

Fire, lichens, and woodland caribou (*Rangifer tarandus caribou*) in Canada's Boreal Shield

by

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Abstract

Threatened woodland caribou (*Rangifer tarandus caribou*) have experienced large range recessions and population declines across much of Canada's boreal forest in the last century and have become a major focus of conservation efforts in the region. Habitat management strategies for woodland caribou seek to minimize the extent of human and fire disturbance on caribou ranges, but there remains conflicting evidence on the effects of fire on woodland caribou. Managers are also encouraged to identify and protect critical habitat for caribou populations, but critical habitat is defined using broad and descriptive definitions that may inadequately represent the functional characteristics needed by caribou. In this thesis, I set out to help refine habitat definitions for woodland caribou in the less studied western Boreal Shield by studying the interactions between fire, lichens, and caribou. I conducted field sampling in northwestern Ontario to map the biomass of ground lichens in a fire-driven landscape and linked this lichen biomass map to GPS collar locations of female caribou to assess seasonal selection for lichen biomass and refuge habitat. I also assessed the short-term response of caribou to fire in Ontario and Saskatchewan by comparing their pre-fire and post-fire space use. I developed a straightforward modelling framework to map lichen biomass that can be refined and adapted for other boreal caribou ranges. Lichen biomass was a strong predictor of winter habitat selection, suggesting lichen biomass maps could be used to improve the identification of winter habitat. I found caribou did not strongly alter their space use in response to fire, particularly during the calving season, suggesting we may need to broaden the interpretation of fire in habitat management strategies. My research provides insight into the ecology of woodland caribou in the western Boreal Shield, a less studied portion of the species range, and suggests changes to habitat management strategies could improve caribou conservation outcomes.

Preface

This thesis is an original work by Joseph Silva.

The title of this thesis pays homage to Klein's 1982 paper on fire, lichens, and caribou.

A previous version of Chapter 1 of this thesis was published as: Silva, J.A., Nielsen, S.E., Lamb, C.T., Hague, C. and Boutin, S, 2019, "Modelling lichen abundance for woodland caribou in a fire-driven boreal landscape," *Forests*, vol. 10, issue 11, article 962. I was responsible for study design, data collection, data analysis and manuscript preparation. S.E. Nielsen assisted with study design, C.T. Lamb with data analysis, and C. Hague with data collection. All coauthors contributed edits to the published manuscript.

Chapter 3 of this thesis was submitted for publication in the Canadian Journal of Zoology as: Silva, J.A., Nielsen, S.E., McLoughlin, P.D., Rodgers, A.R., Hague, C. and Boutin, S, "Comparison of space use before and after fire reveals varied responses by woodland caribou (*Rangifer tarandus caribou*) in Canada's Boreal Shield." I was responsible for study design, data analysis and manuscript preparation. S.E. Nielsen and S. Boutin assisted with study design and data analysis. P.D. McLoughlin and A.R. Rodgers contributed data. All authors reviewed, contributed to, and approved the final manuscript.

No additional manuscripts have been submitted for publication to date.

Dedication

This thesis is dedicated in memory of April Patton (1968–2020). I will remember April for her generosity and kindness. Growing up, she always welcomed me into her home, and she helped welcome me into her parent’s home as I started my post-secondary journey. April had a unique ability to inspire confidence in others. I am grateful for her trust and belief in me.

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This project would not have been possible without my experiences in Woodland Caribou Provincial Park. I started working on this project for my Honours thesis at Lakehead University. I am grateful to Dr. Brian McLaren, Dr. Ulf Runesson and Tomislav Sapic for believing in me and providing me with this opportunity. I will always remember my introduction to the project. Chris Hague guided me on that first trip in Woodland Caribou Provincial Park. Within four hours of the floatplane departing she quipped: “So– you’re going to do your Master’s now, right?” The connection to both place and project was solidified later that trip when we observed caribou in a recent burn. Chris was certain after we saw the caribou that I would come back for a Master’s, and she was right. These experiences provided the inspiration for my Master’s, allowing me to pursue my interest in wildlife ecology and gain valuable skills. I have gone back every summer to work with the staff at Woodland Caribou Provincial Park. Chris has been a friend, mentor, and collaborator throughout my graduate career. I am so fortunate to have spent time shadowing and learning from her.

I am grateful to Dr. Stan Boutin and Dr. Scott Nielsen for their support throughout my Master’s, including answering my unending stream of questions and providing learning opportunities by being a member of both labs. We had many good discussions in Boutin Lab that helped me grow as an ecologist, learn how to ask good scientific questions and how to present scientific research. I was welcomed to the U of A with open arms by ACE Lab and provided all the support I needed to succeed in my fieldwork activities. I continued to learn a lot from being a part of ACE Lab throughout my Master’s. I thank Dr. Evelyn Merrill for acting as the arm’s length examiner for my thesis defence and providing thoughtful insight on my research and thank Dr. Andy Derocher for acting as the Chair of the exam committee.

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INTRODUCTION

Over the course of their evolutionary history, caribou evolved to fill a niche unexploited by other northern ungulates by consuming large quantities of lichens (Klein 1982). This strategy allows caribou to occupy less productive habitat and space away from other ungulates (e.g., moose, *Alces alces*) and wolves (*Canis lupus*), the latter their primary predator (Rettie and Messier 2000). However, it comes at a cost, as caribou require large, contiguous landscapes to space away from moose and wolves, making them highly vulnerable to habitat disturbance (Bergerud 1974).

As human settlement has gradually increased in Canada's boreal forest over the last century, woodland caribou populations have declined (Bergerud 1974) and the species is now classified as Threatened under Canada's *Species at Risk Act*. Habitat disturbance (i.e., resource extraction and fire) has been widely recognized as the primary mechanism driving population declines (Festa-Bianchet et al. 2011; ECCC 2012). In addition to altering or removing the mature, lichen-rich forests caribou rely upon, habitat disturbance can increase the amount of early seral habitat, improving conditions for moose (Street et al. 2015). This facilitates an increase in the density of moose and wolves, increasing predation on woodland caribou (Seip et al. 1992). In addition, linear features such as roads and energy corridors can act as travel routes for wolves, increasing encounter rates between caribou and their predators in heavily fragmented landscapes (Dickie et al. 2016). This process, known as disturbance-mediated apparent competition, has been identified as the primary mechanism driving boreal caribou population declines (Festa-Bianchet et al. 2011; Serrouya et al. 2019).

Because habitat disturbance has been shown to destabilize caribou populations (Courtois et al. 2007; Sorensen et al. 2008), burns <40 years old and human development (e.g., forestry, mining) are classified as disturbance under the federal recovery strategy for woodland caribou

(ECCC 2012). In a national caribou meta-analysis, managers identified a strong negative relationship between cumulative range-level disturbance and population growth rate (λ). They determined that if cumulative, range-level disturbance exceeded 35%, the caribou population had less than a 60% chance of attaining population stability (i.e., $\lambda = 1.0$; ECCC 2012). Since the release of these guidelines, minimizing the extent of disturbances, both natural and anthropogenic, has become a major focus of caribou recovery efforts (ECCC 2017). In addition to minimizing range-level disturbance, managers must also identify and protect critical habitat for woodland caribou populations (ECCC 2012). Critical habitats are defined by ecoregion using broad and descriptive definitions. Without being more explicit and measurable, these habitat definitions may inadequately represent the functional characteristics of suitable habitat for woodland caribou, such as the biomass of forage.

In this thesis, I set out to refine caribou habitat definitions in the less studied western Boreal Shield by studying the interactions between fire, lichens, and woodland caribou. In the first chapter, I mapped the biomass of *Cladonia* spp. ground lichens across the fire-driven landscape of Woodland Caribou Provincial Park in northwestern Ontario, Canada. In the second chapter I applied the lichen biomass map with GPS collar locations to investigate seasonal selection patterns for lichen and refuge habitat by woodland caribou. I placed these results in the context of the annual life history of caribou to gain a deeper understanding of how this species balances nutrition and predator avoidance. In the third chapter, I characterized the short-term response of caribou to fire in the Boreal Shield of Ontario and Saskatchewan by comparing their space use before and after fire events. My findings can be used to improve caribou habitat definitions in the western Boreal Shield, especially as it relates to lichen biomass and fire.

CHAPTER 1 – MODELLING LICHEN ABUNDANCE FOR WOODLAND CARIBOU IN A FIRE-DRIVEN BOREAL LANDSCAPE

Silva, J.A., Nielsen, S.E., Lamb, C.T., Hague, C., Boutin, S.

Abstract

Woodland caribou (*Rangifer tarandus caribou*) are reliant on *Cladonia* spp. ground lichens as a major component of their diet and lichen abundance could be an important indicator of habitat quality, particularly in winter. The boreal forest is typified by large, stand-replacing forest fires that consume ground lichens, which take decades to recover. The large spatial extent of caribou ranges and the mosaic of lichen availability created by fires make it challenging to track the abundance of ground lichens. Researchers have developed various techniques to map lichens across northern boreal and tundra landscapes, but it remains unclear which techniques are best suited for use in the continuous boreal forest, where many of the conflicts amongst caribou and human activities are most acute. In this study, we propose a two-stage regression modelling approach to map the abundance (biomass, kg/ha) of *Cladonia* spp. ground lichens in the boreal forest. Our study was conducted in Woodland Caribou Provincial Park, a wilderness-class protected area in northwestern Ontario, Canada. We used field sampling to characterize lichen abundance in 109 upland forest stands across the local time-since-fire continuum (2–119 years-since-fire). We then used generalized linear models to relate lichen presence and lichen abundance to forest structure, topographic and remote sensing attributes. Model selection indicated ground lichens were best predicted by ecosite, time-since-fire, and canopy closure. Lichen abundance was very low (<1000 kg/ha) across the time-since-fire continuum in dense upland conifer forest. Conversely, lichen abundance increased steadily across the time-since-fire continuum in sparse upland conifer forest, exceeding 3000 kg/ha in mature stands. We interpolated the best lichen presence and lichen abundance models to create spatial layers and

combined them to generate a map that provides a reasonable estimation of lichen biomass ($R^2 = 0.39$) for our study area. We encourage researchers and managers to use our method as a basic framework to map the abundance of ground lichens across fire-prone, boreal caribou ranges. Mapping lichens will aid in the identification of suitable habitat and can be used in planning to ensure habitat is maintained in adequate supply in areas with multiple land-use objectives. We also encourage the use of lichen abundance maps to investigate questions that improve our understanding of caribou ecology.

Introduction

The boreal ecotype of woodland caribou (*Rangifer tarandus caribou*) have evolved to occupy a niche unexploited by other northern ungulates (Rettie and Messier 2000). Caribou tend to select low-productivity forests where ground lichens are a dominant understory component and have evolved physiological adaptations to consume these lichens as a major component of their diet, particularly in winter (Palo 1993, Storeheier et al. 2002, Thompson et al. 2015). By frequenting lichen-rich landscapes, caribou can acquire forage and distance themselves from more productive forests which support higher densities of ungulates (e.g., moose, *Alces alces*) and thus predators (e.g., wolves *Canis lupus*) (Rettie and Messier 2000). However, stand-replacing forest fires are a common occurrence in woodland caribou habitat and because ground lichens are highly flammable, large quantities of lichen are lost in these disturbances (Schaefer and Pruitt 1991). Since lichens are slow growing, they take several decades to recover following fire (Carroll and Bliss 1982, Morneau and Payette 1989). Fires therefore create a constantly shifting mosaic of lichen availability across the landscape, which can influence the distribution and habitat selection of woodland caribou (Schaefer and Pruitt 1991, Joly et al. 2010).

Given the importance of ground lichens in caribou ecology, it may be useful to map the abundance of ground lichens across caribou ranges for research and/or management purposes. Ground lichens are typically found in mature conifer stands with sparse canopy closure and nitrogen-poor, acidic substrate conditions (Bradshaw et al. 1995, Antoniak and Cumming 1998, Keim et al. 2017). Proxies for the growing conditions preferred by ground lichens can be found in forest inventory layers, which often contain attributes for stand age, soil type, tree species composition and forest structure (e.g., canopy closure). Most forest inventories utilize ecological classification systems to divide the landscape into discrete vegetation communities called ‘ecosites’. Each ecosite is characterized by consistent physical features (soil type, soil depth, nutrient availability) and the resulting vegetation community (trees, shrubs, and herbaceous plants) (MNR 2014a). Several researchers have used forest inventory layers to predict the occurrence and abundance of ground lichens (Lesmerises et al. 2011, Boan et al. 2013, Uboni et al. 2019). A disadvantage of forest inventory layers is they are generally unavailable for boreal caribou ranges beyond the range of active forest management. In addition, forest inventory layers are typically updated on long time horizons (e.g., 10–20 years) as part of a forest management planning process, which can make it difficult to update lichen abundance maps to reflect changes to ecosite conditions (Boan et al. 2013).

Remote sensing has become an essential tool in landscape ecology (Kwok 2018), particularly due to the availability of Landsat satellite imagery (Wulder et al. 2012). Landsat satellites capture images of the Earth’s surface approximately bi-weekly, allowing researchers to update spatial layers as conditions change (Wulder et al. 2012). Landsat imagery is composed of several spectral bands that capture different portions of the electromagnetic spectrum. The ground lichens caribou eat contain usnic acid, which produces a unique spectral signature in the

blue and short-wave infrared wavelengths (Nelson et al. 2013). Being pale in colour, lichens can also be distinguished from green vegetation using the normalized difference vegetation index (Keim et al. 2017), which uses the red and near-infrared wavelengths to quantify vegetation greenness (Appendix C) (Tucker and Sellers 1986). The unique spectral properties of usnic lichens in the near- and short-wave infrared wavelengths led to the incorporation of the normalized difference moisture index (NDMI; Appendix C) (Wilson and Sader 2002) in several lichen remote sensing studies (Falldorf et al. 2014, Rickbeil et al. 2017). Studies have proven that Landsat spectral properties can be used to obtain reasonable estimates of lichen abundance in northern boreal and tundra systems (Nelson et al. 2013, Falldorf et al. 2014, Rickbeil et al. 2017). The unique spectral signature of ground lichens can be captured by the moderate spatial resolution of Landsat imagery (30 m pixels) in northern boreal and tundra ecosystems because tree cover is sparse or non-existent (Lesmerises et al. 2011). In the continuous boreal forest, which is characterized by relatively dense tree cover, the unique spectral signature of ground lichens may be masked by the tree canopy (Lesmerises et al. 2011). Higher resolution satellite imagery such as SPOT 6 (6 m pixels) and QuickBird (2.5 m pixels) may be able to capture the unique spectral signature of ground lichens in densely treed areas (Keim et al. 2017), but these platforms do not capture the short-wave infrared portion of the electromagnetic spectrum, which has proven useful in modelling lichens in previous studies (Nelson et al. 2013, Falldorf et al. 2014).

Landscape nutrition models often integrate remote sensing and Geographic Information System (GIS) data (e.g., topography, disturbances, forest structure) to generate spatial predictions of forage abundance from field observations. Such models have been generated for multiple, wide-ranging mammal species, including grizzly bears (Lamb et al. 2017, Nielsen et al.

2017), elk (Proffitt et al. 2016) and woodland caribou (Avgar et al. 2015). Landscape nutrition models can include multiple food types, including seasonally available plant species and prey biomass (Nielsen et al. 2017). Quantifying forage abundance across the landscape can allow researchers to study the influence of nutrition on survival and fecundity (Proffitt et al. 2016). Forage layers can also be used to identify potential high-quality habitats to target for protection or areas of overlap between humans and wildlife that present a high risk of conflict (Lamb et al. 2017). In conjunction with spatial predictions of predation risk, forage layers can be used to study the trade-offs between nutrition and predator avoidance experienced by prey species (Avgar et al. 2015, Gaynor et al. 2019).

In this study, we create a predictive model of lichen abundance in the boreal forest of Woodland Caribou Provincial Park, in Ontario, Canada and interpolate this model to create a spatial prediction (map) of lichen biomass. We use a regression modelling approach, first conducting field sampling within the study area to parameterize relationships between lichen abundance and environmental conditions (forest type, time-since-fire, canopy closure). We then relate lichen presence and lichen abundance to remote sensing and GIS data and use an *a priori* model selection procedure to identify the best explanatory variables. We interpolate the top lichen presence and abundance models across the study area and combine them to generate a map predicting lichen biomass (kg/ha). We show that our approach is straightforward and could be applied in other boreal caribou ranges with site-specific field data. Lichen maps could help managers develop more effective conservation strategies for woodland caribou. Managers could use lichen maps to track the availability of this important food resource over time and ensure a constant supply of lichen-rich habitat through resource or fire management planning. Paired with GPS collar locations, lichen maps could be used to identify the quantity of lichen in stands

selected by caribou, aiding in the delineation of suitable habitat patches based on available forage resources.

Methods

Study Area

Our study area encompasses Woodland Caribou Provincial Park, a 5000 km² wilderness-class protected area in northwestern Ontario, Canada (Figure 1) (MNRF 2004). The park is a part of Pimachiowin Aki, a World Heritage Site that has received international recognition for its intact boreal forest and Indigenous cultural heritage (Parks Canada 2019). The region is characteristic of the continuous boreal forest and is characterized by rolling terrain of bedrock outcrops and numerous small lakes. Elevation varies from 309 m to 430 m above sea level and the park is situated on a plateau slightly elevated above the surrounding area, causing sparse conifer and dense conifer ecosites to compose a large proportion of the study area (Carr et al. 2007). Sparse conifer (ecosite B012) occurs primarily on bedrock outcrops where soils are very shallow (<15 cm) and moisture, nutrient availability, and plant diversity are low (MNRF 2014a). The overstory is dominated by jack pine (*Pinus banksiana* Lamb.) and the understory plant community consists primarily of *Cladonia* spp. ground lichens and velvet-leaf blueberry (*Vaccinium myrtilloides* Michx.). Dense conifer (ecosite B049) dominates upland sites with deeper, rocky soils (>15 cm) and nutrient and moisture conditions are more favourable for plant growth compared to sparse conifer (MNRF 2014a). A mixed overstory of black spruce (*Picea mariana* (Mill.) BSP) and jack pine characterizes dense conifer ecosites and the understory plant community consists primarily of feathermosses (e.g., *Pleurozium schreberi* (Brid.) Mitt.) and herbaceous plants (e.g., bunchberry, *Cornus canadensis* L.). Small peatlands supporting black spruce and tamarack (*Larix laricina* (Du Roi) K. Koch) form in bedrock depressions and support

an understory plant community dominated by *Sphagnum* spp. mosses and ericaceous shrubs (e.g., Labrador tea, *Ledum groenlandicum* Oeder) (MNRF 2004).

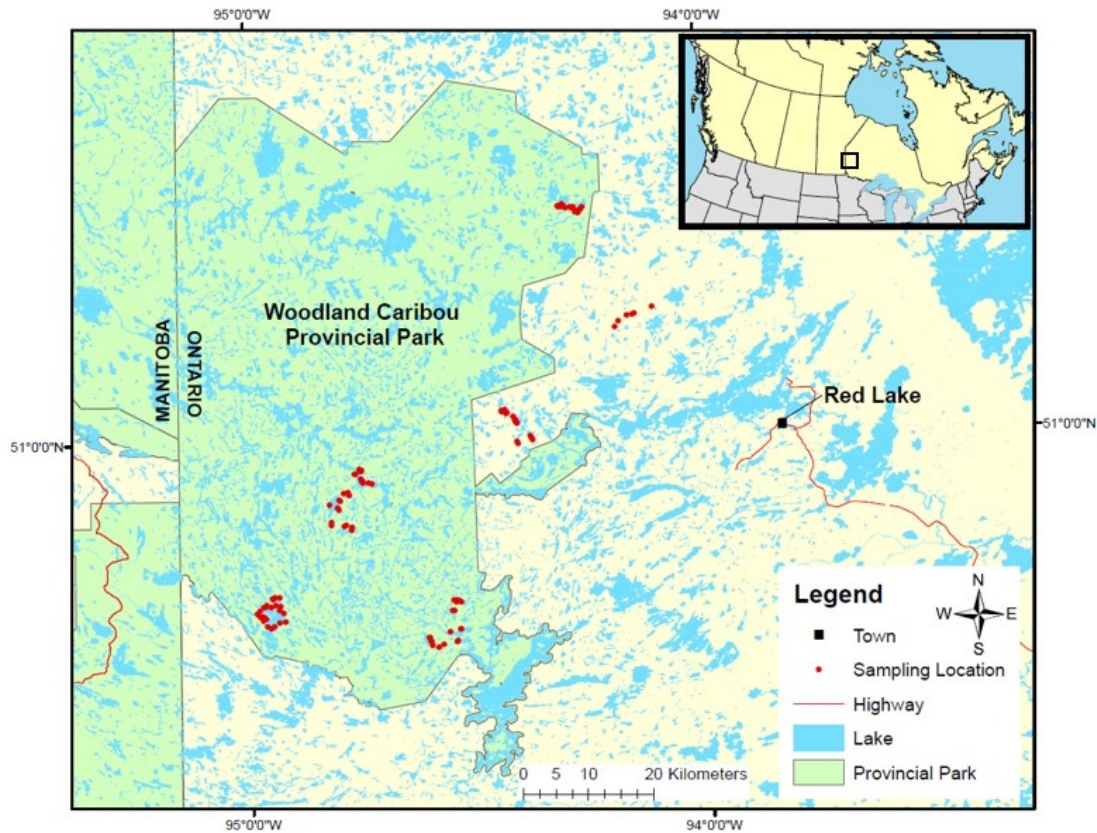


Figure 1. Location of the study area in northwestern Ontario, Canada. Sampling locations, indicated by red dots, are concentrated in and around Woodland Caribou Provincial Park, west of the town of Red Lake.

