Effect of Forest Understorey Stand Density on Woodland Caribou Habitat Use

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Abstract

Woodland caribou (*Rangifer tarandus caribou*) are considered to preferentially use older forests that provide abundant terrestrial lichen forage and refuge from predators. However, structural characteristics vary widely, differing in terms of forage availability but also, perhaps, in the ability of caribou to move freely through forests to access the available forage or to escape predation. We examined the effect of forest understorey stand density, defined as standing and downed biomass, on caribou habitat selection. Because this density is correlated with other features that could also drive habitat selection, we conducted a multivariate analysis of stand conditions in two geographically and biophysically distinct regions to identify the independent effects of various habitat drivers.

We fitted a sample of telemetry locations collected from GPS-collared caribou, along with an equal number of random locations, to Bayesian network models to predict the probability of habitat use (i.e., selection if >50%) based on a set of remotely sensed habitat inputs. Caribou in the Bistcho range (northwestern Alberta) selected non-forest/sparsely forested areas while caribou in the Trout Lake region (northwestern Ontario) used primarily forested habitats. Despite these differences, caribou appeared to pursue the same functional strategies with respect to understorey stand density in both regions, preferring forest stands that allowed greater ease of movement. We suggest that, rather than responding to coarse-scale policy interventions based simply on stand age or stand type, habitat management may require different treatments in different parts of the species' range to address what are nevertheless common pathways to decline.

Keywords**:** woodland caribou, boreal forest, Canada, Bayesian networks

Introduction

Current policy and management for the boreal population of woodland caribou (*Rangifer tarandus caribou*) in Canada is informed by the species' use of largely undisturbed, old stands of conifer forest (Environment and Climate Change Canada, 2020). Specifically, black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), and tamarack (*Larix laricina*)-leading forests and adjacent treed peatlands, muskegs, and bogs are cited as important habitats to restore and maintain to ensure the species' recovery. These forests are associated with abundant terrestrial lichens, on which caribou largely subsist during winter (Webber et al., 2022). Diets are broader in the snow-free season and forage quality is better in more productive forests (Denryter et al., 2022). These are areas where wolves (*Canis lupus*) and their primary prey (e.g., moose [*Alces alces*] and deer [*Odocoileus spp*.]) are more abundant (DeMars and Boutin, 2018; Latham et al., 2011; Serrouya et al., 2021). Caribou generally avoid more productive areas to avoid the elevated risk of predation (Thompson et al., 2015).

Ecological characteristics of boreal forests vary widely (Pojar, 1996) but forest conditions considered in studies of caribou habitat selection generally include only stand age and/or stand type, often because these are the only consistent data layers available at spatial scales typical of such studies. Other, more finely resolved forest characteristics, however, may play functional roles in the behavioural decisions that shape the habitat selection characteristics of caribou.

Here, we characterize the landscapes used by caribou in two, geographically and biophysically distinct regions in central and western Canada, using several remotely sensed structural variables. We include for the first time a measure of understorey forest stand conditions that is assumed to affect the mobility of caribou and therefore influence energetic trade-offs in the context of predation risk (Fryxell et al., 2020; Keim et al., 2021).

Methods

Study Areas

Our study was conducted in the Bistcho boreal caribou range of northwestern Alberta (Environment and Climate Change Canada, 2020) and in the Trout Lake region of northwestern Ontario, Canada. The Bistcho range covers 14,366 km^2 and is contiguous with the Yates range to the east, the Calendar range in northeastern British Columbia and the Cameron Hills region of southern Northwest Territories. Caribou move extensively among these ranges (Wilson et al., 2020). The range is located within the Northern Alberta Uplands and Hay River Plain ecoregions (Strong and Leggat, 1992) and is comprised primarily of lowland black spruce bogs and fens, as well as upland conifer, trembling aspen (*Populus tremuloides*) and mixedwood forests. Elevations varied between approximately 350 and 735 m above sea level.

