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*Research Article*

# Micro-habitat selection by boreal woodland caribou improves access to food

**Ian D. Thompson[1,2], Philip A. Wiebe[1], Arthur R. Rodgers[3], Douglas Reid[3], James A. Baker[4], Brent R. Patterson[5], Eric McNeill[6], Romain Dejeante[7] and John M. Fryxell[3,8]**

[1]Great Lakes Forestry Centre, Canadian Forest Service, Sault Ste. Marie, ON, Canada
[2]Thompson Forest Ltd., West Kelowna, BC, Canada
[3]Ontario Ministry of Natural Resources and Forestry, Centre for Northern Forest Ecosystems Research, Thunder Bay, ON, Canada
[4]Ontario Forest Research Institute, Ontario Ministry of Natural Resources and Forestry, Sault Ste. Marie, ON, Canada
[5]Ontario Ministry of Natural Resources and Forestry, Wildlife Research and Monitoring Section, Trent University, Peterborough, ON, Canada
[6]School of Environmental and Natural Resource Sciences, Fleming College, Lindsay, ON, Canada
[7]Department of Integrative Biology, University of Guelph, Guelph, ON, Canada
[8]Department of Biology, University of Victoria, Victoria, BC, Canada

**Correspondence: Ian D. Thompson (ian.thompsonforest@gmail.com)**

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Bio-logging sensors attached to radiotelemetry receivers have great potential to transform our understanding of the ecological, physiological, and energetic constraints that shape patterns of wildlife movement under field conditions. We used video camera collars to assess microhabitat selectivity by woodland caribou *Rangifer tarandus* in boreal forests of Ontario, Canada. Our study areas provided a range of fine-grain microhabitats within forest stands (>10 ha), drawn from an unlogged forest landscape and a partially commercially-logged landscape. We classified ground-truthed samples within each stand into their sub-stand vegetation types at a scale of <10 m radius. We used a resource selection function to evaluate microhabitat selection by caribou, contrasting their selection of vegetation type by season, study area, calf presence, and behaviour, as identified from 17 384 videos from 19 caribou. Most caribou observations were in upland sites in all seasons and caribou showed seasonal selection among the vegetation types. Most used sites were dominated either by black spruce *Picea mariana* or jack pine *Pinus banksiana* and all other vegetation types were seldomly used. The only favoured lowland vegetation type was poor lowland (low stocking, wet deep organic soils) and wetland types selected in summer. Caribou with calves did not select vegetation types differently from females without calves, nor did they avoid other caribou. Caribou selected for vegetation types with the greatest amount of lichen and other commonly used food types. While habitat selection at landscape scales is important to avoid predation, the videos enabled an understanding of within stand selection among closely-related forest types, indicating habitat selection occurred at a finer spatial scale for different reasons. This new knowledge is useful for identifying silvicultural

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practices needed to restore plant communities most strongly selected by caribou across a managed landscape, which would be expected to improve their energetic balance.

Keywords: boreal forest, lichen, *Rangifer*, resource selection, silviculture, video collar, woodland caribou



## Introduction

Boreal woodland caribou *Rangifer tarandus caribou* are a threatened species in Ontario and throughout much of Canada, with generally declining populations owing primarily to habitat loss contributing to reduced food availability and increased predation risk (Environment and Climate Change Canada 2024). Patterns of space use by woodland caribou measured at the forest stand scale indicate that large tracts of mature (80–100 years) and old (>100 years) conifer forest are selected for in Ontario (Hornseth and Rempel 2016), apparently to avoid predation (Bergerud 1974, Avgar et al. 2013, McGreer et al. 2015) and improve access to lichens and other forage species (Schaefer and Pruitt 1991, Avgar et al. 2013, McGreer et al. 2015, Thompson et al. 2015, Webber et al. 2022). Spatially-explicit population viability analysis (PVA) modelling using such coarse-grained landscape metrics suggests that habitat selectivity is associated with survival, recruitment and long-term viability of woodland caribou (Fryxell et al. 2020).

Scale of observation is fundamental, however, to fully understand the features guiding animal habitat selection. Selection patterns at one scale may not be fully indicative of important features guiding selective space use at other spatial scales (Johnson et al. 2001, Boyce et al. 2003). Caribou may select their habitats in a hierarchical manner such that the important limiting factors that affect choices at coarse scales impose limits on habitat use, and therefore on availability and selection at finer scales (Rettie and Messier 2000, DeCesare et al. 2012). On the other hand, hierarchical selection may simply reflect a scaling-up process. For example, McGreer et al. (2015) suggested that habitat selection by woodland caribou involved a close relationship between selection of habitats at both coarse and fine scales, the latter for areas with high biomass of food, while avoiding predators at the coarser stand level. Dussault et al. (2005) observed a similar selection process for moose *Alces alces* in Quebec. Viejou et al. (2018) inferred that selection within home ranges by female caribou, with or without calves, was related to food availability, predation and/or proximity to a road.

Scale-dependent habitat selection could result from scale-dependent habitat heterogeneity (Boyce et al. 2003, Mayor et al. 2007). For example, Johnson et al. (2001) found that, at the smallest scale of observation (i.e. the feeding site), woodland caribou diet selection was influenced by the availability of certain lichen species, but at the forest stand scale there was no detectable evidence that lichen availability influenced site selection. This latter observation suggests that selection of microhabitats within stands may be important for caribou nutrition and rates of energy gain. There is practical importance to resolving this issue. One of the challenges for recovering caribou populations in disturbed landscapes is to encourage regeneration of local conditions that have a high probability of producing preferred caribou foods. Knowledge of microhabitat selectivity could enable improved silvicultural prescriptions that will encourage improved recovery of important caribou foods.

Testing fine grained features that influence habitat selectivity are often challenging for multiple reasons. Woodland caribou are secretive and therefore difficult to observe, except indirectly by satellite collar technology that has provided considerable information on habitat use, movements, and survival (Fortin et al. 2008, Briand et al. 2009, Avgar et al. 2013). GPS collar technology has limitations, however, including the inability to observe behaviours, errors around locations (D'Eon and Delparte 2005, Hebblewhite and Haydon 2010), and habitat-induced bias (Hebblewhite et al. 2007, Frair et al. 2010). Remote-sensing studies of caribou habitat typically assess 2nd order and 3rd order selection (Johnson 1980), but only at a sub-stand scale when sites are accessible for ground-truthing (Johnson et al. 2001, Briand et al. 2009, McNeill et al. 2020), which can add human bias. Most GPS-based habitat studies are also necessarily based on coarse stand-level typing, often using satellite imagery to classify habitats, such as open woodlands, mature conifer, mixed-woods, treed peatlands, etc. (Avgar et al. 2013, McGreer et al. 2015, Hornseth and Rempel 2016) and provide crude and presumably less reliable information for sub-stand characteristics that could influence habitat selection. Video camera data from GPS camera collars, however, offer a new solution to each of these challenges. Video collars can reveal precise habitat features, to the scale of a few square metres, allowing assessment of microhabitat selectivity (Thompson et al. 2012, 2015, McNeill et al. 2020). More importantly, the cameras eliminate the subjective nature of human observation; instead, the videos show both the precise habitat used as well as the behaviour in that habitat.