There are no roads or resource development activities, historic or current, within Woodland Caribou Provincial Park. Development is limited to portage trails, campsites, and several fly-in fishing camps. Large, frequent forest fires persist as an integral component of the local ecosystem due to a dry, continental climate (MNRF 2004). The average annual area burned in the park over the last 30 years (1985–2015) is 0.6%— above the average for northern protected areas in Canada (Bolton et al. 2019). The study area is home to woodland caribou belonging to the Owl-Flinstone and Atikaki-Berens ranges in Manitoba and the Sydney and Berens ranges in Ontario (ECCC 2012).

Methodology Overview

We combined field sampling with spatial environmental covariates to generate a map of lichen biomass for our study area (Figure 2). First, we conducted vegetation surveys to quantify lichen cover and canopy closure in sparse conifer and dense conifer ecosites. We used conversion factors to estimate the stand-level lichen biomass (kg/ha) of each sampling location. Second, we derived nine environmental covariates from remote sensing and GIS data. We assigned our field observations and environmental covariates to the GPS waypoint of each sampling location. We then used generalized linear models to predict lichen presence and lichen biomass as a function of *a priori* hypotheses built from our environmental covariates. We used model selection to identify the best candidate model and interpolated each top model to generate lichen presence and lichen biomass maps, which we combined to generate a final lichen biomass map for the study area.

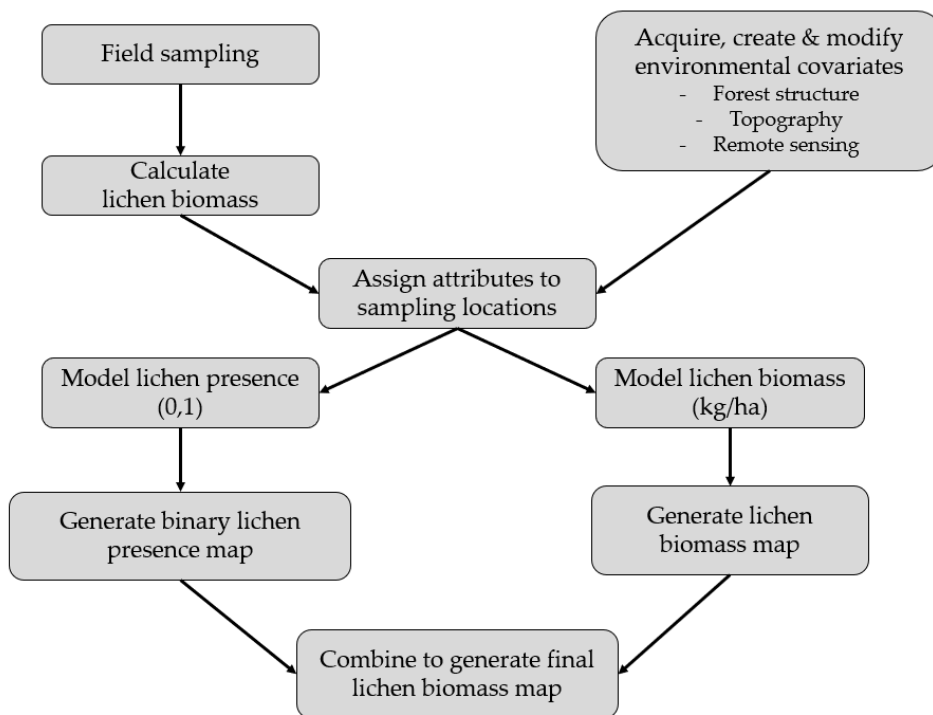


Figure 2. Framework used to generate a lichen biomass map for Woodland Caribou Provincial Park, Ontario, Canada.

Field Sampling

To quantify lichen abundance, we conducted vegetation surveys at 109 sampling locations within and adjacent to Woodland Caribou Provincial Park from June–August 2018. We selected sampling locations based on time-since fire, stratified into decadal classes (Figure 3; range = 2–119 years post-fire). We confirmed time-since-fire at sampling locations using an increment bore. Due to access constraints and the dominance of upland conifer in the study area, we constrained sampling to dense conifer and sparse conifer ecosites. Within each time-since fire class we selected an equal number of sampling locations in each ecosite using a forest inventory map.

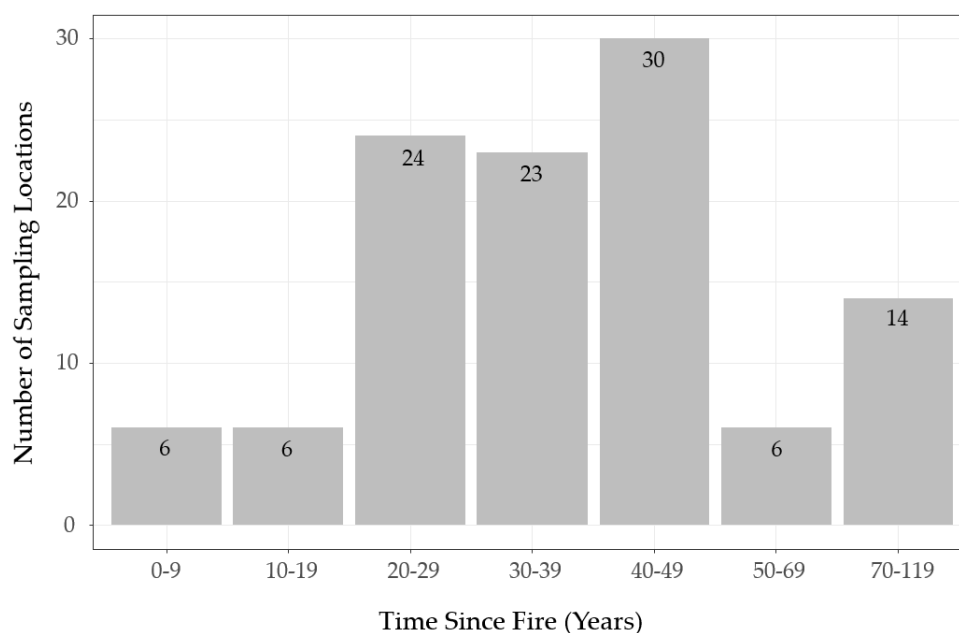


Figure 3. Distribution of sampling locations used to quantify lichen abundance across the local time-since-fire continuum in Woodland Caribou Provincial Park, Ontario, Canada ($n = 109$).

We accessed sampling locations by canoe and portage within the park and by truck in adjacent areas. At each sampling location, we established a start point 25 m from the edge of the mapped ecosite boundary and used a fiberglass tape to establish a 50 m transect oriented in a primary or secondary compass direction (Figure 4). We placed a 1 m² quadrat at the 5 m, 15 m,

25 m, 35 m, and 45 m marks of the transect to conduct five vegetation surveys per sampling location. We recorded the xy coordinates of each sampling location at the 25 m mark of the transect with a handheld GPS unit (accuracy ± 5 m). We spaced sampling locations a minimum of 100 m apart to reduce spatial autocorrelation.

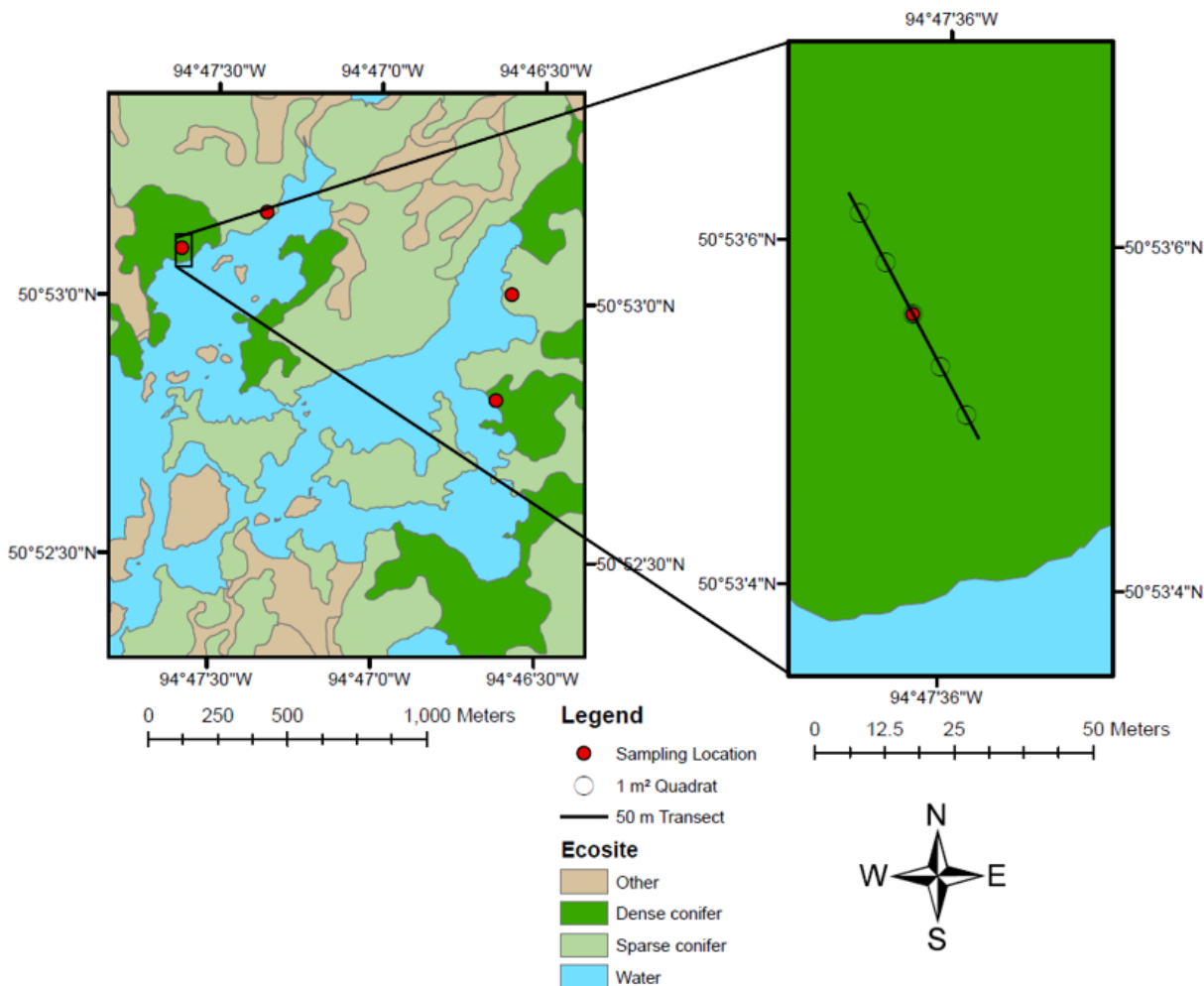


Figure 4. Field sampling protocol used to conduct vegetation surveys in a 12-year-old burn in Woodland Caribou Provincial Park, Ontario, Canada. Sampling was limited to dense conifer (dark green) and sparse conifer (light green) ecosites. Unsampled ecosites are coloured brown, lakes are coloured blue. Sampling locations (red dots) were marked by a GPS waypoint at the 25 m mark of the transect. The 50 m transect is represented by a black line and 1 m² quadrats are represented by open circles (right panel).

For each 1 m² quadrat, a single observer visually estimated the percent cover of each of the six most common *Cladonia* spp. ground lichens in the region (Table 1) and used a concave

spherical densiometer to estimate the canopy closure above the quadrat. We recorded lichen cover for the sampling location by taking the average of the total lichen cover of each quadrat. Similarly, we recorded a single canopy closure value for each sampling location as the average value from the five quadrats. To derive estimates of lichen biomass, we multiplied the cm² area of the quadrat covered by each lichen species by its corresponding cover-to-biomass conversion factor (developed by McMullin et al. (2011); Table 1). We validated the conversion factors for use in our study area using destructive sampling (Appendix A). We estimated stand-level lichen biomass (kg/ha) for each sampling location by adding the biomass estimates for each quadrat, converting from g to kg, and multiplying by 2000 (see Appendix B for example calculation). We assigned the stand level estimates of lichen cover, canopy closure and lichen biomass to the GPS waypoint of each sampling location for use in spatial modelling.

Table 1. Cover-to-biomass (g/cm²) conversion factors for the six most common *Cladonia* spp. ground lichens found in northwestern Ontario, Canada. Species classification and conversion factors are from McMullin et al. (2011).

Lichen Species	Cover-to-Biomass Conversion Factor (g/cm ²)
<i>Cladonia rangiferina</i> (L.) Nyl.	0.10500
<i>Cladonia arbuscula</i> (Wallr.) Flotow	0.08593
<i>Cladonia uncialis</i> (L.) F.H. Wigg.	0.10263
<i>Cladonia gracilis</i> (L.) Willd. ssp. <i>turbinata</i> (Ach.) Ahti	0.14895
<i>Cladonia stellaris</i> (Opiz) Brodo	0.11618
<i>Cladonia stygia</i> (Fr.) Ahti	0.15145

Environmental Covariates

We selected nine environmental covariates (Table 2) supported by the literature to generate spatial models of lichen presence and lichen biomass (Dunford et al. 2006, Nelson et al. 2013, Falldorf et al. 2014, Mallon et al. 2016, Keim et al. 2017, Uboni et al. 2019). The details of how the covariate layers were created are found in Appendix C. Note that the canopy closure layer was generated using a generalized linear model with forest inventory data, field

measurements, time-since-fire and normalized difference vegetation index (NDVI; Appendix C). We converted all polygon datasets to rasters with 30 m pixels in ArcGIS 10.5 (ESRI 2017). We resampled all covariate layers to have matching 30 m pixels and subsequently assigned values of each of covariate to the GPS waypoint of each sampling location using the *mask()* and *extract()* functions in the *raster* package in R version 3.6.0 (Hijmans 2019, R Core Team 2019). This enabled us to subsequently relate lichen presence and biomass to forest structure, topographic and remote sensing attributes.

Table 2. Description of covariates used to model lichen presence and abundance as a function of forest structure, topographic and remote sensing attributes. Additional descriptions of each covariate layer are provided in Appendix C.

Covariate	Source	Data Acquisition	Original Resolution
Ecosite	(MNRF 2019a)	2009–2015	polygons at 1:8000
Canopy closure	(AFFES 2019, MNRF 2019a-b, USGS 2019a-b)	2009–2018	polygons of fires \geq 40 ha; polygons at 1:8000; 30 m
Time-since-fire	(AFFES 2019, MNRF 2019b)	1929–2013	polygons of fires \geq 40 ha
Elevation	(MNRF 2019c)	2019	30 m
Slope	(MNRF 2019c)	2019	30 m
Blue reflectance	(USGS 2019a-b)	2014	30 m
Short-wave infrared (SWIR2) reflectance	(USGS 2019a-b)	2014	30 m
Normalized difference vegetation index (NDVI)	(USGS 2019a-b)	2014	30 m
Normalized difference moisture index (NDMI)	(USGS 2019a-b)	2014	30 m

Spatial Modelling

We used our environmental covariates to generate a set of seven candidate models (Table 3) based on *a priori* hypotheses. Our base model included ecosite, canopy closure and time-since-fire, which we anticipated would be the strongest predictors of lichen abundance. Each additional candidate model built on the base model by adding a topographic or remote sensing covariate. Covariates in the same candidate model had a Pearson's correlation coefficient $< |0.6|$ to reduce collinearity within candidate models. We included a statistical null model (intercept) to assess the robustness of our candidate models.

Table 3. Name and structure of candidate models used to predict lichen presence (0,1) and lichen abundance (biomass, kg/ha) as a function of forest structure, topographic and remote sensing attributes. Covariates within the same model have a Pearson's correlation coefficient $< |0.6|$. TSF = time-since-fire, Canopy = canopy closure, NDVI = normalized difference vegetation index, NDMI = normalized difference moisture index, SWIR2 = short-wave infrared reflectance (details in Appendix C).

Model Name	Model Structure
Base	Lichen ~ TSF + Ecosite + Canopy
Elevation	Lichen ~ TSF + Ecosite + Canopy + Elevation
All Topography	Lichen ~ TSF + Ecosite + Canopy + Elevation + Slope
NDVI	Lichen ~ TSF + Ecosite + Canopy + NDVI
NDMI	Lichen ~ TSF + Ecosite + Canopy + NDMI
Blue Reflectance	Lichen ~ TSF + Ecosite + Canopy + Blue
SWIR2 Reflectance	Lichen ~ TSF + Ecosite + Canopy + SWIR2

To generate a raster with cell values representing lichen biomass (kg/ha), we used our candidate models to conduct a two-stage modelling approach (Nielsen et al. 2017): 1) lichen presence, 2) lichen abundance. We first used generalized linear models (family = binomial, link = logit) to identify the candidate model best explaining lichen presence (0 = absent, 1 = present). Lichen was considered present at sampling locations with $>1\%$ lichen cover ($n = 87$). We ranked competing models using Akaike's Information Criterion corrected for a small sample size (AIC_c ; Hurvich and Tsai 1989) and considered the model with the lowest AIC_c score as the top model.

We interpolated this top model across the study area to create a raster with cell values representing probability of occurrence (0–1) for ground lichens. We used model-based interpolation as defined by Elith and Leathwick (2009), implemented using the *predict()* function in the *raster* package in R (Hijmans 2019). We then created a binary layer where lichen is predicted to be absent (0) or present (1) in each pixel. We used the point on the receiver operator criterion (ROC) curve closest to the top left corner of the graph (0.71) as our presence threshold (Liu et al. 2005). Lichen was classified as present (1) in cells with a probability of occurrence >0.71 and absent (0) in cells with a probability of occurrence ≤ 0.71 . We conducted k -fold cross-validation ($k = 100$; 60% training, 40% testing) to assess the accuracy of the lichen presence raster based on the mean area under the curve (AUC) statistic (Swets 1988).

Once we generated the lichen presence raster, we used generalized linear models (family = Gamma, link = log) to identify the candidate model best explaining lichen biomass (kg/ha). We identified the top model as the candidate model with the lowest AIC_c score and interpolated it across the study area to create a raster with pixel values representing lichen biomass (kg/ha). We multiplied this new layer by the lichen presence raster to create a layer that only predicts biomass in pixels where lichen is predicted to be present. We assessed the accuracy of this final lichen abundance raster by running a simple linear regression (R^2) between observed and predicted lichen biomass at each sampling location.

Results

Lichen Biomass

Preliminary analysis of the field data revealed that post-fire lichen recovery differed markedly between sparse conifer and dense conifer ecosites (Figure 5). Ground lichens were essentially absent from burns 0–19 years old in both ecosites and dense conifer supported low

lichen abundance across the time sequence. Twenty years after fire, lichen biomass began to increase quickly in sparse conifer, reaching a median of 2648 kg/ha 40–49 years post-fire and leveling off thereafter. Mature sparse conifer ecosites supported approximately 2000–3700 kg/ha of ground lichens.

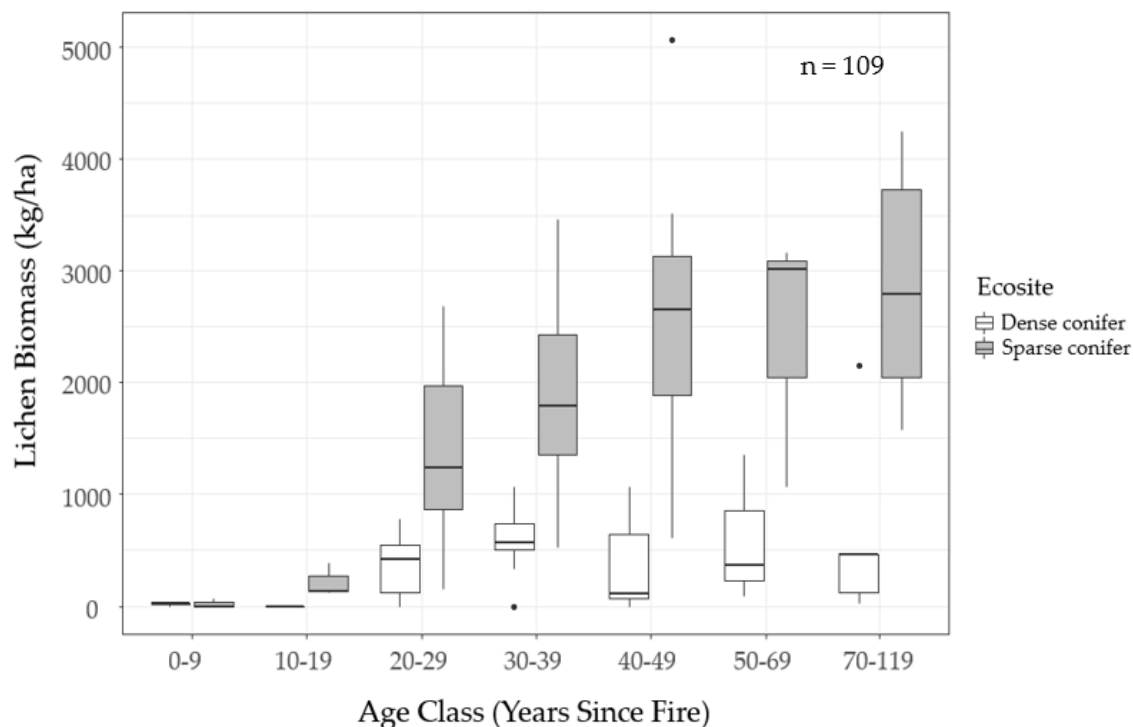


Figure 5. Estimated stand-level lichen biomass (kg/ha) by decadal time-since-fire class in dense conifer (white boxplots) and sparse conifer (gray boxplots) ecosites sampled in Woodland Caribou Provincial Park, Ontario, Canada. The thick black line is the median.