Figure 1. Bistcho woodland caribou range (Alberta) and Trout Lake study area (Ontario).

The Trout Lake region covered 16,476 km^2 and overlaps the Berens, Churchill, Kinloch, and Sydney caribou ranges, which comprise a generally continuous distribution of caribou in northwestern Ontario (Ministry of Natural Resources and Forestry, 2014). The region is located within the Lake St. Joseph and Lake Nipigon ecoregions (Crins et al., 2009) on the Canadian Shield, which is characterized by exposed bedrock with shallow and coarse soils in the uplands, and a high density of small-medium sized lakes and wetland complexes in lowland areas. Black spruce and jack pine are the leading forest species. Elevations in the Trout Lake region varied between approximately 350 and 450 m.

Forest fires are a source of frequent natural disturbances in both regions and climates are similarly continental, with cold and relatively dry winters and short, warm summers. Mean winter and summer temperatures are similar in both regions but Bistcho receives about half the annual precipitation of Trout Lake (Environment Canada climate normals 1981-2010[1] High Level, AB versus Red Lake, ON).

Habitat Variables

We used SkyForest™ mapping products (First Resource Management Group Inc., North Bay, ON, Canada) to provide consistent, seamless, and detailed habitat mapping of forest stand conditions throughout both the Bistcho range and Trout Lake region. SkyForest™ uses open source and commercial satellite data, including optical data and synthetic aperture radar (SAR) data to produce raster products at 5-20 m resolutions.

Understorey stand density was defined as standing and downed biomass that could impede the movement of animals. This was estimated in the field via standardized “steps” within field plots (see Supplementary Information) and then modelled from backscatter data from synthetic aperture radar satellites at different bandwidths.

Canopy height was estimated by the difference in elevation between a digital surface model derived from Tandem-X Interferometric Synthetic Aperture Radar (InSAR) data and the elevations from FRMG’s patented Digital Terrain Model (DTM; US patent 10,095,995 B2. Canadian patent 2,930,989 and patent pending). The DTM was derived from a data fusion of multiple SAR, optical and lidar satellites.

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[1] https://climat.meteo.gc.ca/climate_normals/index_e.html

Conifer basal area is the percentage of total basal area of each 10-m grid cell that is composed of conifer species. It was generated from a proprietary processing of Sentinel-2 optical satellite data and calibrated with field plots (see Supplementary Information).

Crown coverage is the percentage of the ground covered by a vertical projection of the forest canopy. It was generated from a proprietary processing of Sentinel-2 optical satellite data and calibrated with field plots (see Supplementary Information).

Terrain elevation was estimated from the FRMG DTM as described above.

Habitat Disturbance

We used habitat disturbance data developed for the federal recovery strategy for the boreal population of woodland caribou in Canada (Environment and Climate Change Canada, 2020). Habitat disturbances were defined as anthropogenic features visible on 30-m Landsat imagery buffered by 500 m, as well as areas burned by wildfire within the past 40 years, current to 2015.[2] This corresponded to the general vintage of the telemetry data but there were probably some points in areas classified as disturbed that weren't disturbed when the caribou were there.

From this disturbance mapping, sources were stratified into: linear features (e.g., roads, seismic lines; all buffered by 500 m), polygonal anthropogenic features (e.g., recent forest cutblocks, wellpads; all buffered by 500 m), and recent fires (unbuffered). Because these disturbances often overlapped, they were assigned according to the following priority: linear features, otherwise polygonal anthropogenic features, otherwise recent fires.

The two study areas differed significantly in their habitat disturbance profiles. Buffered linear features covered 57% of the Bistcho range but only 5% of the Trout Lake region, while 12% of the Trout Lake region was covered by buffered polygonal disturbance but only 1% of Bistcho. Recent fires covered 17% of Bistcho and 9% of the Trout Lake region.