We examined microhabitat selection by woodland caribou for various behaviours, as revealed by video collars and using a forest ecosystem classification (FEC, 31 vegetation types; Sims et al. 1989). FEC is an ordination of distinct tree, shrub, and ground cover communities that recur across forests in Ontario, at a sub-stand level of tens of $m^2$, based on edaphic factors and the moisture regime. FEC illustrates that, while boreal forests may appear homogeneous at the stand scale, there is in fact a high level of heterogeneity at the sub-stand scale, comprised of multiple FEC types (Sims et al. 1995). Each FEC vegetation type is classified using indicator

ground plant, shrub, and tree species associations that reflect local site conditions.

Our primary goal was to test if selection of microhabitats occurred at the sub-stand level. More specifically, we tested the prediction that caribou would most strongly select microhabitats with the greatest abundance of food plants. We also tested whether females with calves exhibited differential patterns of microhabitat selection than other caribou as a predator avoidance mechanism (Stuart-Smith et al. 1997, Pinard et al. 2012, Viejou et al. 2018, Walker et al. 2024). Gustine et al. (2006) found that female mountain caribou with calves avoided other caribou by segregating at higher elevations, but after losing a calf, they moved down to lower elevations with other caribou. Therefore, we tested predictions of the predation–risk avoidance hypothesis that caribou with calves should spatially segregate from other caribou. We also examined different behaviours at the sub-stand level for resting, travelling and feeding.

## Material and methods

### Study area

We deployed our video collars at two Ontario, Canada, landscapes (Fig. 1) each about 23 000 km$^2$ and separated by 200 km, representing a comparison between a partly managed (harvested) landscape near Nakina (NK), to an unlogged landscape near Pickle Lake (PL), during 2010–2014. Both study areas were in the boreal forest zone, dominated by black spruce *Picea mariana*, jack pine *Pinus banksiana*, trembling aspen *Populus tremuloides*, white birch *Betula papyrifera* and balsam fir *Abies balsamea* (Rowe 1972). Contrasting disturbance regimes had resulted in different proportions of these dominant tree species in the local forests. Of the total land area, the PL study area was 87% conifer, 11% mixed-wood, and < 1% deciduous forest, about 12% had been burned by wildfires in the last 50 years but there had been no logging. The study area at NK had 69% conifer, 24% mixed-wood, and 6% deciduous forest, with approximately 28% and 5% of the area harvested or burned, respectively, over the preceding 50 years.

In boreal forests, seasonal changes can dramatically affect ungulate behaviours and food selection because of snow cover and presence of leaves on shrubs (Pruitt 1959, Gilbert et al. 2017). To establish seasons, we used images from remote trail cameras that took pictures of measuring stakes in forest stands at both study areas at 11:00 h each day, from September to mid-July. Three cameras were located in each study area at least 100 m from the nearest road in three different stand types. One was in an upland stand with at least 80% conifer cover, one in a forested lowland with at least 80% conifer, and one in a mixed conifer-deciduous stand, but placed with primarily deciduous tree cover within a 10 m radius. We defined winter as the period after which snow depth exceeded 10 cm

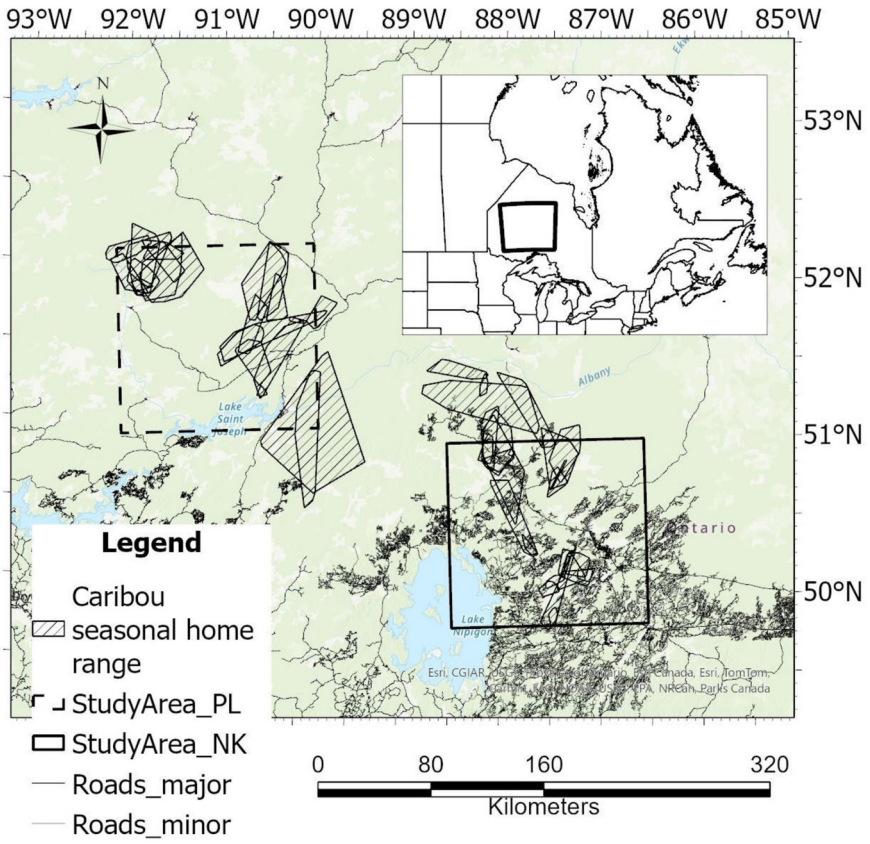



Figure 1. The two study landscapes in Ontario, Canada, with roads and caribou home ranges shown.

for >5 consecutive days for all cameras, and a mean snow ground cover of >50%. Spring was defined as the period after the end of winter until initial leaf-out of deciduous shrubs at all cameras. Summer was the period from initial leaf-out of deciduous shrubs to the time when the chloroplasts began to die, and fall was characterized by no remaining green shrubs and <10 cm of snow cover. These criteria produced different dates for each transition in each study area in each year, with winter ending in late April to early May, summer beginning in mid-May to early June, fall beginning in mid-September, and winter beginning in November. Calves were typically born from mid-May to early June, coinciding closely with the spring to summer transition.