Spatial Modelling

The top candidate model for predicting lichen presence included ecosite, time-since-fire and canopy closure (Table 4). The average AUC score from the k -fold cross-validation for the lichen presence model was 0.80, indicating good model fit (Swets 1988).

Table 4. Ranking of candidate models used to predict lichen presence as a function of forest structure, topographic and remote sensing attributes. Models with a lower Akaike Information Criterion score (AIC_c) better describe the data. k = number of fixed effects (+1 for intercept) and w_i = Akaike weight. SWIR2 = short-wave infrared reflectance, NDVI = normalized difference vegetation index, NDMI = normalized difference moisture index (Appendix C).

Model Name	k	log. lik.	AIC_c	ΔAIC_c	w_i
Base	4	-43.74	95.87	0.00	0.27
SWIR2 Reflectance	5	-42.97	96.52	0.66	0.20
Elevation	5	-43.31	97.20	1.33	0.14
Blue Reflectance	5	-43.42	97.42	1.55	0.13
NDVI	5	-43.58	97.74	1.87	0.11
NDMI	5	-43.62	97.82	1.95	0.10
All Topography	6	-43.28	99.37	3.51	0.05
Null	1	-56.17	114.37	18.50	< 0.01

Beta coefficients from the model describe the direction and magnitude of the effect of a covariate on the response variable. For example, in the top lichen presence model, probability of occurrence is positively associated with time-since-fire, increasing 1.6% per year since fire (Table 5). In the top model, lichen presence is negatively associated with dense conifer ecosites and there is a weak positive association between lichen presence and canopy closure (Table 5).

Table 5. Summary table for the top lichen presence model. TSF = time-since-fire, Canopy = canopy closure. The beta coefficient for ecosite represents probability of occurrence for lichen in dense conifer with sparse conifer as the reference (Appendix C). SE = standard error.

Covariate	Coefficient	SE	z -value	p -value
Intercept	2.33	1.21	1.92	0.05
TSF	0.02	0.01	1.20	0.23
Ecosite	-2.63	0.72	-3.63	2.79×10^{-4}
Canopy	3.94×10^{-4}	0.04	0.01	0.99

The top candidate model for predicting lichen abundance was the same as lichen presence, including ecosite, time-since-fire and canopy closure (Table 6).

Table 6. Ranking of candidate models used to predict lichen abundance (biomass; kg/ha) as a function of forest structure, topographic and remote sensing attributes. Models with a lower Akaike Information Criterion score (AICc) better describe the data. k = number of fixed effects (+ 1 for intercept) and w_i = Akaike weight. SWIR2 = short-wave infrared reflectance, NDVI = normalized difference vegetation index, NDMI = normalized difference moisture index (Appendix C).

Model Name	k	log. lik.	AICc	Δ AICc	w_i
Base	4	-852.14	1714.86	0.00	0.28
Elevation	5	-851.33	1715.48	0.61	0.21
Blue Reflectance	5	-851.75	1716.32	1.45	0.14
NDMI	5	-851.85	1716.52	1.66	0.12
NDVI	5	-852.10	1717.03	2.16	0.09
SWIR2 Reflectance	5	-852.13	1717.09	2.22	0.09
All Topography	6	-851.27	1717.64	2.78	0.07
Null	1	-875.01	1754.14	39.28	0.00

The top lichen abundance model indicates lichen biomass is positively associated with time-since-fire, increasing 1.3% per year since fire (Table 7). Lichen biomass is negatively associated with dense conifer ecosites. There is a weak negative association between lichen biomass and canopy closure, with biomass decreasing by 0.4% per unit increase in canopy closure (Table 7).

Table 7. Summary table for the top lichen abundance model. TSF = time-since-fire, Canopy = canopy closure. The beta coefficient for ecosite represents lichen biomass in dense conifer with sparse conifer as the reference (Appendix C). SE = standard error.

Covariate	Coefficient	SE	z -value	p -value
Intercept	7.10	0.194	36.49	$< 2.00 \times 10^{-16}$
TSF	0.01	0.003	3.96	1.38×10^{-4}
Ecosite	-1.54	0.153	-10.07	$< 2.00 \times 10^{-16}$
Canopy	-4.00×10^{-3}	-4.00×10^{-3}	-0.91	0.36

Figure 6 displays the post-fire recovery of lichen biomass in sparse conifer and dense conifer ecosites as predicted by the top lichen abundance model. Note the shallow slope of the curve for dense conifer– lichen biomass is never predicted to exceed ~ 1000 kg/ha. By

comparison, lichen biomass increases quite steadily in sparse conifer ecosites, reaching 2000 kg/ha 50 years post-fire and exceeding 3000 kg/ha in stands 80–100 years post-fire (Figure 6).

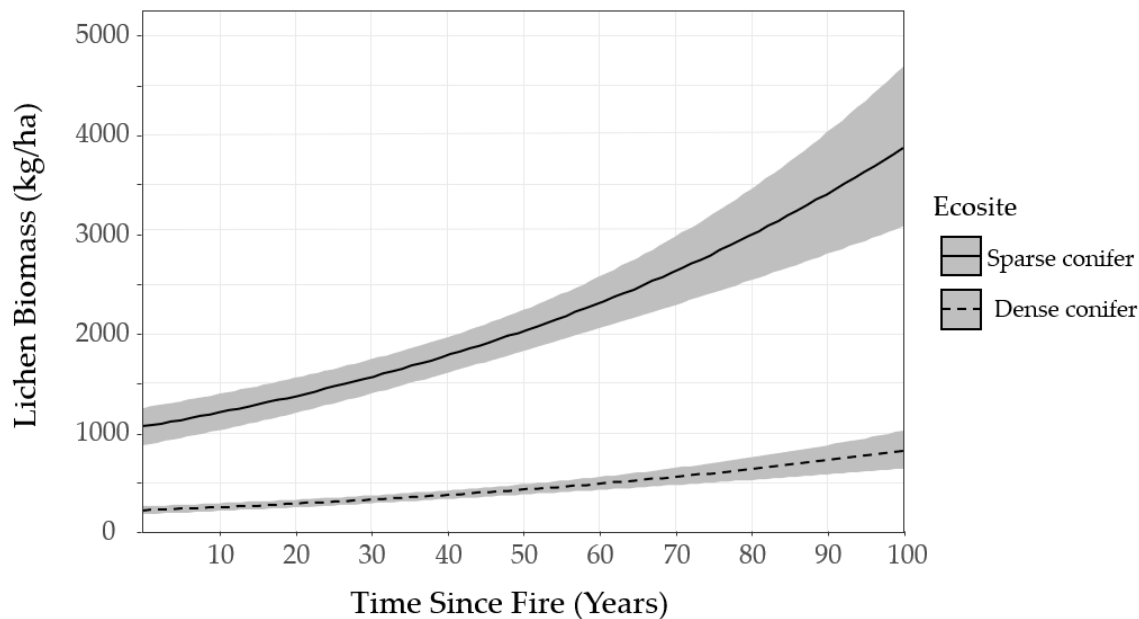


Figure 6. Lichen biomass (kg/ha) in sparse conifer and dense conifer ecosites as time-since-fire increases. Simulated from the top lichen abundance model for Woodland Caribou Provincial Park, Ontario, Canada. The dark lines represent the average trendline for each ecosite and the grey banners represent standard errors.

The final lichen biomass map is displayed in Figure 7. The simple linear regression between observed and predicted lichen biomass at sampling locations ($R^2 = 0.39$) indicates our model performs to a similar standard as previous studies that created forage abundance layers for ungulates (Nelson et al. 2013, Avgar et al. 2015, Proffitt et al. 2016).

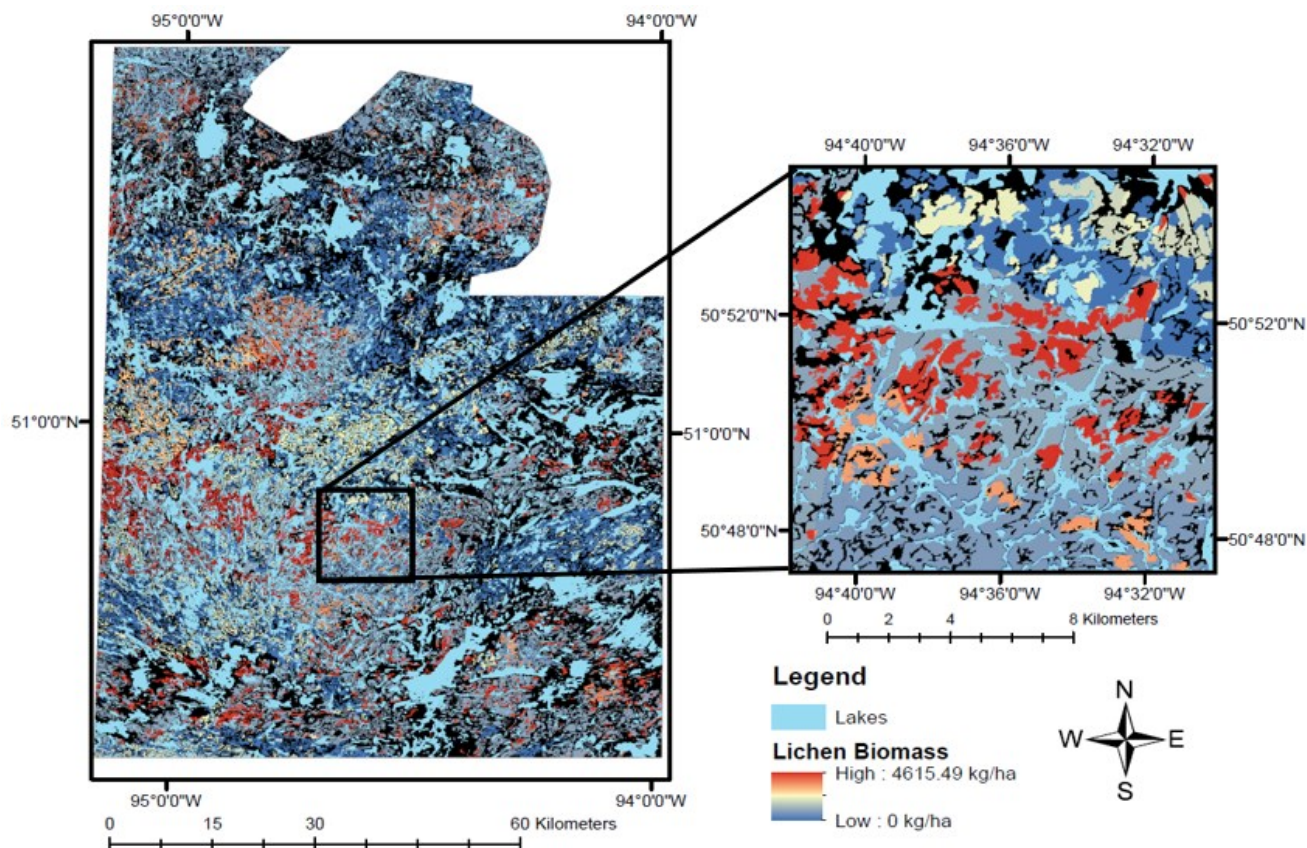


Figure 7. The lichen biomass raster generated for Woodland Caribou Provincial Park, Ontario, Canada. The left panel of the figure shows the entire extent, the right panel shows a small portion in more detail. Pixel values represent lichen biomass (kg/ha) from low (blue) to high (red) in dense conifer and sparse conifer ecosites. Lakes appear in light blue. Unsampled ecosites (NoData; Appendix C) are coloured black.

Discussion

We mapped lichen biomass across Woodland Caribou Provincial Park using a spatial modelling approach that can provide a framework to generate lichen biomass maps for resource management and ecological research in Canada's boreal forest. By relating our field observations of lichen abundance to forest structure, topographic and remote sensing attributes, we were able to identify environmental features useful in predicting ground lichens. We found that time-since-fire and ecosite were important predictors of ground lichens. Probability of occurrence and biomass of ground lichens was negatively associated with dense conifer ecosites and such stands demonstrated low lichen abundance (<1000 kg/ha) across the local time-since-fire continuum.

Conversely, sparse conifer ecosites supported very low lichen abundance in the first 20 years after fire, but lichen biomass increased steadily from 20–50 years post-fire. Mature sparse conifer (≥ 70 years old) supported approximately three times more lichen biomass than dense conifer of the same age.

The lichen abundance model appears to overestimate lichen biomass in young sparse conifer stands (0–19 years post-fire) relative to what was observed in the field. Similarly, the model appears to exaggerate the accumulation of lichen biomass in older stands (≥ 50 years old). These discrepancies could be due to the unbalanced sampling design we employed, as we focused most of our sampling effort on middle-aged stands due to a secondary objective to test post-fire lichen recovery. This resulted in few observations at the young (0–19 years post-fire, $n = 12$) and old (50–119 years post-fire, $n = 20$) portions of the local post-fire continuum. In addition, our field observations suggest lichen biomass may follow a non-linear pattern with time-since-fire in sparse conifer ecosites. We were unable to fully capture this trend in our analysis because generalized linear models assume a linear relationship between the response variable and the predictor variables. Other model types such as generalized additive models can improve predictions of non-linear trends (Elith and Leathwick 2009). Species distribution models such as those developed through MaxEnt, provide a highly flexible workflow for mapping the distribution of plants, and have been used to map the presence of lichens (Merow et al. 2013, Allen and Lendemer 2016). Future research could incorporate these modelling approaches to generate lichen maps for caribou conservation.

In our study, lichen presence was positively associated with canopy closure. Conversely, lichen biomass was negatively associated with canopy closure. Lichen growth is typically maximized at intermediate levels of canopy closure ($\sim 40\%$) (Jonsson Čabrajič et al. 2010),

beyond which the growth of mosses is promoted at the expense of lichens (Morneau and Payette 1989). Thus, lichens may require a minimum amount canopy closure to be present at a site but experience reduced growth at high levels of canopy closure, perhaps explaining the opposing responses of lichen presence and biomass observed here. In the oldest stands we sampled (70–119 years old), high mortality of mature trees created large gaps in the canopy and increased sun exposure at ground level. This promoted the growth of juniper shrubs (*Juniperus communis* L.), which often covered the ground lichens, possibly reducing access to foraging caribou. We had limited observations in over-mature conifer stands ($n = 14$) and suggest future work should measure lichen biomass and caribou habitat selection in mature (50–70 years old) and over-mature stands (≥ 70 years old) to estimate the optimal renewal period for caribou habitat. This information is essential to develop effective fire response and resource management plans that consider caribou conservation.

Most previous studies quantifying lichen over large areas used only remote sensing (Nelson et al. 2013, Falldorf et al. 2014, Keim et al. 2017, Rickbeil et al. 2017) or environmental (Lesmerises et al. 2011, Boan et al. 2013) data. We anticipated that combining forest structure and topographic attributes with remote sensing attributes would provide the best results. Contrary to our expectations, models with only forest structure and/or topographic attributes were just as predictive as models including remote sensing attributes. The candidate models for both lichen presence and lichen abundance had small differences between AICc scores ($\Delta AIC_c < 2$), which would typically indicate support for multiple candidate models (Burnham and Anderson 2002). However, the best candidate model for lichen presence and lichen abundance was the base model, the most parsimonious of the candidate set, only containing ecosite (i.e., dense conifer vs. sparse conifer), time-since-fire and canopy closure as covariates. The penalty

weight assigned by AIC_c to more complex models (Burnham and Anderson 2002) indicates that the additional topographic and remote sensing covariates did not improve explanatory power over the base model.

The lack of support for candidate models with remote sensing covariates could arise from multiple sources. First, environmental and remote sensing covariates are often correlated. We controlled for collinearity within models but because we were interested in predicting lichen abundance rather than inferring ecological relationships, we did not account for correlation amongst models. Second, the coarse spatial resolution of Landsat imagery can cause trees to mask the spectral signature of ground lichens (Lesmerises et al. 2011). Keim et al. (2017) reported an $R^2 = 0.74$ for a lichen map generated using QuickBird satellite imagery (2.5 m pixels) and LiDAR data (1 m pixels). They found that QuickBird imagery predicted lichens better than SPOT (6 m pixels) and Landsat (30 m pixels) imagery in their study area in the continuous boreal forest of northeastern Alberta. We suggest that the continued incorporation of finer resolution satellite (Keim et al. 2017) or UAV imagery (Fraser et al. 2016) may help improve the accuracy of lichen mapping in years to come.

The lichen abundance map we generated in this study highlights the patchy distribution of lichens on the landscape, which is driven primarily by the prevalence of fire in the study area. Lichen-rich forest is relatively restricted on the landscape, only occurring in mature, sparse conifer ecosites (≥ 50 years post-fire), where lichen biomass often exceeds 3000 kg/ha. Historically, researchers have used habitat type as a proxy for lichen abundance (Courbin et al. 2009, Basille et al. 2015, Mason and Fortin 2017); however, some studies have explicitly measured lichen availability and suggest caribou preferentially select stands with ≥ 3000 kg/ha of ground lichens as winter habitat (Trudell and White 1981, Johnson et al. 2001, Joly et al. 2010).

Given that animal nutrition is necessarily related to the amount of available food, ecologists and land managers should strive to understand caribou's use of lichen biomass across time and space. Identifying the use of lichen biomass during different seasons could be used to delineate nutritionally important habitat patches.

The relatively low accuracy of our map ($R^2 = 0.39$) is unsurprising given we used relatively coarse spatial covariates (30 m pixels) to model the presence and abundance of lichens, which are responding to environmental conditions at a very small scale (i.e., microsite). However, we feel that our lichen map provides a reasonable estimation of lichen biomass across our study area and suggest our modelling approach provides a useful framework for researchers to apply and improve in future lichen mapping projects. Most previous research mapped lichen cover (Boan et al. 2013, Nelson et al. 2013, Keim et al. 2017), but we suggest lichen biomass is more biologically relevant than lichen cover as biomass is more closely related to animal energetics and fitness (Avgar et al. 2015). We stress the importance of validating biomass conversion factors and landscape covariates for new study areas, as growing conditions for lichens may vary. For example, in northern Alberta, peatlands are a dominant landscape feature. Previous studies indicate peatlands support much lower lichen abundance than upland sites (Dunford et al. 2006), however raised 'islands' of drier peat within bogs can provide better conditions for lichen growth and support locally abundant ground lichens (Bradshaw et al. 1995, Keim et al. 2017). In other parts of the boreal forest, sandy areas dominated by jack pine support thick mats of ground lichens (McMullin et al. 2011). Integrating abiotic information, such as substrate type, groundwater depth and terrain ruggedness into spatial models may improve lichen predictive mapping, especially when the study area spans multiple biophysical regions. We incorporated data from numerous sources, data types and spatial resolutions to map the

abundance of lichens in our study (Table 2). Researchers must be cognizant of the vintage of the source data in each layer they incorporate in their modelling framework to ensure temporal consistency. We suggest future research should focus on incorporating multiple sources of information, including time-since-fire and attributes derived from high resolution satellite imagery (e.g., spectral values, landcover type, forest structure; Matasci et al. 2018). This will improve spatio-temporal consistency and repeatability. We also encourage researchers to ensure they are selecting the most appropriate model for predicting the distribution of lichens and suggest generalized additive models (Elith and Leathwick 2009) may be of particular utility to address some of the deficiencies of this study. Once a lichen abundance map has been generated, we encourage researchers to conduct independent validation using additional field sampling to improve certainty in their spatial predictions.

In this study, we propose a modelling framework for predicting the abundance of ground lichens in the boreal forest. We show that ecosite, time-since-fire and canopy closure are important drivers of lichen presence and abundance. We encourage researchers to use and improve our modelling framework to generate spatial predictions of lichen across caribou ranges. There is an increasing emphasis in wildlife ecology on including more biologically relevant variables in habitat selection analyses (Hebblewhite and Haydon 2010). Quantifying nutritional landscapes can help researchers and managers measure how food availability changes with succession and varies by habitat type. Explicitly measuring selection for forage abundance can aid in the identification of high-quality habitat and ensure continuous availability through resource planning and fire response. Mapping forage resources can also be used to test hypotheses, such as the effect of forage abundance on fitness or the trade offs between nutrition and predator avoidance. Lichen abundance maps should be applied by researchers to help

improve our understanding of caribou foraging ecology and support better conservation and resource management decisions.

