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Effect of forest understorey stand density on woodland caribou (*Rangifer tarandus caribou*) habitat selection

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Abstract

Woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)) use older forests that provide abundant terrestrial lichen forage and refuge from predators. However, forest structural characteristics vary widely, differing in forage availability but also, perhaps, in the ability of caribou to move freely to access forage or to escape predation. We conducted a multivariate analysis of habitat in two geographically and biophysically distinct regions to identify the independent effects of various attributes, including forest understorey stand density, defined as standing and downed biomass, on caribou habitat selection. We developed Bayesian network models to predict the probability of habitat selection 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) selected primarily forested habitats, nevertheless consistent with selection for reduced predation risk in both cases. Caribou also selected forest stands with lower understorey stand density in both regions, consistent with selection for stands that would allow greater ease of movement. The high-resolution satellite data resolved habitat characteristics more consistently and in greater detail than standard forest cover datasets that are most often used for these analyses, and led us to conclude that habitat management may require different treatments in different parts of the species' range to address what are nevertheless common pathways to decline.

Key words: woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)), boreal forest, Canada, Bayesian networks, remote sensing

Introduction

Current policy and management for the boreal population of woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)) 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* (Mill.) BSP), jack pine (*Pinus banksiana* Lamb.), and tamarack (*Larix laricina* (Du Roi) K. Koch)-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) where wolves (*Canis lupus* Linnaeus, 1758) and their primary prey, primarily moose (*Alces alces* (Linnaeus, 1758)), mule deer (*Odocoileus hemionus* (Rafinesque, 1817)), and white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), are more abundant (Latham et al. 2011; DeMars and Boutin 2018; Serrouya et al. 2021). Caribou generally forego opportunities to forage in these productive forests because of the elevated risk of predation (Briand et al. 2009; 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 habitat selection by caribou.

Here, we characterize the landscapes selected 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).

Fig. 1. Bistcho woodland caribou range (Alberta) and Trout Lake study area (Ontario). Figure was created with QGIS version 3.32.1 using public domain basemap data from https://naturalearthdata.com.

Materials and 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 (Fig. 1). 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. 2022). The range is located within the Northern Alberta Uplands and Hay River Plain ecoregions (Strong and Leggat 1992) and is composed primarily of lowland black spruce bogs and fens, as well as upland conifer, trembling aspen (*Populus tremuloides* Michx.), and mixedwood forests. Elevations vary between approximately 350 and 735 m above sea level.

The Trout Lake region covers 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 vary 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 January and July temperatures in the Bistcho region (−20.4 °C and 16.5 °C) are similar to those of Trout Lake (−18.3 °C and 18.1 °C), but Bistcho receives about half the mean annual precipitation of Trout Lake (372 mm versus 686 mm; Environment Canada climate normals 1981–2010, High Level, AB versus Red Lake, ON; https://climat.meteo.gc.ca/climate_normals/index_e.html).

Habitat variables

We used SkyForest™ mapping products (First Resource Management Group Inc. (FRMG), 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. FRMG has been continuously developing these products since 2013, iteratively testing and applying proprietary indices of earth observation data against field data.

We defined *understorey stand density* as standing and downed biomass that could impede the movement of animals. We modelled this from backscatter data from SAR satellites at different bandwidths and reported for each pixel the number of modelled steps required for a field crew member to traverse plot transects (Figs. S1, S2, S3, and S4, Tables S1 and S2).

We estimated *canopy height* by the difference in elevation between a digital surface model derived from WorldDEM™ elevation data (Airbus Defence and Space SAS, Ottobrunn, Germany) 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). We derived the DTM from a data fusion of multiple SAR, optical, and lidar satellites.

Conifer basal area is the percentage of total basal area of each 10 m grid cell that is composed of conifer species. This definition differs from the standard measure of basal area, which is a volumetric measure (m^2) and does not indicate the relative composition of conifers versus hardwoods. *Crown coverage* is the percentage of the ground covered by a vertical projection of the forest canopy (Fig. S5). We generated these both from a proprietary processing of Sentinel-2 optical satellite data and calibrated them using data collected at field plots.

