nelchina herd (Collins et al. 2011).

The measures of biomass focus on quantity only, not availability of forage lichens. This distinction must be made clear, especially in the context of burns. Other factors (e.g., snow depth and crust, patch size, accessibility, etc.) influence both the availability of forage and the strategies that caribou employ when selecting habitat (Collins and Smith 1991; Johnson et al. 2001). Accessing lichen-rich patches within burns may prove difficult for caribou depending on the size of the burn, presence of downed woody debris, higher snow cover due to a lack of tree interception, and/or the ability of caribou to detect lichen patches (Johnson et al. 2000). Additionally, caribou also select habitat based on a number of non-forage related features, such as slope, elevation, and aspect (Johnson et al. 2000). This highlights the need to further evaluate how selection strategies for the KCH in burns differ from the rest of their winter range.

Conclusions

Data from the KCH range revealed that lichen abundance can be relatively high in stands as young as 45 years post-fire, with biomass levels consistent with stands used by caribou from other herds. At the landscape level, post-fire stand age provides a rudimentary guide for the availability of lichen, but my results suggest that alone it does not explain a large amount of the variability observed at finer scales. Within a burn, there is considerable variability that is likely driven by the presence of microsites favourable to lichen recovery. Identifying these lichen-rich patches can be done on a burn-specific basis using remotely sensed data (Lesmerises et al. 2011; Nelson et al. 2013; Caslys Consulting 2014). However, lichen-rich areas within a burn may be in a transitional, mid-seral phase of succession, and may have reduced lichen abundance over time as climax plant communities begin to dominate.

My results add to the growing body of literature that suggests lichen succession cannot be predicted using only estimates of time since fire. Age-based thresholds, although easy to use and understand, do not capture the variability of lichen abundance within burns. An age-based threshold for burns (e.g., 50 years) provides a conservative evaluation of lichen availability at the landscape level; however, a combination of environmental factors can explain a larger portion of the total variance in lichen abundance within and among burns. The challenge for managers is to have a consistent and robust approach to lichen assessment that can be continually applied over time and space as natural and anthropogenic changes occur within caribou ranges.

CHAPTER THREE: VARIATION IN HABITAT SELECTION STRATEGIES OF WOODLAND CARIBOU IN BURNS

Introduction

The spatial and temporal distribution of caribou manifests as a hierarchy of complex decisions related to the distribution and availability of resources and predation risk (Johnson 1980; Rettie and Messier 2000; Johnson et al. 2001, 2002; Boyce 2006; DeCesare et al. 2012). Disturbance from fire can have resounding effects on forest structure and composition, landscape patterns (Payette 1992), and ultimately influence key components of wildlife habitat (Schaefer and Pruitt 1991; Joly et al. 2003). Caribou may avoid winter habitat for approximately 60 years after a fire due to the time required for terrestrial lichens to recover (Thomas et al. 1996; Joly et al. 2003; Joly et al. 2007; Collins et al. 2011). Nonetheless, locations of satellite-collared caribou reveal that recently burned areas are used by some individuals, even during winter when slow-growing terrestrial lichens are the primary food source (Thomas and Kiliaan 1998; Anderson and Johnson 2014). The nature of this use is not well-understood and is often obscured when studies of habitat selection are conducted at the scale of the population. In such cases, data from multiple individuals are pooled and the collective pattern suggests avoidance of recent burns, whereas some individuals may use those areas (e.g., Hegel and O’Donoghue 2015).

Caribou will use habitat within and adjacent to burns during winter (Thomas et al. 1998; Joly et al. 2003; Anderson and Johnson 2014); however, relative to total range use this habitat is rarely selected by caribou. The use of recently burned stands has been attributed to a number of factors, including the availability of vascular forage in younger regenerating burns (11–20 years old; Joly et al. 2003), reduced predation risk as a result of improved visibility, efficient movement between high-quality habitat patches, and snow conditions (i.e., depth and hardness) that permit relatively easy access to terrestrial vegetation (Miller 1976; Thomas et al. 1998). Conversely, others have suggested that caribou avoid burns because of the presence of predators and other cervids (e.g., wolves and moose), the lack of forage species used by caribou, and unfavourable snow conditions (James et al. 2004; Gustine et al. 2006; Gustine and Parker 2008; Collins et al. 2011).

Resource selection functions (RSFs) have been used to model habitat selection strategies across a variety of spatial scales (Boyce et al. 2002; Manly et al. 2002), often providing an indication of patterns of selection at the population level, but seldom at the individual level (Thomas and Taylor 1990; Gustine et al. 2006; Gillingham and Parker 2008). Examining use and availability of resources by individuals may help to better explain variation in selection strategies (Thomas and Taylor 1990). Such variation is believed to be an important survival strategy (Gustine et al. 2006) that allows individuals to use a range of habitats as they become available. The resource selection strategies of caribou can vary among individuals (Gustine and Parker 2008), but is largely driven by decisions related to forage availability and quality as well as predation risk (Apps et al. 2001; Johnson et al. 2001; Briand et al. 2009). These decisions are complicated by individual responses to the environment at a range of scales (Rettie and Messier 2000; Gustine et al. 2006), where the behavioural and physiological plasticity of an individual is likely more advantageous than a general optimal foraging strategy (Johnson et al. 2001).

The late winter season provides unique challenges to the habitat selection strategies of caribou (Schaefer and Pruitt 1991; Johnson et al. 2001). Cold temperatures and deep, hard snow reduce accessibility to forage and result in high energetic costs of travel on and cratering through snow (Fancy and White 1985; Collins and Smith 1991; Schaefer and Pruitt 1991; Schaefer 1996; Johnson et al. 2001). These energetic demands are exacerbated by the increasing gestational demands experienced by pregnant caribou (Parker et al. 2005; Joly et al. 2015), as the majority of fetal mass is accumulated in the final trimester (Robbins and Robbins 1979), roughly aligning with the late winter season (Hegel and O'Donoghue 2015). The quality of late winter habitat may influence calf condition, recruitment, and the survival of juveniles (White 1983; Gaillard et al. 1998; Post and Klein 1999; Adams 2003).

Habitat selection of caribou during winter in the Yukon has been modeled using fire history, vegetation cover, and terrain (Florkiewicz et al. 2004, 2007; Barker and Hegel 2012). A recent analysis of winter habitat selection revealed that caribou from the KCH avoided burns at the landscape scale. However, these models were dependent on a relatively simple measure of habitat (burned versus unburned) and did not quantify variation in habitat selection among individuals. The relative importance of some habitat variables, such as burns, may vary across scales, and those that are most limiting to individuals should be considered at the broadest scale (Rettie and Messier 2000; Gustine et al. 2006). More complex measures of burns, including multiple age classes, location in burns (core versus edge), and burn size may help to reveal the importance of different burn characteristics at different scales.

Snow conditions have an important influence on the seasonal and finer-scale habitat selection of caribou (Collins and Smith 1991; Russell et al. 1993; Johnson et al. 2001; Tyler 2010). Not only does deep snow restrict movement and increase energetic costs, but it can also hinder the accessibility and detection of lichens (Collins and Smith 1991; Johnson et al. 2000, 2001; Gustine et al 2006). Contrasting habitat selection strategies between the early and late winter seasons can provide a rudimentary proxy for a snow depth metric, as snow conditions are believed to be generally more favourable earlier in the winter (e.g., shallower, less crusty).

In this study, I quantified the habitat selection strategies of the KCH during the winter. These caribou are found across a landscape with a relatively high frequency of forest fire. Thus, I examined range-wide habitat selection strategies during the early and late winter, as well as those strategies employed by caribou that occupied recent burns. Recognising the potential for variation in strategy, I developed resource selection functions for individual caribou that were monitored with GPS collars. I hypothesized that in general, caribou would avoid burns during both early and late winter; however, some individuals would use burns primarily during the early winter season when snow conditions were less limiting. Further, I predicted that this use would be concentrated near high-density patches of lichens at the edge of burns. By focussing on fine-scale selection by individuals and on locations solely within burns, my results provide a unique analysis of burn use by caribou during winter.

Methods

I modelled the habitat selection strategies of the KCH at two ecological scales. First, I used RSFs to model habitat selection of individual caribou across the winter range.

Second, I developed logistic regression models that focused exclusively on the use of recent burns by caribou. These burn-focused models used only early and late winter locations located within recent burns (≤50 years), plus a 500-m buffer outside burns. The 500-m buffer captured imprecision in the burn boundaries and accounted for the influence of edge on habitat selection (Joly et al. 2007).

Caribou locations

From 2012 to 2015, a total of 45 Iridium global positioning satellite (GPS) radio-collars (ATS; Model G211OE) were deployed on Klaza caribou (all females), with fix rates programmed at 5-, 8-, or 13-hour intervals. The fix success (i.e., a successful relocation attempt) was high (>95%; Hegel and O'Donoghue 2015), suggesting that the inference to caribou behaviour, primarily habitat selection, was not impeded by cover or topographic bias (Frair et al. 2010).

The seasons of interest, early and late winter, were defined as 1 November to 31 January and 1 February to 30 April, respectively. This is consistent with Hegel and O'Donoghue's (2015) work on the KCH and is supported by differences in snow depth and density (using NASA's Modern Era Retrospective Analysis for Research and Applications [MERRA] dataset; Russell et al. 2013) between the two seasons during the study period (2012–2016). Both snow depth and density on the annual KCH range were higher during late winter compared to early winter (34% and 23% higher, respectively; Russell et al. 2013). I assumed that the existing collar data were representative of the KCH; however, those data represented only a small proportion of individuals in the herd, over a relatively short time period, and were focused on only one sex and age group (i.e., adult females).

RSF and burn-focused model inputs

I used knowledge of the ecology of woodland caribou, with a focus on factors that may explain the observed distribution of the KCH during the early and late winter seasons, to select candidate environmental variables. These variables represent broad mechanistic processes for habitat selection: vegetation, disturbance as a function of forest fire, and terrain.

As part of an initiative to better understand habitat use by caribou, a model representing the spatial extent of seven lichen cover classes, ranging from 0 to >50% cover, was mapped within the KCH range (Caslys Consulting 2014). The imagery was acquired before the collaring program began in 2012, thus any areas that burned after 22 June 2009 were not represented. Updated Landsat 7 ETM scenes (4 August 2010, 25 June 2013, and 17 July 2015) were used to examine the post-2009 burns and determine if there were any discrepancies (e.g., large, unburned patches) within the recently mapped burn polygons. Where unburned patches were identified within burn polygons, I used ArcMap (version 10.3) to digitize those patches and merge them with the 2009 lichen cover raster (original, unburned lichen cover pixel values were re-assigned). For the purposes of this analysis, I assumed no lichen cover in the remaining burn polygons. I used a moving-window operation to calculate the density of lichen cover in areas defined by the mean 95th centile movement distance of 8-hr fixes across all years during both early and late winter seasons (distance = 4,432 m, SD = 765 m). Thus, my measure of lichen density was considered as the mean percent cover of lichen within a 4,432-m window and served as the principal land cover for the analysis.

Caribou are known to select habitat in proximity to watercourses during winter, as the hard, unobstructed surface may allow for more efficient travel (Schaefer and Pruitt 1991; Thomas et al. 1998; Hegel and O'Donoghue 2015). Thus, I used watercourses from Geomatics Yukon at the 1:1,000,000 scale to determine distance to major watercourses (rivers and named creeks) from telemetered caribou locations.

I generated a number of variables that characterized fire history. Based on the existing literature and findings from the second chapter of this thesis, recently burned areas were considered as any forest stands that were ≤50 years post-fire (Environment Canada 2008). For the RSF models, habitat was represented as burned or unburned (binary term), density of burn patches within a seasonal home range, and distance to burns (Anderson and Johnson 2014). For the burn-focused logistic models, burn variables included time since burn and a categorical term for burn perimeter (core, inner 500 m, and outer 500 m). To represent the burn perimeter, I generated two 500-m buffers inside and outside mapped burn polygons (Joly et al. 2003). The area beyond the inner 500-m buffer was considered the core of the burn, whereas the area beyond the outer 500-m buffer was considered unburned, and was assumed to be beyond the influence of the burn ecotone. The 'unburned' perimeter class was not used for the burn-focused model.

Thomas (1991) reported that during winter, caribou moved through individual burns up to 25 km wide, but avoided large regions with a high density of recent burns. Similarly, Dalerum et al. (2007) suggested that caribou avoided burns at the scale of the home range. Thus, I used a moving window to calculate the density of burns for each season-year. I used the 95% kernel estimate (ArcView 3.2a Home Range Extension) to calculate the seasonal range for each individual. Seasonal range areas for each individual were derived by summing the total area of all estimated kernels (one to seven). These values were then averaged across individuals for each season-year and served to define the extent of the moving window.

Aspect and slope were derived from a 30-m resolution digital elevation model (DEM; Yukon Department of Environment, Information Management & Technology Branch 2015). I used those data to calculate the Topographic Position Index (TPI) representing discrete terrain classes: valley, gentle slope, steep slope, and ridgeline (Jenness 2006; Dickson and Beier 2007; Johnson et al. 2015) in ArcView (V. 3.2a, ESRI 2005). I used my knowledge of the study area in combination with visual aids (hillshade overlaid with TPI model outputs, Google Earth) to select representative values of ridgelines, valleys, and the slope gradient. This resulted in a valley threshold of -20 TPI units, a ridgeline threshold of 100 TPI units, and a slope value of 15 degrees (circular neighbourhood with 1500-m radius).

I used tolerance scores and a threshold of ≤2 to test predictor variables (Table 8) for excessive multicollinearity (Menard 2002). Using deviation coding, I generated a design matrix of dummy variables to represent contrasts between classes of categorical predictor variables (Hendrickx 1999).

Table 8. Environmental variables used in the candidate RSF and logistic models for early and late winter distribution and use of burns by the Klaza caribou herd, west-central Yukon. A single asterisk (*) indicates variables used only in the RSF models, and ** indicates variables used only in logistic models.

Ecological variable	Unit	Description
Slope	degrees	Derived from DEM
Aspect (eastness)	n/a	Derived from DEM, sine-transformed from aspect values (radians)
Aspect (northness)	n/a	Derived from DEM, cosine-transformed from aspect values (radians)
Topographic position index	n/a	Derived from DEM to create categorical classes: valley, ridgeline, steep slope, gentle slope
Lichen density	percent	2009 Landsat imagery representing 0–>50% lichen cover & reclassified areas post-2009
Distance to water	M	Distance to major water courses
Burn variables		
Burn	Binary	Mapped burn polygons (1–50 years post-fire) and ‘unburned’ areas (>50 years)
Burn age**	Years	Mapped burn polygons (1–50 years post-fire) and ‘unburned’ areas (>50 years) within 500-m of burn polygons
Burn density*	ha/km^2	Density of recently burned area (≤50 years post-fire) within individual’s home range
Distance to burns*	M	Distance to the nearest mapped burn polygon
*Location of burn boundary***		
Core**	n/a	Burned area >500-m inside the burn boundary
Burn edge**	n/a	Burned area ≤500-m inside the burn boundary
Outer buffer**	n/a	Unburned area ≤500-m outside the burn boundary

Winter habitat selection: Resource selection function models

Determining use and availability

I determined resource availability (random locations) by calculating the 95th percentile movement rate of an individual within a 5-, 8-, or 13-hour interval (depending on the individual’s GPS collar fix rate) for each season-year. This provided the radius for a circle, centred on each caribou location, representing an individual’s potential for movement within an ecologically relevant time frame (Arthur et al. 1996; Johnson et al.

2005; Gustine et al. 2006; Gillingham and Parker 2008). To reduce bias in the estimated parameters (Northrup et al. 2013), I paired each caribou location with five locations selected randomly from within the circle (Johnson et al. 2005). This resulted in sample sizes of 48,430 and 242,150 used and available (random) locations, respectively.

Statistical model selection and assessment

I constructed a series of individual and season-year specific RSF models that represented plausible hypotheses explaining the distribution of collared caribou during early and late winter. I used paired (one use location to five random locations) conditional logistic regression to parameterise the RSF models (Manly et al. 2002; Johnson et al. 2005).