CHAPTER 2 – SEASONAL SELECTION FOR GROUND LICHENS BY WOODLAND CARIBOU

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Abstract

The persistence of woodland caribou (*Rangifer tarandus caribou*) populations in Canada's boreal forest is threatened by the encroachment of human disturbances. Protection, renewal, and restoration of critical habitat is essential to sustain caribou populations, but current definitions of critical habitat are largely descriptive and may inadequately represent the functional habitat characteristics required by caribou. For example, we have limited knowledge about forage supply (abundance) needed to sustain caribou populations, despite nutrition being an important factor regulating reproductive success in ungulates. *Cladonia* spp. ground lichens form the foundation of the caribou diet and the vast majority of forage intake during winter. In this study, we apply a spatial prediction of lichen biomass to investigate seasonal differences in selection for lichens by ten female woodland caribou near Red Lake, Ontario, Canada. We include proximity to refuge habitat (1. bogs and fens; 2. lakes) to characterize possible trade offs amongst nutrition and predator avoidance that female caribou experience during their annual life history. We found that caribou selected areas with high lichen biomass close to bogs and fens in winter. Caribou also selected areas with high lichen biomass in summer but avoided such areas during calving and autumn. Caribou selected to be close to lakes during calving and summer, but not during autumn. These results suggest caribou may trade off predator avoidance and nutrition depending on the season, representing the need to balance their differing life history requirements. Our study represents a step towards identifying nutritionally important habitat for woodland caribou. We encourage the explicit investigation of the influence of forage availability on caribou demography amongst multiple populations to identify the amount of nutritionally

important habitat required to maintain healthy caribou populations at range scales. This information could be used to inform the delineation of critical habitat and maintain an adequate supply for caribou persistence.

Introduction

Over the last century, human disturbances have gradually increased in intensity and extent in Canada's boreal forest. As a wide-ranging species with low tolerance to human disturbance, woodland caribou (*Rangifer tarandus caribou*) have experienced population declines across much of their range during this same period (Schaefer 2003). Woodland caribou are listed as Threatened under Canada's *Species at Risk Act* (COSEWIC 2002) and government agencies have dedicated significant resources towards maintaining and recovering caribou populations, including identifying and protecting critical habitat across their boreal distribution (ECCC 2017).

The federal government broadly defines critical habitat as areas within the local population range unaffected by fire or human disturbance, based on the understanding that caribou require large, contiguous patches of mature forest to reduce spatio-temporal overlap with other ungulates (e.g., moose, *Alces alces*) and wolves (*Canis lupus*), the latter their primary predator (Rettie and Messier 2000). During the calving season, caribou neonates are highly vulnerable to predation (Gustine et al. 2006) and female caribou use specific habitat features to reduce predation risk, such as bogs and fens (McLoughlin et al. 2005) and lakes (e.g., peninsulas, islands; Carr et al. 2011).

In areas with high rates of habitat disturbance, the spatial isolation strategy employed by caribou is disrupted and predation becomes a proximate factor limiting caribou populations (Seip 1992, Wittmer et al. 2007). Managers attempt to reduce the magnitude of caribou population

declines in areas with human disturbance through habitat restoration (Spangenberg et al. 2019), land-use planning (MNR 2009a), prey control and predator culls (Serrouya et al. 2019). The primary objective of these treatments is to reduce the hunting efficiency and density of wolves. The dominance of predation in caribou management has limited the incorporation of nutritional information in the delineation of critical habitat. Nutrition has important implications for many aspects of ungulate life history including adult survival, reproduction, and population recruitment (Cook et al. 2004, Parker et al. 2009) and requires more explicit inclusion in caribou habitat definitions.

By avoiding areas frequented by moose and wolves, caribou typically occupy low-productivity habitats with poor vascular plant diversity (Mao et al. 2018), but abundant *Cladonia* spp. ground lichens (Rettie and Messier 2000, Keim et al. 2017). Ground lichens are a good source of carbohydrates, particularly in winter when other digestible forages are scarce (Parker et al. 2009). Most herbivores do not consume lichens because of their low protein content and the presence of secondary compounds that reduce digestibility, but caribou evolved a specialized gut microbiome that allows them to metabolize large quantities of *Cladonia* spp. ground lichens (Boertje 1990, Palo 1993). These lichens form the foundation of the woodland caribou diet, especially in winter (Thompson et al. 2015). The relative importance of ground lichens changes throughout the year as caribou manage their annual energy balance by taking advantage of more nutrient-rich forages when available (Trudell and White 1981, Denryter et al. 2017).

Given the importance of ground lichens to caribou ecology, researchers have used spatial modelling and remote sensing techniques to map the distribution of ground lichens for caribou herds across their circumboreal distribution (Nelson et al. 2013, Falldorf et al. 2014, Rickbeil et al. 2017). Mapping lichen abundance enables researchers to investigate habitat selection, provide

information on the quantity of ground lichens, and monitor change over time. Most previous research incorporating spatial predictions of lichens have focused on proportion cover; however, caribou nutrition is largely driven by the intake of digestible biomass. Studying the biomass of ground lichens selected by caribou is therefore an important step towards identifying nutritionally important habitat and investigating potential trade offs with predation risk.

In this study we assess how selection for lichen biomass and proximity to refuge habitat changes seasonally to reflect the annual life history of female caribou. We apply a spatial prediction of lichen biomass for Woodland Caribou Provincial Park in northwestern Ontario, Canada (Silva et al. 2019) by fitting a set of Resource Selection Function (RSF) models to the GPS collar locations of ten adult female caribou. We use these models to investigate trends in selection for lichen biomass and proximity to refuge habitat (1. bogs and fens; 2. lakes) and discuss possible trade offs between nutrition and predator avoidance in each season. We predicted caribou would select lichen-rich areas during winter but would not demonstrate a preference for such habitat during calving, summer, and autumn. We predicted caribou would select areas close to bogs and fens during autumn and winter and areas close to lakes during calving and summer. Our study links caribou habitat selection to the biomass of a key nutritional resource, highlighting the potential value of incorporating such information to obtain ecological inference for caribou. We propose that including lichen abundance in habitat selection models for woodland caribou could improve our ecological understanding of the species and our definition of critical habitat.

Methods

Study Area

Our study was conducted in the area occupied by the Sydney Range caribou west of Red Lake, Ontario, Canada (Figure 8). 62.7% of the Sydney Range is affected by a combination of natural disturbance, resource extraction and infrastructure (MNR 2014b). The Sydney Range was last assessed at a minimum of 55 individuals and low calf recruitment (14–18 calves/100 cows) suggests the population is in decline (MNR 2014b). Most of the occupied portion of the Sydney Range is within Woodland Caribou Provincial Park, a 5000 km² wilderness area. There are no roads or resource extraction activities, historic or current, within the park boundaries, but the area receives moderate recreational use (backcountry canoeing, fishing, and floatplane access). Some logging and recreational use occurs in the areas adjacent to the park.

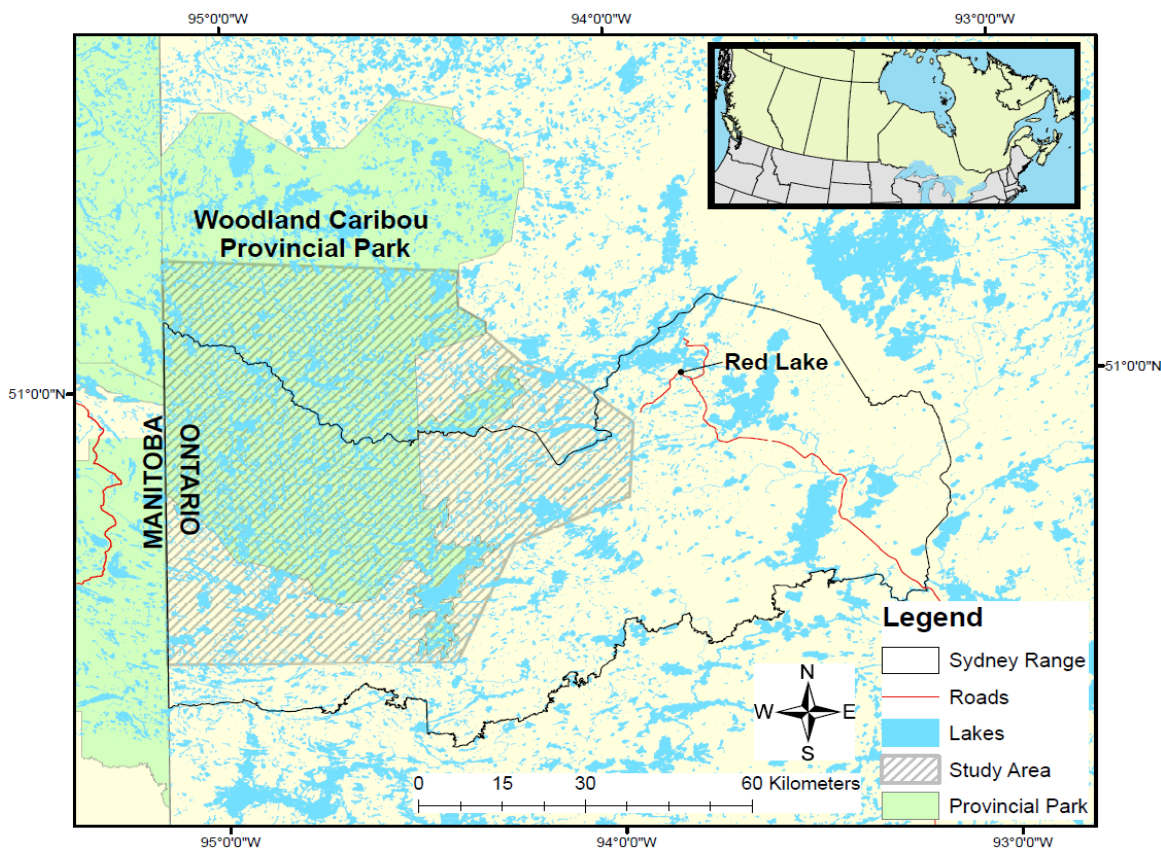


Figure 8. Location of the study area (hatched polygon) in northwestern Ontario, Canada.

The study area is part of the Boreal Shield ecozone, characterized by a rolling terrain of bedrock outcrops, peatlands, and numerous small, interconnected lakes. The study area's slightly elevated topographical position leads to a dominance of upland conifer forest (Carr et al. 2007). Sparse stands of jack pine (*Pinus banksiana* Lamb.) with mats of *Cladonia* spp. ground lichens dominate bedrock outcrops. Upland sites with deeper, rocky soils typically support dense stands of jack pine and black spruce (*Picea mariana* (Mill.) B.S.P) with a ground cover of feathermosses (e.g., *Pleurozium schreberi* (Brid.) Mitt.) (Silva et al. 2019). Mixedwood forests supporting white birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) occur in limited areas on finer-textured soils (MNRF 2014b). Large, frequent forest fires are an integral component of the local ecosystem due to a dry, continental climate (MNRF 2004).

Caribou GPS Locations

As part of the Ontario's Integrated Range Assessment for Woodland Caribou, ten adult female caribou on the Sydney Range were fitted with Argos GPS collars in 2012 (Telonics Inc.; MNRF 2014b). Capture and collar procedures were approved by the Wildlife Animal Care Committee of the Ontario Ministry of Natural Resources and Forestry (2012 Protocol Approval #12-174). We analyzed collar locations from the first year of the study, rarefying to a 5-hour fix rate using the *amt* package in R version 3.6.0 (Signer et al. 2019, R Core Team 2019). We excluded Argos locations due to their low positional accuracy and used topology rules to identify coincident GPS locations (identical xy coordinates) and correct errors in ArcGIS 10.5 (ESRI 2017).

We assigned the rarefied collar locations to one of four biologically-relevant seasons: calving (May 1–July 14), summer (July 15–September 14), autumn (September 15–November 30) or winter (December 1–March 31) (Ferguson and Elkie 2004, MNRF 2013). We estimated

annual home ranges for each individual by generating 95% utilization distributions with the *adehabitatHR* package in R (Calenge and Fortmann-Roe 2019). To define resource availability, we generated 10 random points per used point within each annual home range. We excluded points in lakes during calving, summer and autumn (May 1–November 30) based on the understanding that caribou locations in lakes are caused by GPS error when using island or shoreline habitats and available points are unlikely to represent biologically meaningful habitat during the ice-free seasons. Points in lakes were retained in winter because caribou are known to use frozen lakes for traveling and/or resting (Stardom 1975, Darby and Pruitt 1984). Subsequent analyses are based on 11,482 used locations and 114,820 available locations.

Resource Selection Function

We used Resource Selection Function (RSF) models on our caribou observations to investigate seasonal differences in selection for lichen biomass and proximity to refuge habitat. We created a map of lichen biomass for our study area and generated spatial layers for distance to bog/fen (hereafter distance to bog) and distance to lake from an ecosite layer (Silva et al. 2019; Appendix C). All three spatial covariates were processed to a spatial resolution of 30 m and values for covariates were assigned to each used and available point. The candidate set of RSF models is listed in Table 8, where the response variable is whether a point was used (1) or available (0). Lichen biomass was square root transformed to accommodate non-linear trends in selection. Proximity to refuge habitat was ln transformed after adding a constant of 1 to allow the effect of distance to bog and distance to lake to decay. To obtain population-level inference, we pooled all individuals into a single dataset and fit models separately to each season with the *Resource Selection* package in R (Lele et al. 2019). We estimated model parameters with 99 bootstrap iterations and set the matching parameter to 10 to match each used point with ten

available points from the appropriate annual home range. Covariates in the same model had Pearson's correlation coefficients $\leq |0.25|$. We ranked the RSF models by Akaike Information Criterion score (AIC) and considered the model with the lowest AIC score to be the best of the candidate set (Burnham and Anderson 2002). We simulated relative probability of selection as a function of lichen biomass from the top ranked RSF model in each season (Avgar et al. 2017).

Table 8. Resource Selection Function (RSF) models used to assess differences in selection for lichen biomass and proximity to refuge habitat during calving, summer, autumn, and winter. Models were fit to used (1) and available (0) locations for ten female caribou in northwestern Ontario, Canada. Lichen biomass (Lichen; kg/ha) was square root transformed, distance to bog (m) and distance to lake (m) were ln transformed after adding a constant (+1).

Model	Structure
1	Use ~ Lichen
2	Use ~ Distance to Bog (Dist_Bog)
3	Use ~ Distance to Lake (Dist_Lake)
4	Use ~ Lichen + Dist_Bog
5	Use ~ Lichen + Dist_Lake
6	Use ~ Lichen + Dist_Bog + Lichen:Dist_Bog
7	Use ~ Lichen + Dist_Lake + Lichen:Dist_Lake

Results

Resource Selection Function

Habitat selection was best explained by different variables depending on season (Table 9). The best supported model in winter included lichen biomass and distance to bog: caribou selected areas with higher lichen biomass ($\beta = 0.02 \pm 8.54 \times 10^{-4}$ SE) close to bogs ($\beta = -0.10 \pm 8.94 \times 10^{-3}$; Table 10). During calving, summer and autumn, habitat selection was best predicted by lichen biomass, distance to lake, and an interaction between the two variables. During calving, caribou avoided areas with higher lichen biomass ($\beta = -0.02 \pm 0.01$) and selected areas close to lakes ($\beta = -0.50 \pm 0.04$). There was a positive interaction between lichen biomass and

distance to lake during the calving season ($\beta = 0.01 \pm 1.18 \times 10^{-3}$), suggesting caribou selected areas with higher lichen biomass when far from lakes. In summer, caribou selected areas with higher lichen biomass ($\beta = 0.02 \pm 0.01$) close to lakes ($\beta = -0.29 \pm 0.04$). There was a negative interaction between lichen biomass and distance to lake in summer ($\beta = -3.59 \times 10^{-3} \pm 1.25 \times 10^{-3}$), suggesting caribou avoided areas with higher lichen biomass when far from lakes. In autumn, caribou avoided areas with higher lichen biomass ($\beta = -0.05 \pm 0.01$) and selected areas far from lakes ($\beta = 0.34 \pm 0.04$). The interaction between lichen biomass and distance to lake was positive, indicating caribou selected areas with higher lichen biomass when far from lakes ($\beta = 0.01 \pm 1.64 \times 10^{-3}$).

Table 9. Ranking of Resource Selection Function (RSF) models in each season by Akaike Information Criterion (AIC) score. Models were fit to used (1) and available (0) locations for ten female caribou in northwestern Ontario, Canada. Lichen biomass (kg/ha) was square root transformed, distance to bog (Dist_Bog; m) and distance to lake (Dist_Lake; m) were ln transformed after adding a constant (+1). w_i = Akaike weight.

Season	Model	log likelihood	AIC	Δ AIC	w_i
Winter	Lichen + Dist_Bog	-11180.24	22364.47	0.00	0.65
	Lichen + Dist_Bog + Lichen:Dist_Bog	-11179.87	22365.74	1.27	0.35
	Lichen + Dist_Lake + Lichen:Dist_Lake	-11234.15	22474.30	109.83	0.00
	Lichen + Dist_Lake	-11237.85	22479.70	115.23	0.00
	Lichen	-11239.59	22481.18	116.71	0.00
	Dist_Lake	-11592.06	23186.12	821.65	0.00
	Dist_Bog	-11624.00	23250.00	885.53	0.00
Calving	Lichen + Dist_Lake + Lichen:Dist_Lake	-4726.83	9459.66	0.00	1.00
	Dist_Lake	-4736.08	9474.15	14.49	0.00
	Lichen + Dist_Lake	-4735.88	9475.77	16.11	0.00
	Lichen + Dist_Bog + Lichen:Dist_Bog	-4848.25	9702.49	242.83	0.00
	Lichen + Dist_Bog	-4850.35	9704.70	245.04	0.00
	Dist_Bog	-4853.72	9709.43	249.77	0.00
	Lichen	-4859.54	9721.09	261.43	0.00
Summer	Lichen + Dist_Lake + Lichen:Dist_Lake	-4093.36	8192.72	0.00	0.94
	Lichen + Dist_Lake	-4097.34	8198.67	5.95	0.05
	Dist_Lake	-4099.62	8201.23	8.51	0.01
	Lichen + Dist_Bog + Lichen:Dist_Bog	-4170.04	8346.09	153.37	0.00
	Dist_Bog	-4178.90	8359.81	167.09	0.00
	Lichen + Dist_Bog	-4178.89	8361.78	169.06	0.00
	Lichen	-4181.69	8365.38	172.67	0.00
Autumn	Lichen + Dist_Lake + Lichen:Dist_Lake	-6612.50	13231.00	0.00	1.00
	Lichen + Dist_Lake	-6637.18	13278.36	47.36	0.00
	Dist_Lake	-6645.91	13293.81	62.81	0.00
	Lichen + Dist_Bog	-6821.08	13646.16	415.16	0.00
	Lichen + Dist_Bog + Lichen:Dist_Bog	-6820.97	13647.93	416.93	0.00
	Lichen	-6844.01	13690.01	459.01	0.00
	Dist_Bog	-6845.54	13693.07	462.07	0.00

Table 10. Model summary for the best supported Resource Selection Function (RSF) model in each season. Models were fit to used (1) and available (0) locations for ten female caribou in northwestern Ontario, Canada. Lichen biomass (kg/ha) was square root transformed, distance to bog (Dist_Bog; m) and distance to lake (Dist_Lake; m) were ln transformed after adding a constant (+1).

Season	Covariate	Coefficient	SE	z-value	p-value
Winter	Lichen	0.02	8.54×10^{-4}	25.17	$< 2.00 \times 10^{-16}$
	Dist_Bog	-0.10	8.94×10^{-3}	-11.00	$< 2.00 \times 10^{-16}$
Calving	Lichen	-0.02	0.01	-4.16	3.21×10^{-5}
	Dist_Lake	-0.50	0.04	-13.36	$< 2.00 \times 10^{-16}$
	Lichen:Dist_Lake	0.01	0.00	4.35	1.34×10^{-5}
Summer	Lichen	0.02	0.01	3.17	1.52×10^{-3}
	Dist_Lake	-0.29	0.04	-7.66	1.91×10^{-14}
	Lichen:Dist_Lake	-3.59×10^{-3}	1.25×10^{-3}	-2.86	4.20×10^{-3}
Autumn	Lichen	-0.05	9.40×10^{-3}	-4.90	9.50×10^{-7}
	Dist_Lake	0.34	0.04	8.65	$< 2.00 \times 10^{-16}$
	Lichen:Dist_Lake	8.99×10^{-3}	1.64×10^{-3}	5.50	3.85×10^{-8}

Selection for Lichen Biomass

Selection for lichen biomass varied amongst seasons— caribou selected areas with higher lichen biomass during summer and winter but avoided such habitats during calving and autumn (Figure 9). The selection coefficient for lichen biomass had much lower error in winter compared to the other seasons and relative probability of selection increased in a linear fashion with higher lichen biomass (Figure 10), indicative of caribou targeting lichen-rich stands. By comparison, relative probability of selection was essentially constant with increasing lichen biomass during calving, summer, and autumn (Figure 10).

