Canadian Journal of Zoology
Revue canadienne de zoologie

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Journal:	<i>Canadian Journal of Zoology</i>
Manuscript ID	cjz-2015-0101.R2
Manuscript Type:	Article
Date Submitted by the Author:	15-Oct-2015
Complete List of Authors:	Hornseth, Megan; Ministry of Natural Resources and Forestry, Center for Northern Forest Ecosystem Research Rempel, Robert; Ontario Ministry of Natural Resources and Forestry, Centre for Northern Forest Ecosystem Research
Keyword:	UNGULATES < Taxon, BOREAL < Habitat, HOME RANGE < Habitat, DEER & ETC < Taxon, FOREST < Habitat, FITNESS SELECTION < Discipline, SELECTION < Discipline

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**Seasonal resource selection of woodland caribou (*Rangifer tarandus caribou*) across
a gradient of anthropogenic disturbance**

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Draft

Abstract

Resource selection functions are useful tools for land-use planning, especially for wide-ranging species with sensitivity to anthropogenic disturbance. We evaluated five *a priori* hypotheses describing seasonal habitat selection of woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)) across three regions in northern Ontario. Two regions were Boreal Shield dominated, one area relatively high anthropogenic disturbance (due to commercial forestry) and one relatively low anthropogenic disturbance. The final region was located on the wetland-dominated Hudson Bay Lowlands. Each region encompassed two caribou management ranges: one was used for model development and the other for model evaluation. We developed seasonal resource selection probability functions (RSPFs) using seasonal utilization distributions and isopleths derived from GPS collar data (from 212 caribou) to identify high- and low-use areas. We explored selection across 5 spatial scales; selection patterns were strongest at the 10 000 ha scale. We found temporal and spatial variation in all environmental predictors across ranges and seasons, especially in the Hudson Bay Lowlands. Our results consistently supported the integrated global model (with common variables but range-specific coefficients) where caribou habitat use is related to minimizing apparent competition with moose (*Alces alces* (L., 1958)) while avoiding disturbed areas, and utilizing areas with adequate forage.

Key words: Woodland caribou (*Rangifer tarandus caribou*), resource selection function, boreal, habitat

Introduction

Ontario's Far North constitutes one of the world's last remaining intact landscapes (together with the Russian Taiga and the Amazon (Keddy 2010)). This area is of global significance as it contains the largest wetland complex in North America and provides important ecosystem services such as carbon storage and cycling on a global scale and regulates the effects of climate change (Abraham and Keddy 2005; Abraham and McKinnon 2011; Riley 2011). The Far North Act outlines four land-use planning objectives, and these include developing a network of protected areas to conserve at least 225 000 km² of land and protecting key ecological features for species at risk through engagement with First Nations by developing community land-use plans (Government of Ontario 2010). The Far North supports over 50 mammal species, 190 birds, 9 amphibians and reptiles and at least 50 species of fish. These include several species at risk that are sensitive to anthropogenic development and habitat disturbance, such as wolverine (*Gulo gulo* (L., 1758)), lake sturgeon (*Acipenser fulvescens* (Rafinesque, 1817)), and boreal woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)). However, the future of the Far North is uncertain due to several drivers: climate change, commercial forestry, development associated with transportation and energy for both industry and local communities, and mineral exploration and development (Far North Science Advisory Panel 2010).

Resource selection functions (RSFs) have a variety of applications including identification of critical habitat, risk assessment in land-use planning, spatial population viability analyses, and in estimating connectivity needs and population sizes (Boyce and McDonald 1999; Manly 2002; Aldridge and Boyce 2007; Johnson et al. 2015). RSFs

describe landscapes using probabilistic functions, permitting a spatially explicit examination of resource availability and selection, an improvement from past methods that provided categorical or binary representations of habitat and matrix (Manly 2002; Chetkiewicz et al. 2006). RSFs can be used to project the probability of a species' occurrence on the landscape or be used to assess the cumulative impacts of habitat alteration due to development or climate change (Manly 2002; Chetkiewicz et al. 2006; McLoughlin et al. 2010). Boreal woodland caribou (herein: caribou) are listed as "threatened" under Canada's *Species at Risk Act* (2004) and Ontario's *Endangered Species Act* (2007).

Spatially explicit estimates of "critical habitat" are vital for land-use planning and conservation strategies and are required by the *Species at Risk Act* in Canada. Critical habitat is defined as "the resources and environmental conditionals required for persistence of local populations of boreal caribou throughout their current distribution in Canada" (Environment Canada 2008). This requires a scale-appropriate approach, which was identified as the local population range (Environment Canada 2008). However, caribou select habitat at a range of scales to attain their life history needs. Patterns of selection can vary with spatial scale; at a fine scale caribou select habitats with adequate forage, while at a broad scale caribou select habitats with lower predation risk (Rettie and Messier 2000). As a result, the effects of some variables, such as anthropogenic disturbance, may be scale-dependent and have different influences at fine and broad spatial scales (DeCesare et al. 2014).