The most parsimonious model(s) were identified using Akaike's Information Criterion difference corrected for small sample sizes (ΔAIC_c; Akaike 1973; Burnham and Anderson 1998) and Akaike weights ($AIC_c w_i$). Models with a ΔAIC_c of ≤2 were considered plausible (Richards 2005; Symonds and Moussalli 2011). Then, for all caribou in each season-year, I tabulated the number of times each of the five candidate models was determined to be plausible ($\Delta AIC_c \leq 2.00$). I used weighted counts (each individual divided by its total number of top models) to account for bias resulting from a different number of top models per individual (one to five top models possible). The unweighted coefficients for each individual's single top model were averaged over each season-year to provide an indication of overall consistency in herd selection strategies (Anderson and Johnson 2014). Error was represented using 95% confidence intervals derived from the variance of averaged coefficients. Variance was estimated using the following equation (Marzluff et al. 2004):

$$\mathrm{Var}\,(\widehat{\widehat{\beta_{\mathrm{J}}}}) = \frac{1}{(n-1)}\sum_{i=1}^{n}\left(\widehat{\beta_{iJ}} - \hat{\hat{\beta}}_{\mathrm{J}}\right)^2$$

where β represents individual coefficient values, and n represents the number of animal-model combinations. Evaluating predictive capability is essential, as model selection is a relative measure of the most parsimonious model within the candidate set, not a measure of model fit. I used the Receiver Operating Characteristic (ROC) with independent cross validation to assess the predictive accuracy of the RSF models. Using a jackknifing procedure, I sequentially withheld the data for one cluster group (one used and five paired availability locations) during the model-fitting process; the resulting model (N-1) and the withheld record were then used to generate an independent prediction. I then calculated the area under the curve (AUC) generated from the nonparametric ROC. An AUC of 0.50 suggests a model has no predictive power, while a score of 1.00 suggests perfect prediction (Boyce et al. 2002). The ROC was a conservative measure of predictive accuracy as it assumed a case-control sample design (Boyce et al. 2002). For each individual caribou and season-year, model fit was assessed for the top-selected model only (i.e., the highest $\mathrm{AIC}_c w_i$ value).

Selection ratios for burn variables

For the RSF models, categorical burn age classes, burn perimeter use, and burn size classes (small, medium, and large) were initial model inputs; however, several of these classes had to be dropped due to near-complete separation (i.e., complete avoidance of an available resource; Gillingham and Parker 2008). To incorporate these resources of interest, I determined the ratio of used (GPS collar locations) to available (random) locations across years for each season; with available locations divided by five (the number of available locations generated per used location; Gillingham and Parker 2008). The selection ratio for each individual caribou was treated as a replicate after which I averaged ratios to represent selection for the sampled population.

Burn use: Logistic regression models

Approximately 12% of winter locations (*n* = 5,663) were located within 500 m of the boundaries of a mapped burn polygon. Thus, I used a grid of habitat selection units (HSUs) overlaid on burns to define individual sampling units for modeling the use of burns by caribou relative to ecological variables (Figure 10). HSUs were contained within a defined area of use (AOU) where one or more caribou were located within a 500-m buffer of recent burns within the KCH annual range. With all burns within the AOU identified, I used two techniques to define the size of the HSU: 1) the 2.5th centile area (representing the lower end of values in the 95% central range) of burns in the AOU, and 2) the smallest individual burn with >10 caribou locations, >1 individual, and >1 season of use. Both techniques resulted in a HSU size of 47 ha (a length of 686 m per side).

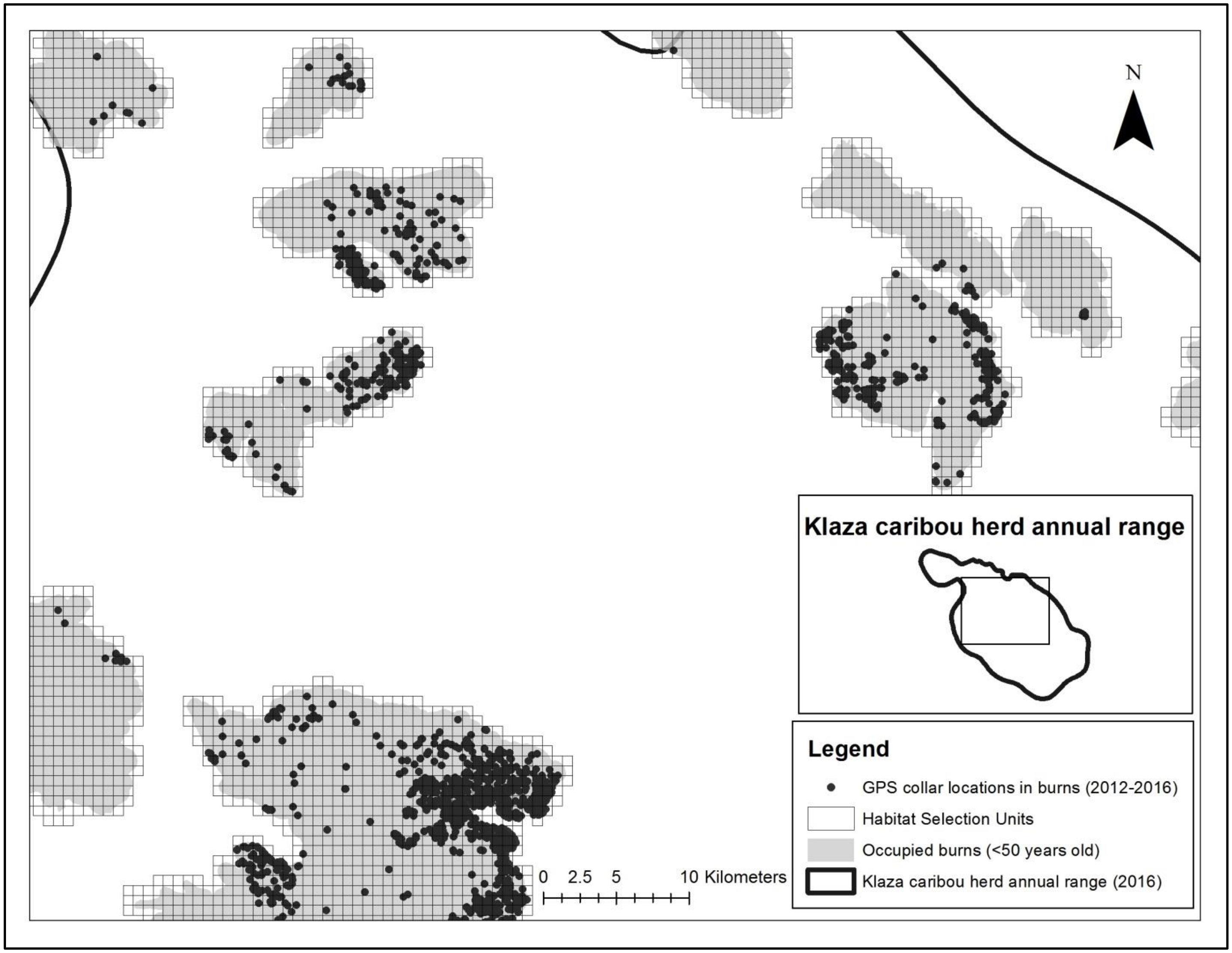

Figure 10. Example of the sampling design used for the burn-focused models. Habitat selection units (HSUs) were a grid overlaid on recent (≤50 years old), occupied burns (plus a 500-m buffer) in the Klaza caribou range, west-central Yukon.

I quantified use as the product of the proportion of collared caribou and the median duration of use of individual caribou within each HSU:

$$\boldsymbol{HSU_i} = \frac{\boldsymbol{N}(\textbf{caribou})_{\boldsymbol{i}}}{\sum_{\boldsymbol{j}} \boldsymbol{N}(\textbf{caribou})} \cdot \widetilde{\boldsymbol{X}} \left(\frac{\boldsymbol{N}(\textbf{locations})_{\boldsymbol{ik}}}{\sum_{\boldsymbol{jk}} \boldsymbol{N}(\textbf{locations})} \right)$$

The proportion of individual caribou in each HSU was defined as the total number of collared caribou in that HSU (N(caribou)$_i$) divided by the total number of collared caribou occupying any HSU during that season-year ($\sum_j N$(caribou)). The relative duration of use reflected the number of collar locations in that HSU for each individual (N(locations)$_{ik}$) divided by the total number of locations in any HSU ($\sum_{ik} N$(locations)) for that individual in that season-year. I calculated the median relative duration of use ($\widetilde{\boldsymbol{X}}$) for all collared caribou that occupied the HSU. For example, if Caribou #1 had three locations in HSU #A1 and a total of 30 locations in all HSUs during late winter 2014, ‘use’ would equal 0.1. Given the relatively small number of samples in each HSU, the median value was then derived from all individuals in a given HSU. To prevent one metric, proportion of caribou or median proportion of locations, having a greater influence on the final score for the HSU, prior to calculating the product of these two, I performed a linear stretch to scale the values of each metric between 0 and 1 (Johnson et al. 2004b):

$$\widehat{\boldsymbol{w}} = \frac{\boldsymbol{w}(\boldsymbol{x}) - \boldsymbol{w_{min}}}{\boldsymbol{w_{max}} - \boldsymbol{w_{min}}}$$

Where $w(x)$ is the proportion of caribou or median proportion of locations and w_{min} and w_{max} are the smallest and largest use values, respectively.

After multiplying the two stretched proportions, the values characterizing use were relatively small, thus I transformed each continuous HSU score into a binary variable. For this purpose, I used the ROC to identify the classification breakpoint between HSUs with high (1) versus low (0) use. I fit the most parameterized model (greatest number of predictor variables) with the dependent variable defined by percentile values of the HSU scores (e.g., 10th, 25th...90th). The percentile with the greatest area under the curve defined the breakpoint for the continuous HSU values for that season-year. To avoid creating an unbalanced data set (e.g., considerably more high (1) versus low (0) use values as the threshold approaches the 5th percentile), I selected threshold values identified between the 10th and 90th percentiles.

Statistical model selection and assessment

I used logistic regression (binomial family, logit link function) to identify environmental and terrain factors that differentiated HSUs with high (1) versus low (0) use (Table 8). As with the RSF analysis, I used AIC_c to select the most parsimonious model(s) and the jackknifing cross-validation procedure to test the predictive ability of those models. All statistical analyses were completed using Stata/IC (Version 12.1; StataCorp 2011) statistical software with the desmat add-in (Hendrickx 1999) for deviation coding of categorical variables.

Results

Forty-two GPS-collared female caribou provided 48,430 locations across nine season-years from 2012–2016 (Table 9). Only two individuals were collared during late winter 2012, providing an insufficient sample for modelling habitat selection during that season; those data were excluded from seasonal comparisons across years. Most collared individuals had more than one season-year of location data, and some had up to four season-years. Of these locations, 5,663 (12%) were located within 500 m of recent burns (≤50 years old), and included locations from 64–100% of collared individuals, depending on year and season (early and late winter; Table 9).

Table 9. Summary of GPS-collar locations within 500-m of burns in early and late winter for the Klaza caribou herd, west-central Yukon, 2012–2016.

Season	Year	Total collared individuals (within 500 m of burns)	Locations within 500-m of burns	Total locations	% of locations within 500 m of burns	Number of individuals with *x* years of data			
						1	***2***	***3***	***4***
Early winter	2012/2013	28(18)	572	7,159	8	*12*	*12*	*18*	*0*
	2013/2014	24(19)	466	6,965	7				
	2014/2015	28(19)	295	8,234	4				
	2015/2016	10(9)	323	2,618	12				
	All years	-	**1,656**	**24,976**	**7**				
Late winter	2012	2(2)	158	257	61	*11*	*12*	*15*	*2*
	2013	27(23)	1,019	6,775	15				
	2014	23(20)	1,235	6,882	18				
	2015	27(24)	1,199	7,136	17				
	2016	10(10)	396	2,404	16				
	All years	-	**4,007**	**23,454**	**17**				

Resource selection function models

Five candidate models were developed to explore individual seasonal habitat selection strategies for the KCH (Table 10), totaling 885 individual by season-year model combinations. Due to the high number of individual-season-year combinations, the candidate model set was limited to five, relatively complex models. These models represented ecologically plausible hypotheses explaining the distribution of collared caribou without comprising the inherent complexity of resource selection (Boyce and McDonald 1999).

Table 10. Candidate resource selection function models for the Klaza caribou herd of west-central Yukon, during the early and late winter, 2012–2016. GM = general model, BM = burn model.

Model name	**Model parameters**
GM1	Eastness+Northness+Slope+Slope^2+Elevation+Elevation^2+TPI+Lichen density+Distance to water+Distance to water^2
BM1	Eastness+Northness+Slope+Slope^2+Elevation+Elevation^2+TPI+Lichen density+Distance to water+Distance to water^2+Burn density+Distance to burns+Distance to burns^2+Burned
BM2	Eastness+Northness+Slope+Slope^2+Elevation+Elevation^2+TPI+Lichen density+Distance to water+Distance to water^2+Burned
BM3	Eastness+Northness+Slope+Slope^2+Elevation+Elevation^2+TPI+Lichen density+Distance to water+Distance to water^2+ Distance to burns+Distance to burns^2+Burned
BM4	Eastness+Northness+Slope+Slope^2+Elevation+Elevation^2+TPI+Lichen density+Distance to water+Distance to water^2+Burn density

Model selection

For the early winter season, there was considerable model selection uncertainty, with no single model consistently selected more than others (Figure 11). Model BM1 (the most parameterized model) was selected as a top model in three of four years. For the late winter season, all models that included burn variables (BM1–4) were selected as top models more often than the general model (GM1). Model BM1 was selected as a top model (ΔAIC ≤2) for all years, with BM3, differing only by the exclusion of burn density, as the second most selected model (Table 10, Figure 12).

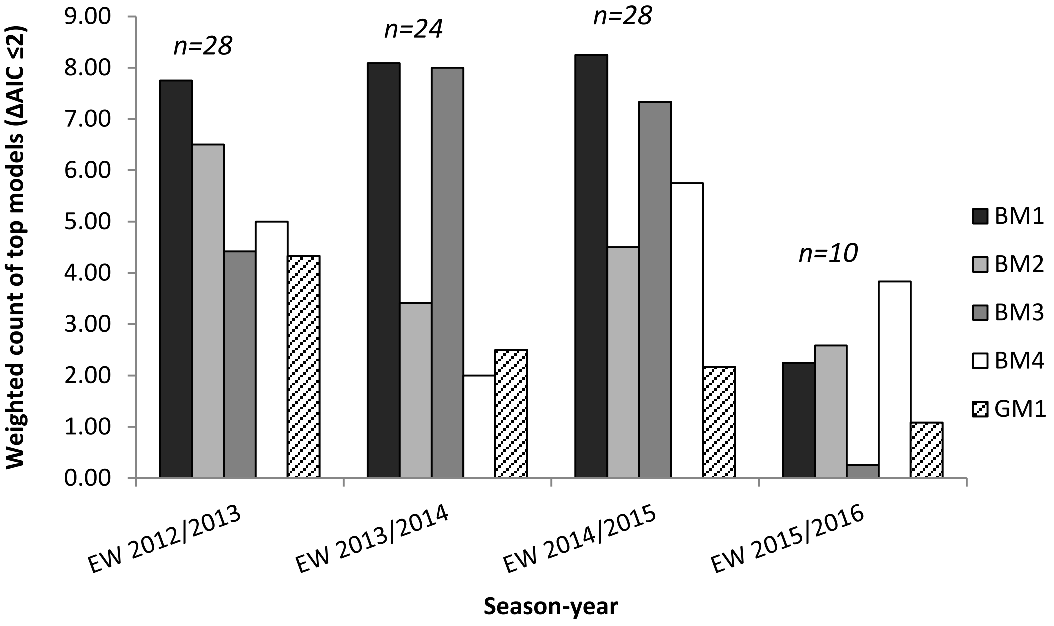

Figure 11. Weighted count of each candidate RSF model, as defined in Table 10, selected as a top model (ΔAIC ≤2) for the early winter season (2012–2016). The number of collared individuals in the Klaza caribou herd in each season-year is indicated above the bars.

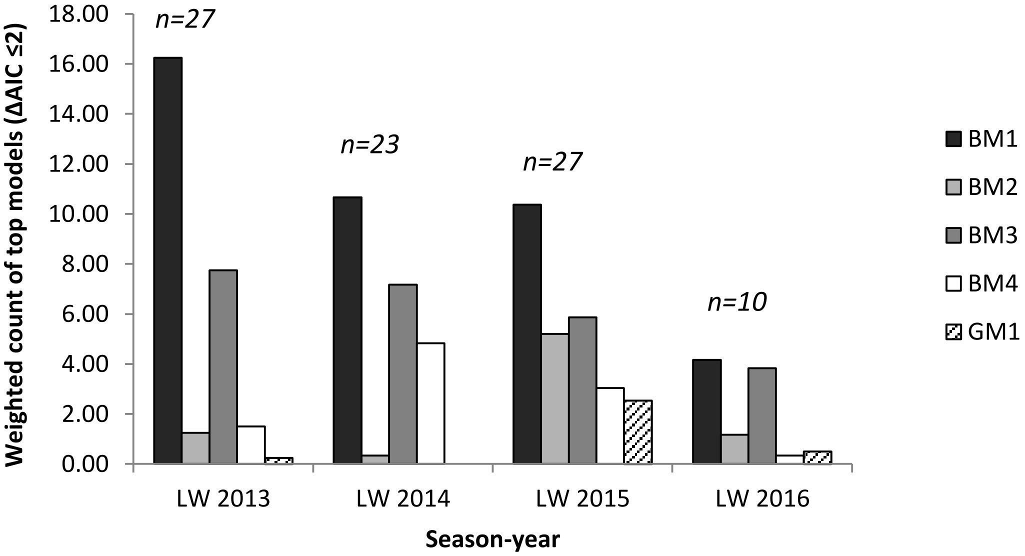

Figure 12. Weighted count of each candidate RSF model, as defined in Table 10, selected as a top model (ΔAIC ≤2) for the late winter season (2013–2016). The number of collared individuals in the Klaza caribou herd in each season-year is indicated above the bars.