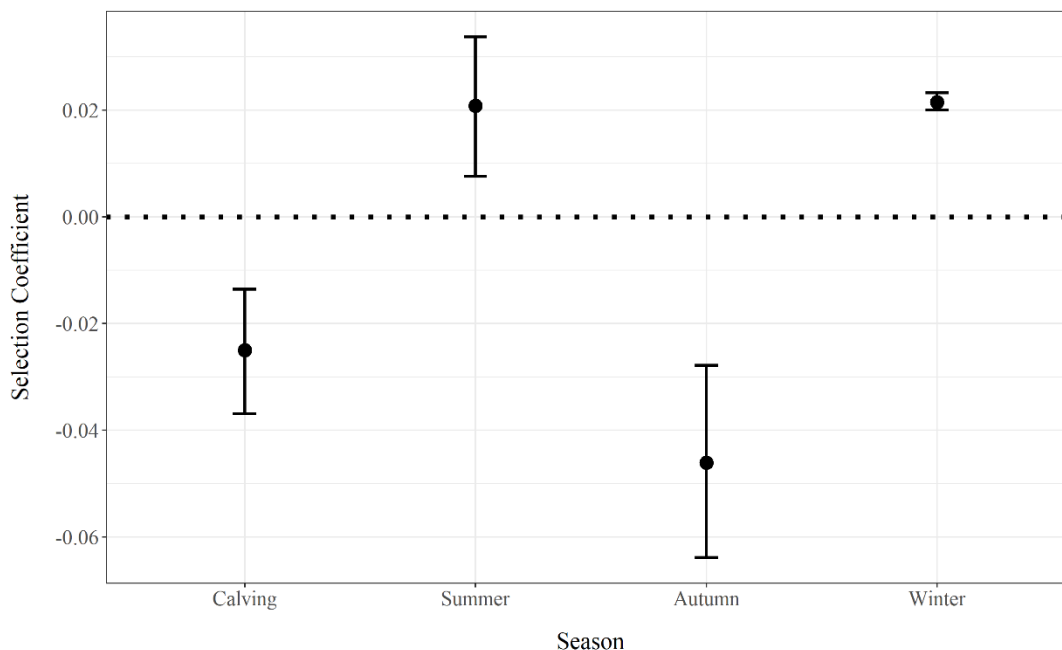


Figure 9. Selection coefficients for lichen biomass by season for ten female woodland caribou in northwestern Ontario, Canada. Estimates are based on the best supported Resource Selection Function (RSF) model in each season. Points above the zero lines represent selection, points below the zero line represent avoidance. Error bars represent 95% confidence intervals.

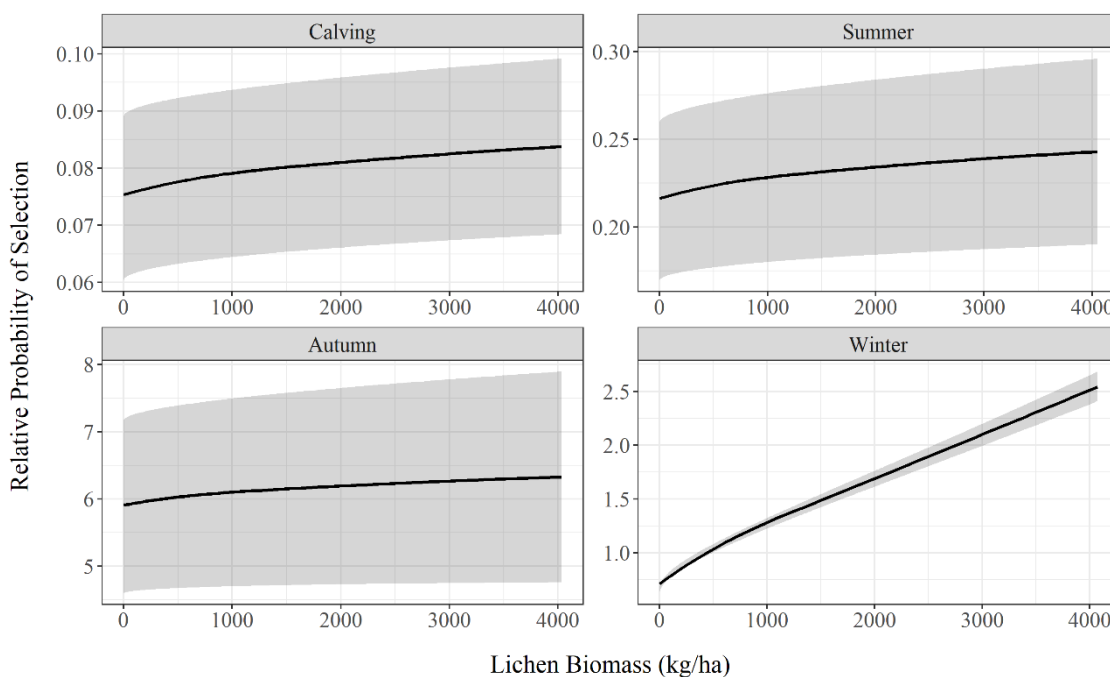


Figure 10. Relative probability of selection by season as a function of increasing lichen biomass (kg/ha) for ten female woodland caribou in northwestern Ontario, Canada. These response curves were simulated from the best supported Resource Selection Function (RSF) model in each season. Lichen biomass was back transformed for ease of interpretation. The dark line represents the average trend line, the grey banners the associated standard errors.

Discussion

Caribou habitat selection patterns differed amongst seasons, consistent with hypothesized trade offs between nutrition and predator avoidance (Mason and Fortin 2017, Viejou et al. 2018). These trade offs were most evident during calving and summer when caribou selected to be close to lakes and avoided lichens during the calving season but selected for lichens in summer. Caribou are known to use islands and peninsulas as refuge habitat during calving and summer, as they are excellent swimmers and can use lakes to escape predators (Cumming and Beange 1987, Carr et al. 2011). For the first few weeks after birth, calves are highly vulnerable to predation (DeMars et al. 2013). Selecting less productive habitats with low forage biomass during the calving season could reduce the risk of calf mortality (Gustine et al. 2006, Viejou et al. 2018). Low forage availability could be of little consequence to female caribou as they rely primarily on body reserves to meet their energy needs during the calving season (Parker et al. 1990). This strategy could enable caribou to spend the calving season in relatively safe habitats near lakes and forgo using riskier lichen-rich stands (Basille et al. 2015), increasing the level of protection for their calf from predators.

Unlike the calving season, caribou selected for lichens during summer. Body condition declines into mid-summer and female caribou must quickly replenish their depleted body reserves to support the energetic costs of lactation and prepare for the upcoming winter (Parker et al. 2009). To restore their protein reserves, caribou must increase their diet breadth during the summer to incorporate nitrogen-rich forages such as deciduous shrubs, forbs, and mushrooms (Denryter et al. 2017). Despite increasing their diet breadth, caribou still consume lichens in large quantities during summer (Thompson et al. 2015). As a good source of digestible energy, lichens could help caribou replenish their body reserves. Notably, caribou were less likely to

select lichens when far from lakes in summer, suggesting females preferentially forage in lichen-rich stands near lakes to increase the likelihood of predator escape.

In this study, we used distance to bog and distance to lake as proxies to represent areas with lower predation risk for woodland caribou. Although caribou are known to use bogs and fens (McLoughlin et al. 2005) and lakeshore features (e.g., islands, peninsulas; Carr et al. 2011) as refuge habitat, without specific observations of predators in our study area we cannot confirm that caribou experienced lower predation risk near these habitats. Using habitat types as a proxy for predation risk is common in the literature but can lead to unfounded or incorrect ecological conclusions (Keim et al. 2011). Therefore, we encourage researchers to include explicit measures of predation risk (e.g., wolf density, encounter rates) where possible to more accurately characterize the trade offs female caribou face between nutrition and predator avoidance (e.g., Avgar et al. 2015).

In autumn, caribou avoided lichen biomass, suggesting ground lichens are not a strong predictor of habitat selection during this time of year. Caribou maintain a varied diet during autumn, foraging on sedges, forbs, and other plants in addition to ground lichens (Bergerud 1972). Avoidance of lichens in calving and autumn highlights the importance of incorporating non-lichen forage in caribou nutrition models to fully describe the characteristics of caribou foraging habitats in different seasons. Caribou avoided lakes in our study and models including distance to bog were poorly supported, suggesting caribou do not emphasize refuge habitat during this time of year, perhaps because they maintain higher movement rates as they travel from their summer to their winter range (Ferguson and Elkie 2004). Our knowledge of autumn habitat selection patterns is quite limited and additional research is warranted to understand

caribou behavior during this time of year given the importance of autumn body mass on parturition success (Cameron and Ver Hoef 1994).

In winter, caribou selected for lichens and relative probability of selection increased steadily as lichen biomass increased. The highest relative probability of selection occurred in areas with >3000 kg/ha of ground lichens, corresponding to the most lichen-rich stands available (Silva et al. 2019) and consistent with caribou winter habitat characteristics in Alaska (Trudell and White 1981, Joly et al. 2010) and British Columbia (Johnson et al. 2001). Within the study region, lichen-rich stands are found on bedrock outcrops, where snow is softer and shallower than low-lying areas (Stardom 1975). By targeting these habitats, caribou expend less energy cratering, maximizing energy gain for foraging effort (Johnson et al. 2001). Lichen-rich bedrock outcrops are typically interspersed with numerous small bogs and fens, perhaps explaining the tendency of caribou to select areas close to bogs and fens in winter. However, bogs and fens could provide numerous other functions as caribou winter habitat. Caribou could shelter in bogs and fens between foraging bouts on exposed bedrock outcrops and lowlands tend to have less favourable snow conditions (Stardom 1975) which could impede wolf movement and reduce predation risk (Droghini and Boutin 2018). Mature bogs and fens can be a rich source of arboreal lichens (Darby and Pruitt 1984) and raised areas of peat or bedrock within the bog complex can support locally abundant ground lichens (e.g., Bradshaw et al. 1995). Because our spatial prediction of lichen abundance was restricted to upland conifer forest, additional field sampling would be required to determine whether caribou select to be close to bogs and fens to access the terrestrial and/or arboreal lichens therein.

Availability of lichen-rich stands as winter habitat could have important consequences to the fitness and reproductive success of female caribou. Ground lichens are a good source of

digestible energy (Parker et al. 2009) that help caribou maintain their body condition over the winter (Kojola et al. 1995). An adequate supply of lichens in winter may be important to offset the increased energetic costs associated with thermoregulation (Parker and Robbins 1985), moving through snow (Stardom 1975), and gestation (Ofstedal 1985), improving overwinter adult survival and calf birth weight (Rognmo et al. 1983). Caribou have relatively high pregnancy rates, but low neonate survival, suggesting winter nutrition could be an important factor influencing successful parturition and calf recruitment (Cameron and Ver Hoef 1994). Once a calf is born, the female faces even higher energetic costs associated with lactation (Ofstedal 1985, Chan-McLeod et al. 1994), but frequently occupy less productive habitat to reduce predation risk (Viejou et al. 2018). Therefore, adequate winter nutrition could have important carryover effects in the calving season to sustain females until mid-summer when the calf is mobile enough to spend more time in productive, but riskier foraging habitats.

To effectively manage caribou winter habitat, we need to know what qualifies as lichen-rich habitat (i.e., stand-level biomass) and how much lichen-rich habitat is required to maintain a healthy caribou population. Due to our small sample size, more research is required to address these needs. Researchers with a larger sample size should investigate the use of Resource Selection Probability Functions (Lele and Keim 2006), which can link absolute probability of selection to changes in lichen abundance, helping verify important thresholds in stand-level lichen biomass. Creating spatial predictions of lichen biomass for multiple caribou populations and comparing demographic parameters (e.g., adult survival, calf recruitment) could help determine the quantity of lichen-rich habitat required to sustain a healthy caribou population. For example, Keim et al. (2012) used scat samples to correlate glucocorticoid and progesterone levels, indicators of glucose nutrition and pregnancy health, with lichen abundance across three

caribou ranges in northern Alberta. Caribou living in ranges with low lichen abundance had lower glucocorticoid and progesterone levels, indicative of poor nutrition and pregnancy health (Seckl 2001, Monfort et al. 1993). This study suggests there may be a link between caribou demography and lichen availability, and further research could help determine the lichen biomass needed to sustain caribou populations at a range scale.

In this study, we demonstrated that selection for ground lichens by female caribou varies throughout the year, which may reflect trade offs between nutrition and predator avoidance. Ground lichens can be a useful predictor of caribou space use and provide more biologically meaningful information than habitat variables alone. Lichen biomass is especially important during winter and the availability of lichen-rich habitat could influence female body condition and reproductive success. Incorporating lichen abundance in the delineation of winter critical habitat could improve the retention of functional characteristics necessary to sustain caribou populations.

CHAPTER 3 – COMPARISON OF SPACE USE BEFORE AND AFTER FIRE REVEALS VARIED RESPONSES BY WOODLAND CARIBOU (*RANGIFER TARANDUS CARIBOU*) IN CANADA’S BOREAL SHIELD

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Abstract

By regulating successional dynamics in Canada’s boreal forest, fires can affect the distribution of Threatened woodland caribou (*Rangifer tarandus caribou* Gmelin, 1788). Caribou tend to avoid areas burned within the last 40 years; however, few studies have compared observations before and after fire. In this study, we employ a ‘before-after, control-impact’ design to assess the short-term response of caribou to fire in the Boreal Shield of Ontario and Saskatchewan ($n = 169$), comparing the overlap of pre-fire and post-fire seasonal home ranges to the overlap of year to year seasonal home ranges. Caribou rarely encountered recent burns and when they did, they adjusted their space use in variable and complex ways that were largely indistinguishable from interannual variation. Caribou tended to reduce use of recent burns in summer-autumn and winter but not during the calving season, in some cases intentionally shifting their home range to incorporate more burned habitat. We conclude that woodland caribou may not view recent burns as maladaptive habitat in the first few years post-fire, requiring a more flexible approach to interpret fire in habitat management strategies.

Introduction

Woodland caribou (*Rangifer tarandus caribou* Gmelin, 1788) have developed a unique ecology that makes them vulnerable to habitat disturbance. Caribou evolved a specialized gut microbiome (Boertje 1990, Palo 1993) and nitrogen conservation strategies (Parker et al. 2009) to consume terrestrial lichens as the primary component of their diet (Thompson et al. 2015). Relying on lichens enables caribou to occupy unproductive mature conifer forest and peatlands, spatially separating themselves from more productive habitats that support higher densities of

moose (*Alces alces* L., 1758) and wolves (*Canis lupus* L., 1758), the latter their primary predator (Rettie and Messier 2000). Terrestrial lichens are often completely consumed and slow to recover following the stand-replacing fires that typify the boreal forest (Morneau and Payette 1989, Silva et al. 2019), causing concern over the destruction of caribou foraging habitat by fire (Klein 1982). Human disturbance (e.g., forestry, energy, mining) has expanded into the range of woodland caribou over the past century (Schaefer 2003) and can cause temporary or permanent habitat loss and fragmentation (Hins et al. 2009). Like fire, human disturbance increases the proportion of early seral stands on the landscape, which can increase the abundance of deciduous plants and support higher densities of moose and wolves (Seip 1992, Street et al. 2015). This facilitates the process of disturbance-mediated apparent competition, where caribou experience high wolf predation in disturbed landscapes (Rudolph et al. 2017). Invoking these mechanisms, numerous studies have documented a tendency of caribou to avoid burns and human disturbance (Joly et al. 2003, Vors et al. 2007, Faille et al. 2010, MacNearney et al. 2016, Lafontaine et al. 2019). Disturbance-mediated apparent competition has been implicated as the primary mechanism driving woodland caribou population declines across Canada (Courtois et al. 2007, Festa-Bianchet et al. 2011, Serrouya et al. 2019, Fryxell et al. 2020).

Given the importance of disturbance-mediated apparent competition in population declines, Environment Canada developed a recovery strategy for woodland caribou that aims to minimize the cumulative footprint of fire (burns <40 years old) and human disturbance on population ranges (ECCC 2012). An empirical study determined a less than 60% probability of population stability (i.e., $\lambda = 1$) when cumulative range-level disturbance exceeded 35% (ECCC 2012). Keeping range-level disturbance below this 35% threshold or recovering habitat to reach this threshold has become a focus of caribou conservation over the past decade. However,

because woodland caribou occupy a broad geographic distribution across Canada, there is high regional variation in caribou ecology and disturbance history that may make a generalized disturbance classification untenable (DeMars et al. 2019, Neufeld et al. 2020). For example, the Boreal Shield of northern Saskatchewan has high fire (57%) but low human disturbance (3%), and the local caribou population is stable despite cumulative, range-level disturbance 1.7 times the recommended limit (Johnson et al. 2020). Johnson et al. (2020) found the negative effects of human disturbance on calf recruitment and adult survival were three to five times greater than the equivalent effects of fire. There is mounting evidence that fires do not have a strong influence on calf recruitment, adult survival, and population viability (Dalerum et al. 2007, ECCC 2011, Johnson et al. 2020, Konkolics 2020).

Several mechanisms could explain the weak effect of fire on caribou demography. Caribou evolved with fire and have likely developed strategies to respond to the shifting habitat mosaic (Klein et al. 1982). Occupying large home ranges could allow caribou to redirect their activity to unburned portions of their home range when they experience fire (Dalerum et al. 2007). Fires burn in heterogeneous patterns across the landscape due to the complex interplay of fuel, weather, and topography (Johnson 1992), resulting in a patchwork of burned and unburned forest within the fire perimeter (Kansas et al. 2016). Patches of unburned forest, often called post-fire residuals, may retain some habitat value to caribou (Schaefer and Pruitt 1991, Skatter et al. 2017) and slow tree recruitment in the surrounding burn complex (Gutsell and Johnson 1992) could temporarily improve predator detectability (Skatter et al. 2017). Coniferous forests frequented by caribou tend to self-replace after fire (Hart et al. 2019), especially in northern boreal and taiga regions where low productivity and poor edaphic conditions inherently limit post-fire increases in deciduous plants (Neufeld et al. 2020). Due to poor forage prospects,

moose (Maier et al. 2005, Street et al. 2015, DeMars et al. 2019) and subsequently wolves (Ballard et al. 2000, Kittle et al. 2015) avoid recent burns (<10 years), reducing disturbance-mediated apparent competition (Neufeld et al. 2020). As burns age, deadfall accumulation and tree recruitment increase the energetic costs of moving through the burn (Schaefer and Pruitt 1991). Moose and wolves tend to gradually increase use of burns as they age (Maier et al. 2005, Ballard et al. 2000). As a result, caribou may gradually shift away from burned habitats (Schaefer et al. 1991). The contemporary treatment of fire in habitat management strategies could mask this temporal variation in the response of moose, wolves, and caribou to fire, leading to inappropriate management recommendations.

The conflicting evidence of the effect of fire on woodland caribou has ignited debate surrounding its treatment in habitat management strategies. Understanding regional and individual variation in the response of caribou to fire is required to decide how managers can best address fire in conservation actions. One can assess the response of caribou to fire by observing changes in their space use. Woodland caribou tend to demonstrate interannual fidelity to seasonal home ranges (Schaefer et al. 2000, Wittmer et al. 2006, Lafontaine et al. 2019). The degree of home range overlap is often used to assess fidelity to seasonal ranges year to year and can be related to social or environmental conditions, such as disturbance, to study the drivers of space use behavior (Peignier et al. 2019). For example, Faille et al. (2010) found caribou in heavily burned areas tended to demonstrate lower home range overlap, whereas Dalerum et al. (2007) found caribou did not shift their home range after large fires. In this study, we employed a ‘before-after, control-impact’ design (Stewart-Oaten and Murdoch 1986) to assess the short-term response of caribou to fire by comparing the overlap of pre-fire and post-fire seasonal home ranges to the overlap of year to year seasonal home ranges. We contrasted the two groups to

determine whether caribou adjusted their space use more strongly in response to fire than they typically would year to year. We predicted caribou would reduce use of burns, resulting in lower overlap of seasonal home ranges before and after fire than year to year. By characterizing the real-time response of caribou to fire, we seek to broaden the interpretation of fire in habitat management strategies for woodland caribou.

Methods

Study Area

Our study encompassed the SK1 caribou range in Saskatchewan and portions of several woodland caribou ranges in Ontario (Figure 11). The area is part of the Boreal Shield West and Boreal Shield West Central ecoregions, part of the traditional territories of the Anishinaabe, Cree and Dene peoples. The Boreal Shield is characterized by a rolling topography of upland forest, peatlands, and numerous lakes. Dominant tree species include jack pine (*Pinus banksiana* Lamb., 1803) and black spruce (*Picea mariana* B.S.P., 1888), with lesser amounts of trembling aspen (*Populus tremuloides* Michx., 1803), paper birch (*Betula papyrifera* Marsh., 1785) and tamarack (*Larix laricina* (Du Roi) K. Koch, 1873). Lowland areas commonly support *Sphagnum* spp. mosses and ericaceous shrubs (e.g., Labrador tea, *Ledum groenlandicum* Oeder, 1771). Productive uplands support a moderate diversity of herbaceous plants and shrubs, whereas sandy or rocky uplands with shallow soils tend to be dominated by blueberry (*Vaccinium myrtilloides* Michx., 1803) and terrestrial lichens (*Cladonia* spp.) (Silva et al. 2019). The climate is continental, with mean annual temperatures of -2.7°C and -1.1°C and mean annual precipitation of 503 mm and 726 mm in Saskatchewan and Ontario, respectively (Fick and Hijmans 2017). The Boreal Shield of Saskatchewan has comparatively lower human disturbance (~3%) than the Boreal Shield of Ontario (~20%). Low human settlement combined with a drier climate means

Saskatchewan experiences higher annual area burned than Ontario (Stocks et al. 2002). During the study period, 8.4% and 2.5% of the study area burned in Saskatchewan and Ontario, respectively.



Figure 11. Map of the study area in central Canada, encompassing the SK1 range in Saskatchewan and parts of several woodland caribou ranges in Ontario. Only areas that burned while animals were collared in each province are displayed.