Caribou are sensitive to development, prefer intact landscapes and select habitat at broad spatial scales, so they can be used as an indicator of ecosystem health and are an

important focal species in land-use planning (Schneider et al. 2003). Given the broad range of landscapes that caribou inhabit across the Boreal Shield and Hudson Bay Lowlands, understanding the relationship between caribou and landscape features can inform ecosystem conservation and land-use planning. In Ontario, caribou exist in a largely continuous distribution, from Manitoba to Quebec, southwards to the approximate edge of human development and forestry (with remnant populations on the coast of Lake Superior), and northwards overlapping with the eastern migratory population (Schaefer 2003; Vors et al. 2007; COSEWIC 2011; Berglund et al. 2014). Caribou are divided into two ecotypes in Ontario: forest-dwelling and forest-tundra caribou; forest-dwelling caribou are listed as ‘threatened’, while forest-tundra animals are considered ‘not at risk’ (OMNR 2014b). Our study focused on the forest-dwelling ecotype. Development has been pushing northwards into the caribou range in Ontario for close to 200 years, which has resulted in habitat loss and fragmentation. Consequently, caribou have been extirpated from about 50% of their historic range in Ontario and the range limit has receded by approximately 34 km per decade (de Vos and Peterson 1951; Thompson 2000; Schaefer 2003). Following suggestions from Environment Canada’s scientific review of critical habitat (Environment Canada 2008, 2011), the Ontario Ministry of Natural Resources (OMNR 2014b) adopted a Range Management Approach, whereby ranges are considered to be an appropriate scale to assess whether resource management actions are consistent with caribou conservation (OMNR 2014a).

Over recent years, RSFs have been developed for caribou in Alberta (McLoughlin et al. 2005), British Columbia (Johnson et al. 2004; DeCesare et al. 2012), Manitoba (Gustine et al. 2006) and Quebec (Leblond et al. 2013). However, patterns of caribou

habitat use across their range are variable and are not well understood in Ontario (but see Berglund et al. 2014). Generally, there is a consensus on the importance of peatland complexes and old-growth conifer stands as caribou habitat, as well as the avoidance of linear features and disturbed areas (Bradshaw et al. 1995; Dyer et al. 2001, 2002; McLoughlin et al. 2005; Bowman et al. 2010). Johnson et al. (2015) have recently explored the differences in avoidance of disturbances among Central Mountain caribou herds in British Columbia, and determined that the zone of influence of linear features and non-linear disturbances differs among 5 caribou herds within a 41,000 km² study area. However, few studies have examined how patterns of selection can vary across different environmental conditions such as the presence of roads and development, peatland-dominated and forest-dominated areas. Such studies are costly due to the expense and effort required to implement and maintain the large research programs necessary for such analyses, especially in areas with minimal infrastructure. Recent studies have shown that caribou can alter their patterns of habitat selection based on landscape context (Moreau et al. 2012), so a range-based approach could improve our understanding of the influence of landscape heterogeneity on habitat requirements.

After a thorough review of recent literature and the hypotheses proposed by the Collaborative Woodland Caribou Research Program (Rodgers et al. 2007), we established five alternate hypotheses in a hierarchical structure to explain caribou habitat selection. Lichen is the principal, but not the only browse species for caribou, and the first two hypotheses consider the availability of browse and the habitats that produce it. The *Browse* hypothesis predicts that caribou will select areas of high browse availability, whereas the *Browse Refuge* hypothesis builds on the first hypothesis and predicts that

caribou will select areas of high browse availability and will utilize lakes to avoid predation. The *Apparent Competition* hypothesis predicts that caribou will avoid areas of high moose density (e.g., because moose can result in increased wolf (*Canis lupus* (L., 1758)) densities, increasing the predation risk for caribou (James et al. 2004; Wittmer et al. 2007). The *Disturbance* hypothesis suggests that caribou habitat selection can be predicted based on avoidance of disturbed areas, where disturbance includes both natural disturbance, such as fire, and anthropogenic disturbance, such as forest harvest and land clearing. Finally, the *Global* model integrates factors from each of the preceding hypotheses, suggesting that habitat selection is best explained by caribou avoiding areas of high apparent competition, and selecting areas with high browse and low predation risk. We examined environmental variables across a range of spatial scales and developed seasonal resource selection probability functions (RSPFs) for caribou under each of the proposed hypotheses to (i) identify the important features associated with habitat selection, (ii) determine if there are distinct differences in caribou habitat selection among different analysis regions across the north of Ontario and among seasons, and (iii) assess the likelihood of alternative hypotheses about the mechanisms that drive habitat selection. The resulting models are a useful a tool in land-use planning to identify areas in need of protection and to evaluate alternative development scenarios.