Winter habitat selection coefficients

During early winter, individual caribou consistently demonstrated nonlinear selection for lichen density, elevation, and distance to water (Table 11; Appendix D: Figure 18). Caribou consistently avoided valleys, demonstrated a nonlinear avoidance of increasing slopes, and variation among individuals in selection or avoidance of aspect, ridgelines, and gentle and steep slopes varied across years. Individuals generally avoided recent burns and selected for areas further from burns; however, individual strategies for burn density varied across the years.

During late winter, RSF models indicated that the KCH collectively demonstrated nonlinear selection for increasing lichen density, elevation, slope, and distance to water, and southern aspects and ridgelines (Table 12; Appendix D: Figure 19). Valleys and north-facing aspects were consistently avoided, while selection strategies for east and west-facing slopes and gentle and steep slopes were inconsistent across all years. The selection of recent burns was variable across year and among caribou. Individuals generally avoided recent burns in 2014 and 2015, and selected for recent burns in 2016, whereas the overall selection strategy of individuals monitored during 2013 was unclear. Overall, individuals selected for increasing distance to burns in all years except in 2013, lower burn density in 2014 and 2016, and higher burn density in 2013 and 2015.

For the burn-related variables (burned/unburned, burn density, and distance to burns), individuals with three season-years of data were examined for consistency in selection strategies across years (Appendix D: Figure 20 and Figure 21). During early winter, one individual consistently selected for increasing distance to burns, while another consistently selected for decreasing distance to burns (N = 5; Appendix D: Figure 20d), and one individual consistently avoided burned areas (N = 13; Appendix D: Figure 20a,b). One individual consistently selected for decreasing burn density (N = 13; Appendix D: Figure 20c). During late winter, five of nine individuals consistently selected for increasing distance to burns (Appendix D: Figure 21d), two and three individuals consistently selected for burned and unburned areas, respectively, and one individual consistently selected for increasing burn density (N = 12; Appendix D: Figure 21a,b).

Table 11. Weighted counts for each coefficient by early winter season (EW) from top-ranked (ΔAIC ≤ 2) resource selection models for individual caribou in the Klaza herd of west-central Yukon. For each year, the number under the – indicates the weighted count of individual top models that showed significant avoidance for that parameter; the number under the + indicates the weighted count of individual top models that showed significant selection for that parameter. The count of significant β coefficients ($P<0.05$) in each year is shown in bold italics for each – or + coefficient.

Parameter	EW 2012/2013				EW 2013/2014				EW 2014/2015				EW 2015/2016			
	-	*P<0.05*	+	*P<0.05*	-	*P<0.05*	+	*P<0.05*	-	*P<0.05*	+	*P<0.05*	-	*P<0.05*	+	*P<0.05*
Burned	12.13	***9.98***	6.49	***4.00***	7.66	***5.66***	11.80	***7.64***	14.55	***8.15***	4.73	***1.33***	2.25	***0.50***	1.83	***1.00***
Unburned	6.49	***4.00***	12.13	***9.98***	11.80	***7.64***	7.66	***5.66***	4.73	***1.33***	14.05	***8.15***	1.83	***1.00***	2.25	***0.50***
Burn density	8.89	***4.83***	3.82	***2.83***	7.73	***2.66***	2.33		3.49	***1.83***	10.80	***1.33***	0.25	***0.25***	4.83	***1.50***
Distance to burns	4.08	***3.00***	8.07	***5.24***	3.58	***1.50***	12.48	***10.15***	6.41	***4.66***	9.14	***2.16***	0.75		0.75	
Distance to burns^2	8.90	***6.91***	3.25	***2.00***	13.56	***10.15***	2.50	***0.50***	9.81	***3.66***	5.74	***1.00***	1.00		0.50	
Lichen density	4.31	***1.00***	23.58	***11.96***	2.98		20.96	***9.65***	0.00		27.91	***22.43***	1.00	***4.00***	7.99	***5.00***
Lichen density^2	21.26	***10.96***	6.63	***1.99***	20.21	***5.99***	3.73		27.25	***16.44***	0.66		7.99		1.00	
Elevation	4.98		22.91	***14.31***	2.00		21.94	***17.29***	0.00		27.91	***22.60***	0.00		8.99	***8.99***
Elevation^2	20.42	***13.65***	7.47	***0.66***	21.94	***17.95***	2.00		27.91	***20.95***	0.00		8.99	***8.99***	0.00	
Slope	21.07	***6.98***	6.82	***2.00***	18.96	***7.16***	4.98	***0.99***	25.92	***10.95***	1.99		8.99	***5.33***	0.00	
Slope^2	16.93	***4.00***	10.96	***3.00***	12.97	***0.99***	10.97	***3.00***	9.98		17.93	***1.00***	2.00		6.99	***2.00***
Northness	21.91	***10.47***	5.98	***1.00***	12.98	***5.00***	10.96	***1.00***	16.95	***4.99***	10.96	***2.99***	4.00	***1.00***	4.99	
Eastness	13.98	***4.74***	13.91	***2.31***	17.13	***8.98***	6.81	***2.00***	11.60	***1.33***	16.31	***5.00***	3.99		5.00	***1.00***
Ridgeline	10.95	***1.99***	16.94	***1.00***	7.82	***1.00***	16.12	***4.16***	9.32	***1.00***	18.59	***3.98***	7.33	***1.00***	1.66	
Steep slope	10.95		16.94		6.00	***1.00***	17.94	***3.00***	7.97	***1.00***	19.94	***4.99***	3.00		5.99	***2.00***
Gentle slope	10.48		17.41		11.97	***1.99***	11.97		13.94	***1.99***	13.97	***3.00***	1.00		7.99	***1.00***
Valley	5.72		22.17	***2.00***	3.00		20.94	***5.33***	6.65		21.26	***5.00***	2.00		6.99	***2.66***
Distance to water	8.97	***2.82***	18.92	***9.96***	7.47	***1.00***	16.47	***6.99***	13.97	***4.99***	13.94	***5.96***	5.00	***1.00***	3.99	***0.99***
Distance to water^2	20.92	***11.63***	6.97	***3.99***	15.96	***6.99***	7.98	***1.33***	10.95	***5.30***	16.96	***5.32***	3.99		5.00	***1.00***

Table 12. Weighted counts for each coefficient by late winter season (LW) from top-ranked (ΔAIC ≤ 2) resource selection models for individual caribou in the Klaza herd of west-central Yukon. For each year, the number under the – indicates the weighted count of individual top models that showed significant avoidance for that parameter; the number under the + indicates the weighted count of individual top models that showed significant selection for that parameter. The count of significant β coefficients ($P<0.05$) in each year is shown in bold italics for each – or + coefficient.

Parameter	**LW 2013**				**LW 2014**				**LW 2015**				**LW 2016**			
	-	$P<0.05$	+	$P<0.05$	-	$P<0.05$	+	$P<0.05$	-	$P<0.05$	+	$P<0.05$	-	$P<0.05$	+	$P<0.05$
Burned	11.00	***5.50***	11.99	***6.33***	8.99	***1.99***	8.16	***6.33***	11.09	***5.09***	10.31	***3.99***	1.00	***1.00***	8.15	***2.00***
Unburned	11.99	***6.33***	11.00	***5.50***	8.16	***6.33***	8.99	***1.99***	10.31	***3.99***	11.09	***5.09***	8.15	***2.00***	1.00	***1.00***
Burn density	2.50	***1.00***	14.33	***13.33***	7.49	***4.99***	8.00	***6.00***	7.69	***4.53***	5.69	***3.00***	1.66	***0.66***	2.83	***1.33***
Distance to burns	6.16	***2.33***	17.50	***12.50***	4.66	***3.33***	13.16	***9.83***	7.50	***5.50***	8.72	***3.86***	2.99	***2.33***	5.00	***3.00***
Distance to burns^2	19.50	***12.50***	4.16	***0.66***	13.49	***10.50***	4.33	***2.00***	10.72	***4.66***	5.50	***3.00***	5.00	***3.00***	2.99	***2.33***
Lichen density	3.00		23.99	***14.00***	4.00		18.98	***14.48***	5.16		21.78	***11.47***	0.83		9.15	***5.99***
Lichen density^2	23.50	***15.50***	3.49		16.98	***7.66***	6.00	***3.00***	21.45	***11.98***	5.49	***0.33***	8.49	***5.99***	1.49	
Elevation	0.00		26.99	***24.99***	1.99		20.99	***17.99***	0.99		25.95	***23.96***	0.00		9.98	***9.98***
Elevation^2	26.99	***24.99***	0.00		21.98	***19.99***	1.00		25.95	***23.96***	0.99		9.98	***9.98***	0.00	
Slope	9.00	***1.00***	17.99	***7.49***	3.00		19.98	***6.99***	7.98	***1.00***	18.96	***6.98***	4.00	***1.00***	5.98	***1.00***
Slope^2	22.99	***12.99***	4.00	***1.00***	20.98	***10.99***	2.00		19.96	***9.98***	6.98		7.98	***2.33***	2.00	***1.00***
Northness	25.99	***23.99***	1.00		20.98	***16.98***	2.00		24.94	***23.94***	2.00		5.98	***2.32***	4.00	
Eastness	18.00	***9.00***	8.99	***1.99***	10.00		12.98	***4.00***	12.96	***1.00***	13.98	***4.99***	3.98		6.00	***2.00***
Ridgeline	4.00	***1.00***	22.99	***10.00***	1.00	***1.00***	21.98	***12.99***	4.00	***1.00***	22.94	***5.98***	5.00		4.98	***1.99***
Steep slope	14.99	***1.00***	12.00		12.48	***2.99***	10.50	***1.00***	17.44	***1.99***	9.50	***1.00***	4.98		5.00	
Gentle slope	13.00		13.99	***3.99***	15.99	***3.00***	6.99		12.63	***3.49***	14.31	***1.50***	3.98		6.00	
Valley	20.99	***3.00***	6.00		19.98	***3.99***	3.00		20.28	***5.66***	6.66		6.48	***1.00***	3.50	
Distance to water	12.00	***5.00***	14.99	***5.99***	3.00	***1.00***	19.98	***13.99***	5.16	***1.00***	21.78	***13.96***	2.00		7.98	***2.00***
Distance to water^2	17.49	***8.99***	9.50	***4.00***	17.32	***12.99***	5.66	***1.00***	21.94	***8.97***	5.00	***1.00***	7.99		1.99	

Model fit

ROC scores were generally higher for the top-ranked (highest overall AIC_w) late winter RSF models when compared to early winter models. Not all seasonal RSFs had good predictive power, but the average scores across the late winter seasons consistently exceeded the 0.7 threshold for good model performance (Table 13).

Table 13. Mean Receiver Operating Characteristic (ROC) scores (area under the curve) for top-ranked (highest AIC_w) resource selection function (RSF) models for individual Klaza caribou, 2012–2016.

Season-year	**Individuals**	**ROC (mean)**	**ROC (min)**	**ROC (max)**
All years (early winter)	*89*	*0.70*	*0.53*	*0.87*
EW 2012/2013	28	0.68	0.58	0.87
EW 2013/2014	24	0.67	0.53	0.79
EW 2014/2015	28	0.72	0.63	0.84
EW 2015/2016	9[1]	0.76	0.70	0.82
All years (late winter)	*87*	*0.75*	*0.61*	*0.91*
LW 2013	27	0.77	0.67	0.87
LW 2014	23	0.76	0.61	0.88
LW 2015	27	0.74	0.66	0.89
LW 2016	10	0.76	0.67	0.91

[1] The jackknifing procedure for one individual would not converge, thus it was excluded.

Seasonal selection ratios

Seasonal selection ratios were derived for measures of burn age, burn perimeter, and burn size (Figure 13). During early winter, many individual caribou selected the 21–30 and 31–40 year burn age classes. During late winter, there was relatively little variability around the pooled ratio estimates for all burn age classes, with the exception of the 1–10 year age class, which showed more selection than other age classes. For both early and late winter, there was considerable individual variation in the selection or avoidance of the outer 500-m perimeter of burns, although individuals selected this class more than others (Figure 13). Similarly, individuals had a variable response to small burns, with greater selection of this size class compared to others.

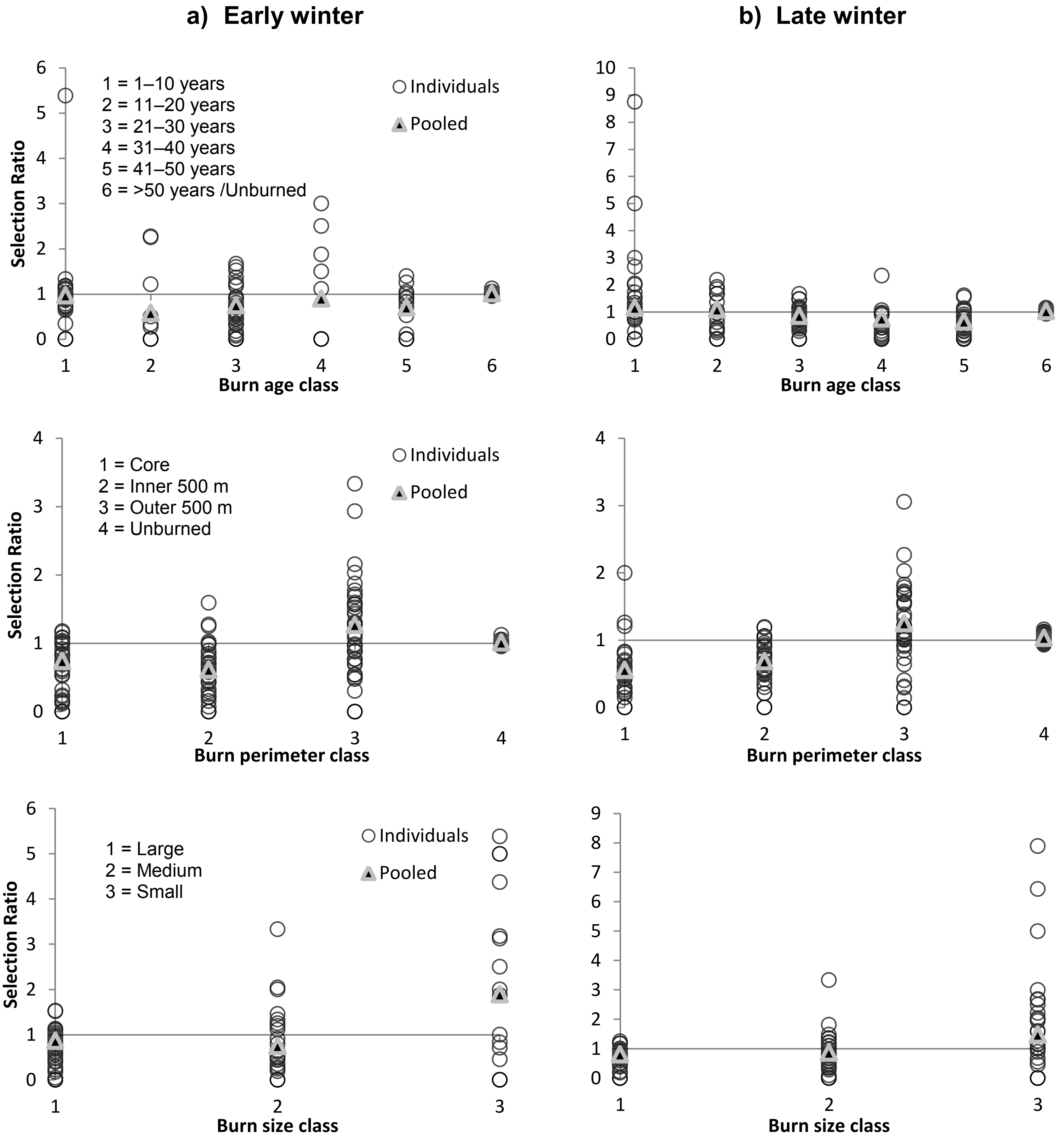

Figure 13. Individual and pooled (across all animals) seasonal selection ratios (used versus available locations) of burn attributes (burn age, burn perimeter, and burn size) for Klaza caribou during early (a) and late (b) winter, 2012–2016. Selection ratios greater than one indicate selection, whereas values less than one indicate avoidance.