GPS Location Data

We obtained GPS locations for 230 adult female caribou from telemetry studies in Ontario and Saskatchewan. Caribou locations in Ontario (2009–2015, $n = 136$) were collected by the Ontario Ministry of Natural Resources and Forestry as part of the Integrated Range Assessment for Woodland Caribou (MNRF 2014c). Caribou locations in Saskatchewan (2014–2018, $n = 94$) were collected as part of a research project led by the University of Saskatchewan

(McLoughlin et al. 2019). Capture and collaring procedures were carried out following Canadian Council on Animal Care guidelines as approved by the Wildlife Care Committee of the Ontario Ministry of Natural Resources and Forestry (Approvals 09-174, 10-174, 11-174, 12-174), the University of Saskatchewan (protocol: 20130127) and the Saskatchewan Ministry of Environment (permit: 14FW037).

Seasonal Home Range Estimation & Overlap

GPS collar fix rates varied between 5–25 hours in Ontario and remained constant at 5 hours in Saskatchewan. To ensure consistency in the amount of data used to estimate home ranges within individuals, we rarefied GPS locations to the individual's longest fix rate, either 5, 10 or 25 hours, using the *amt* package in R version 3.6.0 (Signer et al. 2019, R Core Team 2019). We defined three biologically-informed seasons based on Ferguson and Elkie (2004) and McLoughlin et al. (2019): Calving (May 1–July 31), Summer-Autumn (August 1–November 30) and Winter (December 1–March 31). To minimize the effect of missing fixes, we eliminated seasons with a low rate of fix success (<66% of days) and individuals with insufficient collar life to facilitate interannual home range comparisons.

We used the *adehabitatHR* package in R (Calenge and Fortmann-Roe 2019) to estimate seasonal home ranges as 95% utilization distributions (UDs) for each individual/year/season (e.g., SK115-1-Winter). We generated a 100% minimum convex polygon in ArcGIS 10.5 (ESRI 2017) surrounding all seasonal home ranges to define the study area in each province. We calculated Bhattacharyya's Affinity (hereafter, BA overlap) for each individual's seasonal home range dyads (e.g., SK115-1-Winter to SK115-2-Winter). BA overlap describes the degree of three-dimensional similarity between two UD's (Fieberg and Kochanny 2005). Values range from 0–1 with higher values representing greater similarity in space use. Unlike overlap metrics that

rely solely on home range boundaries, BA overlap incorporates intensity of use within the UD, providing a more detailed representation of space use similarity between two home ranges (Fieberg and Kochanny 2005, Clapp and Beck 2015).

Identifying Caribou that Interacted with Recent Burns

To determine whether individuals interacted with recent burns, we first rasterized provincial fire polygons (CFS 2019) and waterbodies (NRCAN 2017) to a 30 m pixel size. We then created rasters with cell values representing waterbodies, areas that burned prior to caribou being collared, and areas that burned while caribou were collared (ON: 2009–2014, SK: 2014–2017). We used the *raster* package in R (Hijmans 2019) to determine the proportion of each home range burned and the proportion of caribou GPS locations within recent burns for each individual/year/season.

We employed a ‘before-after, control-impact’ design to compare the overlap of pre-fire and post-fire seasonal home ranges to the overlap of year to year seasonal home ranges. We used GPS locations to identify use of recent burns and hereafter refer to the proportion of pre-fire GPS locations within the burn as an index of use (i.e., how heavily affected an individual was by a fire event). We deemed an animal interacted with recent burns when $\geq 5\%$ of the GPS locations for a single individual/year/season were within a recent burn. Individuals that did not meet this criterion were considered control cases for the purposes of comparison and the BA overlap of their seasonal home ranges was considered an index of interannual space use similarity. For animals that interacted with recent burns, we assigned the seasonal home ranges in each dyad as combinations of pre, during or post fire based on the fire’s start and end dates (CFS 2019). We then restricted to pre-fire/post-fire ($n = 96$) and year to year ($n = 807$) seasonal home range dyads for our analyses.

Statistical Modelling

To quantify the response of caribou to fire, we ran a series of beta regression models and a logistic regression model for each season (Table 11) using the *glmmTMB* package in R (Magnusson et al. 2020). Where appropriate, proportion response variables were transformed to exclude values of 0 and 1 (Cribari-Neto and Zeileis n.d.). All models included a random effect for animal ID nested in province, and a random effect for the years in the involved dyad (Peignier et al. 2019, Harrison et al. 2018). Due to lack of normality, we used median and 95% median confidence intervals (Le Boudec 2016) as a measure of central tendency of the BA overlap of year to year seasonal home ranges (hereafter, population median).

Table 11. Overview of statistical models used to assess the effects of recent burns on space use by woodland caribou in the Boreal Shield of Ontario and Saskatchewan. BA overlap (0–1) describes the overall similarity in space use based on the pair of seasonal home ranges. “Home range comparison” is a binary variable denoting year to year (0) or pre-fire, post-fire (1) seasonal home ranges. “Pre-fire prop. use of burn” is the proportion of GPS locations within the burn pre-fire. “ Δ Prop. use of burn” is based on the absolute difference in the proportion of GPS locations in the burn post-fire compared to pre-fire. Increase is a binary variable for the change in use of the burn from pre-fire to post-fire (0 = constant/decrease, 1 = increase).

Prediction	Model Structure	Model type	Prediction supported
Overlap of pre-fire/post-fire home ranges < year to year home ranges	BA overlap ~ Home range comparison	Beta	Partially supported
Overlap of pre-fire/post-fire home range is lower if more heavily affected by the burn	BA overlap ~ Pre-fire prop. use of burn	Beta	Refuted
Caribou will alter use of the burn more strongly if more heavily affected by the burn	Δ Prop. use of burn ~ Pre-fire prop. use of burn	Beta	Partially supported
Caribou will be more likely to reduce use of the burn if more heavily affected by the burn	Increase ~ Pre-fire prop. use of burn	Logistic	Partially supported

Results

Fire Occurrence

Over six fire years in Ontario and four in Saskatchewan, caribou rarely encountered burns that occurred while they were collared (Figure 12). Figure 12 suggests it is rare for a large part of a caribou’s home range to be actively burned by a fire, as 84% of the time, <5% of an animal’s seasonal home range burned.

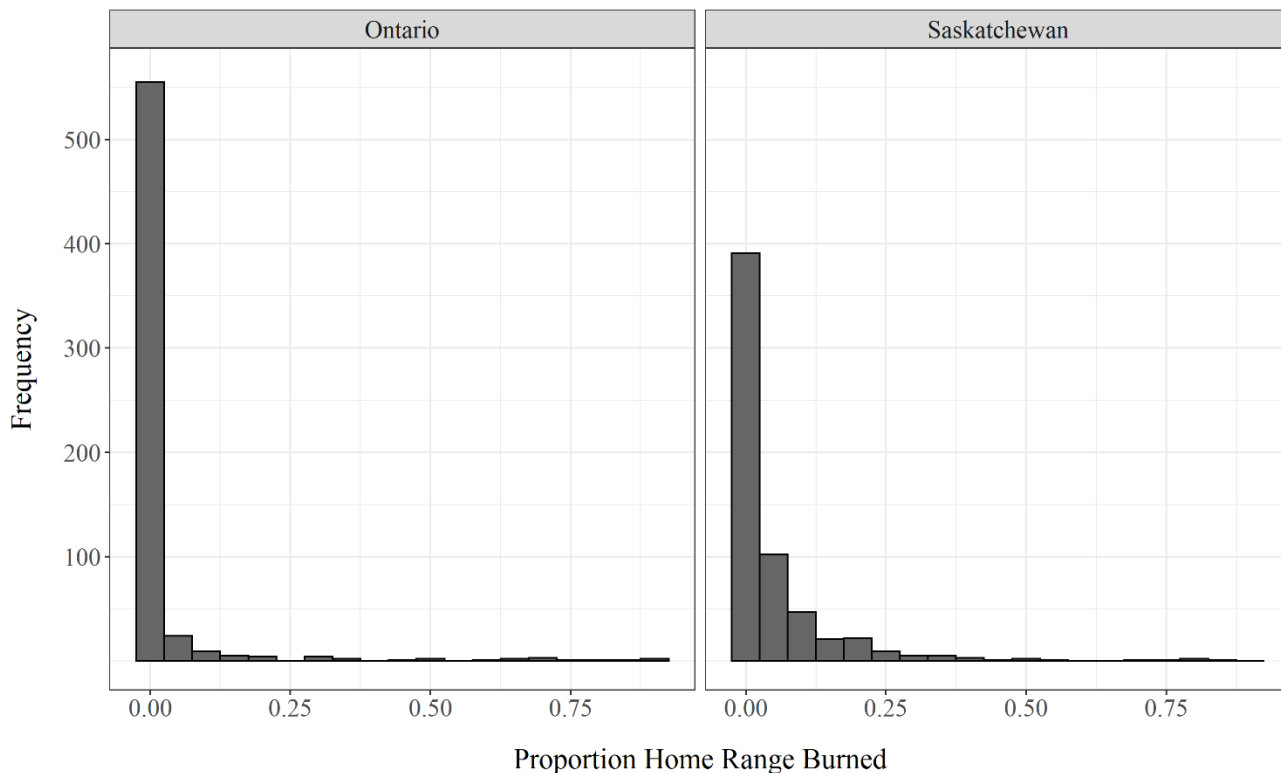


Figure 12. Frequency distribution of proportion seasonal home range burned for caribou in the Boreal Shield of Ontario and Saskatchewan ($n = 1231$ seasonal home ranges).

Regional Variation

Caribou in Saskatchewan encountered recent burns more frequently than caribou in Ontario (Figure 12): only fourteen of the ninety-six pre-fire/post-fire home range comparisons were in Ontario. This small sample size prevented us from assessing regional differences in response to fire. Population-level trends in interannual seasonal home range fidelity were similar between the two provinces (Appendix D) and inferences were unaffected by excluding the Ontario data. All subsequent analyses are based on the two provinces pooled together.

Home Range Fidelity

Overall, we found negligible differences in BA overlap of pre-fire/post-fire and year to year seasonal home ranges (Figure 13). During calving and winter, BA overlap was not significantly different for pre-fire/post-fire or year-to-year home ranges (Table 12). In summer-

autumn, BA overlap was significantly lower for pre-fire/post-fire home ranges than year to year home ranges (Table 12). Contrary to expectations, in all seasons, caribou more heavily affected by fire did not alter BA overlap more strongly (Table 12).

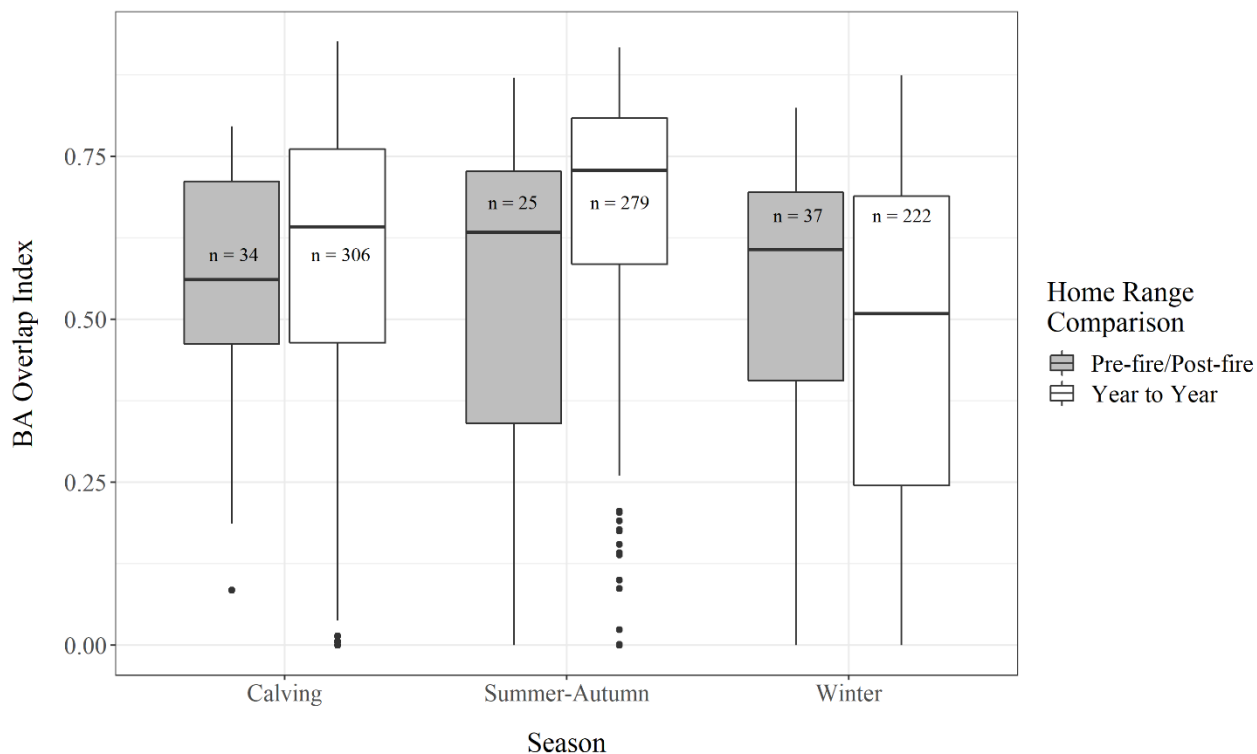


Figure 13. Boxplots of BA overlap for pre-fire/post-fire and year-to-year seasonal home ranges for caribou in the Boreal Shield of Ontario and Saskatchewan. BA overlap (0–1) describes the overall similarity in space use based on the pair of seasonal home ranges. “n” = number of seasonal home range dyads.

Individual Responses to Fire

We expected caribou that interacted with recent burns would alter their home range and reduce use of an area after it burned. Therefore, we expected these animals to demonstrate lower home range overlap than the population median, coinciding with a reduction in use of the burn (i.e., bottom left corner of graphs in Figure 14). Contrary to our expectations, caribou demonstrated high variation within and amongst individuals and seasons in their response to fire (Figure 14). During calving, caribou often made small adjustments to use of the burn and increased use 44% of the time. In several cases where caribou increased use of the burn post-fire,

home range overlap was lower than the population median, suggesting caribou intentionally shifted their home range to incorporate more burned habitat (Figure 14, Figure 15a). In summer-autumn, caribou reduced use of the burn 76% of the time. BA overlap frequently fell below the median of the population, suggesting caribou made larger adjustments to their home range during this season (Figure 14). In winter, caribou increased use of the burn 30% of the time; however, most individuals reduced use of the burn (Figure 14, Figure 15b), particularly when they were more heavily impacted by the fire. Most caribou that interacted with recent burns in winter had higher home range overlap than the population median, suggesting they maintained relatively similar home ranges before and after fire. In the calving season, when caribou were more heavily affected by fire they did not strongly alter or reduce use of the burn (Table 12), whereas in summer-autumn and winter caribou altered use of the burn more strongly and tended to reduce use when more heavily impacted by fire (Table 12).

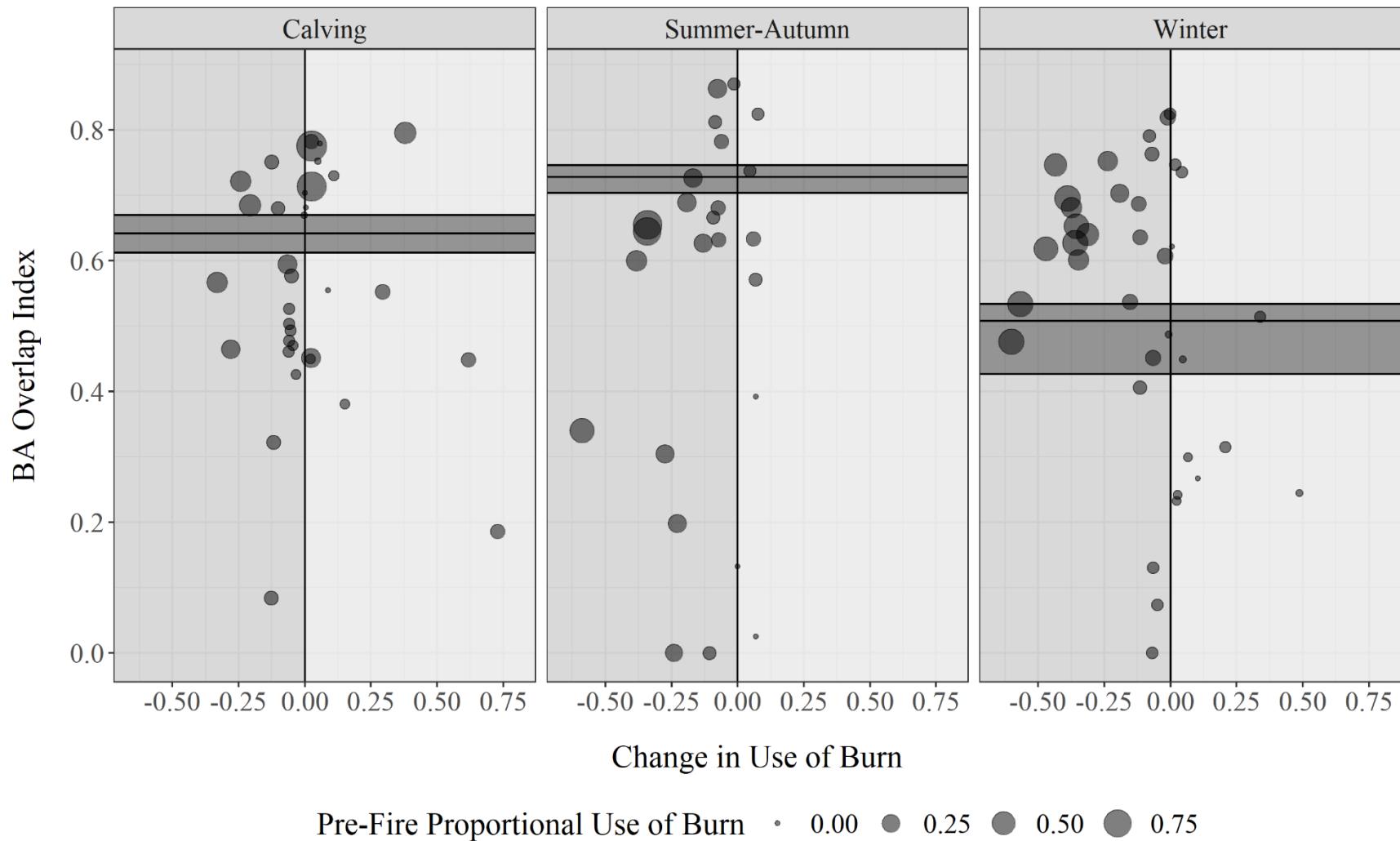


Figure 14. Response of woodland caribou to recent burns in the Boreal Shield of Ontario and Saskatchewan during calving, summer-autumn, and winter. BA overlap (0–1) describes the overall similarity in pre-fire and post-fire space use based on the pair of seasonal home ranges. The horizontal line represents the median BA overlap of year to year home ranges in each season, bound by 95% median confidence intervals. Change in use of burn is the difference in the proportion of GPS locations within the burn post-fire compared to pre-fire. The size of data point corresponds to the proportion of pre-fire GPS locations within the burn.

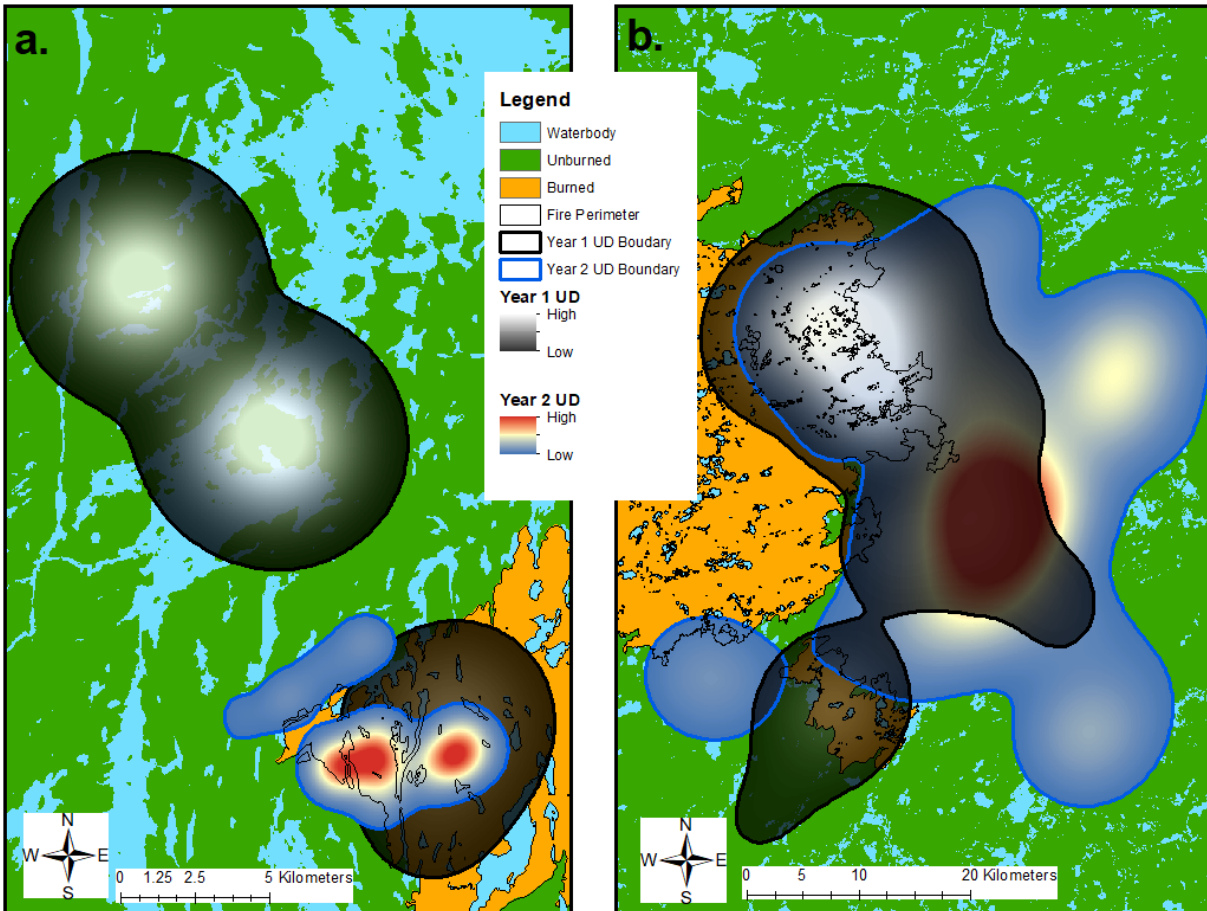


Figure 15. Example comparisons of pre-fire and post-fire seasonal home ranges for woodland caribou in the Boreal Shield of Saskatchewan: a. This individual substantially altered its home range amongst calving seasons (BA overlap = 0.19) to increase use of the burn post-fire (14% pre-fire use → 87% post-fire use); b. This individual reduced use of the burn post-fire (65% pre-fire use → 8% post-fire use) but showed moderate overall similarity in home ranges amongst winters (BA overlap = 0.53).