Ground Calibration of Landscape Variables

Remotely sensed understorey stand density, crown coverage, and conifer basal area coverages were calibrated using field data collected at 107 plots in the Bistcho range and 109 plots in the

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[2] https://open.canada.ca/data/dataset/a71ab99c-6756-4e56-9d2e-2a63246a5e94

Trout Lake region. Methods used to determine sample plot locations and details of the data collected are presented in the Supplementary Information.

Calibration involved regressing various transformations of the remote-sensed spectral bands (single images or multi-temporal images) or of SAR polarizations (or of both) against field data and predicting attributes from the regression function.

Caribou Habitat Use

Caribou telemetry data were accessed from Province of Alberta and Province of Ontario government databases for the most recent, approximately 5-year periods available. All were GPS locations collected on adult female caribou collared by net-gunning individuals from helicopters in late winter. Seasons were assigned to each location based on the following: snow-free: 15 April-14 November and winter: 15 November-14 April.

There were 90,540 telemetry locations available for the analysis that fell within the bounds of the Bistcho range, collected on 31 collared caribou between 1 January 2015 and 5 November 2019. Within the Trout Lake region, there were 102,667 locations collected from 60 caribou between 22 February 2010 and 8 July 2015.

Analysis and Modelling

Telemetry points were overlaid on each landscape habitat variable to assemble the dataset for the analysis. Random locations were generated to represent habitats “available” to caribou. A number of random points equal to the number of observations was used to prevent overfitting to an oversampled class. Telemetry and random points that were located within mapped lakes and double-lined rivers were removed.

Using the binary target variable *Location*, consisting of both random and telemetry points, a Bayesian Network model was fit to the data to predict the probability that a location was either a telemetry point or a random point, based on the evidence provided by the predictors.

Model structures were fit using Sons and Spouses structural learning and feature selection (Costello et al., 2020), and parameters were then fit using expectation maximization (Bilmes, 1998). The resulting networks predicted the probability of a location being a telemetry or random point, based on evidence provided by the values of habitat predictors at the location. We interpreted a probability of >50% of being classified as a telemetry point to be evidence of selection by caribou and <50% as evidence of avoidance (Wilson and Demars, 2015). While states were discretized, “virtual evidence” (Bilmes, 2004; Mrad et al., 2015) was interpolated to generate continuous response curves for predictor variables.

We assessed the fit of the final models using k-fold ($k = 10$) cross-validation (Fielding and Bell, 1997), resulting confusion matrices, and by receiver-operator characteristics (Metz, 1978). BayesiaLab 10.2 (Bayesia SAS, Laval, France) was used for all analyses.

Results

Models for both Bistcho and Trout Lake excluded season as a predictor, and it was not considered further in analyses. For Bistcho, edges were included in the final model among all the other predictors and the target variable (Figure 2). There were strongly positive associations among several predictors; notably, understorey stand density, conifer basal area, crown coverage, and canopy height. Model structure was similar for Trout Lake, with similarly strong correlations among the same predictors but weaker relationships with the target variable (Figure 3).