### Vegetation sampling and habitat classification

We sampled forests based on the typing from the Ontario Far North Land Cover (FNLC; Supporting information) ver. 1.3.1, which used 2009–2011 Landsat imagery with 30 m resolution (OMNR 2013). This classification product covered 89.4% of our study area. The remaining area was at the PL site where the earlier (from 2000) but compatible Ontario Provincial Land Cover was used for site selection (Spectranalysis 2004). Ground truthing of forest characteristics was done for eight common forest types: coniferous trees, mixed-wood treed, deciduous treed, sparse treed, open lowland, treed lowland, harvested (<10 years ago), and recently burned (<10 years ago). Landsat-derived classes for bogs and fens are known to be poorly distinguished (Brown et al. 2006, Maxie et al. 2010) and so open bogs and open fens were grouped as 'open lowland' and treed bogs and treed fens were grouped as 'treed lowland'.

The landscape area for available habitats was constrained by the minimum convex polygon that was used by all radio-collared caribou at each study location. Within that area, stands were randomly selected among locations where access was possible. We sampled at the stand scale, with stands defined as areas >10 ha, within which the overstory plant community was uniform and distinct from other surrounding stands (Forestry Canada 1992). Identification of stands for sampling was conducted using ArcMap ver. 9.3.1 and 10.1. The raster layers were converted to polygons with contiguous, uniform FNLC cover types. To ensure that we obtained a representative sample of stands for each FNLC type, we assigned stands to three age classes: young (10–29 years), middle-aged (30–69 years), and old (70+ years), using a stratified random design. At NK, stand age was obtained from forest resource inventory (FRI) data. For PL, there was no FRI for most (79%) candidate stands, so Ontario Ministry of Natural Resources and Forestry (OMNRF) fire records were used, and aerial reconnaissance of candidate stands was conducted to ensure that sampling was proportional across age classes. Where FRI data were available, FNLC polygons were clipped to the FRI polygons at the same location. Any clipped FNLC polygons with cover types not corresponding to the overlapping FRI polygons were removed. 'Available' habitats were chosen randomly to provide approximate proportional representation across cover types and age classes for both study areas.

Within each stand, three to five points were established 100 m apart and at least 50 m from a stand edge along an arbitrary transect oriented through the longest axis of the stand. At each point, 50 $m^2$ plots were used to conduct ocular estimates of cover by species to determine food availability for ungulates. We recorded the percent cover of each species with >1% cover except for lichen coverage that was estimated regardless of amount. The species and abundance of understory plants was estimated separately for the shrub layer (woody plants 0.4–2.0 m tall) and for the ground layer (all plants and lichens <0.4 m). While ocular estimation of coverage can produce inconsistent results (Floyd and Anderson 1987, van Hees and Mead 2000, Godinez-Alvarez et al. 2009), we overcame this issue by ensuring that selected observers were trained on plots with known coverage until all observers were in close agreement.

We were interested in understanding microhabitat use and selectivity by caribou that would influence caribou energetic gain, at a scale representing their perceptual range of detection, much finer grain than the forest stand scale. Vegetation type microhabitats (Sims et al. 1989) represent local plant communities that are relatively consistent across areas of approximately 100 $m^2$, an order of magnitude finer scale than typical of forest stand categories of the FNLC (see the Supporting information for details on classifications). We assigned a vegetation type microhabitat category to each plot using indicator plant species and soil types based on the categories from Sims et al. (1989). During three summer seasons from June to August in 2010 to 2012, we conducted vegetation typing and plot sampling at 302 and 164 plots at NK and PL, respectively.

Diet composition for caribou on both study areas were obtained from Thompson et al. (2015) and food cover refers to mean proportional area of plots covered by food items. Mean dietary abundance was calculated for each vegetation type by summing cover values of each known forage species for each vegetation plot. We quantified the top seven diet items to generate food cover values: Graminoids (grasses and sedges), *Maianthemum canadense*, *Maianthemum trifolium*, *Equisetum* spp., *Clintonia borealis*, *Cladina/Cladonia* spp. and *Menyanthes trifoliata*. Sample sizes among the vegetation types ranged from 29 to 151 plots (see the Supporting information for coverage of food items within vegetation types).

### Caribou capture and video sampling of habitats used

Adult female woodland caribou were captured by a commercial capture company using a helicopter and net gun in March 2011 and 2012. Capture and collaring procedures followed the Canadian Council on Animal Care Guidelines (2003) and were approved by the Ontario Ministry of Natural Resources Animal Care Committee (Protocol 11-183). We deployed 19 GPS camera-collars on caribou over the 2 years, nine at NK and ten at PL. The cameras were housed in a hard plastic case suspended from an upper modified GPS satellite-collar housing (model GPS7000MA, Lotek Wireless Inc.), which included an Argos transmitter for remote data uplink,

and a back-up VHF beacon with mortality sensors for collar recovery. GPS locations were acquired at intervals ranging from hourly to every 5 h, and the positional data were uploaded to Argos satellites every 2 days.

Behaviours and the habitats used were recorded by the remote video camera units (see Thompson et al. 2012 for technical specifications). We pre-programmed the video cameras to record 10-s video segments every 5 min on a duty-cycle from 08:00 to 10:00 h and again from 15:00 to 17:00 h each day. The total video data storage capacity was 32 or 64 gigabytes and other limitations were provided by battery size and optimal collar weight. Our choice of recording time and available battery size enabled recording for a 36-week period from late winter to fall. As ungulates can feed at any time, we selected morning and afternoon to ensure daylight and a possibility of at least some feeding events. Each video recording was labelled electronically with a file number, date, and time. The recorded video data were too large to use the satellite uplink for retrieval, so we recovered the collars to obtain the data cards. In 2011–2012, automatic drop-off mechanisms were deployed on camera collars. When the mortality signal was obtained (indicating 16 h of inactivity), a crew was dispatched to recover the collar either by aircraft, or by vehicle if the collar was within 5 km of a road. In 2012–2013, the drop-off mechanisms failed and the caribou had to be recaptured to obtain the data.