Burn-focused logistic models

During early winter, the proportion of collared caribou in a HSU was relatively consistent across years, with the highest use by collared individuals in 2015/2016. The mean duration of use was lowest in 2015/2016 (Figure 14). During late winter, the mean proportion of collared caribou in a burn (i.e., HSU) varied throughout the study period, but was greatest in 2016, and the mean duration of use was greatest in 2013 (Figure 14). Overall mean combined use (proportion and use) of burns by the KCH was highest during late winter 2013, although the use of burns during late winter decreased considerably from 2014 to 2016 (Figure 14).

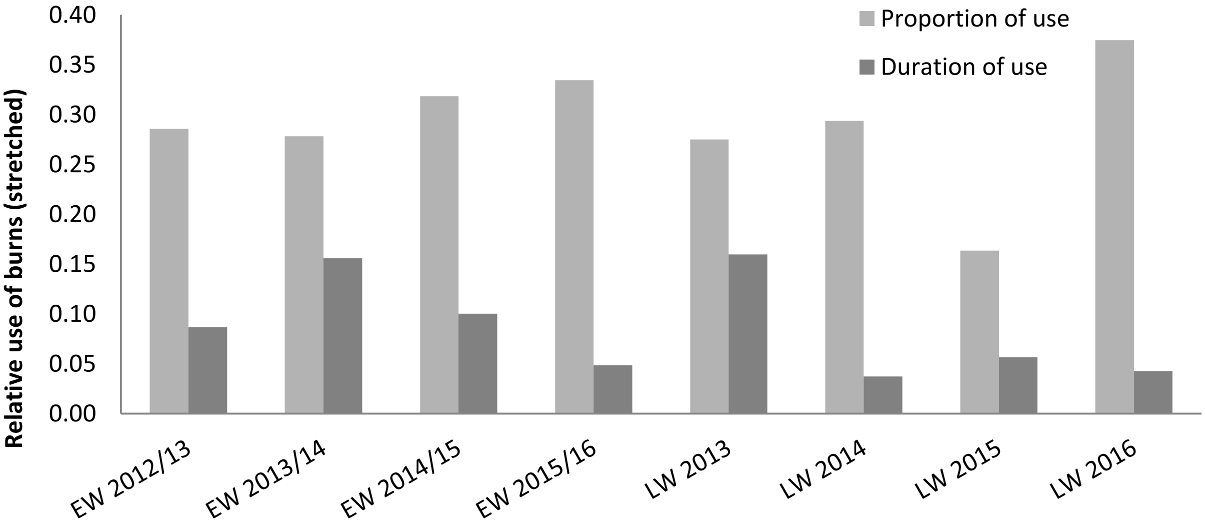

Figure 14. Relative mean proportion and duration of burn use by collared caribou during individual early (EW) and late (LW) winter seasons by Klaza caribou, west-central Yukon, 2012–2016. All values were scaled between 0 and 1 using a linear stretch.

Model selection

A set of eight candidate models (M1–8) were developed to explain the relative use of HSUs by caribou, with all but one (M1) containing variables that represented burn characteristics (Table 14). For each season-year, one to three models were identified as a top model ($\Delta_i \mathrm{AIC}_c \leq 2.00$). Model M2 (Table 14) was selected the most often across all season-years (seven times), whereas models M4 and M7 (Table 14), which contained the most parameters, were never selected as a top model (Table 15). Model M2, which explained use with burn age, lichen density, and burn perimeter, had relatively few parameters compared to the other models, but it was selected more often than a simpler model (M3) that did not include burn age.

Table 14. Candidate logistic regression models used to differentiate Habitat Selection Units (HSU) with relatively high and low use by monitored caribou of the Klaza herd during early and late winter, west-central Yukon, 2012–2016.

Model name	**Model Parameters**
M1	Northness+Eastness+Slope+Elevation+Elevation^2+TPI+Lichen density+Lichen density^2+Distance to water
M2	Burn age+Lichen density+Lichen density^2+Burn perimeter
M3	Lichen density+Lichen density^2+Burn perimeter
M4	Northness+Eastness+Slope+Elevation+Elevation^2+TPI+Lichen density+Lichen density^2+Distance to water+Burn age+Burn perimeter
M5	Slope+Elevation+Elevation^2+Lichen density+Lichen density^2+Burn age+Burn perimeter
M6	Elevation+Elevation^2+TPI+Lichen density+Lichen density^2+Burn age+Burn perimeter
M7	Northness+Eastness+Slope+Elevation+Elevation^2+TPI+Lichen density+Lichen density^2+Distance to water+Burn perimeter
M8	Elevation+Elevation^2+Lichen density+Lichen density^2+Burn age+Burn perimeter

TPI = Topographic Position Index

Table 15. Summary of statistics used to select the most parsimonious logistic regression models for understanding caribou use of Habitat Selection Units in the Klaza caribou herd range, west-central Yukon.

Season-year	Rank	Model name	AIC_{ci}	$AIC_c\ w_i$	$\Delta_i\ AIC_c$
Early winter 2012/2013	1	M2	197.57	0.80	0.00
Early winter 2013/2014	1	M2	113.91	0.33	0.00
	2	M8	113.96	0.32	0.05
	3	M6	115.57	0.14	1.66
Early winter 2014/2015	1	M6	59.38	0.42	0.00
	2	M2	59.85	0.33	0.48
Early winter 2015/2016	1	M6	134.48	0.39	0.00
	2	M1	136.00	0.18	1.51
	3	M3	136.01	0.18	1.53
Late winter 2013	1	M3	255.04	0.64	0.00
	2	M2	256.88	0.26	1.84
Late winter 2014	1	M8	179.86	0.84	0.00
Late winter 2015	1	M5	224.80	0.65	0.00
	2	M8	226.64	0.26	1.84
Late winter 2016	1	M2	230.28	0.65	0.00

Caribou use of burns

In early winter, burn age, burn perimeter use, lichen density, and TPI classes (ridgeline, steep slope, gentle slope, and valley) were significant predictors of the use of HSUs by caribou (Appendix E: Table 26). Use increased with burn age, lichen density, and within the inner and outer 500 m of burns, and decreased within the core of burns. Compared to other TPI classes, ridges and gentle slopes had a positive influence on use, whereas steep slopes did not. The influence of valleys on use was not consistently positive or negative (Appendix E: Table 26). In late winter, burn age, burn perimeter use (core, inner 500 m, and outer 500 m), slope, and elevation were significant predictors of the use of HSUs by caribou (Appendix E: Table 27). Use increased with burn age, elevation, and within the outer 500 m of burns, whereas the core of the burn and decreasing slope had a negative influence on use (Appendix E: Table 27).

Model fit

The ability of logistic regression models to explain caribou use of burns, ranged from relatively poor (AUC = 0.55, SE = 0.05) to very good (AUC = 0.89, SE = 0.04); however most were considered fair (i.e., ~0.70; Table 16). On average, models for early winter had more power to explain the distribution of caribou in burns than the models for late winter ($\bar{x}$ = 0.73, SD = 0.08; $\bar{x}$ = 0.66, SD = 0.07, respectively).

Table 16. Area under the curve for Receiver Operating Characteristic (ROC) scores calculated for the top models representing caribou use of Habitat Selection Units (HSUs) in the Klaza caribou herd range. The threshold percentiles that differentiated high and low use HSUs are indicated at the bottom along with the number of HSUs used in each season-year. LW = late winter, EW = early winter.

Model name	**EW 2012/2013**	**EW 2013/2014**	**EW 2014/2015**	**EW 2015/2016**	**LW 2013**	**LW 2014**	**LW 2015**	**LW 2016**
M1	-	-	-	0.75	-	-	-	-
M2	0.71	0.60	0.83		0.61			0.55
M3	-	-	-	0.73	0.61	-	-	-
M4	-	-	-	-	-	-	-	-
M5	-	-	-	-	-	-	0.73	-
M6	-	0.68	0.89	0.74	-	-	-	-
M7		-	-	-	-	-	-	
M8	-	0.67	-	-	-	0.76	0.69	-
Threshold percentile	*50*	*10*	*90*	*75*	*75*	*10*	*90*	*25*
n (HSUs used)	*172*	*200*	*125*	*139*	*234*	*397*	*388*	*210*

Discussion

These findings substantiate conclusions from other studies suggesting that caribou (both woodland and migratory) collectively avoid recent burns during winter (Schaefer and Pruitt 1991; Thomas et al. 1996; Joly et al. 2003, 2007, 2009; Collins et al. 2011; Hegel and O'Donoghue 2015). While much of the previous research has focused on population-level selection patterns, I observed considerable variation in habitat selection strategies among individuals, years, and winter seasons. That variation was most apparent when considering burn-related resources.

A large number of past works have documented the winter ecology of caribou on burned landscapes. However, this is one of the first studies to quantify the resource selection strategies of caribou that have chosen to occupy burns. For the KCH, 12% of locations were located within 500 m of recent burns and 20% of the annual range was burned in the last 50 years. Active use of burns is not a trivial component of the winter distribution and behaviour of these caribou and likely other herds that are found in fire-prone ecosystems. Use of burns by the KCH varied by season and year; however, burns were used more consistently during early winter. Recent burns (≤50 years old) are likely sub-optimal habitat for the KCH (see Chapter 2), but observed selection for areas with a high density of lichen suggests that caribou seek out remnant and re-establishing terrestrial lichen across burned areas.

Variation of habitat selection strategies in burns

As expected, there were differences in the selection and avoidance of habitats among individual caribou (Gillingham and Parker 2008; Lesmerises and St-Laurent 2017); however, selection coefficients revealed some consistent strategies. During late winter, caribou consistently selected for areas with relatively greater lichen density and higher elevations, and avoided northern aspects (Table 12; Appendix D: Figure 19). Although somewhat less consistent, caribou typically selected for steeper slopes, ridgelines, and areas further from major watercourses (Table 12; Appendix D: Figure 19). During early winter, the selection strategies of caribou were more variable, with only increasing elevation and lichen density being consistently important (Table 11; Appendix D: Figure 18).

The collective response of the KCH to burns is similar to other studies that used pooled models to examine the selection strategies of caribou during the winter (Robinson et al. 2012; Hegel and O'Donoghue 2015). Averaged model coefficients indicated that the KCH avoided burns in all years except early and late winter 2015/2016 (Appendix D: Figure 18 and Figure 19). This could be a result of the reduced number of collared individuals in 2015/2016 (*n* = 10) compared to other years (*n* = 23–28). With a small sample of individuals, the average response to burns could be skewed by outliers (Gillingham and Parker 2008). Also, as the collective response of the KCH is merely an averaged value, there is likely bias towards individuals that had more model selection uncertainty (i.e., more top models selected). Contrary to the averaged selection strategies of caribou, counts of significant burn coefficients (when adjusted for the number of top models per individual) demonstrated that more individuals were selecting for burns in three out of four late winter seasons (2013, 2014, and 2016; Table 12), whereas more individuals were selecting for burns in only one out of four early winter seasons (2014; Table 11). The discrepancy between averaged coefficients and coefficient counts suggests that negative responses to burns, as indexed by the magnitude of the coefficients, may be greater than positive responses. The scope of this analysis was also limited to averaging coefficients from the top selected model only to provide a simple indication of overall consistency in herd selection strategies. Using AIC_c weights to average all plausible models for each individual may have reduced the discrepancy between averaged coefficients and coefficient counts.

Selection for the factors that define habitat can vary among scales (Rettie and Messier 2000; Johnson et al. 2001), thus inferences made at one scale do not necessarily hold true at another (Apps et al. 2001; Johnson et al. 2001; Shepard et al. 2007). While other studies have focused on selection strategies at the scale of the seasonal, home, or annual range (e.g., Dalerum et al. 2007; Anderson and Johnson 2014; Hegel and O'Donoghue 2015), I examined habitat selection at the individual level. This allowed me to better understand the fine-scale foraging behaviour of individual caribou in relation to burns. Population-level analyses represent the average response of the sample, yet no one individual may be represented by the 'average' animal. Although more difficult to interpret, the generation of RSF models for each individual allowed me to document the full range of selection strategies demonstrated by collared caribou.

Individuals were not uniform in their selection strategies across seasons or years, with few exhibiting consistent selection or avoidance of burns (Appendix D: Figure 20 and Figure 21). This variability is likely due to a number of interacting factors, including nutritional and maternal condition, predation risk, landscape diversity, and differences in winter or range conditions among years. Lone caribou behave differently than adult females with calves (Bergerud et al. 1984; Rettie and Messier 2000; Lesmerises et al. 2016), with resource use most variable when females and calves are more vulnerable to predation or when food resources are limited (Gustine and Parker 2008). This variability creates a difficult challenge for wildlife managers: meaningfully incorporating individual variability in selection strategies into population-level management objectives.

Habitat selection strategies were more variable and the use of burns was greater during early winter than during late winter. That variability in habitat selection also resulted in reduced predictive accuracy of individual models compared to late winter models (Table 13). During early winter, snow depths are lower and energetic reserves are higher, allowing for greater ease of movement on the landscape. By late winter, caribou have reduced forage intake and instead focus on minimizing energetic costs, especially those related to movement (Gustine et al. 2006).

Snow conditions vary annually and seasonally, influencing the distribution of caribou. Previous late winter RSF models completed for the KCH were limited by the lack of a snow depth metric (EDI 2013; Hegel and O'Donoghue 2015). I used the contrast between early and late winter as a coarse representation of snow conditions throughout a typical winter. Hegel and O'Donoghue (2015) noted that typical snow conditions on the KCH range were reversed in the winter of 2013, with low snow depths at high elevations and deeper snow at low elevations. This year-to-year variation in snow conditions affects seasonal distribution, potentially resulting in different parts of the range being used, including burns. Although I could not measure range-wide snow conditions, such data could considerably improve our understanding of selection strategies among years.

Close encounters: How Klaza caribou use burns during winter

Analyses focused on the use of burned habitat suggested that the KCH did not actively select recent burns. Instead, caribou appear to regularly encounter burns, primarily small ones (Figure 13), and opportunistically use remnant lichens within the burn perimeter. During early winter, burn use models with higher threshold values (e.g., 90th percentile; 2014/2015, 2015/2016) performed better than lower threshold models (e.g., 10th percentile); however, there was no apparent pattern for late winter models

(Appendix E: Table 25). Lower threshold values of high versus low use HSUs were representative of more general use, whereas higher threshold values represented more selective use of HSUs. This indicates that caribou in burns during early winter are using them more selectively, and caribou in burns during late winter are encountering and using them randomly, potentially for traveling between high density lichen patches. Joly et al. (2003) found a similar pattern, and suggested it was a result of early successional vascular forage being more accessible in burns during the early winter season. The use of early seral habitats, including burns, was also observed by Anderson and Johnson (2014), indicating that early successional forage in burns, in addition to lichen, may supplement winter diets. This is paralleled by the fact that burn age was generally a poor predictor of burn use by caribou (Appendix E: Table 26 and Table 27), suggesting that use is temporally non-linear and reflects the successional patterns of both lichen and non-lichen forage species (e.g., herbs, horsetails, shrubs, etc.).

My data suggest that caribou focus their use of burns at the edges (both the inner and outer 500 m); typically in proximity to areas of high lichen density (Figure 15), which is consistent with findings from other herds (Joly et al. 2003, 2007; Anderson and Johnson 2014). The core of burns is often where the most intense and severe effects to vegetation and overall forest structure are observed (Joly et al. 2007). Additionally, the core of burns may be more exposed to sun and wind, resulting in crusty, high-density snow that restricts movement (Thomas et al. 1998). Use of burn edges and strong avoidance of the core indicates that edges not only provide nutritional advantages, but may also facilitate caribou movement within the winter range (Thomas et al. 1998).

The analysis of burn use is limited to revealing ecological factors that explain the intensity of occurrence of caribou in burns; we cannot infer the behaviour of caribou that occupy burns. Movement analyses may provide some insight on the activities of caribou as they interact with burned habitats (e.g., foraging, quickly transiting burns, bedding down). Although beyond the scope of this research, this highlights the need to better understand caribou movement patterns as they relate to burned and unburned habitats.