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

Habitat disturbance

We defined habitat disturbances 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 (https://open.canada.ca/data/dataset/a71ab99c-6756-4e56-9d2e-2a63246a5e94). This is the same definition developed for the federal recovery strategy for the boreal population of woodland caribou in Canada (Pasher et al. 2013; Environment and Climate Change Canada 2020). This corresponded to the general vintage of the telemetry data but there were probably some points in areas classified as disturbed that were not disturbed when the caribou were there.

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

The two study areas differed in their habitat disturbance profiles (ignoring overlapping disturbance features). Buffered linear features covered 57% of the Bistcho range but only 6% of the Trout Lake region, while 15% of the Trout Lake region was covered by buffered polygonal disturbance and 13% of Bistcho. Recent fires covered 44% of Bistcho and 17% of the Trout Lake region.

We also included time since disturbance as a predictor, based on Landsat data from 1985 to 2018 and from provincial fire databases for older disturbances. We stratified fire disturbance in the analysis into the following states: $\leq$40 years, 40–80 years, and $>$80 years.

Ground calibration of landscape variables

We calibrated remotely sensed estimates of understorey stand density, crown coverage, and conifer basal area coverages using field data collected at 107 plots in the Bistcho range and 109 plots in the Trout Lake region. We present methods to determine sample plot locations and details of the data collected and calibration in the Supplementary Material.

Caribou habitat use

We acquired caribou telemetry data from Alberta and 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. We assigned seasons to each location based on the following: snow-free: May–October and snow-covered: November–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

We overlaid telemetry points on each landscape habitat variable to assemble the dataset for the analysis. We then generated random points from within 100% minimum convex polygons of the telemetry points to represent habitats "available" to individual caribou. We used a number of random points equal to the number of observations to prevent overfitting to an oversampled class. We removed telemetry and random points that were located within mapped lakes and double-lined rivers, along with any caribou with <200 telemetry points. The resulting dataset for Bistcho was 57 076 telemetry points collected from 20 caribou and for Trout Lake was 98 590 telemetry points collected from 50 caribou.