Methods

Study Area

Northern Ontario has been divided into 14 caribou ranges that reflect a combination of factors including animal movements and distribution, behavioural

responses, and predominant risk factors as well as existing administrative boundaries to facilitate management at a broad spatial scale (OMNR 2009, 2014a). We used 6 of these ranges to delineate the study area and created 3 regions based on ecological and anthropogenic differences, the *Undeveloped Boreal Shield* (UBS), the *Developed Boreal Shield* (DBS), and the *Hudson Bay Lowlands* (HBL; Fig. 1). Each region consisted of two paired ranges: Kinloch and Spirit, Nipigon and Pagwachuan, and Missisa and James Bay, respectively. For each study area, the first of these ranges had a higher sampling effort and was used for model development, and the second used for model evaluation.

The UBS region was dominated by sparse and coniferous forests followed by mixed forest. While there was no active forestry in either the Kinloch or Spirit Range, there was one active mine in the Spirit Range (Fig. 2). There was a highway to Pickle Lake in the Kinloch Range, seasonal ice roads to other communities, and an all-season gravel road to the mine. In the Spirit Range the predominant tree species were black spruce (*Picea mariana* (P. Mill)), followed by jack pine (*Pinus banksiana* (Lamb.)) and white birch (*Betula papyrifera* (Marsh.)) on upland sites. The UBS region had an aggressive natural disturbance regime, where burns ≤ 30 years old occupied $>15\%$ of the landscape and the average fire return interval was short (50-187 years) (Crins et al. 2009). This was the highest percentage of anywhere in Ontario as this area was not under fire suppression (Crins et al. 2009). In Kinloch, upland areas were comprised of jack pine and black spruce, with white spruce (*Picea glauca* ((Moench) Voss)) and trembling aspen (*Populus tremuloides* (Michx.)). Large peatlands (fens and bogs) dominated lowland areas in both Kinloch and Spirit, with black spruce and tamarack (*Larix laricina* ((Du Roi) K. Koch)) in treed areas (Crins et al. 2009).

The DBS region consisted of the Nipigon and Pagwachuan Ranges. The Nipigon Range was on the central Boreal Shield and was dominated by mixed and coniferous forests. The vegetation consisted of black spruce and jack pine, with mixtures of balsam fir (*Abies balsamea* ((L.) Mill)), trembling aspen, white birch, and white spruce (Rowe 1972). Most of this range (>90%) was within the area of active forestry so there was a substantial anthropogenic footprint due to forestry as well as roads, small settlements, and mineral exploration (Crins et al. 2009). Pagwachuan straddled the southern extent of the James Bay Lowlands and the transition into the Boreal Shield; it also included areas of the Clay Belt. The dominant tree species were black spruce with mixtures of jack pine, balsam fir, white spruce, trembling aspen, and balsam poplar (*Populus balsamifera* (L.)) (Rowe 1972; Crins et al. 2009). Lowland areas were common in this range, especially towards the north. In the southern part of the range there was a substantial anthropogenic footprint due to forestry, mineral exploration, small settlements, and roads (Crins et al. 2009). While the Nipigon and Pagwachuan ranges have some ecosystem-based differences, we were interested in comparing the responses to disturbance in these ranges based on their proximity to the 'Ring of Fire', an area recently discovered to be rich in chromite, nickel, copper, platinum, and vanadium centred around McFauld's Lake ([52°46'06"N 86°03'26"W](#)) (Far North Science Advisory Panel 2010) with potential for future development (Fig. 2).

The HBL Region consisted of the Missisa and James Bay ranges. The Missisa range encompassed the transition zone between the Boreal Shield and the Lowlands, as well as the western part of the Lowlands. In a transition zone, vegetation species from both regions co-dominate the landscape; there were extensive peatlands with poor

drainage, as well as bedrock outcroppings and upland areas. The James Bay Range was located entirely within the Lowlands region, dominated by extensive peatlands and poor drainage. Treed and open fens and bogs comprised 68.5% of the landscape by land cover (Wiken 1986; Crins et al. 2009). The dominant forest class was conifer and dominant trees were stunted black spruce and tamarack, with a low fire regime (Crins et al. 2009). There was no active forestry in either range; anthropogenic disturbance was limited to small First Nation settlements, winter ice roads, and one active mine. While current anthropogenic disturbance was limited, the Missisa range contains the ‘Ring of Fire’, an area which may be developed for mineral extraction in the near future (Far North Science Advisory Panel 2010). There is the potential for development of this area, and possible options include one of 2 proposed all-season roads or a railway (Fig. 2).