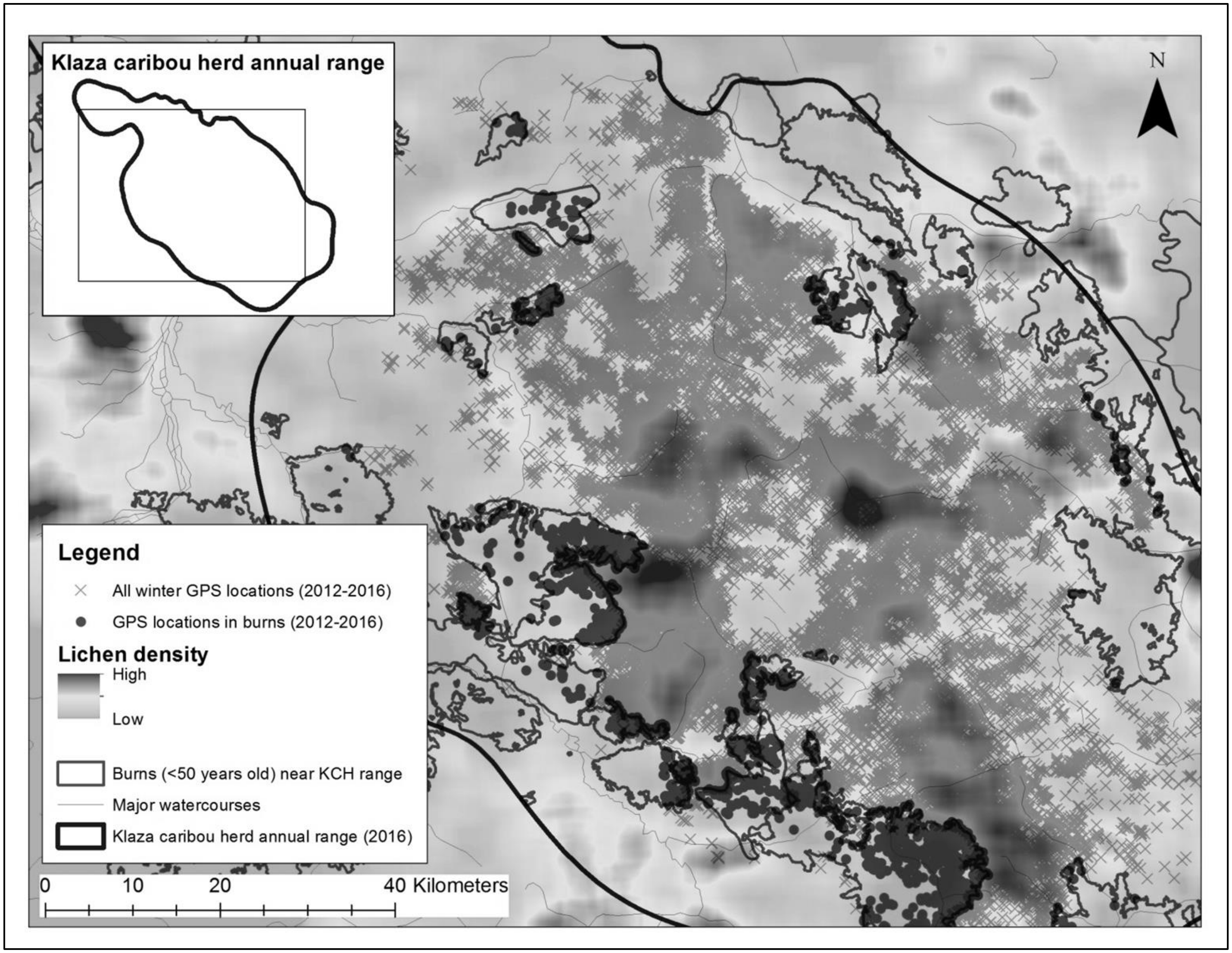

Figure 15. GPS collar locations of Klaza caribou during winter (2012–2016) in relation to recent burns (≤50 years old) and lichen density, west-central Yukon.

Conclusions

On average, burns were avoided during winter; however, individual Klaza caribou may benefit from the use of burns during early winter and to a lesser degree during late winter when access to remnant patches of lichen is limited by snow conditions. I observed that individual Klaza caribou exhibited considerable variability in how they selected habitat during winter, especially during early winter, when snow conditions were presumably more favourable to movement and accessing terrestrial lichens or vascular plants (Pruitt 1959; Fleishman 1990; Joly et al. 2003). Recent burns (≤50 years) were used by Klaza caribou, but similar to the conclusions from Chapter Two of this thesis, the individual RSF and burn-focused models demonstrated that burn age alone did not provide a consistent indication of habitat selection or burn use. In addition to age, managers should consider the season of use, the effect of burn size, and the burn landscape — burn edges near lichen patches are used more than the core of burns, but areas generally further from burns are selected.

This study demonstrates that collective behaviour does not necessarily mirror that of individuals. Although the variability of habitat selection strategies among individuals may hinder the applicability of these models to management (Gustine and Parker 2008), it is important to understand that variation (Thomas and Taylor 1990) and assess differences between pooled and individual models. As noted by others, (e.g., Gustine et al. 2006; Gustine and Parker 2008), wildlife managers should aim to identify this variability within a population by using a multi-scale approach to define availability, quantifying individual variation, and then pooling similar strategies. This will result in better predictions of habitat selection that account for the diversity of strategies within the population.

CHAPTER FOUR: THESIS CONCLUSIONS

Summary

Lichens are essential winter forage for woodland caribou, with almost 80% of the KCH winter diet composed of terrestrial lichens (Farnell et al. 1991). Terrestrial lichens consumed by caribou are susceptible to forest fires and are known to grow slowly when compared to other early successional vegetation (Bliss and Wien 1972). Due to the slow growth and recovery of terrestrial lichens, forest fires are the most dominant natural disturbance process influencing the habitat use and distribution of caribou in winter (Scotter 1970; Thomas et al. 1996; Environment Canada 2012; Anderson and Johnson 2014). While forest fires reduce the abundance of forage lichens in the short term, in the long term fire can enhance overall lichen diversity and productivity (Kershaw 1978; Klein 1982).

Caribou may avoid recently burned habitat until forage lichens recover. Recent burns also influence snow conditions and may inhibit movement due to increased deadfall (Schaefer and Pruitt 1991; Thomas et al. 1998). Approximately 50 years is required for burned areas to regenerate enough lichen to be used consistently by caribou (Thomas et al. 1996; Joly et al. 2003, 2007; Collins et al. 2011; Environment Canada 2011). Nonetheless, 12% of collar locations from the KCH were located within 500 m of recent burns (≤50 years old), suggesting that some caribou have chosen to occupy burns despite the apparent disadvantages to foraging and movement. The use of recent burns has been attributed to a number of factors, including the availability of vascular forage in younger regenerating burns (11–20 years old; Joly et al. 2003), reduced predation risk as a result of improved visibility, efficient movement between high-quality habitat patches, and selection of remnant patches of forage within the burn boundary (Miller 1976; Thomas et al. 1998).

Cumulative disturbance to boreal caribou ranges has been linked to a herd's probability of persistence (Environment Canada 2011). Although a different ecotype, NM caribou may also be limited by disturbance within their ranges. For the KCH, where approximately 24% of the current late winter range is disturbed by recent burns (Table 1), knowledge of caribou-fire dynamics is essential to better manage cumulative landscape change. The diverse landscapes within the KCH's annual range result in burns of different intensities, severities, and ultimately, value as habitat.

I studied the determinants of lichen succession post-fire (Chapter Two) and collective and individual habitat selection strategies in burns (Chapter Three) to determine when and how burned landscapes are used by caribou. In Chapter Two I used vegetation field data collected on the KCH range to evaluate lichen abundance in different age burns. I then tested the ability of a number of environmental characteristics to explain the variation in lichen abundance in burns of a similar age.

With respect to lichen succession in burns, I observed that:

- The sequence of lichen succession was consistent with stand-replacing burns in the boreal forest; however, *Cladina stellaris* did not dominate the late succession phase of the post-fire community. The relative absence of this late-seral lichen suggests that the fire interval was too short to allow for the establishment of climax stands across the range of the KCH.

- Burns of the same age had considerable variation in lichen abundance. This variation was best explained by greater canopy openness, tree height, stand basal area, and coniferous cover types. Although not a significant parameter in models of volume or percent cover of forage lichen, time since burn improved model performance; however, models performed better with it included as a predictor, suggesting it does help to explain some variability in lichen abundance.
- 50 years provides a conservative estimate of lichen recovery post-fire; however, other environmental characteristics should be used in combination with burn age to better assess the abundance of forage lichens on a burn-specific basis.

In Chapter Three I explored the factors explaining the use of recent burns by the KCH. I applied locations from GPS-collared caribou to resource selection functions and quantified the habitat selection strategies of caribou during the early and late winter relative to topography, density of terrestrial lichen, and fire history. I used those RSFs to understand variation in selection among individual caribou as well as the population, as represented by the pooled sample of caribou locations. Further, I isolated locations of caribou that occurred in or adjacent to burns and determined factors that were important for explaining the relative use of Habitat Selection Units that were representative of burned habitat.

With respect to habitat selection strategies, I observed that:

- Averaged selection coefficients indicated that the KCH avoided burned habitats during winter in most years. In some season-years, more individual caribou selected for burned habitat; however, this selection was weak compared to individuals who avoided burns (Appendix D: Figure 18 and Figure 19).

- Caribou used burns selectively during early winter when snow conditions were less limiting, and focused their use at the edges and in proximity to areas of high lichen density.
- During late winter, when snow was deeper, denser, and crustier, caribou encountered and used burns randomly.
- Variability in selection strategies was observed for individual caribou that were monitored for multiple seasons and among caribou within any one season. Few caribou exhibited consistent selection or avoidance of burns across seasons and years, suggesting that, on average, burns provided sub-optimal habitat (Appendix E: Table 26 and Table 27).

Together, the findings from Chapters Two and Three suggest that the relationship between forest fire and the KCH is both complex and non-linear. In general, burns in the KCH annual range are not beneficial to caribou during winter until at least 50 years post-fire; however, there was considerable variability in lichen abundance observed within recent burns. When caribou encounter recent burns during winter, they can take advantage of available forage; however, the ability to do so likely decreases when snow conditions deteriorate as winter progresses.

Management considerations and future research

In this research, I explored a limited set of methods for understanding the resource selection strategies and use of burns by woodland caribou during the winter. I recommend exploring other measures of caribou distribution and behaviour. Movement parameters, an index of behaviour, can improve our understanding of how caribou use landscapes altered by forest fire. Few studies have explicitly explored the relationship between movement and fire history (e.g. Thomas et al. 1998). Winter is an energetically stressful time for caribou (Fancy and White 1985; Schaefer and Pruitt 1991; Schaefer 1996; Johnson et al. 2001) and burn history is important for range planning and management, thus, it is essential to understand how or if caribou alter movement and behaviour in response to burns. This would include migratory movements among seasonal ranges.

Additionally, the availability of some resources influences diet and habitat selection strategies (Boyce and McDonald 1999). An analysis of caribou faecal pellets collected during winter could provide further insight into winter forage characteristics and perhaps habitat selection strategies on a burned landscape. Winter diet should be considered on a herd-specific basis. The use of early-seral habitats, including burns (Joly et al. 2003; Anderson and Johnson 2014), suggests that early successional forage may play an important role in winter diet for some herds. A singular focus on lichen abundance in burns could result in a more limited understanding of caribou-fire dynamics.

In both Chapters Two and Three, my results provide further evidence that burn age or time since fire, often used for conservation and management planning purposes, is not a comprehensive metric for understanding the spatiotemporal effects of fire on the habitat selection of caribou during winter. It has become increasingly apparent that wildlife managers need to look beyond simple age thresholds to better account for the effects of fire on the availability and quality of habitat for caribou.

This research demonstrates that the relationship between caribou and burns is complicated and requires careful consideration in the context of cumulative landscape change. Where snow conditions allow, caribou will use sites within burns that provide lichen forage or other components of winter diet. In high-priority areas, wildlife managers should develop a more comprehensive inventory of existing and new burns that quantify not only burn area, but also lichen cover, forest cover type, canopy openness, some measure of burn intensity or severity, and through digital terrain models, characterisation of terrain (i.e. slope, aspect, and elevation). Finally, when evaluating caribou habitat, managers face the difficult challenge of recognising the variability in caribou behaviour while developing tractable land-use strategies that represent the requirements of the population. As a starting point, we can assess differences between pooled and individual habitat selection models. The challenge of interanimal variability becomes less when most animals act similarly or respond to only a few habitat features differently. Where there are considerable differences in resource selection among animals we can identify and manage for the dominant selection strategy or strategies. Alternatively or in combination with that approach, we can bound management prescriptions according to the range of selection strategies demonstrated by monitored individuals or weight the value we place on particular elements or components of habitat according to observed selection. In the case of the KCH during late winter, this would mean a general focus on lichen density, elevation, slope, distance to water, aspect, and the contrast between valleys and ridgelines, while other elements, such as burn characteristics, may need to be assessed on an annual basis.

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Appendix A Field data collection details

Table 17. Fire history, terrain, and vegetation variables recorded during field sampling in 2014 within the Klaza caribou herd annual range, west-central Yukon.

Variable	Description
Fire-related variables	
Burn age class	Derived from mapped polygons from the 2013 Yukon Fire History database + tree core samples
1-10 years	
11–20 years	
21–30 years	
31–50 years	
51–70 years	
>70 years/unburned	Age post-fire derived from tree core samples
Burn size	Size of burn polygon in hectares, from Yukon Fire History database
Distance to burn edge/closest burn	Distance in metres from plot centre to nearest edge of burn or closest burn (if in unburned plot)
Terrain variables	
Elevation	Metres above sea level
Aspect	0–360° (converted to northness and eastness using cosine and sine)
Slope	Percent slope angle
Slope position	Level, depression, toe, lower, mid, upper, crest
Moisture regime[1]	0 = very xeric, 1 = xeric, 2 = subxeric, 3 = submesic, 4 = mesic, 5 = subhygric, 6 = hygric, 7 = subhydric
Vegetation variables	
Top tree species	Most dominant tree species in plot
Tree height	Average height (m) of the most dominant tree species
Stand basal area	Basal area factor; determined using a rod relascope
Top tall shrub species	Most dominant tall shrub species in plot (>0.5 m in height)
Cover of tall shrubs	Percent cover of tall shrubs (> 0.5 m in height)
Canopy openness	Percent canopy openness; determined using Gap Light Analyzer software
Ground cover	
Bryophytes	Percent cover of non-vascular plants
Dwarf shrubs	Percent cover of shrubs <0.5 m tall
Forbs	Percent cover of herbaceous flowering plants
Graminoids	Percent cover of grasses, sedges, and rushes
Horsetails	Percent cover of plants in the genus *Equisetum* (spore-producing, vascular)
Mushrooms	Percent cover of fungus species (aboveground fruiting bodies)
Litter	Percent cover of leaf, needle, or small woody debris
Soil or Rock	Percent cover of exposed mineral soil or rock (bedrock or large boulders)
Lichens	Percent cover of *Cladina mitis/arbuscula* (not distinguished in the field), *C. rangiferina, C. stellaris, Cladonia* spp., *Cetraria cucullata, C. ericetorum/ islandica* (not distinguished in the field), *C. nivalis, Stereocaulon* spp., and *Peltigera* spp.
Lichen height	Height (cm) of lichen thallus measured from beginning of living stem for all species except *Peltigera* spp.

[1] During modeling, some categorical predictor variables had too few samples per category, thus requiring fewer categories per variable. The categories for moisture regime were re-categorized to: Dry (very xeric, xeric, subxeric, submesic), Moist (mesic), and Wet (subhygric, hygric, subhydric).

Table 18. Protocol for determining the age class of vegetation plots as determined using mapped burn age and/or tree core ages from trees sampled in field plots within the Klaza caribou herd annual range, west-central Yukon.

Tree core result	Assigned age	Justification/assumptions
Inside mapped burn		
Minimum core age within 10 years of mapped burn age	Mapped burn age	Some trees established post-burn, but there may have been some survivors.
Minimum or maximum core age >10 years younger than mapped burn age	Mapped burn age	It may have taken longer for trees to establish post-burn, and there may have been some survivors.
Minimum core age >10 years older than mapped burn age	Minimum core age	Suggests that no new trees established post-burn, and the stand is made up of survivors.
Outside mapped burn		
Maximum-minimum core age ≤50 years	Median core age	Suggests that the stand is relatively even-aged, and the median value is representative of the site age.
Maximum-minimum core age ≥50 years	Maximum core age	Suggests the stand is multi-aged and it is assumed the oldest tree core represents the age class

Table 19. Average values (with standard error) of the percent cover of non-lichen ground cover in vegetation plots in burns by 15-year intervals, Klaza caribou range, west-central Yukon, summer 2014. Plots aged 100–149 and ≥150 years were grouped together rather than by 15-year intervals due to low sample sizes.