We recorded three behaviours: feeding, resting, and travelling, where travelling was walking or running, and resting was either standing but not travelling (usually ruminating) or lying down. For each video, a primary behaviour was identified based on the highest proportion of time within the video spent on each behaviour, and secondary behaviours were identified if switching occurred. Only the primary behaviours were used for the classifications in this study. Videos for which the field of view was obscured by snow or condensation were rejected, but for those with clear views, the designation of these three behavioural states was straight-forward. Except for two caribou that were sampled completely, a random sample, stratified by animal and season, was analysed for each caribou to identify behaviours displayed, and vegetation type occupied. We kept the sample sizes as balanced as possible among animals within seasons. Six observers who were trained in the field to identify all plant species and vegetation types in the study areas classified a total of 17 384 videos, which represented approximately 15.4% of the total number of videos recorded by the collars in these study areas. We could not identify soil types from the videos but we could identify all indicator plants needed for the vegetation typing, except during winter. For the winter videos, most indicator plants were still available, but herbaceous plants are needed to distinguish seven of the 31 vegetation types found on our study area. To avoid possibly incorrect typing, we pooled some vegetation types and used seven vegetation types or groups of vegetation types for all seasons based on the ordination and cluster diagram provided by Sims et al. (1989). With these groups, only non-herbaceous plant indicator species were required (Table 1). Wetland classes (open bogs, fens and swamps; Harris et al. 1996) were pooled with FEC vegetation type 38 (black spruce–leatherleaf–*Sphagnum*) that is characterized by few stunted trees. Some further pooling of categories was required to satisfy statistical modelling requirements where categories with small sample sizes led to empty categories for some caribou (see the Supporting information for sample sizes of vegetation types).

From the videos, we were able to ascertain which females had calves for how long and if they associated with other caribou. Among the 19 females, ten had calves across the two study areas for at least part of the year. We used the first and last dates that calves were observed in a video file for each female and assumed that the calf was with the female for all observations in between, even if the calf was not seen in the video sample. We tested for differences in habitat selection between females with and without calves, by including 'with calf' as a fixed effect in the models for females with calves. We used observations of other caribou appearing in the videos to test for evidence of segregation of caribou with calves from those that did not have calves. For each month, we used a linear mixed effect regression model with frequency of detections of other caribou as the response, a binary variable for calf presence as the explanatory variable, and animal identifier as the random intercepts.

### Generation of vegetation types for availability sample

The FEC vegetation types available to each caribou were derived from the distribution of FNLC types within individual winter and non-winter home ranges. Using program R (www.r-project.org), the telemetry data for each caribou was reduced to a random sample of 1 point per day that had at least 2D or 3D accuracy (excluding less accurate ARGOS points) that were expected to have a high probability that the animal was within the stand suggested by the location. Using 'adehabitatHR' (Calenge 2006), seasonal (winter or non-winter) home ranges were calculated, and a shape file was generated containing the 95% minimum convex polygons. Random points were generated within the polygon extents using the 'spatstat.geom' package (Baddeley and Turner 2005), so that at least 25 000 points were included in each home range. The FNLC stand types were applied to the random points using a spatial join function. The proportional availability of vegetation types within each FNLC stand type was assessed from 302 and 164 vegetation plots at NK and PL, respectively. We applied vegetation types to the random points within home ranges using the proportional availability within FNLC types (see the Supporting information for values used). These vegetation type values applied to the random points within home ranges were used as the availability sample for resource selection analysis. The proportional availability of FNLC categories was also calculated from the areas of each stand type within study areas, and proportional availability of vegetation types from plots within FNLC categories were applied to estimate vegetation type habitat proportions for each study area using a similar method to the home ranges (Table 1). The forests at PL and NK were dominated by a

Table 1. Sub-stand vegetation types, grouped by similarity, with their descriptions following the forest ecosystem classification by Sims et al. (1989) and their corresponding proportion of foods eaten by caribou according to Thompson et al. (2015), available to caribou populations on two landscapes in northern Ontario boreal forest (NK = Nakina, PL = Pickle Lake). Landscape coverage is based on vegetation ground sampling adjusted to satellite-derived far north land cover (FNLC) classes. [1]Predominantly *Cladina rangiferina*. [2]Predominantly *Pleurozium schreberi*.

| Vegetation type groups | Corresponding FNLC classes | Sub-stand vegetation type | (%) Food cover/m$^2$ | Proportion of the landscape (%) | | Complete description |
|---|---|---|---|---|---|---|
| | | | | NK | PL | |
| 23, 35, 36, 37 | 9, 11, 12, 13, 14, 15, 18, 19, 20 | Lowland conifers | 6.4 | 20.5 | 17.8 | Lowland conifer types with black spruce, white cedar, balsam fir, and American larch, with shrub communities. V37 is a rich lowland black spruce with ericaceous shrubs and *Sphagnum* spp. |
| 24, 25, 28, 29, 30 | 13, 15, 17, 18, 19, 20 | White spruce and balsam fir | 4.9 | 6.1 | 1.1 | White spruce and balsam fir forest types, with scattered black spruce or jack pine. V29 is a minor jack pine type. V30 is a jack pine/black spruce with blueberry and lichen[1]. |
| 31, 32 | 14, 15, 17, 18, 19, 20 | Jack pine and moss | 9.2 | 10.3 | 18.8 | V31 is black spruce/jack pine with tall shrubs and feather moss[2]. V32 is a jack pine/ black spruce with ericaceous shrubs and feather moss |
| 33 | 17, 18, 20 | Upland black spruce and moss | 14.2 | 10.1 | 11.8 | Upland black spruce and moss |
| 34 | 1, 14, 17, 18, 19 | Mesic black spruce | 13.7 | 4.8 | 4.8 | Mesic black spruce with Labrador tea, feather moss, and *Sphagnum* |
| 22, 38 | 11, 12, 13, 14, 15, 18, 19, 20 | Poor lowland and wetlands | 10.7 | 15.6 | 16.2 | Poor lowland, very open black spruce with leatherleaf and *Sphagnum* spp., and wetland types |
| 1, 4, 5, 6, 7, 8, 9, 10, 11, 14, 15, 16, 17, 18, 19, 20 | 12, 15, 16, 17, 18, 19, 20 | Mixed woods | 3.8 | 29.1 | 20.4 | Deciduous and mixed wood forests |

mixture of coniferous vegetation types, mostly upland vegetation types 31–34 and lowland vegetation types 35–38 (Table 1). Within the vegetation types 31–34 group, 32 (jack pine–black spruce–ericaceous shrub–feathermoss) and 33 (black spruce–feathermoss) were the most common at both study areas. Vegetation type 34 represents a mesic black spruce forest type that is transitional between uplands and lowlands. Among the vegetation types 35–38 lowland black spruce group, 35 (black spruce–speckled alder–*Sphagnum*) and 38 (black spruce–leatherleaf–*Sphagnum*) dominated at NK, while 37 (black spruce–ericaceous shrub–*Sphagnum*) and 38 were dominant at PL. Combined mixed-woods and deciduous forest types accounted for 29% and 20% of the plots at NK and PL, respectively.