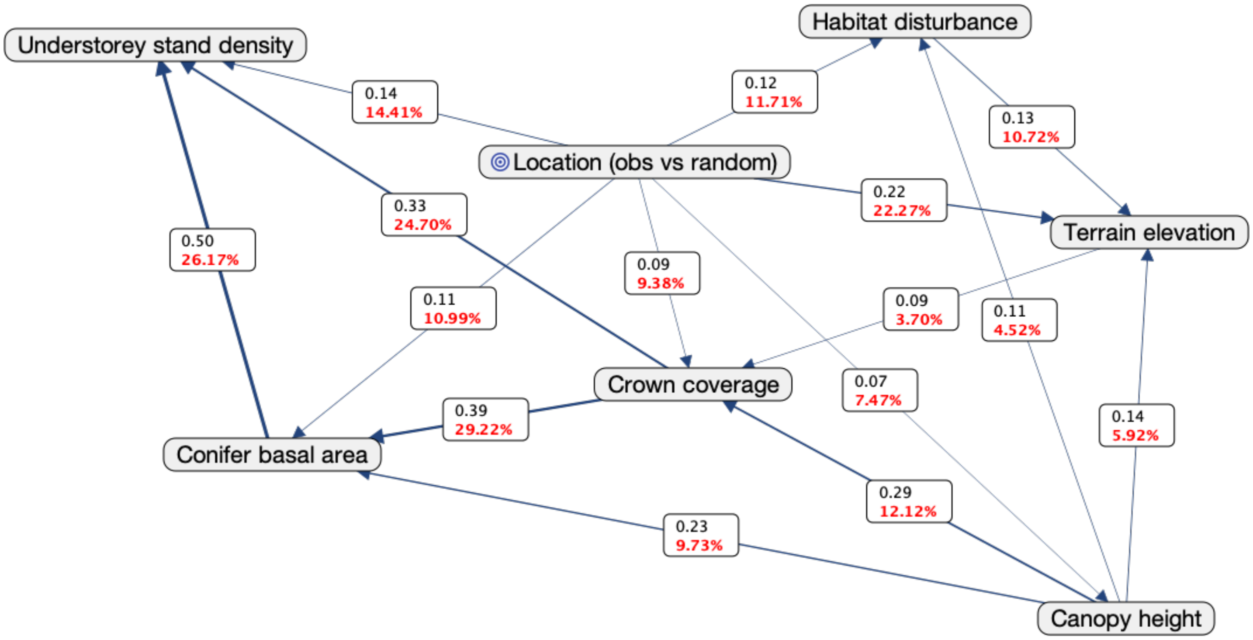

Figure 2. Bayesian network illustrating the relationship between the target variable *Locations,* representing the set of caribou telemetry locations (obs) and random locations, and the habitat predictor variables for the Bistcho caribou range. By convention, arcs are directed from the target variable to predictors and direction is arbitrary among predictors. Labels on arcs are mutual information and relative mutual information (%) from child to parent nodes.