Age group (years)	*n*	Bryophyte		Dwarf shrub		Forb		Graminoid		Horsetail		Mushroom		Litter		Soil		Rock		Fern	
		%	**SE**	**%**	**SE**	**%**	**SE**	**%**	**SE**	**%**	**SE**	**%**	**SE**	**%**	**SE**	**%**	**SE**	**%**	**SE**	**%**	**SE**
<25	18	11.5	2.7	29.7	7.0	4.6	1.1	16.9	4.0	1.0	0.2	0.2	0.0	3.6	0.8	10.4	2.4	5.6	1.3	0.0	0.0
25–39	8	5.6	1.3	45.3	10.7	3.9	0.9	10.6	2.5	0.0	0.0	0.0	0.0	9.1	2.2	1.8	0.4	18.8	4.4	0.0	0.0
40–54	14	17.7	4.2	33.7	7.9	1.9	0.4	8.3	1.9	0.5	0.1	0.1	0.0	6.2	1.5	0.2	0.1	10.7	2.5	0.0	0.0
55–69	18	16.1	3.8	37.1	8.8	8.4	2.0	8.8	2.1	1.6	0.4	0.1	0.0	10.0	2.4	0.6	0.1	0.0	0.0	2.8	0.7
70–84	8	15.4	3.6	21.8	5.1	2.9	0.7	11.8	2.8	0.1	0.0	0.1	0.0	3.6	0.8	0.0	0.0	0.0	0.0	0.0	0.0
85–99	5	17.8	4.2	21.1	5.0	1.5	0.4	7.7	1.8	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
100–149	16	23.8	5.6	28.6	6.7	4.8	1.1	7.3	1.7	0.4	0.1	0.0	0.0	2.9	0.7	0.1	0.0	15.6	3.7	0.0	0.0
≥150	13	23.1	5.4	28.3	6.7	3.6	0.9	8.2	1.9	1.5	0.3	0.1	0.0	0.8	0.2	0.0	0.0	0.0	0.0	0.0	0.0

Appendix B Lichen model outputs and prediction

Table 20. Summary of model selection statistics for candidate *a priori* models used to select the most parsimonious count model for understanding the volume of forage lichens in the Klaza caribou herd range, west-central Yukon. Parameters are defined in Table 2.

Rank	Model parameters	AIC_{ci}	$AIC_c\ w_i$	$\Delta_i\ AIC_c$
1	TSB+CO+SBA+TH+TH^2+CT	782.58	0.95	0.00
2	CO+SBA+TH+TH^2+CT	788.57	0.05	6.00
3	TSB+TH+TH^2+CT	808.89	0.00	26.31
4	TH+TH^2+CT	829.70	0.00	47.12
5	TSB+CO+SBA+TH+TH^2+Elev+North+East	884.66	0.00	102.08
6	TSB+CO+SBA+TH+TH^2+TSC	888.61	0.00	106.04
7	CO+SBA+TH+TH^2+Elev+North+East	893.06	0.00	110.48
8	TSB+CO+SBA+TH+TH^2+SMR	893.38	0.00	110.81
9	TSB+CO+SBA+TH+TH^2	894.35	0.00	111.78
10	CO+SBA+TH+TH^2+SMR	902.93	0.00	120.36
11	CO+SBA+TH+TH^2+TSC	905.96	0.00	123.38
12	TSB+CO+TH+TH^2+TSC	913.05	0.00	130.48
13	CO+SBA+TH+TH^2	914.07	0.00	131.49
14	TSB+CO+TH+TH^2	917.37	0.00	134.80
15	CO+TH+TH^2+TSC	950.64	0.00	168.06
16	CO+TH+TH^2	959.94	0.00	177.37
17	TSB+SMR+S	1267.83	0.00	485.26
18	TSB+Elev+North+East+S	1290.62	0.00	508.04
19	SMR+S	1331.04	0.00	548.47
20	Elev+North+East+S	1369.99	0.00	587.41

Table 21. Summary of model selection statistics for candidate *a priori* models used to select the most parsimonious fractional logit model (binomial family, logit link function) for understanding the cover of forage lichens in the Klaza caribou herd range, west-central Yukon. Parameters are defined in Table 2.

Rank	Model parameters	AIC_{ci}	$AIC_c\ w_i$	$\Delta_i\ AIC_c$
1	CO+SBA+TH+TH^2	71.37	0.17	0.00
2	CO+TH+TH^2	71.43	0.16	0.06
3	TH+TH^2+CT	71.79	0.13	0.42
4	TSB+CO+TH+TH^2	72.07	0.12	0.70
5	TSB+CO+SBA+TH+TH^2	72.96	0.08	1.59
6	TSB+TH+TH^2+CT	73.02	0.07	1.65
7	CO+TH+TH^2+TSC	73.36	0.06	1.99
8	CO+SBA+TH+TH^2+TSC	73.45	0.06	2.08
9	CO+SBA+TH+TH^2+CT	73.94	0.05	2.57
10	TSB+CO+TH+TH^2+TSC	74.15	0.04	2.78
11	TSB+CO+SBA+TH+TH^2+TSC	75.15	0.03	3.78
12	TSB+CO+SBA+TH+TH^2+CT	75.95	0.02	4.58
13	CO+SBA+TH+TH^2+SMR	77.60	0.01	6.23
14	TSB+SMR+S	79.08	0.00	7.71
15	TSB+CO+SBA+TH+TH^2+SMR	79.54	0.00	8.16
16	SMR+S	79.67	0.00	8.30
17	CO+SBA+TH+TH^2+Elev+North+East	80.05	0.00	8.68
18	TSB+Elev+North+East+S	81.70	0.00	10.33
19	TSB+CO+SBA+TH+TH^2+Elev+North+East	81.85	0.00	10.48
20	Elev+North+East+S	83.67	0.00	12.30

Table 22. Coefficients and statistical parameters generated from the top-ranked (Δ_i AIC_c differed by ≤2 points) zero-inflated Poisson (ZIP) regression models for *Cladina* spp. and *Cetraria* spp. lichen volume (dm^3/m^2) in the Klaza caribou herd annual range, west-central Yukon. Coefficients and statistical parameters for the count and binary parts of the ZIP models are distinguished.

Parameter	**β**	**Robust SE**	**Z**	**P**	**95% CI**	
					Lower	**Upper**
Count						
Time since burn	0.002	0.001	1.27	0.21	-0.001	0.005
Canopy openness	0.011	0.009	1.21	0.23	-0.007	0.028
Stand basal area	0.034	0.016	2.12	0.03	0.003	0.065
Tree height	0.271	0.101	2.69	0.01	0.073	0.469
Tree height^2	-0.022	0.006	-3.55	0.00	-0.034	-0.010
Cover type						
Deciduous	-0.736	0.342	-2.15	0.03	-1.406	-0.066
Open	-0.697	0.327	-2.13	0.03	-1.338	-0.057
Coniferous	1.433	0.265	5.41	0.00	0.914	1.952
Constant	-0.460	0.900	-0.51	0.61	-2.224	1.304
Binary						
Time since burn	-0.015	0.016	-0.95	0.34	-0.046	0.016
Canopy openness	-0.076	0.036	-2.13	0.03	-0.146	-0.006
Stand basal area	-0.665	0.140	-4.75	0.00	-0.939	-0.390
Tree height	1.997	0.995	2.01	0.05	0.046	3.948
Tree height^2	-0.076	0.035	-2.21	0.03	-0.144	-0.009
Cover type						
Deciduous	3.543	0.481	7.37	0.00	2.601	4.485
Open	-6.514	0.983	-6.62	0.00	-8.441	-4.586
Coniferous	2.971	0.968	3.07	0.00	1.073	4.869
Constant	-7.080	7.808	-0.91	0.37	-22.383	8.223

Table 23. Coefficients and statistical parameters generated from the top ranked ((Δ_i AIC$_c$ differed by ≤2 points) fractional logit models for the prediction of *Cladina* spp. and *Cetraria* spp. lichen cover (%, expressed as a proportion) in the Klaza caribou herd annual range, west-central Yukon.

AIC$_c$ rank	**Parameter**	**β**	**Robust SE**	**Z**	**P**	**95% CI**	
						Lower	**Upper**
1	Canopy openness	0.044	0.012	3.66	0.000	0.020	0.067
	Stand basal area	0.108	0.038	2.86	0.004	0.034	0.183
	Tree height	0.527	0.106	4.99	0.000	0.320	0.734
	Tree height^2	-0.032	0.008	-4.07	0.000	-0.048	-0.017
	Constant	-7.231	1.132	-6.39	0.000	-9.449	-5.014
2	Canopy openness	0.029	0.010	2.9	0.004	0.009	0.049
	Tree height	0.578	0.112	5.17	0.000	0.359	0.797
	Tree height^2	-0.032	0.008	-3.88	0.000	-0.048	-0.016
	Constant	-5.891	0.958	-6.15	0.000	-7.768	-4.014
3	Tree height	0.222	0.152	1.46	0.145	-0.076	0.520
	Tree height^2	-0.019	0.009	-2.20	0.027	-0.037	-0.002
	Cover type						
	Deciduous	-1.168	0.400	-2.92	0.004	-1.953	-0.384
	Open	-0.427	0.344	-1.24	0.214	-1.100	0.246
	Coniferous	1.595	0.331	4.82	0.000	0.946	2.244
	Constant	-2.974	0.384	-7.74	0.000	-3.727	-2.221
4	Time since burn	0.006	0.003	2.52	0.012	0.001	0.011
	Canopy openness	0.028	0.009	3.18	0.001	0.011	0.045
	Tree height	0.498	0.116	4.29	0.000	0.270	0.725
	Tree height^2	-0.030	0.008	-3.67	0.000	-0.046	-0.014
	Constant	-5.915	0.847	-6.98	0.000	-7.575	-4.254
5	Time since burn	0.005	0.002	1.92	0.055	0.000	0.009
	Canopy openness	0.040	0.011	3.53	0.000	0.018	0.063
	Stand basal area	0.088	0.038	2.33	0.020	0.014	0.163
	Tree height	0.482	0.110	4.39	0.000	0.267	0.698
	Tree height^2	-0.031	0.008	-3.95	0.000	-0.046	-0.016
	Constant	-7.032	1.083	-6.49	0.000	-9.155	-4.910
6	Time since burn	0.005	0.002	2.14	0.032	0.000	0.010
	Tree height	0.205	0.145	1.41	0.158	-0.080	0.489
	Tree height^2	-0.020	0.008	-2.36	0.018	-0.036	-0.003
	Cover type						
	Deciduous	-1.119	0.404	-2.77	0.006	-1.911	-0.327
	Open	-0.318	0.336	-0.95	0.344	-0.976	0.340
	Coniferous	1.437	0.334	4.31	0.000	0.783	2.091
	Constant	-3.187	0.375	-8.50	0.000	-3.922	-2.452
7	Canopy openness	0.033	0.010	3.26	0.001	0.013	0.053
	Tree height	0.587	0.115	5.1	0.000	0.361	0.813
	Tree height^2	-0.032	0.008	-3.9	0.000	-0.049	-0.016
	Shrub cover	-0.006	0.003	-1.86	0.063	-0.012	0.000
	Constant	-6.097	0.952	-6.41	0.000	-7.963	-4.232

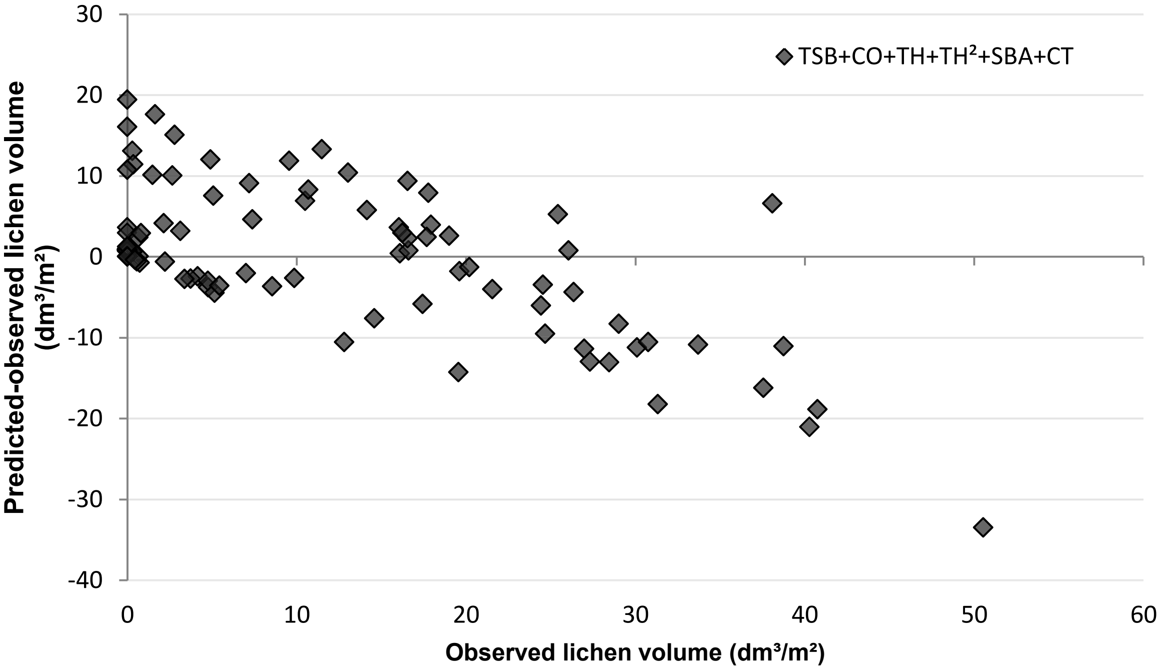

Figure 16. Difference in the observed and predicted volume of forage lichens generated using the top-ranked zero-inflated Poisson model for vegetation plots in the Klaza caribou herd range, west-central Yukon. A value of zero suggests perfect prediction, whereas negative values indicate model under-prediction and positive values indicate over-prediction.

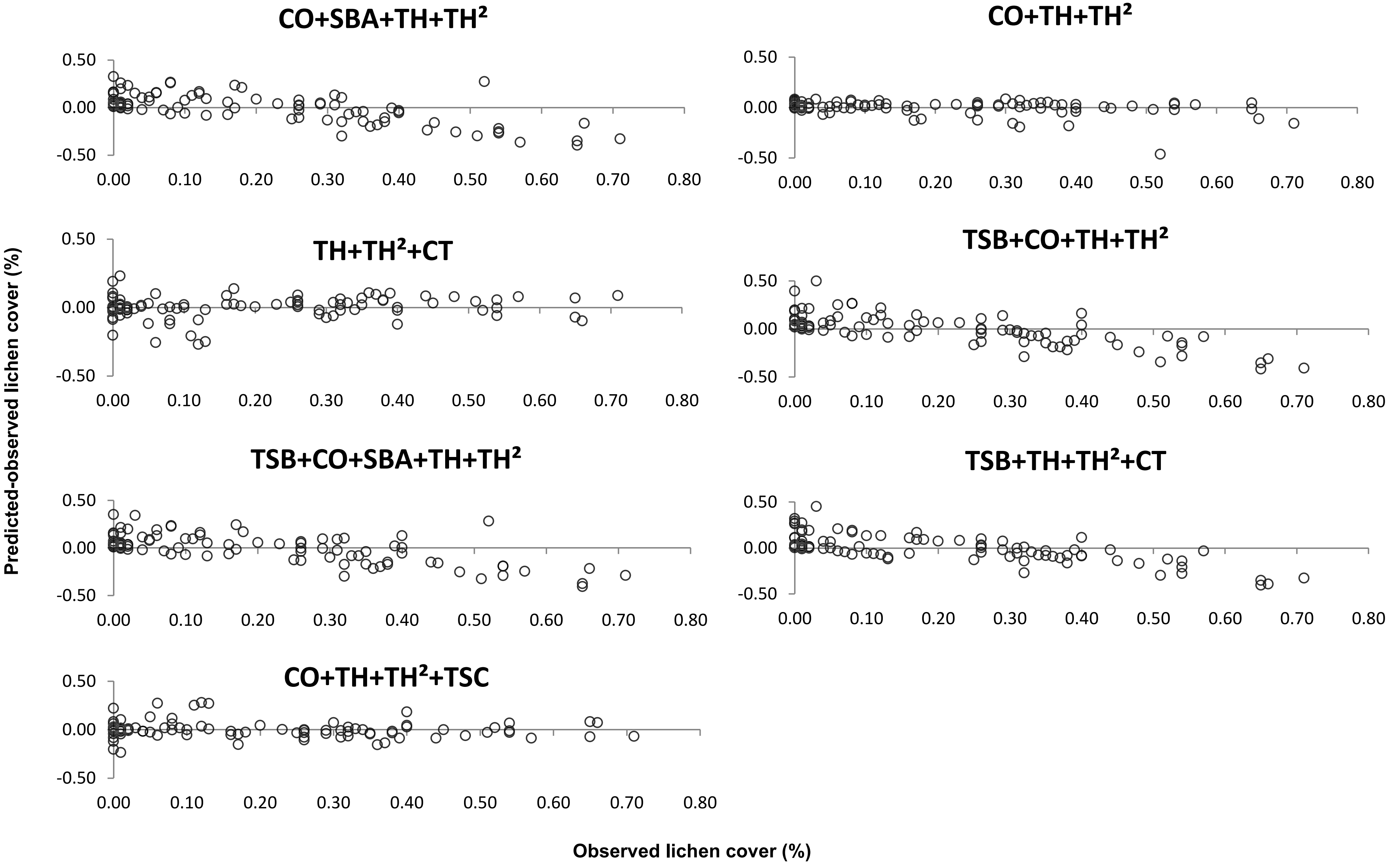

Figure 17. Difference in the observed and predicted cover of forage lichens generated using the top-ranked fractional logit models for vegetation plots in the Klaza caribou herd range, west-central Yukon. A value of zero suggests perfect prediction, whereas negative values indicate model under-prediction and positive values indicate over-prediction. Parameters are defined in Table 2; model statistics are given in Table 6.