## Statistical analysis

We used a resource selection function (RSF) to estimate caribou selection for the FEC vegetation types available in their seasonal home ranges. For each caribou, we sampled ten times as many random points as the number of used points within its seasonal home range to evaluate habitat availability. We extracted the vegetation types associated to used and available points. To measure differences in microhabitat selection based on caribou behaviours (travelling, resting, feeding), we randomly assigned a behaviour to each available point, ensuring that the proportion of available points in each behaviour matched the proportion of used points for each behaviour. We then fitted a RSF using a generalised linear mixed model with a logit link and a binomial distribution of errors, with the type of point (used versus available) as response variable, and vegetation types, behaviour, calf presence, season, and study area as predictor variables. We added interaction terms between these four latter variables and the vegetation type variable to address whether caribou could select sub-stand vegetation types differently depending on their behaviour, calf presence, study area, or season. To account for individual-specific variation in microhabitat selection among caribou, we added a random intercept and a random slope with caribou identity as random factor with the 'glmmTMB' package in R (Magnusson et al. 2017). We performed different models with different combinations of multiplicative effects among the vegetation types and the behaviour, season, and study area variables and used the Akaike information criterion corrected for small sample size (AICc) to determine the most parsimonious model (Burnham and Anderson 2004).

We present results obtained from the most parsimonious models, i.e. with both $\Delta$AICc < 2 and the lowest number of explanatory variables, as recommended by Arnold (2010). Estimates of habitat selection obtained from the competing-best model ($\Delta$AICc < 2 but higher number of explanatory variables) are available in the Supporting information and suggest that some included variables were uninformative for

caribou micro-habitat selection (Arnold 2010). Very similar results were obtained when assigning a large weight (5000) to each available location and a weight of 1 to all observed locations, or when using unweighted models (Supporting information). Similarly, we tested whether microhabitat selection was related to the abundance of preferred and common foods eaten by caribou. To do so, we fitted a RSF using the type of point (used versus available) as response variable but using the percentage of cover of foods eaten by caribou as a predictor variable instead of the vegetation type variable. We added an interaction term between this variable and behaviour, calf presence, season, and study areas, as well as a random intercept and random slope with caribou identity as a random factor. For interpretability, RSF scores were then converted to a selection ratio for habitat type *i* (Chamaillé-Jammes 2020, Dejeante et al. 2024):

$$S_i = \exp\left(\beta_0 + \beta_1 x_1 + \cdots + \beta_n x_n\right)\frac{N_a}{N_u}$$

where $N_a$ = the number of available points and $N_u$ = the number of used points used to calculate the resource (habitat) selection function. A selection ratio >1 indicated selection for the corresponding vegetation type and, conversely, a selection ratio <1 indicated avoidance. We used the Spearman rank correlation based on k-fold cross-validation (Boyce et al. 2002) to evaluate the goodness-of-fit of our models, with 10 folds, 10 bins and 10 repetitions.

## Results

For our 19 female caribou, we obtained habitat use of sub-stand vegetation types by behaviours from 17 384 video records sampled at NK (n = 4020 in winter; n = 3584 in non-winter) and PL sites (n = 4151 in winter, n = 5629 in non-winter). All videos were in unlogged forests aged from 70–120 years at both study areas. For females with calves, the number of videos was 1537 and 1519 (n = 4 females with calves) in winter and non-winter seasons, respectively, at NK, and 2742 and 4750 (n = 6 females with calves) in winter and non-winter seasons, respectively, at PL. We found little evidence that females with calves segregated from females without calves. Other caribou were seldom seen in summer videos by any caribou, with monthly incidence rates of 0.68, 0.62, 0.12 and 0.32% for May, June, July and August, respectively, using the full collection of videos. A significant difference for June was found in the frequency of caribou with calves near other caribou versus caribou with calves alone (n = 18, estimate = −0.94, SE = 0.001, $p < 0.001$). The result is unlikely to be biologically meaningful given the very small numbers of observations.

### Caribou selection of sub-stand vegetation types

Microhabitat selection by woodland caribou varied by study area, season, and year but not with the presence of a calf (Table 2, Supporting information). We note that the second-best, competing model included a term for the 'white spruce and balsam fir vegetation type'. The model shows that the effect of calf is positive compared to the 'selection' without calf, but in this case 'selection' coefficient without calf is negative indicating 'lower avoidance'. The most parsimonious RSF model had a high predictive power (cross-validation: $\bar{r}_s = 0.85 \pm 0.01$, mean ± SE). Consistently across seasons and study sites, caribou avoided mixed woods and, to a lesser extent lowland conifers (Fig. 2a–b). Among mixed-wood vegetation types, only those dominated by black spruce or jack pine (vegetation types 17–20) were used. Conversely, caribou strongly selected for sub-stand vegetation types composed of upland black spruce with feathermoss at both areas and in all seasons (Fig. 2c). Averaged across study areas and seasons, the caribou selection ratio for upland black spruce-feathermoss was 5.6 [95% CI: 4.7–6.5], i.e. caribou used this habitat

Table 2. Summary table of the RSF candidate models used to evaluate the selection of sub-stand vegetation types by woodland caribou. All models included a random intercept and a random slope with caribou identity as random effect to account for individual-level variations in habitat selection. The most parsimonious model (ΔAICc < 2 and lowest number of parameter *K*) is shown in bold.

| Model | K | ΔAICc | AICc weight |
|---|---|---|---|
| **Vegetation type:(Behaviour + Season + Study area)** | **63** | **0.0** | **0.7** |
| Vegetation type:(Behaviour + Season + Study area + Calf) | 70 | 1.6 | 0.3 |
| Vegetation type:(Behaviour + Season) | 56 | 24.7 | 0.0 |
| Vegetation type:(Behaviour + Season + Calf) | 63 | 27.5 | 0.0 |
| Vegetation type:(Season + Study area) | 49 | 299.8 | 0.0 |
| Vegetation type:(Season + Study area + Calf) | 56 | 301.3 | 0.0 |
| Vegetation type:Season | 42 | 324.5 | 0.0 |
| Vegetation type:(Season + Calf) | 49 | 327.2 | 0.0 |
| Vegetation type:(Behaviour + Study area) | 56 | 642.1 | 0.0 |
| Vegetation type:(Behaviour + Study area + Calf) | 63 | 644.5 | 0.0 |
| Vegetation type:Behaviour | 49 | 670.7 | 0.0 |
| Vegetation type:(Behaviour + Calf) | 56 | 673.3 | 0.0 |
| Vegetation type:Study area | 42 | 941.8 | 0.0 |
| Vegetation type:(Study area + Calf) | 49 | 944.0 | 0.0 |
| Vegetation type | 35 | 970.6 | 0.0 |
| Vegetation type:Calf | 42 | 973.1 | 0.0 |