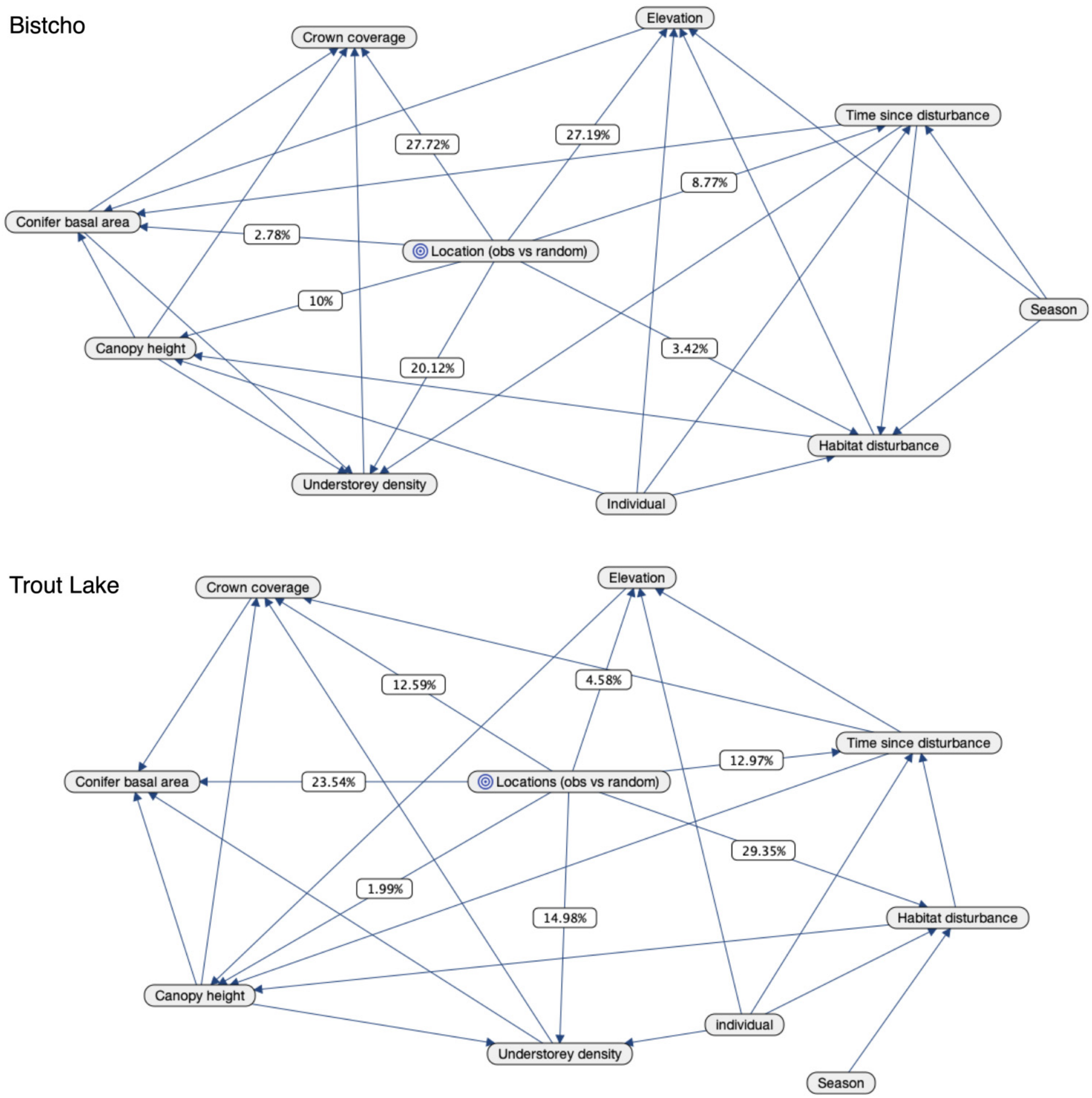
Using the binary target variable *Location*, consisting of both random and telemetry points, we fit a Bayesian network model to the data. A Bayesian network is a directed acyclic graph consisting of nodes (random variables) and edges (arrows between nodes) that represent probabilistic relationships among variables, in this case various landscape predictors and the target node, *Location*. Each variable is assigned two or more "states" that represent the range of values that the variable can take. States can be categorical or ordinal, with continuous values stratified or "discretized" into ordinal bins. The probabilistic relationships are encoded in either marginal (for nodes with no incoming edges) or joint (for nodes with one or more incoming edges) probability tables associated with each node in the graph.

We generated model structures using the Sons and Spouses structural learning algorithm (Costello et al. 2020) and fit parameters by 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 the habitat predictors at the location. For example, in the case of a habitat vector (i.e., a set of habitat predictors and their values) within which an equal number of observations and random points are located, the probability of a location being classified as an observation would be 50%, indicating no selection by caribou. Therefore, 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). Note that this differs from the definition of selection typically applied in resource selection functions (Lele et al. 2013) and that the reported inferences are exact probabilities and have no confidence intervals.

While states were discretized, we used "virtual evidence" (Bilmes 2004; Mrad et al. 2015) to interpolate continuous response curves for predictor variables. We generated response curves for each predictor in turn, holding all other predictors constant, by employing Jouffe's likelihood matching (Conrady and Jouffe 2015). Matching ensures that the multivariate distributions of the subsamples being compared are as similar as possible, except for the predictor of interest, to isolate its independent effect. Matching is a common statistical technique that usually relies on subsetting samples to achieve similar distributions; however, likelihood matching achieves the same effect on the basis of the joint probability distribution represented by the Bayesian network.