Appendix C Lichen biomass estimates on winter ranges of caribou

Table 24. Lichen biomass of various winter range types, both used and unused (random) by *Rangifer* (caribou or reindeer; adapted from Barrier 2011).

Location	**Herd**	**Range Type**	**Thallus**[a]	**Biomass (kg/ha)**	**Reference**
Northwest Territories	Bathurst	Used unburned forest	No	2,412	Barrier 2011
Northwest Territories	Bathurst	Random unburned forest	No	2,516	Barrier 2011
Northwest Territories	Beverly (west block)	Used, >60 years old	No	2,594	Thomas et al. 1996
Northwest Territories	Beverly (east block)	Used, >60 years old	No	6,250	Thomas et al. 1996
N. Saskatchewan	Beverly/Qamanirjuaq	Lichen-dominant	No	810	Scotter 1970
N. Saskatchewan	Qamanirjuaq	Lichen-dominant	Yes	5,850	Miller 1976
N. Manitoba	Qamanirjuaq	Lichen-dominant	Yes	4,270	Miller 1976
Ungava	Leaf River	Lichen-dominant	Unknown	1,223	Crete et al. 1990
Ungava	George River	All present	Unknown	3,170	Bergerud et al. 2008
N. Quebec	George/Leaf River	Forests <30 years	No	530	Arseneault et al. 1997
N. Quebec	George/Leaf River	All present	No	2,800	Arseneault et al. 1997
N. Quebec	George/Leaf River	Forests >90 years	No	8,010	Arseneault et al. 1997
N. Quebec	George/Leaf River	Lichen-dominant	No	5,440	Arseneault et al. 1997
Northern Yukon	Porcupine	All present	Yes	508	Russell et al. 1993
Central Alaska	Delta (traditional areas)	All present	Unknown	100–850	Fleischman 1990
Central Alaska	Delta (peripheral areas)	All present	Unknown	>2,000	Fleischman 1990
NW Alaska	Western Arctic	Used unburned forest	Unknown	3,007	Joly et al. 2010
NW Alaska	Western Arctic	Random unburned forest	Unknown	1,260	Joly et al. 2010
NW Alaska	Western Arctic	Random burned forest	Unknown	818	Joly et al. 2010
N. Finland	Reindeer	Heath forest	No	520	Helle 1981
Norway	Reindeer	Climax forest stands	Unknown	11,000	Gaare and Skogland 1980
Finland[b]	Reindeer	Random burned forest	No	38–1,272	Kumpula et al. 2000
Alberta[b]	Woodland	Used	Unknown	4,017	Edmonds and Bloomfield 1984
Alberta[b]	Woodland	Random	Unknown	Random	Edmonds and Bloomfield 1984
British Columbia[b]	Wolverine	Used	Unknown	1,730–3,450	Johnson et al. 2001
Alaska[b]	Nelchina	Used	Unknown	1,250	Collins et al. 2011
Alaska[b]	Nelchina	Unused, abandoned stands	Unknown	400	Collins et al. 2011

Quebec[b]	Forest-dwelling	Used	Unknown	1082–3054	Briand et al. 2009

[a] Indicates whether or not dead bases of lichen thalli were included in the biomass estimates (Barrier 2011).

[b] Addition to Barrier's (2011) original table.

Appendix D RSF model outputs

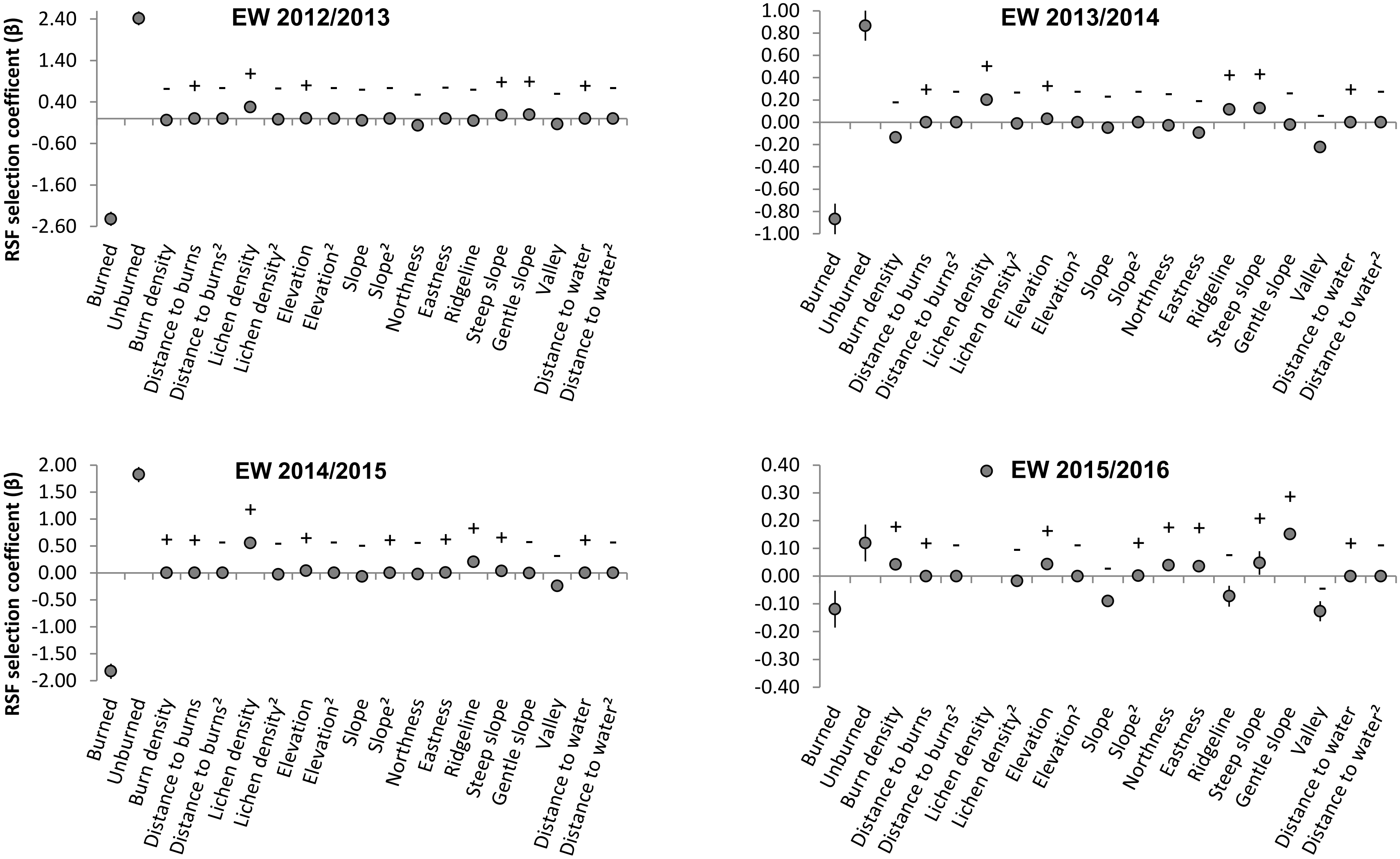

Figure 18. Averaged, unweighted selection coefficients with 95% confidence intervals (representing variability of averaged coefficients) for early winter resource selection function models of individual Klaza caribou. For very small values, positive and negative (+/-) signs above coefficient values are provided for clarity.

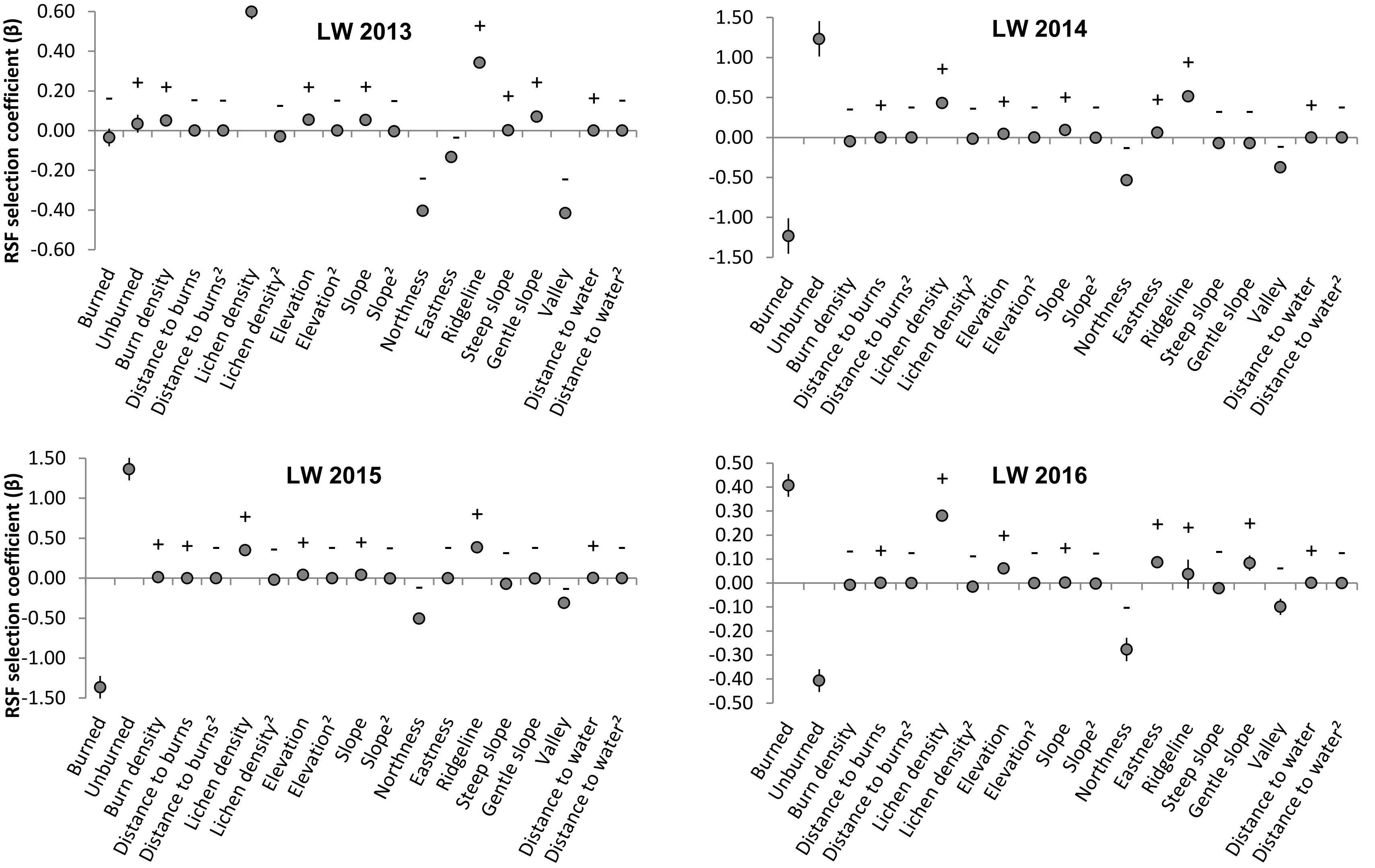

Figure 19. Averaged unweighted selection coefficients with 95% confidence intervals (representing variability of averaged coefficients) for late winter resource selection function models of individual Klaza caribou. For very small values, positive and negative (+/-) signs above coefficient values are provided for clarity.

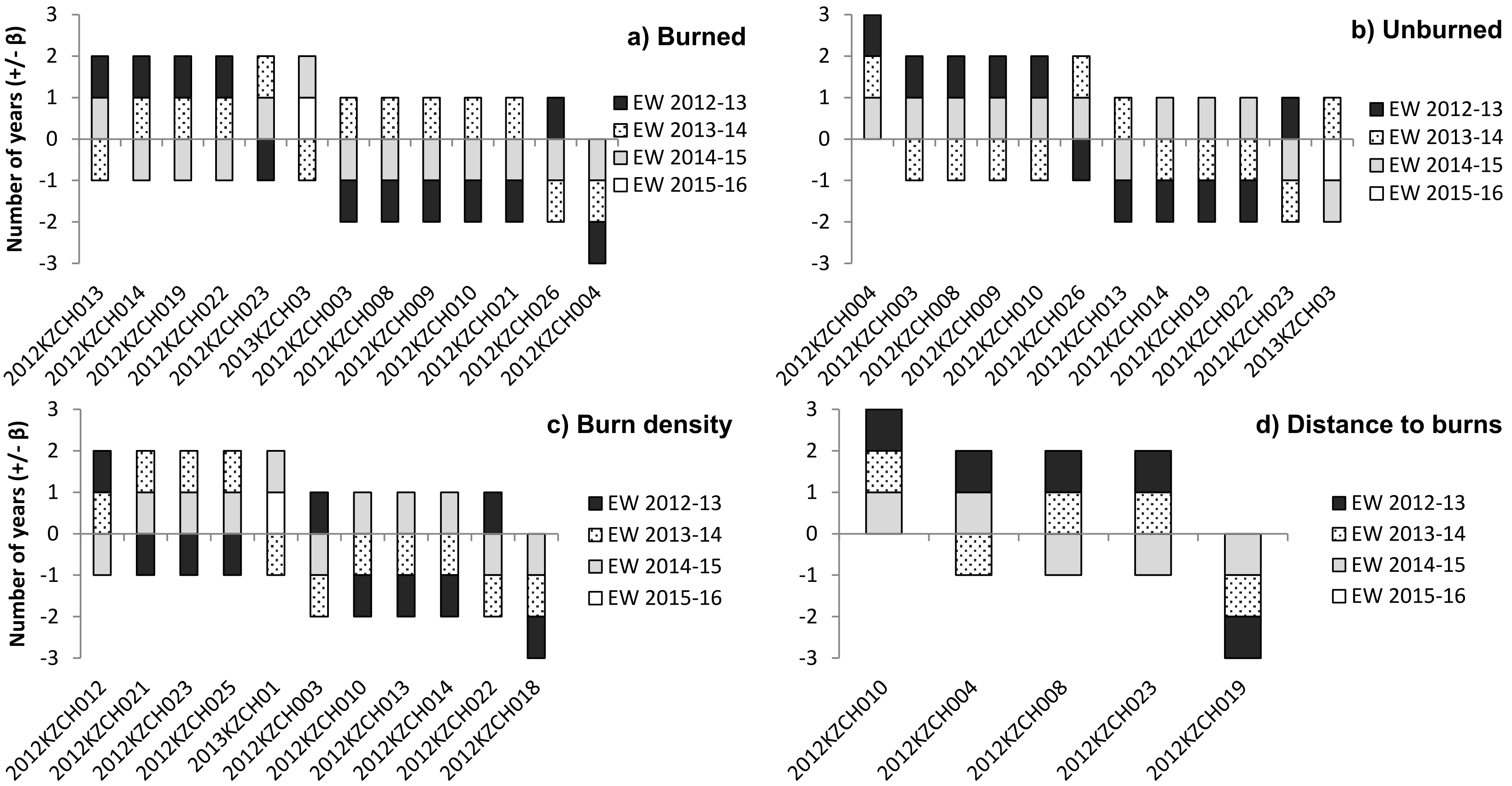

Figure 20. Number of years during the study period (2012–2016) that individual Klaza caribou with three years of data demonstrated positive or negative responses to burn characteristics during the early winter season.