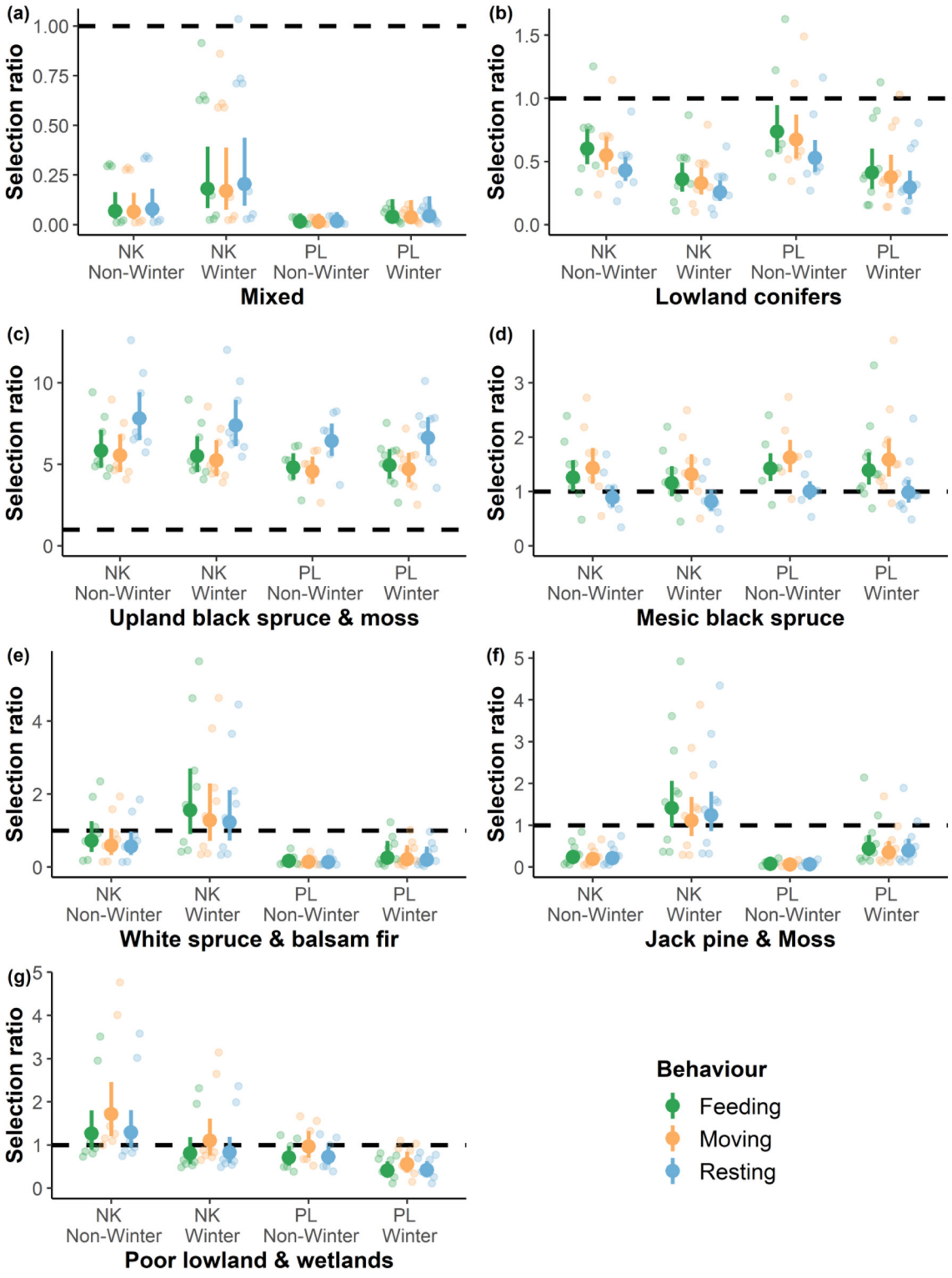



Figure 2. Estimations of the selection ratio for sub-stand vegetation types (a–g) by caribou during the winter and non-winter seasons, according to their behavioural states and to the study site (NK = Nakina, PL = Pickle Lake) obtained using a RSF. The dashed horizontal line indicates a selection ratio of one, that is habitat use proportional to habitat availability. Selection ratios higher than one indicate positive selection of sub-stand vegetation types (a–g) by caribou in the corresponding study site, behaviour and season, while values less than one indicate avoidance. Solid points show mean values of the selection ratio estimated at the population level, with extremities indicating the 95% confidence intervals. Translucent points show the selection ratio estimated per individual.

about 5.6 times more than its availability in their home range. The latter selection ratio was greater when caribou rested (SR = 7.1 [95% CI: 6.0–8.3]) than when they fed (SR = 5.0 [95% CI: 4.3–5.9]) or travelled (SR = 4.9 [95% CI: 4.1–5.8]). Caribou also selected for mesic black spruce (vegetation type 34), which they used more than its availability in the landscape, both to feed (SR = 1.3 [95% CI: 1.1–1.60]) and travel (SR = 1.5 [95% CI: 1.2–1.8]) but not to rest (SR = 0.9 [95% CI: 0.8–1.1]). This difference in microhabitat selection by behaviour was slightly more important at PL than at NK (Fig. 2d). Caribou selection for sub-stand vegetation types also varied between the study sites. At PL, caribou avoided sub-stand vegetation types composed of white spruce and balsam fir types with scattered black spruce or jack pine, while they used them proportionally to their availability at NK, with no effect of season (Fig. 2e). We found differences between seasons in selection for sub-stand vegetation types composed of black spruce or jack pine with tall or ericaceous shrubs and feather moss. Although caribou from both areas avoided these latter vegetation types during non-winter seasons, their use was proportionate to availability in NK during winter (Fig. 2f).

### Caribou selection of food resources

Commonly eaten and preferred food species included terrestrial lichens (mostly *Cladina* spp.), *Maianthemum* spp., graminoids (including sedges), *Equisetum* spp., *Clintonia borealis* and *Menyanthes trifoliata* (Thompson et al. 2015). Sub-stand vegetation types with the highest values for those foods, often dominated by lichens and to a lesser extent by graminoids, were black spruce or jack pine with tall shrubs, upland black spruce, mesic black spruce, rich lowland black spruce with ericaceous shrubs, poor lowland with very open black spruce, and wetland types (Table 1). Sites with at least 11% cover of preferred food species were preferred (Fig. 3). An important food plant in lowlands, *Menyanthes trifoliata*, was only abundant in poor lowland with very open black spruce and wetland types. This vegetation type was commonly used less (at PL during winter) or proportionally (in NK during winter and at PL during non-winter seasons) to its availability in the landscape, except for caribou travelling during non-winter seasons at NK, where it was selected (Fig. 2g). Other lowland conifer types had low food values and were avoided. Generally, caribou showed increased selection for vegetation types with increasing cover of preferred foods, with only minor influences of the study area, season, and behaviour (Fig. 3).