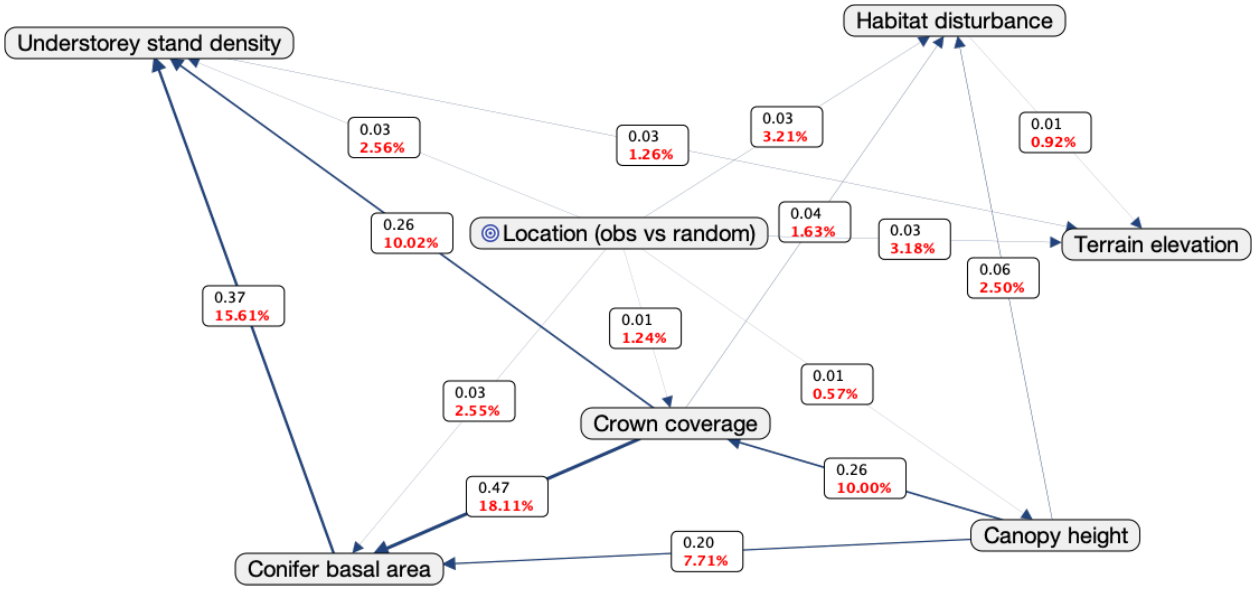

Figure 3. Bayesian network illustrating the relationship between the target variable *Locations,* representing the set of caribou telemetry locations (obs) and random locations, and the predictor variables for the Trout Lake study area. By convention, arcs are directed from the target variable to predictors and direction is arbitrary among predictors. Labels on arcs are mutual information and relative mutual information (%) from child to parent nodes.

K-folds cross-validation indicated a good fit of the final Bistcho model with an ROC index of 88.2% (Figure 4) and a mean precision (percentage of points correctly classified by the model) of 83.5% for telemetry points and 76.6% for random points. The mean reliability (percentage of modelled points correctly classified) was 78.1% for telemetry points and 82.3% for random points. Fit of the Trout Lake model poorer than that for the Bistcho, with an ROC index of 73.0% (Figure 4) and a mean precision (percentage of points correctly classified by the model) of 75.0% for telemetry points and 58.5% for random points. The mean reliability (percentage of modelled points correctly classified) was 64.4% for telemetry points and 70.0% for random points.

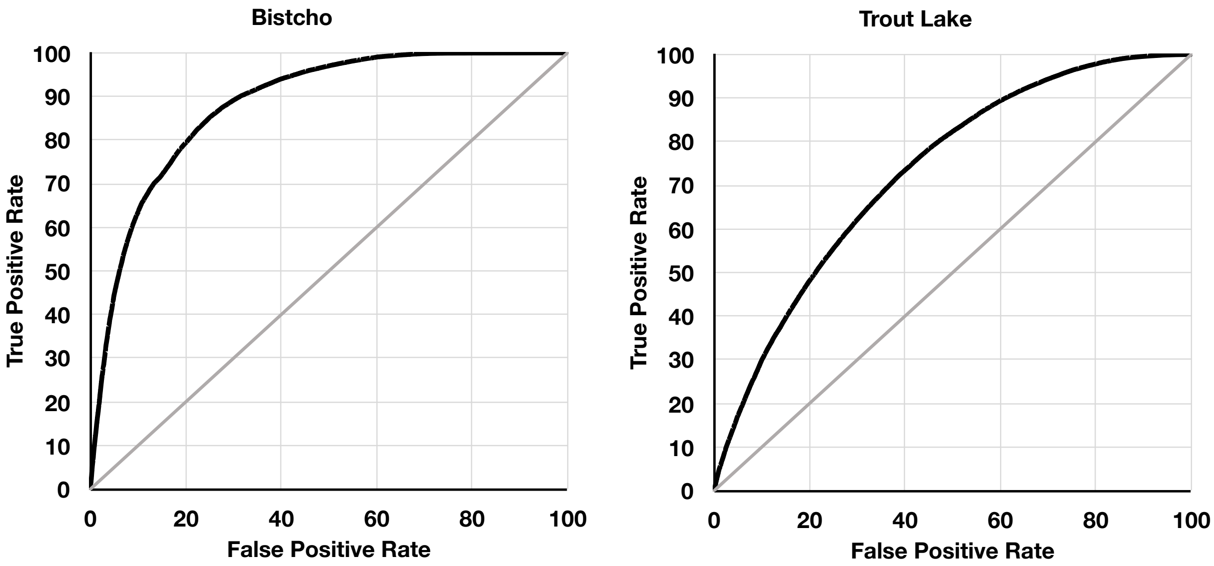

Figure 4. Receiver Operator Characteristic (ROC) curves for Bistcho and Trout Lake models.