Table 12. Summary of statistical models used to assess the effects of recent burns on space use by woodland caribou in the Boreal Shield of Ontario and Saskatchewan. BA overlap (0–1) describes the overall similarity in space use based on the pair of seasonal home ranges. “Home range comparison” is a binary variable denoting year to year (0) or pre-fire, post-fire (1) seasonal home ranges. “Pre-fire prop. use of burn” is the proportion of GPS locations within the burn pre-fire. “ Δ Prop. use of burn” is the proportion of GPS locations within the burn post-fire minus pre-fire (absolute value). Increase is a binary variable for the change in use of the burn from pre-fire to post-fire (0 = constant/decrease, 1 = increase). Random effect estimates are presented in Appendix E.

Model	Calving			Summer-Autumn			Winter		
	β	SE	<i>p</i>	β	SE	<i>p</i>	β	SE	<i>p</i>
BA overlap ~ Home range comparison	-0.13	0.21	0.54	-0.66	0.30	0.03	0.24	0.25	0.34
BA overlap ~ Pre-fire prop. use of burn	0.82	0.55	0.13	1.61	1.82	0.38	1.64	0.70	0.02
Δ Prop. use of burn ~ Pre-fire prop. use of burn	0.24	0.59	0.68	2.95	0.57	< 0.001	3.70	0.46	< 0.001
Increase ~ Pre-fire prop. use of burn	1.62	1.83	0.38	-17.98	9.25	0.05	-48.30	20.37	0.02

Discussion

Despite inhabiting boreal ecosystems with high fire frequency, our study suggests it is rare for a large part of a caribou’s home range to be actively burned. Large parts of each study area burned while animals were collared (ON = 2.5%, SK = 8.4%), yet 84% of the time, less than 5% of an individual’s seasonal home range burned while the animal was collared. Caribou in Saskatchewan interacted with recent burns more frequently than those in Ontario, likely due to lower fire suppression (Stocks et al. 2002), a more aggressive fire regime (Parisien et al. 2004), and a higher density of collared animals across the landscape (SK = 1 caribou/1000 km², ON = 0.5 caribou/1000 km²).

Unpredictability in the occurrence of fires relative to the timing and duration of GPS collar projects inherently limits the sample size in studies of this nature. Collecting GPS

locations repeatedly for the same population or including other collaring projects would improve the sample size and the robustness of our results. This study only considered interactions with recent burns (i.e., fires that occurred while caribou were collared), but burns are considered disturbed habitat for caribou until 40 years post-fire (ECCC 2012). Caribou must constantly adapt to the shifting mosaic of habitat created by fire histories and this temporal element means fire has a nuanced influence on caribou distribution. Future research could incorporate burns already present on the landscape at the onset of collaring to investigate how local fire history influences the response of caribou to recent burns.

Prevailing theory and policy predicts caribou should shift their home range to reduce use of an area after it burns because burned landscapes have poor habitat quality compared to alternate, unburned ranges (Schaefer and Pruitt 1991, Switzer 1993, Joly et al. 2003, Faille et al. 2010). Home range fidelity should only be favoured if the current home range is of equal or higher quality than the alternate range (Switzer 1993). Therefore, we expected the overlap of pre-fire and post-fire seasonal home ranges to be significantly lower than the overlap of year to year seasonal home ranges. BA overlap was significantly lower for pre-fire/post-fire home ranges in summer-autumn, but we found no such trend during calving and winter. In these seasons, a caribou's response to fire was indistinguishable from regular, interannual variation in home range overlap in these populations. Many factors influence interannual variation in space use including weather, body condition, reproductive status, social interactions, predation, and disturbance (Wittmer et al. 2006, Faille et al. 2010, MacNearney et al. 2016, Lafontaine et al. 2017, Peignier et al. 2019). Our results do not indicate a lack of adjustment in space use after fire during calving and winter, but rather that recent burns do not cause adjustments outside the observed range of variability in interannual home range overlap in these seasons.

Caribou were least averse to recent burns during calving. Caribou showed similar fidelity of pre-fire/post-fire and year to year home ranges during calving, and individuals more heavily impacted by fire did not strongly alter or reduce use of the burn. Caribou increased use of the area after it burned 44% of the time during the calving season, with some individuals appearing to intentionally shift their home range to incorporate more burned habitat. Following the logic of Switzer (1993), caribou should only demonstrate these behaviors if recent burns are of equal or greater habitat quality than alternate ranges.

There are several ways in which recent burns may provide habitat value to caribou during the calving season. In the Boreal Shield, it is common for $\geq 25\%$ of the area within a burn to consist of post-fire residuals (Kansas et al. 2016). Bogs and fens are less likely to burn due to high soil moisture and sparse tree cover (Turetsky et al. 2004, Hart et al. 2019) and are common as post-fire residuals (Silva 2018). Skatter et al. (2017) documented caribou calving in lowland post-fire residuals in northern Saskatchewan. Islands and peninsulas can be protected by the fire breaks created by lakes and could also serve as calving habitat (Carr et al. 2011, Nielsen et al. 2016). As fires reduce the density of understory vegetation, predator detectability could be enhanced when caribou use these features in recent burns (Skatter et al. 2017). Predation risk could be further reduced due to the high resiliency of coniferous forest types that prevents an extensive influx of deciduous plants (Neufeld et al. 2020), leading to low habitat value for moose and wolves in recent burns (DeMars et al. 2019). Calving in recent burns with relatively low forage biomass may help reduce predation risk (Viejou et al. 2018) and females could compensate by drawing from their body reserves, a common behavior in the calving season (Parker et al. 1990). Females may also take advantage of the protein-rich, new growth in recent burns to help meet the high energetic needs of lactation (Gustine et al. 2006, Oftedal 1985, Chan-

McLeod et al. 1994). Maintaining fidelity to a burned calving range or shifting to calve in a recent burn may be an adaptive strategy enabling caribou to spatially isolate themselves from conspecifics, competing ungulates and predators in regions with high fire frequency to reduce predation on calves (Bergerud 1996, Walker et al. 2020). Therefore, we believe recent burns can provide similar habitat value as alternate, unburned areas during the calving season.

Contrary to the calving season, caribou were most averse to fires in summer-autumn. The overlap of pre-fire/post-fire home ranges was significantly lower than year to year home ranges in summer-autumn and caribou reduced use of the burn 76% of the time. When caribou were more heavily impacted by fire in summer-autumn, they were more likely to reduce use of the burn. Together, these results suggest caribou tended to shift their home range out of recent burns in summer-autumn.

Female body condition reaches a low point in mid-summer due to the high nutritional demands of lactation and caribou must quickly replenish their body reserves prior to the upcoming winter to survive and reproduce (Parker et al. 2009). Caribou can take advantage of high-protein vascular forage during the growing season (Denryter et al. 2017) but lichens remain an important component of the diet (Thompson et al. 2015). Caribou typically maintain strong fidelity to their summer-autumn range (Schaefer and Mahoney 2013, this study). Peignier et al. (2019) hypothesized that caribou demonstrate high fidelity to productive summer ranges because forage is homogeneously distributed and easily accessible. By increasing heterogeneity, burns could reduce the quality of affected home range below that of alternate ranges, promoting caribou to shift to unburned ranges where the abundance and quality of forage, especially lichens, is more predictable (Switzer 1993). Spending more time in unburned habitats would allow females to restore their body condition but could increase predation risk (Gustine et al.

2006, Basille et al. 2015). Approximately four weeks after birth, caribou calves are more mobile and are less vulnerable to predation (DeMars et al. 2013). Since parturition in our study area occurs from early May to mid-June (McLoughlin et al. 2019, Walker et al. 2020), by the onset of summer-autumn (August 1), calves should be quite mobile and predator avoidance may be a less acute concern than during the calving period. This could enable cow-calf pairs to spend more foraging time in riskier, productive habitats (Basille et al. 2015), in this case outside of recent burns.

Because caribou rely heavily on lichens in winter (Thompson et al. 2015), one would expect caribou to be most averse to recent burns during this season. However, caribou demonstrated similar levels of overlap of pre-fire/post-fire and year to year home ranges in winter and did not alter their home range more strongly when more heavily impacted by fire. Despite maintaining relatively similar home ranges, caribou often reduced use of the burn in winter, especially if they were more heavily impacted by the fire.

Caribou demonstrate low fidelity to winter home ranges (Schaefer et al. 2000, Wittmer et al. 2006, Lafontaine et al. 2017, this study), as terrestrial lichens and snow conditions are patchy across the landscape (Mayor et al. 2009). Caribou tend to congregate in groups during winter to access lichens at feeding craters and the location of these social associations can be highly variable year-to-year (Peignier et al. 2019). The tendency of caribou to reduce use of burns in winter is consistent with alternate ranges being of higher quality (Switzer et al. 1993), likely due to more predictable lichen availability, but these adjustments in space use were apparently achievable within the range of interannual variation in home range overlap in these populations. Surprisingly, caribou did increase use of the burn 30% of the time, in some cases quite substantially (e.g., + 49%). This suggests caribou may not view recent burns as maladaptive

winter habitat. Schaefer et al. (1991) observed caribou grazing lichens in post-fire residuals during winter. Caribou may also feed on graminoids (e.g., cotton grass, *Eriophorum vaginatum* L., 1753), which can be more plentiful in recent burns, as a relatively nutritious supplement to their winter diet (Klein 1982, Ballard et al. 2000).

Additional research is required to verify the mechanisms of habitat selection by woodland caribou within recent burns (e.g., protein-rich new growth, lichens in post-fire residuals, predator refuge). Tracking the spatio-temporal dynamics of moose, wolves, and caribou over several decades would provide insights into how these species respond to the shifting habitat mosaic, which could help to design more effective resource management strategies. Additional research would provide a more holistic understanding of the interactions between caribou and fire, potentially leading to new insights in caribou ecology that could inform more effective conservation actions for this species.

Superficially, fire can appear to be a destructive disturbance for woodland caribou. To date, most caribou-disturbance research has been conducted in ranges with high cumulative fire and human disturbance (e.g., Sorensen et al. 2008). Behavioral plasticity is likely critical for caribou populations to respond to changing environmental conditions (Gustine et al. 2006). A lack of alternate ranges and enhanced disturbance-mediated apparent competition in areas with high human disturbance could hinder the ability of caribou to respond to recent burns and exaggerate the negative effects of fire on caribou demography (Sorensen et al. 2008, Faille et al. 2010). In the present study, caribou rarely experienced fire and when they did, they adjusted their space use in variable and complex ways that were largely indistinguishable from the regular, interannual variation in space use of the population. Therefore, we contend that recent burns are not a major concern to woodland caribou and may even provide some habitat value, particularly

in the immediate years post-fire (<5 years; Schaefer and Pruitt 1991) and during the calving season. We believe the generalized treatment of fire in habitat management strategies deflects from human disturbance as the primary mechanism influencing population stability and ignores temporal variation in the effects of fire on moose, wolves, and caribou. We echo the call by DeMars et al. (2019) and Neufeld et al. (2020) for a regionally-informed, flexible approach to interpret fire in habitat management strategies.

CONCLUSION

Woodland caribou are a challenging species to manage due to their wide geographic distribution and sensitivity to habitat disturbance. In the context of recovery actions, this makes it challenging to ensure habitat definitions are appropriate and specific enough to support effective conservation actions when local caribou ecology and disturbance history vary widely across the species range. In this thesis, I set out to refine caribou habitat definitions in the less studied western Boreal Shield by investigating the interactions between fire, lichen, and woodland caribou. I mapped the biomass of ground lichens in a fire-driven landscape and linked the map to caribou GPS collar locations to characterize seasonal selection patterns for this important food source. I then characterized the short-term response of caribou to fire by comparing their pre-fire and post-fire GPS locations. My research suggests our identification of caribou winter habitat could be improved using lichen biomass maps and suggests a need to broaden our interpretation of fire in habitat management strategies. Together, these changes could improve habitat definitions for woodland caribou in the western Boreal Shield and support more effective conservation actions.

I developed a simple, user-friendly framework that can be adapted to model and map the biomass of ground lichens for woodland caribou ranges in Canada. I found the biomass of ground lichens to be distributed in a heterogenous pattern in the fire-driven landscape of

Woodland Caribou Provincial Park in northwestern Ontario. Ecosite, time-since-fire, and canopy closure were important predictors of lichen presence and abundance. Most of the landscape was relatively poor in lichen abundance, as lichen-rich areas were restricted to mature stands of sparse conifer forest on bedrock outcrops.

I demonstrated the utility of the lichen biomass map by analyzing seasonal selection patterns for lichen biomass by woodland caribou. I found caribou strongly selected for lichen biomass during winter, especially stands with >3000 kg/ha of ground lichens. My findings and those of previous studies (Trudell and White 1981, Johnson et al. 2001, Joly et al. 2010) suggest this could be an important threshold to identify nutritionally important patches of winter habitat. I encourage policymakers and managers to incorporate measures of forage availability when delineating winter critical habitat for woodland caribou.

I found that caribou responded to fire in variable and complex ways. The overlap of pre-fire and post-fire home ranges was indistinguishable from the overlap of year to year home ranges in most seasons. Caribou adjusted their space use at a smaller scale during summer-autumn and winter, showing a tendency to reduce use of the burn. However, during the calving season, caribou did not strongly alter their space use in response to fire and in some cases intentionally shifted their home range to incorporate more burned habitat. These findings suggest we may need to broaden our interpretation of fire in habitat management strategies.

In this thesis, I developed a straightforward modelling framework that can be adapted to map the biomass of ground lichens in other boreal caribou ranges. By linking the lichen biomass map the caribou GPS locations, I found lichen biomass was a strong predictor of winter habitat selection and suggest lichen biomass maps could be used to improve the delineation of winter habitat. I found caribou responded to fire in variable and complex ways that were largely

indistinguishable from regular, interannual variation, suggesting we may need to broaden the interpretation of fire in habitat management strategies. Together, my research can be used to improve habitat definitions for woodland caribou in the western Boreal Shield and support better conservation decisions.

Management Recommendations

My research suggests we could improve habitat definitions for woodland caribou in the western Boreal Shield by better understanding lichens and fire, two important components of the species' ecology. Specifically, we encourage managers to use lichen biomass maps to identify caribou winter habitat in a more direct and measurable way. We also encourage managers to broaden their interpretation of fire in habitat management strategies by recognizing temporal variation in the effects of fire and the weak demographic effects of fire in landscapes with low human disturbance. Across much of the western Boreal Shield, caribou ranges remain relatively intact. This presents managers with an opportunity to conserve caribou while contributing to larger conservation objectives. As a wide-ranging species with high sensitivity to habitat disturbance, woodland caribou are a good indicator of intact boreal landscapes, which safeguard a variety of other biodiversity values such as carbon stores and migratory bird habitat. Caribou are also part of the livelihood and culture of many northern communities and our identity as Canadians. As resource interests continue to expand into these relatively intact landscapes, society will decide on the fate of the local caribou populations. Effective co-existence will likely require a commitment to large protected areas and gradual, limited development.

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Appendix A

To validate the cover-to-biomass conversion factors from McMullin et al. (2011) for our study area, we collected a subsample of the lichen material in one 1 m² quadrat at 34 randomly selected sampling locations. Within each selected quadrat, we placed a 25 cm × 25 cm square subplot and recorded the percent cover of all six lichen species. We then collected all thallus material of each *Cladonia* spp. ground lichen in the subplot, placing each species in a separate, labelled paper bag.

We air-dried our lichen samples after returning from the field to prevent mold and decomposition. We later cleaned the lichens of debris (moss, needles, etc.) and dried each sample in a biomass oven at 60°C for 24 hours. We weighed the dried samples using a digital scientific balance (measured in grams to two decimal places) and recorded a g/cm² value for each sample by dividing the weight of the dried sample (g) by the area it covered in the subplot (cm²). We derived a cover-to-biomass conversion factor (g/cm²) for each lichen species by taking the average g/cm².

We compared our conversion factors to McMullin's using two-tailed T-tests. We considered conversion factors not statistically different at an α -level = 0.05. The validation procedures could not be performed for *C. stellaris* or *C. stygia* because their rarity precluded them from being present in the destructive samples. There was considerable overlap in the conversion factors for each lichen species (Figure A1). In the two-tailed T-test for each lichen species, the p -values (all ≥ 0.43) exceeded the α -level = 0.05, indicating the conversion factors developed by McMullin do not differ significantly from those recorded in this study. We therefore concluded that McMullin's conversion factors were appropriate for our study area and applied them to our subsequent analyses.

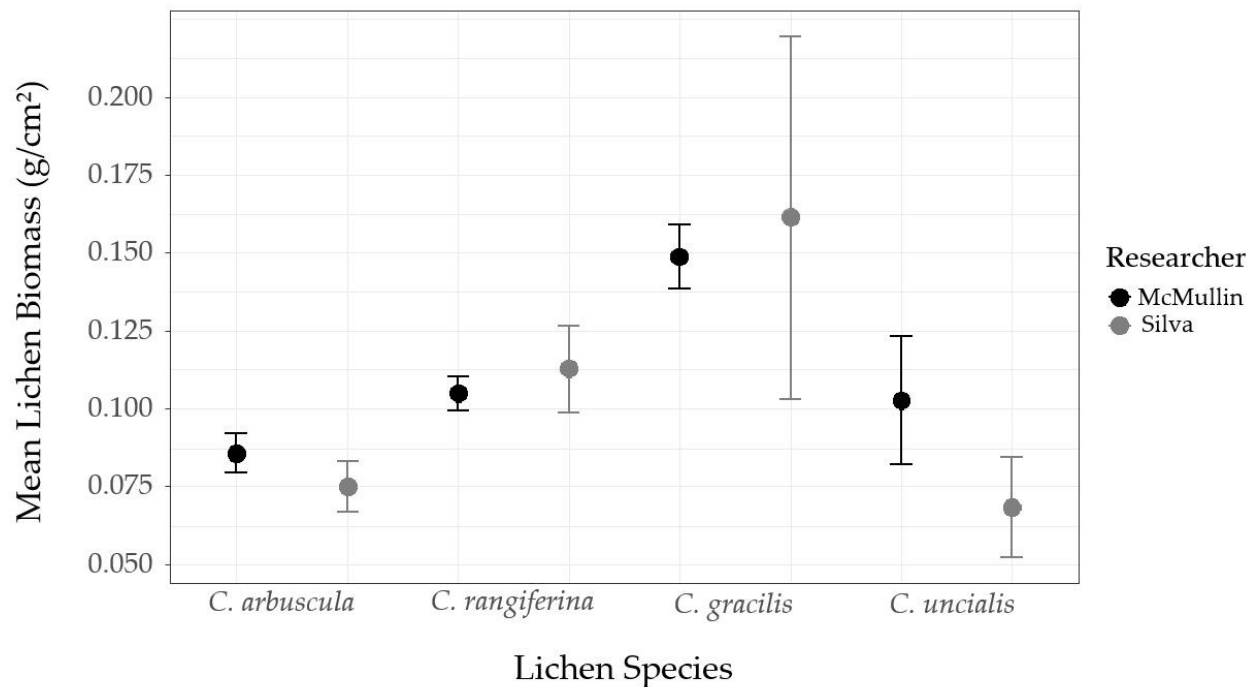


Figure A1. Mean biomass (g/cm^2) recorded for each *Cladonia* spp. ground lichen destructively sampled by McMullin et al. (2011) and Silva (this study). Error bars represent ± 1 SE.

Appendix B

To estimate lichen biomass in each 1 m^2 quadrat, we visually estimated the percent cover of each lichen species and converted to proportions (Table B1). We multiplied each proportion by 10,000 ($10,000 \text{ cm}^2 = 1 \text{ m}^2$) to determine the square centimetre area covered by each lichen species in the quadrat. We multiplied the square centimetre area covered by each lichen species by its conversion factor to derive a biomass estimate (g/m^2) and added the biomass of all species present in the quadrat to determine a biomass estimate for the quadrat (Table B1).