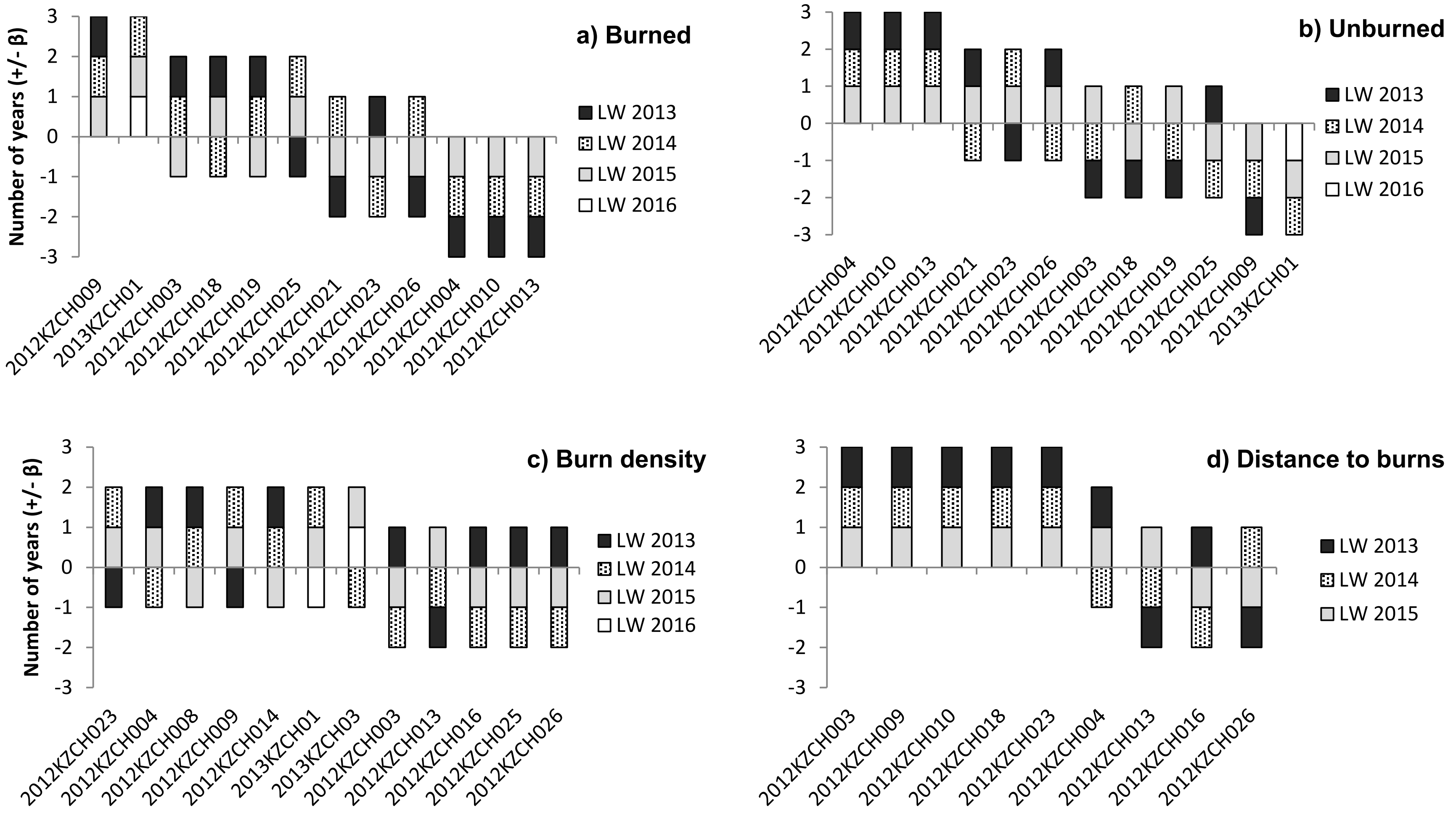

Figure 21. Number of years during the study period (2012–2016) that individual Klaza caribou with three years of data demonstrated positive or negative responses to burn characteristics during the late winter season.

Appendix E Burn-focused logistic model outputs

Table 25. Area under the Receiver Operating Characteristic (ROC) curve scores calculated for each percentile differentiating Habitat Selection Units with low versus high use by Klaza caribou, west-central Yukon. Values in bold indicate the highest scores and the corresponding percentile was used to set the threshold for that season-year.

Percentile of combined use metric	**Early winter**				**Late winter**			
	2012/13	**2013/14**	**2014/15**	**2015/16**	**2013**	**2014**	**2015**	**2016**
5	0.45		-	-	0.47	0.76	0.58	0.42
10	0.60	**0.71**	-	-	0.47	**0.76**	0.55	0.42
25	0.65	0.65	0.71	0.74	0.50	0.67	0.66	**0.58**
50	**0.69**	0.64	0.66	0.72	0.57	0.66	0.66	0.50
75	0.56	0.60	0.80	**0.75**	**0.59**	0.62	0.58	0.54
90	0.53	0.58	**0.98**	0.44	0.57	0.56	**0.71**	0.35
95	0.66	0.42	0.00	0.44	0.50	0.63	0.75	0.21
99	-	-	0.78	-	-	0.46	0.01	-

Note: To avoid creating an unbalanced data set, only ROC scores identified within the 10th to 90th percentiles were considered.

Table 26. Coefficients and statistical parameters generated from the top-ranked (Δ_i AIC_c differed by ≤2 points) logistic models representing the relative use of Habitat Selection Units by caribou during early winter in the Klaza herd annual range, west-central Yukon (2012–2016).

Year	**AIC_c rank**	**Parameter**	**β**	**Robust SE**	**Z**	**P**	**95% CI**	
							Lower	**Upper**
2012/2013	1	Burn age	***0.158***	0.036	4.380	0.000	0.087	0.228
		Lichen density	***0.488***	0.245	2.000	0.046	0.009	0.968
		Lichen density²	***-0.036***	0.018	-1.960	0.050	-0.072	0.000
		Burn perimeter use						
		Core	0.468	0.468	1.000	0.317	-0.449	1.384
		Inner 500	-0.250	0.372	-0.670	0.503	-0.979	0.480
		Outer 500	-0.218	0.336	-0.650	0.517	-0.877	0.441
		Constant	-1.935	0.639	-3.030	0.002	-3.188	-0.682
2013/2014	1	Burn age	0.938	0.956	0.980	0.326	-0.935	2.811
		Lichen density	-0.229	0.256	-0.890	0.371	-0.731	0.273
		Lichen density²	0.012	0.020	0.570	0.568	-0.028	0.052
		Burn perimeter use						
		Core	-0.632	0.496	-1.280	0.202	-1.604	0.339
		Inner 500	0.433	0.428	1.010	0.312	-0.406	1.273
		Outer 500	0.199	0.436	0.460	0.647	-0.655	1.053
		Constant	-0.224	2.887	-0.080	0.938	-5.883	5.435
	2	Elevation	-0.102	0.072	-1.400	0.160	-0.243	0.040
		Elevation²	0.000	0.000	1.540	0.125	0.000	0.000
		Valley	***1.257***	0.572	2.190	0.028	0.135	2.378
		Gentle slope	-0.272	0.504	-0.540	0.590	-1.259	0.716
		Steep slope	0.224	0.726	0.310	0.758	-1.200	1.648
		Ridge	-1.209	1.121	-1.080	0.281	-3.407	0.988
		Lichen density	-0.297	0.303	-0.980	0.328	-0.891	0.297
		Lichen density²	0.019	0.022	0.870	0.383	-0.024	0.061
		Burn age	1.252	0.932	1.340	0.179	-0.575	3.078
		Burn perimeter use						
		Core	-0.294	0.581	-0.510	0.613	-1.433	0.846
		Inner 500	0.448	0.497	0.900	0.368	-0.526	1.422
		Outer 500	-0.154	0.464	-0.330	0.740	-1.063	0.756
		Constant	50.528	39.869	1.270	0.205	-27.615	128.671
	3	Elevation	-0.105	0.059	-1.770	0.076	-0.221	0.011
		Elevation²	0.000	0.000	1.840	0.066	0.000	0.000
		Lichen density	-0.244	0.262	-0.930	0.353	-0.758	0.271
		Lichen density²	0.013	0.021	0.630	0.529	-0.027	0.053

Year	AIC$_c$ rank	Parameter	β	Robust SE	Z	P	95% CI	
							Lower	Upper
		Burn age	0.977	0.891	1.100	0.273	-0.770	2.724
		Burn perimeter use						
		Core	-0.505	0.511	-0.990	0.323	-1.505	0.496
		Inner 500	0.315	0.436	0.720	0.470	-0.539	1.168
		Outer 500	0.190	0.462	0.410	0.681	-0.716	1.096
		Constant	56.786	32.605	1.740	0.082	-7.118	120.690
2014/2015	1	Burn age	***0.251***	0.061	4.150	0.000	0.133	0.370
		Lichen density	***1.262***	0.591	2.140	0.033	0.105	2.420
		Lichen density²	-0.060	0.035	-1.730	0.084	-0.127	0.008
		Burn perimeter use						
		Core	***-9.615***	0.699	-13.750	0.000	-10.985	-8.244
		Inner 500	***4.647***	0.560	8.300	0.000	3.550	5.744
		Outer 500	***4.967***	0.594	8.370	0.000	3.804	6.131
		Constant	-14.515	2.670	-5.440	0.000	-19.748	-9.282
	2	Elevation	-0.054	0.055	-0.990	0.322	-0.161	0.053
		Elevation²	0.000	0.000	1.100	0.271	0.000	0.000
		Valley	***2.723***	1.325	2.050	0.040	0.126	5.320
		Gentle slope	***5.701***	0.851	6.700	0.000	4.033	7.368
		Steep slope	***-12.436***	1.186	-10.490	0.000	-14.760	-10.112
		Ridge	***4.013***	0.771	5.210	0.000	2.502	5.523
		Lichen density	***2.089***	0.747	2.800	0.005	0.625	3.553
		Lichen density²	***-0.100***	0.041	-2.440	0.015	-0.181	-0.020
		Burn age	***0.377***	0.091	4.140	0.000	0.199	0.556
		Burn perimeter use						
		Core	***-8.831***	0.919	-9.610	0.000	-10.632	-7.030
		Inner 500	***4.541***	0.720	6.310	0.000	3.131	5.951
		Outer 500	***4.290***	0.651	6.590	0.000	3.014	5.565
		Constant	7.127	34.934	0.200	0.838	-61.342	75.596
2015/2016	1	Northness	0.218	0.348	0.620	0.532	-0.465	0.900
		Eastness	-0.383	0.340	-1.130	0.259	-1.050	0.283
		Slope	0.044	0.068	0.650	0.516	-0.089	0.177
		Elevation	0.077	0.045	1.720	0.085	-0.011	0.166
		Elevation²	0.000	0.000	-1.790	0.074	0.000	0.000
		Valley	-0.746	0.502	-1.490	0.137	-1.729	0.237
		Gentle slope	-0.191	0.518	-0.370	0.712	-1.207	0.824
		Steep slope	***-1.398***	0.631	-2.220	0.027	-2.634	-0.162
		Ridge	***2.336***	0.524	4.460	0.000	1.308	3.363
		Lichen density	***2.277***	0.485	4.690	0.000	1.325	3.228

Year	AIC_c rank	Parameter	β	Robust SE	Z	P	95% CI	
							Lower	Upper
		Lichen density^2	***-0.151***	0.036	-4.230	0.000	-0.222	-0.081
		Distance to water	0.000	0.000	-1.540	0.123	-0.001	0.000
		Constant	-53.985	28.401	-1.900	0.057	-109.651	1.680
	2	Lichen density	***1.803***	0.398	4.530	0.000	1.023	2.582
		Lichen density^2	***-0.123***	0.028	-4.340	0.000	-0.179	-0.068
		Burn perimeter use						
		Core	0.093	0.429	0.220	0.828	-0.747	0.934
		Inner 500	-0.381	0.346	-1.100	0.271	-1.059	0.297
		Outer 500	0.288	0.322	0.890	0.372	-0.343	0.918
		Constant	-6.643	1.253	-5.300	0.000	-9.099	-4.187
	3	Elevation	0.056	0.042	1.320	0.187	-0.027	0.139
		Elevation^2	0.000	0.000	-1.370	0.171	0.000	0.000
		Valley	***-1.137***	0.555	-2.050	0.041	-2.225	-0.048
		Gentle slope	-0.340	0.396	-0.860	0.391	-1.116	0.437
		Steep slope	***-1.096***	0.533	-2.060	0.040	-2.141	-0.051
		Ridge	***2.572***	0.567	4.540	0.000	1.461	3.684
		Lichen density	***2.295***	0.496	4.630	0.000	1.323	3.267
		Lichen density^2	***-0.153***	0.036	-4.190	0.000	-0.224	-0.081
		Burn age	-0.026	0.023	-1.130	0.258	-0.071	0.019
		Burn perimeter use						
		Core	0.620	0.562	1.100	0.270	-0.481	1.722
		Inner 500	-0.657	0.430	-1.530	0.127	-1.500	0.186
		Outer 500	0.037	0.381	0.100	0.923	-0.709	0.783
		Constant	-40.593	26.575	-1.530	0.127	-92.679	11.493

Table 27. Coefficients and statistical parameters generated from the top-ranked (Δ_i AIC_c differed by ≤2 points) logistic models representing the relative use of Habitat Selection Units by caribou during late winter in the Klaza herd annual range, west-central Yukon (2013–2016).

Year	*AIC_c rank*	Parameter	β	Robust SE	Z	P	95% CI	
							Lower	Upper
2013	1	Lichen density	0.120	0.202	0.600	0.551	-0.275	0.515
		Lichen density^2	0.012	0.016	0.720	0.472	-0.020	0.438
		Burn perimeter use						
		Core	-0.207	0.286	-0.730	0.468	-0.767	0.352
		Inner 500	0.168	0.241	0.700	0.486	-0.305	0.641
		Outer 500	0.039	0.230	0.170	0.865	-0.412	0.490
		Constant	-2.058	0.562	-3.660	0.000	-3.159	-0.958

Year	AIC_c rank	Parameter	β	Robust SE	Z	P	95% CI	
							Lower	Upper
	2	Lichen density	0.156	0.208	0.750	0.454	-0.252	0.564
		Lichen density^2	0.009	0.017	0.540	0.591	-0.024	0.042
		Burn age	-0.007	0.013	-0.520	0.600	-0.031	0.018
		Burn perimeter use						
		Core	-0.151	0.291	-0.520	0.604	-0.722	0.420
		Inner 500	0.151	0.242	0.620	0.533	-0.324	0.626
		Outer 500	0.000	0.233	0.000	1.000	-0.457	0.457
		Constant	-1.989	0.570	-3.490	0.000	-3.105	-0.872
2014	1	Elevation	-0.030	0.024	-1.260	0.208	-0.077	0.017
		Elevation^2	0.000	0.000	1.120	0.261	0.000	0.000
		Lichen density	0.140	0.313	0.450	0.654	-0.473	0.753
		Lichen density^2	0.010	0.036	0.280	0.782	-0.060	0.080
		Burn age	***0.083***	0.029	2.890	0.004	0.026	0.139
		Burn perimeter use						
		Core	***-0.771***	0.283	-2.720	0.006	-1.326	-0.216
		Inner 500	-0.007	0.289	-0.020	0.981	-0.573	0.560
		Outer 500	***0.778***	0.351	2.210	0.027	0.090	1.466
		Constant	17.182	11.927	1.440	0.150	-6.194	40.559
2015	1	Slope	***-0.063***	0.031	-2.000	0.045	-0.125	-0.001
		Elevation	***0.076***	0.028	2.770	0.006	0.022	0.130
		Elevation^2	***0.000***	0.000	-2.840	0.005	0.000	0.000
		Lichen density	0.541	0.336	1.610	0.108	-0.118	1.200
		Lichen density^2	-0.029	0.027	-1.080	0.281	-0.082	0.024
		Burn age	-0.027	0.015	-1.810	0.070	-0.055	0.002
		Burn perimeter use						
		Core	-0.584	0.472	-1.240	0.216	-1.508	0.341
		Inner 500	-0.259	0.357	-0.730	0.467	-0.958	0.440
		Outer 500	***0.843***	0.295	2.860	0.004	0.264	1.421
		Constant	-40.099	13.973	-2.870	0.004	-67.485	-12.713
	2	Elevation	***0.065***	0.026	2.480	0.013	0.014	0.116
		Elevation^2	***0.000***	0.000	-2.590	0.010	0.000	0.000
		Lichen density	0.574	0.326	1.760	0.078	-0.064	1.212
		Lichen density^2	-0.029	0.026	-1.130	0.257	-0.080	0.021
		Burn age	-0.024	0.014	-1.750	0.081	-0.051	0.003
		Burn perimeter use						
		Core	-0.534	0.467	-1.140	0.253	-1.449	0.382
		Inner 500	-0.308	0.359	-0.860	0.391	-1.011	0.395
		Outer 500	***0.842***	0.291	2.890	0.004	0.271	1.412

Year	***AIC$_c$ rank***	**Parameter**	**β**	**Robust SE**	**Z**	**P**	**95% CI**	
							Lower	**Upper**
		Constant	-35.082	13.393	-2.620	0.009	-61.332	-8.833
2016	1	Burn age	***0.034***	0.012	2.760	0.006	0.010	0.058
		Lichen density	-0.417	0.260	-1.600	0.109	-0.926	0.093
		Lichen density^2	0.037	0.021	1.790	0.073	-0.003	0.077
		Burn perimeter use						
		Core	-0.207	0.299	-0.690	0.488	-0.794	0.379
		Inner 500	-0.047	0.244	-0.190	0.848	-0.525	0.431
		Outer 500	0.254	0.240	1.060	0.291	-0.217	0.725
		Constant	1.254	0.675	1.860	0.063	-0.069	2.577