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 characteristic (ROC) curves (Metz 1978). We measured the relative contribution of each predictor to the target node by the mutual information shared by the predictor and target (Scutari and Denis 2021). We used BayesiaLab 10.2 (Bayesia SAS, Laval, France) for all analyses.

Fig. 2. Bayesian networks 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 and Trout Lake study area. By convention, arcs are directed from the target variable to predictors and direction is arbitrary among predictors. Labels on arcs indicate the relative mutual information shared between each predictor and the target node, expressed as a percentage of the total mutual information shared between all of the predictors and the target.



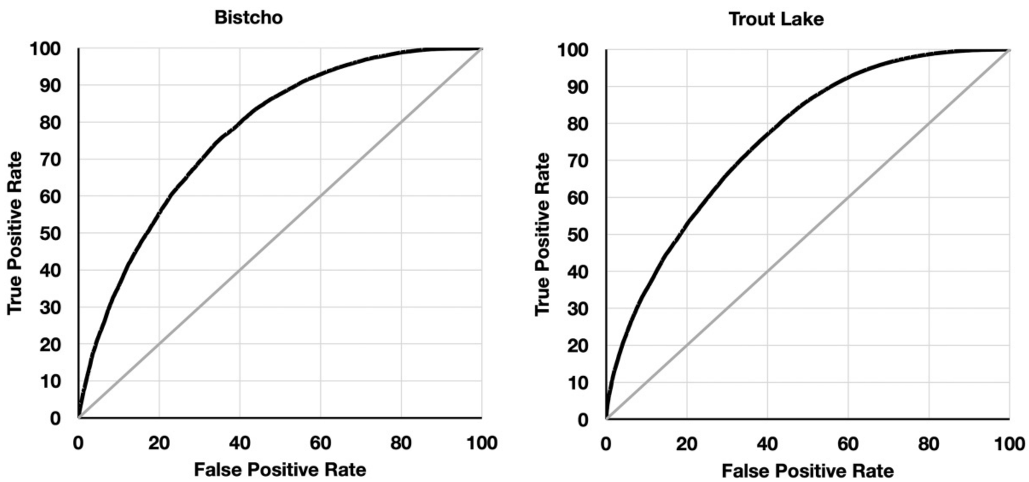
Results

For the Bistcho range, model edges linked all but the individual and season predictors to the target variable (Fig. 2). There were also strong associations among several predictors, notably, understorey stand density, conifer basal area, crown coverage, and canopy height (Table S3). The predictors with the strongest relative associations with the target node were crown coverage, followed by elevation and understorey stand density. Collectively, these three factors explained >75% of the mutual information with the target node described by all of the predictors.

Model structure was similar for Trout Lake, with the learned model structure excluding links between individual and season with the target node, and similar correlations among the predictors (Fig. 2, Table S4). The predictors with the strongest relative associations with the target node were habitat disturbance, conifer basal area, and understory stand density (explaining >67% of the total mutual information).

K-fold cross-validation indicated a reasonable fit of the final Bistcho model with an ROC index of 77.1% (Fig. 3) and a mean precision (percentage of *actual* telemetry or random points *predicted* by the model to be telemetry or random

Fig. 3. Receiver–operator characteristic curves for the Bayesian network habitat selection models for the Bistcho and Trout Lake study areas. The true positive rate in this study was the proportion of telemetry points predicted by the model to be telemetry points out of all of the points (telemetry and random) predicted to be telemetry points. The false positive rate was the proportion of random locations predicted by the model to be telemetry points out of all of the points predicted to be random points.



points, respectively) of 76.7% for telemetry points and 63.5% for random points. The mean reliability (percentage of *predicted* telemetry or random points that were *actual* telemetry or random points, respectively) was 67.7% for telemetry points and 73.1% for random points. Fit of the Trout Lake model was similar to that for the Bistcho, with an ROC index of 76.0% (Fig. 4) and a mean precision of 75.6% for telemetry points and 61.5% for random points. The mean reliability was 66.3% for telemetry points and 71.6% for random points.