Caribou responded similarly to understorey stand density in both study areas, selecting lower densities, adjusting for all other predictors (Figure 5). However, caribou in the different regions responded differently to the other modelled predictors. Specifically, Bistcho caribou preferred non-forested or sparsely forested areas with low crown coverage and moderate stand canopy heights, while Trout Lake caribou selected forested stands with moderate crown coverages and taller canopies. Both Bistcho and Trout Lake caribou favoured purer conifer stands over mixedwood forests.

Caribou in the Trout Lake region selected upland areas while in the Bistcho they selected lowland areas. In both study areas, caribou selected undisturbed habitat and avoided buffered linear and polygonal disturbances. Trout Lake caribou avoided fire but caribou in the Bistcho did not.

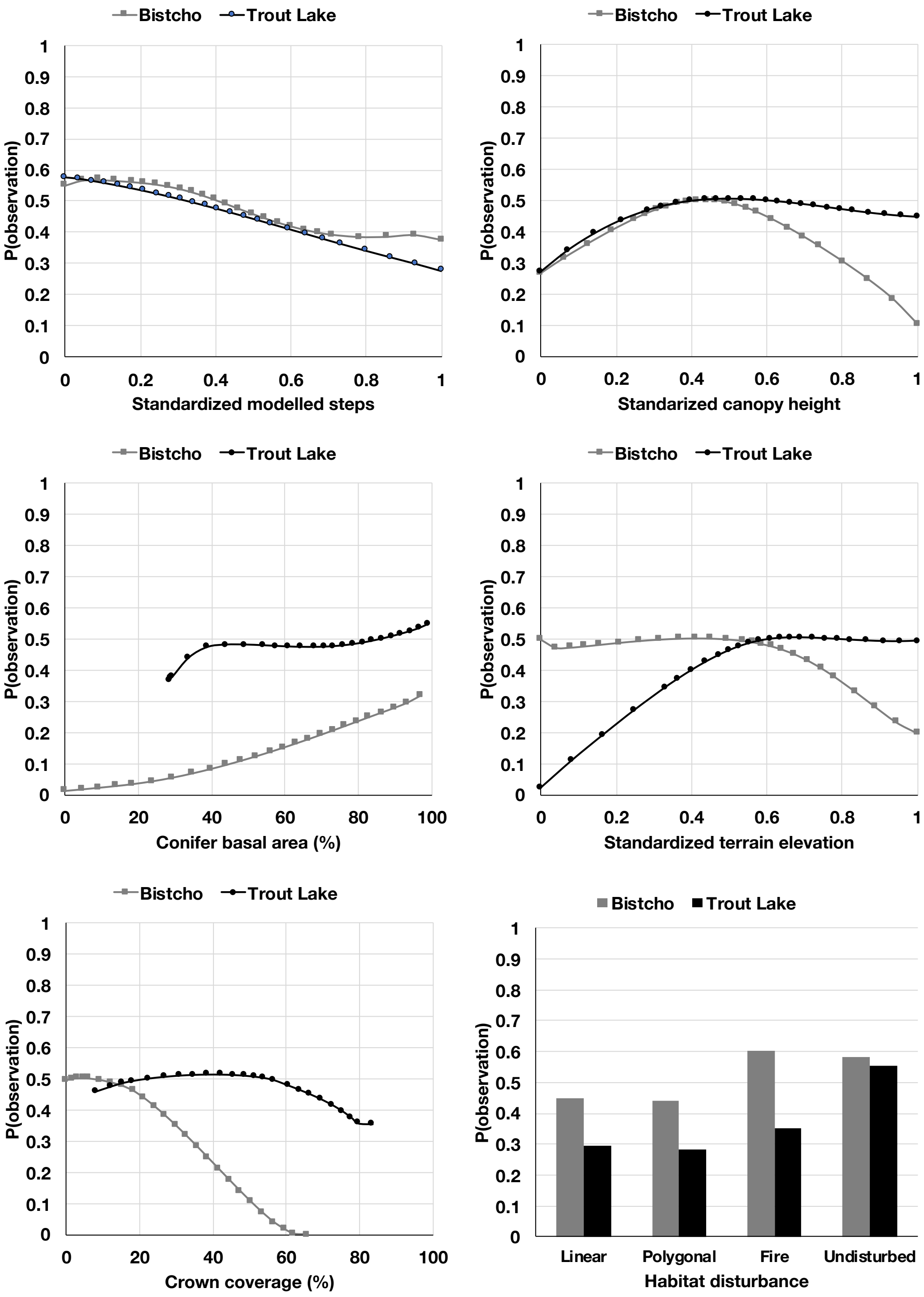

Figure 5. Direct effects of predictor habitat variables on the probability of a location being an observation. Y-axis values >0.5 represent habitat selection for a predictor, adjusting for all other predictors. The conifer basal area relationship was restricted to forested stands.

Discussion

This is the first study to measure understorey stand density based on remotely sensed data and to estimate its effect on habitat selection by caribou. We demonstrate the consistent effect of understorey stand density in two regions otherwise differing significantly in the way caribou responded to other biophysical characteristics of the forests. Research has linked small-scale, cognitive foraging behaviour by caribou faced with predation risk (Avgar et al., 2015, 2013) to the viability of entire caribou populations (Fryxell et al., 2020) under large-scale habitat change (Mallon et al., 2016; McGreer et al., 2015). These studies suggest that habitat suitable for caribou depends not only on the type and quality of available food, but also on the energy costs of movement to obtain that food and to avoid predators. That caribou in both of our study areas selected areas of lower understorey stand density supports this.