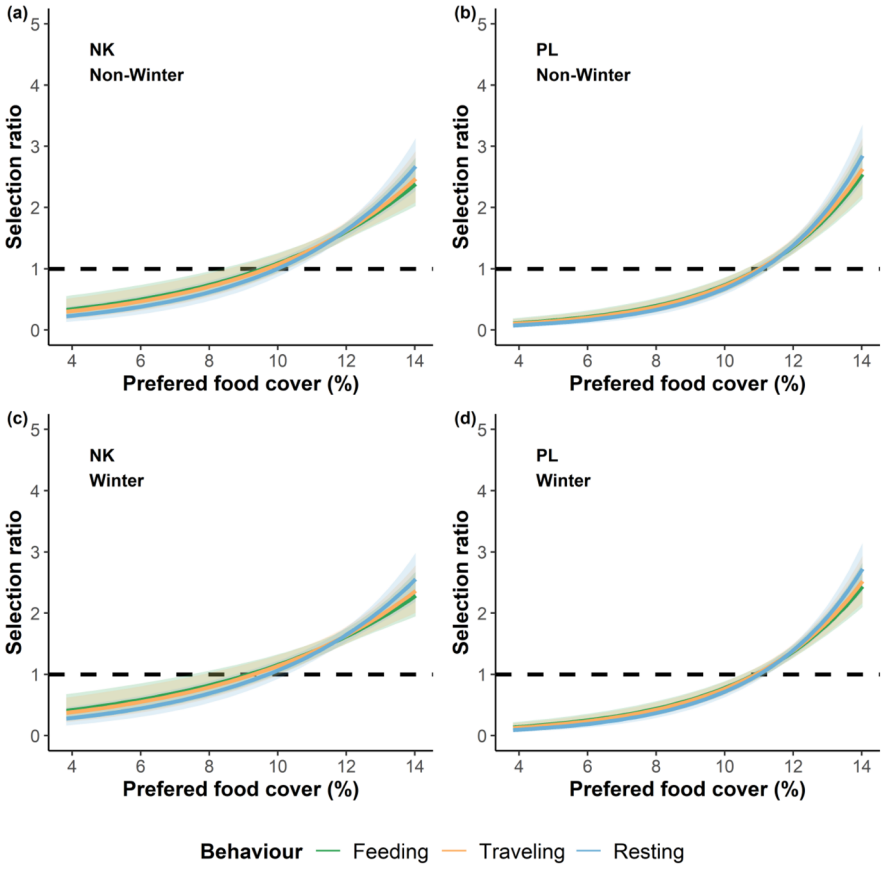



Figure 3. Estimations of the selection ratio for the percentage cover of preferred foods eaten by caribou during the winter and non-winter seasons, according to their behavioural states and to the studied areas (NK = Nakina, PL = Pickle Lake). The dashed horizontal line indicates a selection ratio of one, that is habitat use proportional to habitat availability. Lines show mean values of the selection ratio estimated at the population level, with ribbon extremities indicating the 95% confidence intervals.

## Discussion

Microhabitat selection is difficult to demonstrate for secretive species and our study affirmed the value of video technology to assist in understanding habitat use behaviours by woodland caribou, also recently demonstrated by Ehlers et al. (2024). Earlier fine-grained studies required accessing sites located by radio-telemetry and then inferring caribou behaviour. For example, Serrouya et al. (2007) observed fine-scale choice among forest types by mountain caribou in British Columbia where, in deep snow conditions, caribou selected habitats rich in arboreal lichens at low elevations. In Quebec, Briand et al. (2009) accessed stands used by eight radio-collared caribou to study fine-scale use of habitats. Such studies are limited by weather (snow hides tracks and hampers access), stand accessibility (especially in mountains and in winter), cost of access, and small sample size owing to the time required to collect samples. Video collar information is only limited by the number of collars that can be deployed, and the time to interpret the large number of samples, while providing the unbiased opportunity to directly observe habitat selection in real time. Ehlers et al. (2024) pointed out that studies, such as ours using video cameras, open exciting possibilities of improved prediction of fine-scaled habitat use for conservation.

Our observation of microhabitat selection, coupled with our earlier results illustrating food plant electivity (Thompson et al. 2015), indicated that a small number of microhabitat types and associated ground covers were actively selected within individual home ranges. Caribou at both landscapes selected particular types of black spruce and/or jack pine habitats. Favoured vegetation types 33 (black spruce/feathermoss) and 34 (black spruce/labrador tea/feathermoss) occurred on relatively poor upland or mesic sites. Vegetation type 33 is an upland black spruce type that is drier and tends to have more jack pine in the overstory than vegetation type 34 (up to 40% versus <20% in type 34), while the latter vegetation type is a transitional forest type dominated by black spruce between uplands and the adjacent wetter lowland black spruce types (i.e. vegetation types 35–38; Sims et al. 1989). McNeill et al. (2020) argued that because high value food patches of some preferred species occurred in other vegetation types (e.g. higher density of *Clintonia* spp. in mixed-woods) that caribou were not optimally selecting stands for these species. It is likely, however, that total biomass of all common and preferred species is more important than maximising for a single species, as was observed at both study areas (Fig. 2). Our data suggested that caribou had preferentially occupied areas of their home ranges where lowlands were adjacent to uplands of vegetation type 33, with an abundance of mesic vegetation type 34 in between, enabling them to find high total biomass of all preferred foods.

We found that most caribou activity, including all females with calves, occurred in upland conifer forest types during all seasons, similar to findings from habitat selection research in Quebec (Courbin et al. 2009, Hins et al. 2009, Leclerc et al. 2012), elsewhere in Ontario (Brown et al. 2007), and in Manitoba (Schaefer and Pruitt 1991), but different from Alberta, where lowlands are used most heavily (Bradshaw et al. 1995, Latham et al. 2011). Kittle et al. (2015) reported that wolf use of lowlands was low on our study areas, so the limited use of lowland habitats by our caribou was accordingly unexpected. Many studies have found selection for lowland areas for at least part of the year, and have suggested this as a possible predator avoidance mechanism, especially when neonates are present (Bradshaw et al. 1995, McLoughlin et al. 2005, Hins et al. 2009).