At the home range scale modelled in this study, caribou responded similarly to understorey stand density in both study areas by selecting lower densities (Fig. 4). However, caribou in the different regions responded differently to the other modelled predictors. Specifically, Bistcho caribou preferred nonforested or sparsely forested areas as indicated by low crown coverage and moderate stand canopy heights, while Trout Lake caribou selected moderate crown coverages and taller canopies, indicating selection for denser forests than caribou in the Bistcho range. Both Bistcho and Trout Lake caribou favoured purer conifer stands over mixedwood forests, with Bistcho caribou avoiding forested stands altogether (i.e., selection consistently <0.5), but avoiding conifer stands less than mixedwood (i.e., still a positive slope with increasing conifer basal area).

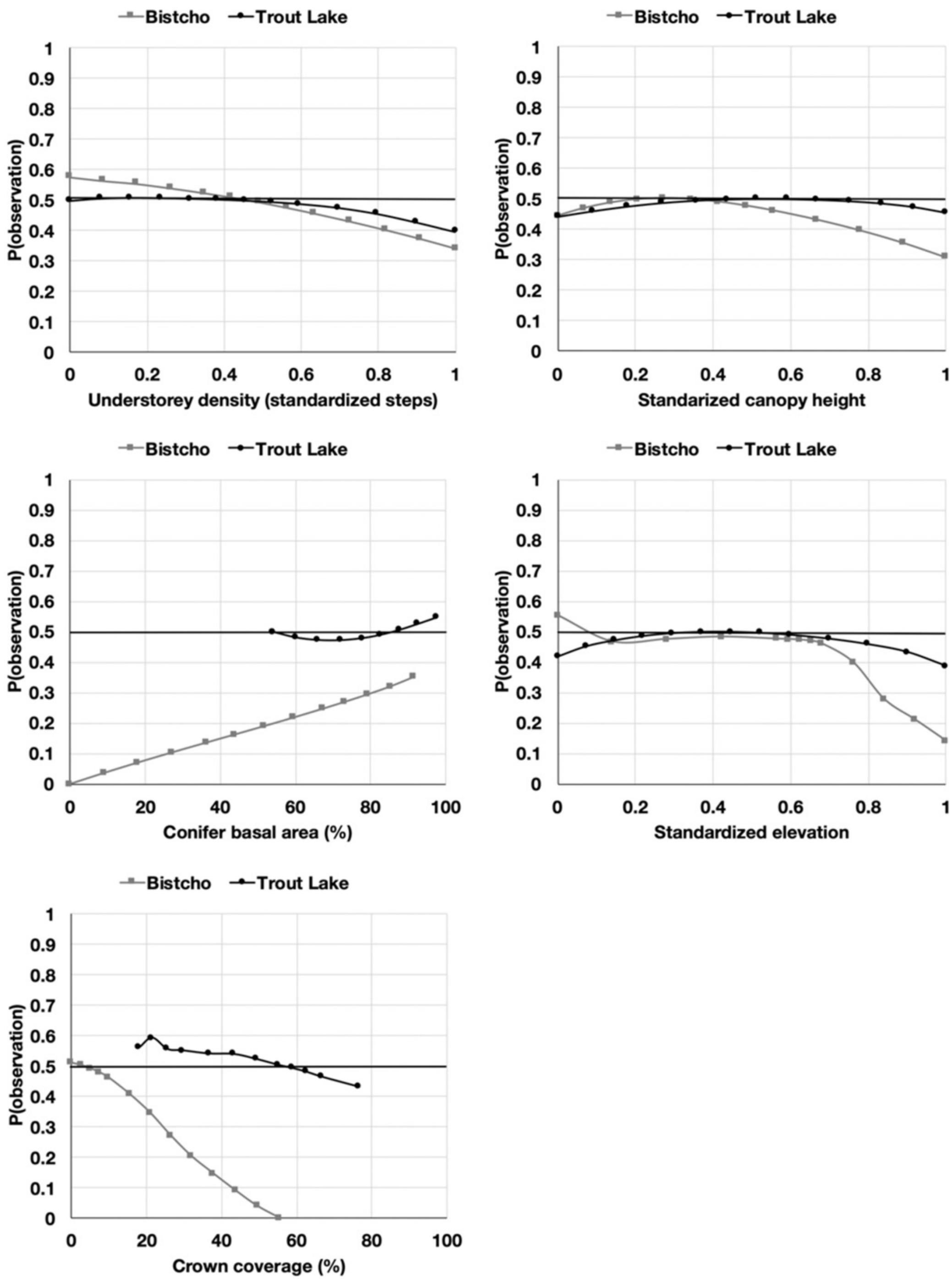
Caribou in the Trout Lake region selected moderate elevations, while in the Bistcho they avoided uplands. In both study areas, caribou selected undisturbed habitat and avoided buffered linear and polygonal disturbances (Fig. 5). Trout Lake caribou avoided recently burned areas within their home ranges but caribou in the Bistcho did not.