Some ground lichens on which caribou depend thrive under semi-open forest canopies (Brodo et al., 2001; Lesmerises et al., 2011; Silva et al., 2019), perhaps coincident with lower understorey stand densities. We were not able to link a commensurate estimate of lichen abundance to our remotely sensed estimate of understorey stand density that would enable an adjustment for a potential forage effect. As a result, we cannot infer that caribou selected stands solely because of lower understorey stand density, potentially greater lichen abundance, or both. To infer a sole causal effect of understorey stand density based on our statistical design would be to submit to an "omitted variable bias", i.e., conclude that stand density causes the observed habitat selection only because that was the variable for which data could be included in the model while lichen abundance remained unobserved and excluded. To infer causation, a model must include all of the observed and unobserved common causes (Wilson et al., 2021). Regardless, management interventions that reduce understorey stand density could be neutral or positive for caribou on sites that are otherwise favourable for lichens.

The response by caribou to understorey density was remarkably similar in both study areas, given the wide variation in their response to other habitat predictors. In the Bistcho, caribou selected sparsely treed, lowland habitats over densely forested uplands while caribou in the Trout Lake region were less discriminating but made opposite selection decisions, staying predominantly in upland forests, and avoiding lowlands.

In northwestern Alberta, lowland treed bogs and fens are low productivity environments that are generally avoided by moose and their main predator, wolves (DeMars and Boutin, 2018; Latham et al., 2011; Serrouya et al., 2021). Moose in that region are more common in productive upland forests and, in particular, those with a significant deciduous component (Routh and Nielsen, 2021). That caribou are largely segregated spatially from moose via their habitat preferences is hypothesized to be key to sustaining caribou populations, due to their susceptibility to apparent competition with moose (DeCesare et al., 2009; James et al., 2004). On the other hand, in northwestern Ontario, the exposed bedrock and shallow soils of the Canadian Shield can limit the productivity of upland coniferous forests and caribou select low-volume jack pine and black spruce forests with abundant lichen and few shrubs (Antoniak and Cumming, 1998). In contrast, moose in this region use lowland aquatic areas and more productive deciduous and mixedwood forests (Street et al., 2015). Nevertheless, the result is spatial segregation between caribou and moose in a manner similar to the Bistcho (Cumming et al., 1996).