Canopy cover in the preferred black spruce vegetation types 33 and 34 ranged from 40 to 85% (OMNR 1997), indicating variability among individual stands that probably reflected the variance that we observed in food abundance, especially for terrestrial lichens. Open upland forests generally provide a higher density of terricolous lichens than closed forests or lowlands (Lesmerises et al. 2011, McMullin et al. 2013), and lichens were an important year-round food for caribou on our study areas, especially in winter (Thompson et al. 2015). Some studies have found that caribou selected closed canopy boreal forest for at least part of the year (Brown et al. 2007, Courtois et al. 2008). Use of closed forests under deep snow conditions was also reported by Johnson et al. (2001) for mountain caribou in British Columbia although there, arboreal lichens were a common food item, unlike on our study areas (Thompson et al. 2015). Caribou have difficulty digging through > 50 cm of snow or crusted snow (Pruitt 1959, Johnson et al. 2001, Mosnier et al. 2003) and deep snow is understood to inhibit movements reducing habitat permeability (Stuart-Smith et al. 1997, Johnson et al. 2001). While open canopy conifer forests support more lichens than closed forests, there is a tradeoff because of the amount of extra energy required to dig in and travel through deep snow to access large lichen mats. With deep snow, caribou may be forced into closed canopy stands, while preferring more open stands whenever possible, and vegetation types 33 and 34 occur in both conditions. Further, closed canopy forests have a low shrub density in Ontario boreal forests (Sims et al. 1989, Mallon et al. 2016), which would enhance predator detection, contrary to the suggestion that closed-canopy forests may actually reduce predation risk because of low prey detectability through heavy cover (Kunkel and Pletscher 2000, Pierce et al. 2004).

Based on previous studies (Bergerud and Page 1987, Gustine et al. 2006, Pinard et al. 2012, Viejou et al. 2018, Walker et al. 2024), we expected that there would be some habitat segregation between females with and without calves. However, we did not detect any major influence of calf presence on microhabitat selection by caribou. Further, Thompson et al. (2015) reported that there was no detectable difference in diet choice between females with or without calves. Viejou et al. (2018) demonstrated that females with calves showed much stronger selection for land cover types with lower predation risk and greater distance from roads than females without a calf. Females with calves could also have segregated spatially from other caribou, but the video analyses showed that there was very low interaction

with other caribou, regardless of whether females had a calf or not.

Microhabitat selection by female caribou (with or without calves) on a seasonal basis, for specific stand types and certain behaviours, was strongly related to their dietary preferences which should consequently have a pronounced impact on rates of energy gain. Caribou also used the same vegetation types for travelling and feeding, but we observed differences when resting. The latter differences occurred across two habitat types with similar overstory composition of black spruce, but with upland versus mesic soils and corresponding understory vegetation. The upland black spruce and moss vegetation type typically has a very open understory where resting caribou could see for long distances, whereas the mesic black spruce category contains a thicker shrub layer composed of alder (*Alnus* spp.) and ericaceous shrubs, in which caribou would not be able to see approaching predators until they were close. This relationship is probably not related to differential habitat permeability, nor was there obvious movement from feeding habitats to other habitat types for resting. Caribou avoided mixed-wood forest types for all behaviours. Mixed-woods, especially in the younger age classes, are well-understood to be avoided by caribou, a behaviour attributed to higher predator and moose density in these habitat types (Fortin et al. 2008, Losier et al. 2015, McGreer et al. 2015).

Woodland caribou select certain preferred foods that contribute to the majority of dietary biomass (Thompson et al. 2015). Avgar et al. (2013) and McGreer et al. (2015) found a positive relationship between caribou habitat use and high plant biomass at a large scale on our study areas, but had no data on the actual plant or lichen species. Here we have shown that caribou recognized and preferentially used microhabitats with the greatest cover in preferred and common forage species and that food abundance and quality are key factors determining how caribou allocate time among mature forest vegetation types within their home ranges. Such behaviour suggested optimal foraging (Stephens and Krebs 1986) by maximising energy gain in the most profitable vegetation types (Cameron et al. 1993, Gaillard et al. 2010), similar to selection patterns observed in other ungulates (Renecker et al. 1986, Fryxell et al. 2004, 2008).

Lichens are clearly an important food item for woodland caribou but surprisingly little information is available on the long-term recovery of boreal ground covers, especially lichens, after forest harvesting. Studies of the oldest managed forests, where machine-harvesting was used, have shown that terrestrial lichen cover was substantially reduced for at least 60 years (Coxson and Marsh 2001, Berg et al. 2008, Kivinen et al. 2010). McMullin et al. (2011) found lower lichen biomass in 40-year-old harvested stands that had been treated with herbicide than in unmanaged stands. Several authors have shown that partial opening of closed canopy conifer forest enhances terrestrial lichen biomass (Sulyma and Coxson 2001, McMullin et al. 2013, Boudreault et al. 2013), especially if the stands were harvested in winter (Coxson and Marsh 2001, Lafleur et al. 2016). Nevertheless, for most boreal forests clear-cutting is the preferred silvicultural system, resulting in reduced terrestrial lichen biomass (Hart and Chen 2008). Collectively, these studies suggest that there is high uncertainty about lichen recovery in boreal forests managed by clearcutting, especially when post-harvest treatments are applied. We recommend that managers consider leaving legacy stands of the preferred vegetation types as source populations for lichens, where caribou management is an objective.

Many studies on woodland caribou have suggested a top–down basis for habitat selection. That is, to avoid predation, caribou select landscapes with low predator density, primarily in unmanaged older forests with low alternative ungulate biomass (Seip 1992, Rettie and Messier 2000, Latham et al. 2011). This study used video cameras to show that caribou also select microhabitat types within their home ranges based on high value foods, indicating that the hierarchy of habitat selection at each scale can contribute to fitness, based on choices made that increase efficiency of resource use while avoiding predation.

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## Author contributions

**Ian D. Thompson**: Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Validation (equal); Writing – original draft (lead); Writing – review and editing (equal). **Philip A. Wiebe**: Formal analysis (equal); Investigation (equal); Methodology (equal); Validation (equal). **Douglas Reid**: Data curation (equal); Investigation (equal); Methodology (equal); Supervision (equal). **Arthur R. Rodgers**: Conceptualization (equal); Funding acquisition (equal); Investigation (equal);

Methodology (equal); Project administration (equal); Supervision (equal); Visualization (equal). **James A. Baker**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Project administration (equal); Resources (equal). **Brent R. Patterson**: Conceptualization (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal). **Eric McNeill**: Investigation (equal). **Romain Dejeante**: Data curation (equal); Formal analysis (equal); Validation (equal). **John M. Fryxell**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (equal).

### Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/wlb3.01503.

### Data availability statement

Data are available from the Zenodo: https://doi.org/10.5281/zenodo.17868950 (Thompson et al. 2025).

### Supporting information

The Supporting information associated with this article is available with the online version.

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