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 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. 2013, 2015) to the viability of entire caribou populations (Fryxell et al. 2020) under large-scale habitat change (McGreer et al. 2015; Mallon et al. 2016). 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 is consistent with this.

Some ground lichens on which caribou depend thrive on low productivity sites that are often associated with open forest canopies (Brodo et al. 2001; Lesmerises et al. 2011; Silva et al. 2019; Hämäläinen et al. 2020), 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. However, we were able to adjust for crown coverage and found that caribou still selected stands with lower understorey stand density. This provided some confidence that our results were not confounded by the unobserved abundance of ground lichens, but the addition of reliable lichen mapping might improve model performance. Regardless, management interventions that reduce understorey stand density could be neutral or positive for caribou on sites that are otherwise favourable for lichens, if such treatments were sufficient to improve caribou energy balance. Lamont et al. (2019) recommended removing standing dead and downed trees in stands killed by mountain pine beetle (*Dendoctronus ponderosae* (Hopkins, 1902)) to reduced locomotion costs of elk (*Cervus canadensis* (Erxleben,

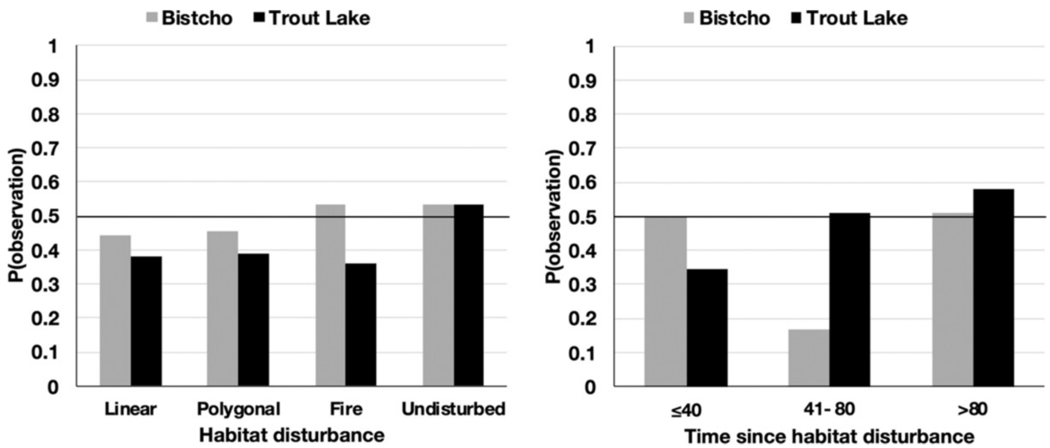
Fig. 4. Direct effects of predictor habitat variables on the probability of a location being an observation. *Y*-axis values >0.5 (above the horizontal line) represent habitat selection for a predictor, adjusting for all other predictors by likelihood matching. The conifer basal area relationship was restricted to forested stands only to omit stands with no basal area. Understorey density is estimated by the number of steps required to traverse study plots. Understorey density, elevation, and canopy height were standardized to allow for relative comparisons between study areas. See Fig. 2 for the relative strengths of these variables in contributing to the habitat selection behaviour of caribou in the two study areas.