While caribou in Bistcho and Trout Lake regions pursued different tactics with respect to uplands and lowlands, and forested versus sparsely forested habitats, overall, the results suggested caribou were following a similar strategy: selection for forest stands with higher conifer components and away from areas with significant deciduous components – a known habitat feature favoured by moose. We contend that both the differences and similarities in habitat use exhibited by caribou in the two study areas were consistent with respect to seeking refuge from predators.

Habitat disturbance caused by anthropogenic activity and fire is correlated with demographic decline among woodland caribou subpopulations in Canada (Johnson et al., 2020) and recovery from disturbance is a focus of the national recovery strategy (Environment and Climate Change Canada, 2020). The disturbance profiles of the two study areas differed significantly due to differences in land use. The Bistcho range has experienced significant oil and gas exploration and development while forestry is restricted to the productive uplands of the southeastern portion of the range. As a result, the Bistcho range is associated with a high density of seismic lines, pipeline corridors, and associated industrial roads. Well pads are common but relatively small clearings (<2 ha), and the limited spatial extent of forestry means that there is little anthropogenic polygonal disturbance. In contrast, forestry is the main industrial driver of anthropogenic activity in the Trout Lake region, which has resulted in less linear development, but a higher proportion of recent forestry cutblocks than in the Bistcho.

High densities of linear features provide efficient travel corridors for wolves (Dickie et al., 2017) and can lead to the loss of the predation refugia thought necessary to sustain caribou (DeMars and Boutin, 2018). Consistently, juvenile recruitment rates in the Bistcho range are less than half the estimates for subpopulations overlapping the Trout Lake study area (Johnson et al., 2020).

Caribou in both study areas selected undisturbed habitat, but avoidance of fire was evident only in the Trout Lake region, despite recent burns being a common characteristic of both study areas. Recent fires have occurred throughout the Bistcho, both in productive forest and in the open and sparsely treed habitats that caribou select. Caribou in Bistcho selected burned areas, but only those in open or sparsely forested areas, avoiding recently burned areas associated with previously dense forests. Caribou in Trout Lake avoided burns wherever they occurred. In contrast, both buffered linear and polygonal disturbance were avoided in both areas. This builds on recent evidence that the relationship between caribou and fire is complex (Dalerum et al., 2007; DeMars et al., 2019; Konkolics et al., 2021; Skatter et al., 2017) and our study suggests that different habitat characteristics can lead to different responses to fire.

This study underlines the importance of addressing the functional basis for caribou habitat selection behaviour when planning recovery actions. While analyses revealed both similarities (i.e., stand density, conifer basal area) and differences (i.e., upland versus lowland, open versus forested habitats) in habitat selection patterns between geographically and biophysically distinct regions, caribou appeared to be pursuing similar strategies, albeit with different tactics. Using high-resolution satellite data provided the opportunity to resolve habitat characteristics more consistently and in greater detail than previous studies and allowed us to link structural elements of the forest to the functional requirements of caribou. We conclude that applying coarse-scale policies based simply on stand age or stand type may not be appropriate in different parts of caribou range, and that prescriptions necessary to restore or sustain caribou habitat will need to be adapted to local conditions, despite caribou facing common pathways to decline.

CRediT Authorship Contribution Statement

S.F. Wilson: Conceptualization, data curation, methodology, formal analysis, writing, editing. **T.D. Nudds:** Conceptualization, methodology, writing, editing. **P. Green:** Conceptualization, data curation, methodology, writing, editing. **A. de Vries:** Funding acquisition, supervision, conceptualization, reviewing.

Declaration of Competing Interest

Phil Green is CEO of First Management Resource Group, Inc., which was contracted to produce the SkyForest™ digital mapping products for the study. The other authors declare that they have no known competing financial interests or personal relationships that influenced the work reported in this paper.

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