Table B1. Example calculation to estimate the biomass of *Cladonia* spp. ground lichens in a 1 m² quadrat. Species classification and conversion factors are adapted from McMullin et al. (2011).

Lichen Species	Cover	Quadrat 1	
		cm ²	Biomass
<i>C. rangiferina</i>	0.10	$0.10 \times 10,000 = 1,000 \text{ cm}^2$	$1,000 \text{ cm}^2 \times 0.10500 \text{ g/cm}^2 = 105.00 \text{ g}$
<i>C. arbuscula</i>	0.15	$0.15 \times 10,000 = 1,500 \text{ cm}^2$	$1,500 \text{ cm}^2 \times 0.08593 \text{ g/cm}^2 = 128.90 \text{ g}$
<i>C. uncialis</i>	0.25	$0.25 \times 10,000 = 2,500 \text{ cm}^2$	$2,500 \text{ cm}^2 \times 0.10263 \text{ g/cm}^2 = 256.58 \text{ g}$
<i>C. gracilis</i>	0.00	0 cm ²	0 g
<i>C. stellaris</i>	0.20	$0.20 \times 10,000 = 2,000 \text{ cm}^2$	$2,000 \text{ cm}^2 \times 0.11618 \text{ g/cm}^2 = 232.36 \text{ g}$
<i>C. stygia</i>	0.05	$0.05 \times 10,000 = 500 \text{ cm}^2$	$500 \text{ cm}^2 \times 0.15145 \text{ g/cm}^2 = 75.72 \text{ g}$
<i>Quadrat Biomass</i>		$105.00 + 128.90 + 256.58 + 0 + 232.36 + 75.72 = 798.56 \text{ g}$	

We repeated this procedure (Table B1) for all five 1 m² quadrats along the transect, resulting in five estimates of lichen biomass per sampling location (Table B2). To determine the stand-level lichen biomass for the sampling location (kg/ha), we add the biomass estimates for the five quadrats (g/5 m²). We then divided by 1,000 (1,000 g = 1 kg) to convert to kilograms and multiplied the result by 2,000 (5 m² × 2,000 = 10,000 m² = 1 ha), resulting in a stand-level biomass estimate (Table B2; kg/ha).

Table B2. Example calculation to derive a stand-level estimate of lichen biomass (kg/ha) for a sampling location using the protocol described in this paper. Species classification and conversion factors are adapted from McMullin et al. (2011).

Lichen Species	Quadrat 1			Quadrat 2			Quadrat 3			Quadrat 4			Quadrat 5		
	Cover	cm ²	Biomass	Cover	cm ²	Biomass	Cover	cm ²	Biomass	Cover	cm ²	Biomass	Cover	cm ²	Biomass
<i>C. rangiferina</i>	0.10	1000	105.00	0.05	500	52.50	0.20	2000	210.00	0.10	1000	105.00	0.00	0	0.00
<i>C. arbuscula</i>	0.15	1500	128.90	0.15	1500	128.90	0.00	0	0.00	0.15	1500	128.90	0.00	0	0.00
<i>C. uncialis</i>	0.25	2500	256.58	0.05	500	51.32	0.00	0	0.00	0.07	700	71.84	0.00	0	0.00
<i>C. gracilis</i>	0.00	0	0.00	0.00	0	0.00	0.01	100	14.90	0.00	0	0.00	0.00	0	0.00
<i>C. stellaris</i>	0.20	2000	232.36	0.00	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0	0.00
<i>C. stygia</i>	0.05	500	75.73	0.00	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0	0.00
		Sum	798.56		Sum	232.71		Sum	224.90		Sum	305.74		Sum	0.00
		Quadrat Biomass		$798.56 + 232.71 + 224.90 + 305.74 + 0 = 1,561.91 \text{ g}$											
		Stand-level Biomass		$1,561.91 \text{ g} \div 1,000 \text{ g/kg} = 1.56 \text{ kg}$											
		$1.56 \text{ kg} \times 2,000 = 3,120 \text{ kg/ha}$													

Appendix C

We used nine environmental covariates to construct a set of candidate models for predicting lichen presence and lichen abundance: ecosite, canopy closure, time-since-fire, elevation, slope, blue reflectance, short-wave infrared (SWIR2) reflectance, normalized difference vegetation index (NDVI) and normalized difference moisture index (NDMI). The pre-processing details for these datasets are described in the following sections.

Ecosite

We created an ecosite layer from the primary ecosite attribute (PRI_ECO; MNRF 2009b) for each polygon in the forest resource inventory datasets for Woodland Caribou Provincial Park (2009) and the surrounding Forest Management Units: Kenora (2015), Red Lake (2013) and Whiskey Jack (2015) (MNRF 2019a). We grouped the 68 ecosites present in our study area into eleven broad categories: sparse conifer, dense conifer, anthropogenic, bog, fen, hardwood swamp, mixedwood, rock, shrubland and upland mixed conifer (Table C1). Lakes were classified based on the water (WAT) polygon type (POLYTYPE; MNRF 2009b). We assigned the simplified forest classification to each inventory dataset, merged them together, clipped them to the study area and created an ecosite raster in ArcGIS 10.5 (ESRI 2017). We only sampled sparse conifer (ecosite B012) and dense conifer (ecosite B049) in our study, so the ecosite variable used for modelling was a factor with two levels: 1 = sparse conifer, 2 = dense conifer. The beta coefficient for ecosite in the lichen presence and lichen abundance models indicates the effect of dense conifer relative to sparse conifer. Unsampled ecosites were assigned 'NoData' in the lichen presence and abundance rasters.

Table C1. Categorization of boreal ecosites of Ontario (MNR 2014a) into eleven categories used to model lichen presence and lichen abundance for the study area.

Ecosite Number	Ecosite Name	Landcover Category
12	Very shallow, dry to fresh: pine-black spruce conifer	Sparse conifer
49	Dry to fresh, coarse: jack pine-black spruce dominated	Dense conifer
189	Constructed vertical surface	Anthropogenic
195	Active fine clean fill	Anthropogenic
197	Pavement/concrete	Anthropogenic
198	Compact gravelled surface	Anthropogenic
997	Anthropogenic	Anthropogenic
999	Anthropogenic	Anthropogenic
126	Treed bog	Bog
127	Organic poor conifer swamp	Bog
128	Organic intermediate conifer swamp	Bog
129	Organic rich conifer swamp	Bog
137	Sparse treed bog	Bog
138	Open bog	Bog
222	Mineral poor conifer swamp	Bog
223	Mineral intermediate conifer swamp	Bog
136	Sparse treed fen	Fen
139	Poor fen	Fen
140	Open moderately rich fen	Fen
141	Open extremely rich fen	Fen
146	Open shore fen	Fen
147	Shrub shore fen	Fen
130	Intolerant hardwood swamp	Hardwood swamp
133	Hardwood swamp	Hardwood swamp
14	Very shallow, dry to fresh: conifer	Mixedwood
16	Very shallow, dry to fresh: aspen-birch hardwood	Mixedwood
37	Dry, sandy: spruce-fir conifer	Mixedwood
40	Dry, sandy: aspen-birch hardwood	Mixedwood
52	Dry to fresh, coarse: spruce-fir conifer	Mixedwood
55	Dry to fresh, coarse: aspen-birch hardwood	Mixedwood
67	Moist, coarse: spruce-fir conifer	Mixedwood
70	Moist, coarse: aspen-birch hardwood	Mixedwood
71	Moist, coarse: elm-ash hardwood	Mixedwood
88	Fresh, clayey: aspen-birch hardwood	Mixedwood
101	Fresh, silty to fine loamy: spruce-fir conifer	Mixedwood
104	Fresh, silty to fine loamy: aspen-birch hardwood	Mixedwood
119	Moist, fine: aspen-birch hardwood	Mixedwood
7	Active mineral barren	Rock
158	Cliff	Rock
159	Open cliff	Rock
161	Bedrock shoreline	Rock
162	Open bedrock shoreline	Rock

164	Rock barren	Rock
62	Moist, coarse: sparse shrub	Shrubland
63	Moist, coarse: shrub	Shrubland
96	Fresh, silty to fine loamy: shrub	Shrubland
134	Mineral thicket swamp	Shrubland
135	Organic thicket swamp	Shrubland
142	Mineral meadow marsh	Shrubland
143	Rock meadow marsh	Shrubland
144	Organic meadow marsh	Shrubland
24	Very shallow, humid: black spruce-pine conifer	Upland mixed conifer
33	Dry, sandy: red pine-white pine conifer	Upland mixed conifer
34	Dry, sandy: jack pine-black spruce dominated	Upland mixed conifer
35	Dry, sandy: pine-black spruce conifer	Upland mixed conifer
48	Dry to fresh, coarse: white pine conifer	Upland mixed conifer
50	Dry to fresh, coarse: pine-black spruce dominated	Upland mixed conifer
65	Moist, coarse: pine-black spruce conifer	Upland mixed conifer
68	Moist, coarse conifer	Upland mixed conifer
82	Fresh, clayey: black spruce-jack pine dominated	Upland mixed conifer
83	Fresh, clayey: pine-black spruce conifer	Upland mixed conifer
85	Fresh, clayey: spruce-fir conifer	Upland mixed conifer
98	Fresh, silty to fine loamy: black spruce-jack pine dominated	Upland mixed conifer
99	Fresh, silty to fine loamy: pine-black spruce conifer	Upland mixed conifer
100	Fresh, silty to fine loamy: cedar (hemlock) conifer	Upland mixed conifer
114	Moist, fine: pine-black spruce conifer	Upland mixed conifer
116	Moist, fine: spruce-fir conifer	Upland mixed conifer

Time Since Fire

We created a time-since-fire layer using the fire perimeters captured into two provincial GIS polygon datasets: FiresByDecade (1929-1959) (MNRF 2019b) and Fire Disturbance Area (1960–2013) (AFFES 2019). We clipped the two datasets to the extent of the study area, merged them and converted the new layer to a raster format in ArcGIS 10.5 (ESRI 2017). We calculated time-since-fire by subtracting the fire year from 2014 (the study year for producing the lichen map). Areas unaffected by fire since 1929 were assigned a uniform value of 100.

Canopy Closure

We created a canopy closure layer from the overstorey crown closure attribute (OCCLC) (MNRF 2009b) for each polygon in the forest resource inventory datasets for Woodland Caribou

Provincial Park (2009) and the surrounding Forest Management Units: Kenora (2015), Red Lake (2013) and Whiskey Jack (2015) (MNR 2019a). We merged the individual inventory datasets together, clipped them to the study area and created a single canopy closure raster in ArcGIS 10.5 (ESRI 2017).

Simple linear regression indicated poor agreement ($R^2_{adj} = 0.17$) between our canopy closure layer and our field observations. To improve the accuracy of our canopy closure layer, we used generalized linear models (family = Gamma, link = logit) to predict our field observations as a function of four environmental covariates: canopy closure derived from the inventory datasets (OCCLO), ecosite (1 = sparse conifer, 2 = dense conifer), time-since-fire (TSF) and normalized difference vegetation index (NDVI) (Table C2).

Table C2. Name and structure of candidate models used to create the canopy closure layer for modelling lichen presence and abundance. Obs = canopy closure recorded in the field, OCCLO = canopy closure derived from the forest inventory datasets, TSF = time since fire (years), NDVI (normalized difference vegetation index).

Model Name	Model Structure
Null	Obs ~ OCCLO
Ecosite	Obs ~ Ecosite + OCCLO
TSF	Obs ~ TSF + OCCLO
NDVI	Obs ~ NDVI + OCCLO
Ecosite + TSF	Obs ~ Ecosite + TSF + OCCLO
Full	Obs ~ Ecosite + TSF + NDVI + OCCLO

We ranked the candidate models by AIC_c score (Hurvich and Tsai 1989) and considered the model with the lowest AIC_c score as the best of the candidate set (Burnham and Anderson 2002). The model with the lowest AIC_c score included canopy closure derived from the inventory datasets, ecosite, time-since-fire and NDVI (Table C3).

Table C3. Ranking of candidate models used to create the canopy closure layer for modelling lichen presence and abundance. k = number of fixed effects (+ 1 for intercept), w_i = Akaike weight. TSF = time-since-fire, NDVI = normalized difference vegetation index.

Model Name	k	log likelihood	AIC _c	Δ AIC _c	w_i
Full	4	-436.16	885.15	0	0.91
Ecosite	2	-441.03	890.44	5.29	0.06
Ecosite + TSF	3	-440.71	892.01	6.86	0.03
NDVI	2	-444.63	897.65	12.50	0.00
Null	1	-452.89	912.01	26.86	0.00
TSF	2	-452.87	914.13	28.98	0.00

The model summary for the top model is presented in Table C4. We interpolated this top model across the study area using the *raster* package in R version 3.6.0 (Hijmans 2019, R Core Team 2019) to create the canopy closure layer we used to model lichen presence and abundance. Simple linear regression indicated the new canopy closure layer showed greater agreement with our field observations ($R^2_{adj} = 0.40$).

Table C4. Model summary for the model used to create the canopy closure layer for modelling lichen presence and abundance. TSF = time-since-fire, NDVI = normalized difference vegetation index, OCCLO = canopy closure derived from the forest inventory datasets. *SE* = standard error.

Covariate	Coefficient	<i>SE</i>	<i>z</i> -value	<i>p</i> -value
Ecosite	-8.15×10^{-3}	2.01×10^{-3}	-4.06	9.55×10^{-5}
TSF	-4.978×10^{-5}	2.86×10^{-5}	-1.742	0.08
NDVI	-4.14×10^{-2}	1.30×10^{-2}	-3.19	< 0.01
OCCLO	-1.19×10^{-4}	4.87×10^{-5}	-2.44	0.02

Elevation and Slope

Elevation (metres above sea level) was obtained from a provincial digital elevation model (MNR 2019c). Slope values were derived from the digital elevation model using ArcMap 10.5 (ESRI 2017).

Remote Sensing Covariates

We derived our remote sensing covariates from the spectral bands of two Landsat 8 Surface Reflectance datasets (captured July 31, 2014; USGS 2019a-b). The individual spectral bands used in this study are:

Band 2: Blue (Blue reflectance)

Band 4: Red (used in NDVI)

Band 5: Near infrared (NIR; used in NDVI and NDMI)

Band 6: Shortwave infrared 1 (SWIR1; used in NDMI)

Band 7: Shortwave infrared 2 (SWIR2 reflectance)

The equations for the spectral indices are:

$$\text{NDVI} = [\text{NIR} - \text{Red}] / [\text{NIR} + \text{Red}] \quad (1)$$

(normalized difference vegetation index; Tucker and Sellers 1986)

$$\text{NDMI} = [\text{NIR} - \text{SWIR1}] / [\text{NIR} + \text{SWIR1}] \quad (2)$$

(normalized difference moisture index; Wilson and Sader 2002)

Appendix D

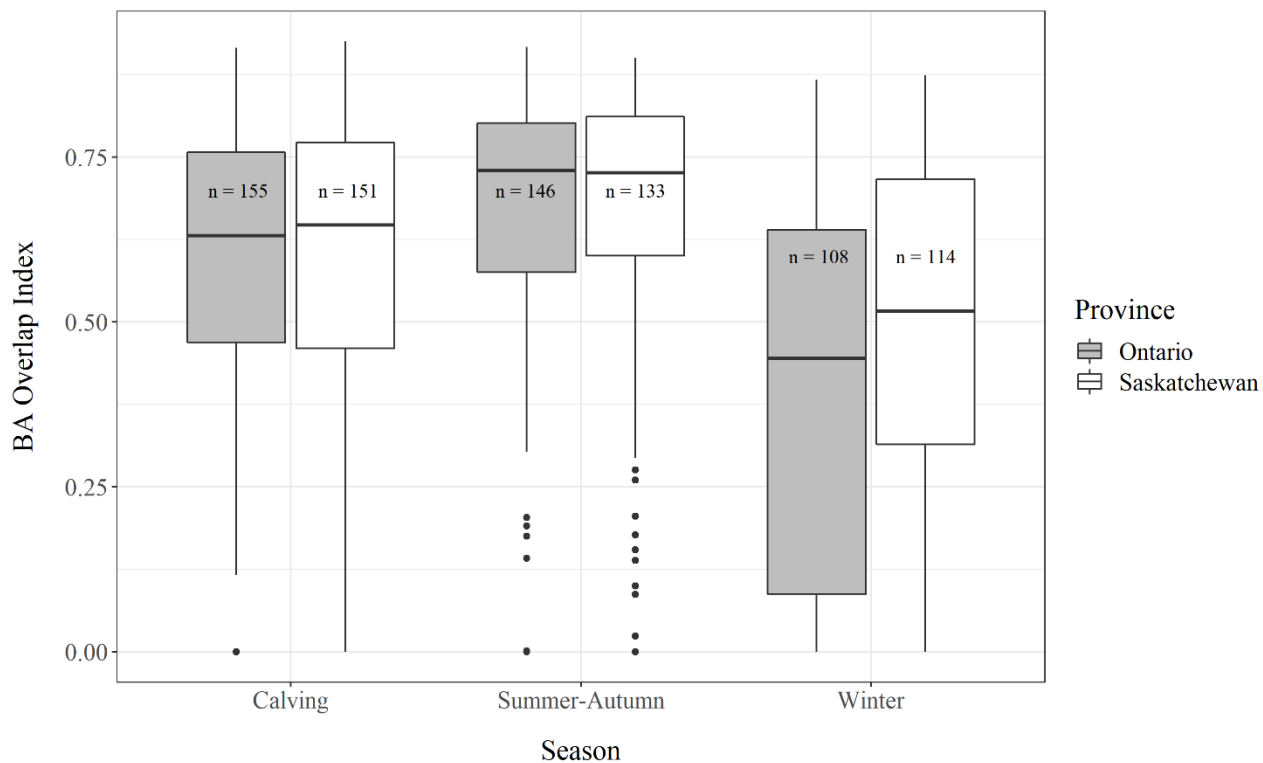


Figure D1. Interannual space use similarity for animals that did not interact with recent burns in the Boreal Shield of Ontario and Saskatchewan by season. BA overlap (0–1) describes the overall similarity in space use based on the pair of seasonal home ranges. “n” = number of seasonal home range dyads.

Appendix E

Table E1. Variance and standard deviation (*sd*) of random effects for statistical models used to assess the effects of recent burns on space use by woodland caribou in the Boreal Shield of Ontario and Saskatchewan. BA overlap (0–1) describes the overall similarity in space use based on the pair of seasonal home ranges. “Home range comparison” is a binary variable denoting year to year (0) or pre-fire, post-fire (1) seasonal home ranges. “Pre-fire prop. use of burn” is the proportion of GPS locations within the burn pre-fire. “ Δ Prop. use of burn” is the proportion of GPS locations within the burn post-fire minus pre-fire (absolute value). Increase is a binary variable for the change in use of the burn from pre-fire to post-fire (0 = constant/decrease, 1 = increase).

Model	Random Effect	Calving	Summer-Autumn	Winter
		Variance ($\pm sd$)	Variance ($\pm sd$)	Variance ($\pm sd$)
BA overlap ~ Home range comparison	Animal ID:	0.43 (± 0.65)	0.85 (± 0.91)	0.55 (± 0.74)
	Province			
	Province	1.82×10^{-7} ($\pm 4.26 \times 10^{-4}$)	1.32×10^{-10} ($\pm 1.15 \times 10^{-5}$)	0.04 (± 0.21)
	Year	1.98×10^{-4} (± 0.01)	0.01 (± 0.11)	0.16 (± 0.40)
BA overlap ~ Pre-fire prop. use of burn	Animal ID:	0.04 (± 0.19)	0.77 (± 0.88)	0.20 (± 0.44)
	Province			
	Province	2.32×10^{-15} ($\pm 4.82 \times 10^{-8}$)	0.29 (± 0.54)	7.94×10^{-11} ($\pm 8.91 \times 10^{-6}$)
	Year	2.62×10^{-10} ($\pm 1.62 \times 10^{-5}$)	0.13 (± 0.36)	0.09 (± 0.30)
Δ Prop. use of burn ~ Pre-fire prop. use of burn	Animal ID:	0.03 (± 0.18)	0.24 (± 0.49)	6.77×10^{-11} ($\pm 8.23 \times 10^{-6}$)
	Province			
	Province	2.28×10^{-12} ($\pm 1.51 \times 10^{-6}$)	4.12×10^{-10} ($\pm 2.03 \times 10^{-5}$)	4.25×10^{-15} ($\pm 6.52 \times 10^{-8}$)
	Year	2.84×10^{-10} ($\pm 1.68 \times 10^{-5}$)	0.03 (± 0.16)	1.62×10^{-10} ($\pm 1.27 \times 10^{-5}$)
Increase ~ Pre-fire prop. use of burn	Animal ID:	0.30 (± 0.55)	2.05×10^{-12} ($\pm 1.43 \times 10^{-6}$)	1.94×10^{-11} ($\pm 4.40 \times 10^{-6}$)
	Province			
	Province	1.29×10^{-12} ($\pm 1.14 \times 10^{-6}$)	1.07×10^{-11} ($\pm 3.27 \times 10^{-6}$)	2.56×10^{-15} ($\pm 5.06 \times 10^{-8}$)
	Year	5.51×10^{-10} ($\pm 2.35 \times 10^{-5}$)	7.28×10^{-10} ($\pm 2.70 \times 10^{-5}$)	2.87×10^{-9} ($\pm 5.36 \times 10^{-5}$)