1777)), after observing that elk avoided beetle-killed areas. Nobert et al. (2020) suggested that mountain caribou populations might benefit from similar treatments where infestations affected pine–lichen winter ranges but cautioned that wolves might also benefit from such clearing.

The risk of confounding by the abundance of forest shrubs is more difficult to estimate. Open forest canopies can promote shrub growth on productive sites (e.g., Paulson et al. 2021), and caribou have broad diets during the snow-free season (Denryter et al. 2017); however, we found little evidence

Fig. 5. Selection by caribou of habitats with different disturbance causes and times since habitat disturbance. Values >0.5 (above the horizontal line) represent habitat selection for the class.



of seasonal variation in habitat selection by caribou on either study area.

Understorey density might reduce the travel speed of caribou. Dickie et al. (2022) found that caribou movements on seismic lines slowed when lines were subject to various restoration treatments intended to impede the movements of wolves, including the roll-back of coarse woody debris and the felling of trees. There was no indication from our analysis that caribou travelling more slowly through denser understorey was sufficient to bias our estimates of selection in favour of these habitats.

The response by caribou to understorey density was remarkably similar in both study areas, given the wider variation in their response to other habitat predictors. In the Bistcho, caribou avoided forested uplands, while caribou in the Trout Lake region were less discriminating, generally selecting forests at moderate elevations with moderate crown coverages.

In northwestern Alberta, lowland treed bogs and fens are low productivity environments that are generally avoided by moose and their main predator, wolves (Latham et al. 2011; DeMars and Boutin 2018; 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 (James et al. 2004; DeCesare et al. 2009). 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 (Cumming et al. 1996) in a manner similar to the Bistcho.

While caribou in Bistcho and Trout Lake regions pursued different tactics with respect to uplands and lowlands, and forested versus open habitats, overall, the results suggested that 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 selection 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 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 industrial roads. Well pads are common but are 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 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. In contrast, both buffered linear and polygonal disturbances were avoided in both areas. This builds on recent evidence that the relationship between caribou and fire is complex (Dalerum et al. 2007; Skatter et al. 2017; DeMars et al. 2019; Konkolics et al. 2021) and our study suggests that different habitat characteristics may 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 pursue similar strategies (i.e., avoiding predators, selecting for ease of movement), albeit with different tactics. Using high-resolution satellite data provided the opportunity to resolve habitat characteristics more consistently, in greater detail, and over larger areas 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.

As recommended for mountain caribou (Nobert et al. 2020), forest management prescriptions to address ease of movement by caribou might be appropriate in boreal ranges. Best practices could include harvesting strategies such as thinning, log processing and brush piling at roadsides to avoid high volumes of on-site coarse woody debris, burning and light scarification for site preparation (except where lichen mats are intact), and replanting at low stocking densities. Further work is required to understand how wolf mobility may also be enhanced by these treatments and whether interventions can be designed to avoid enhancing habitat suitability for, and mobility of, primary prey and wolves.

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Data availability

Use of caribou telemetry data was governed by limited agreements with the Province of Ontario and the Province of Alberta. Mapping products were developed commercially by First Resource Management Group, Inc. but coverages for the study areas, as well as plot data and model script files, are available for download (https:doi.org/10.17605/OSF.IO/GDNC9).

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Writing – original draft: SFW, TDN, PEJG
Writing – review & editing: TDN, PEJG, AdV

Competing interests

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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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfr-2023-0105.

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