Environmental Conditions

The 27 land cover classes of the Provincial land cover were interpreted from 1999/2000 imagery (Spectranalysis Inc 2004) and were grouped into 7 land cover classes based on principal patterns found in previous studies of caribou that we believed were sufficient to discriminate habitat selection (see Bradshaw et al. 1995; Bowman et al. 2010; Leblond et al. 2011). Clear open and turbid water classes were combined as “water”; open fen and open bogs were combined as “open peatland” class; treed fen and treed bogs were combined as “treed peatland”. Four of the original upland land cover classes were retained: sparse forest, deciduous forest, coniferous forest, and mixed forest (Spectranalysis 2004), while classes found only on the Hudson Bay coastline or southern Ontario were omitted from this analysis. We used more recent imagery containing disturbances from pre-1990 up to and including 2011 (from the OMNR satellite-derived

disturbance mapping program) to identify both natural and anthropogenic disturbance across the study site (OMNR 2013), as well as recent silvicultural harvest (OMNR, *unpublished data*). Mapped linear features included all road types, including permanent primary, long-term secondary, short-term tertiary, and seasonal winter roads, as well as hydro lines, and railways. Eskers, a natural geological land feature, were mapped by the Ontario Geological Survey (1997). We used correlation analysis to identify any collinearity among variables, and found that linear features were highly correlated with anthropogenic disturbance (i.e. clear cuts, human settlements). As development proceeds in the Ring of Fire, the number of linear features will increase while the amount of clear cuts will be limited due to the growth rates of forests in the Far North. In order to address the magnitude of this type of disturbance on caribou, only linear features were included in the models as an indicator of overall anthropogenic disturbance. Additionally, mixed and deciduous land cover types were highly correlated within the Lowland ranges (but not on the Boreal Shield), so within the James Bay and Missisa ranges we combined these two land covers to a single land cover group (Mixed/Deciduous).

We used the spatial analysis programming language, LSL (Kushneriuk and Rempel 2011) to capture environmental variables and response data. A hexagonal grid comprised of 16 ha cells was used to build nested gridsets (pseudo-hexagons) of increasingly larger sizes (100 ha, 500 ha, 1 000 ha, 5 000 ha, and 10 000ha) corresponding to a range of spatial analysis scales relevant to caribou (DeCesare et al. 2012). These hexagonal gridsets were used to determine the most relevant spatial scale for caribou habitat selection, a critical step in the development of RSFs (Boyce 2006). Land cover and disturbance variables were summarized as the proportion of each

hexagon. Eskers were summarized on the Boreal Shield ranges, but not on the lowlands, where eskers were rare; both eskers and linear features were summarized as m/ha.

Caribou Response

Caribou telemetry location data used in this study was collected through two projects. To help meet the caribou monitoring and assessment commitments in the Caribou Conservation Plan, 140 animals were collared with GPS transmitters across the Far North distribution of woodland caribou in February 2009 and 2010, and an additional 31 collars were deployed across southern ranges and fell into our study area (Avgar et al. 2013). This study area included animals from the eastern migratory and boreal populations (COSEWIC 2011), so we removed 47 eastern migratory caribou from this analysis based on location of calving sites (B. Pond, *pers. comm.*). The Collaborative Woodland Caribou Research Program was the second project and focussed on study sites corresponding to the Kinloch, Nipigon, and Kesagami ranges (Kesagami range not included in analysis) and maintained at least 50 GPS-collared animals in each study site from 2010 to 2013 (see description in OMNR 2012), since some collars failed or fell outside of our study area, an additional 88 caribou were included in this analysis. Since we used data from two different projects with different fix rates, we randomly selected 1 fix per day (of the most accurate fixes) for each animal to even sampling effort. In total, >120 000 GPS locations from 212 female caribou between April 2009 to April 2013 were used to develop seasonal resource selection probability functions (RSPFs) across six caribou ranges.

There are principally three ways to define seasons: as a function of calendar date, biological or physiological factors, or weather conditions. Due to the variability in

calving dates even within a single range (Wilson 2013) as well as the large geographic extent and subsequent variability in climatic patterns, we chose to establish 4 seasons based on calendar dates to ensure consistency both within and across ranges. The seasons were: Spring (including the pre-calving and calving periods): April 15-June 21, Summer: June 22-September 21, Fall: September 22-December 21, Winter: December 22-April 14. All animals were collared in February, so new animals were not included in the analysis until the beginning of the subsequent season (spring). See Appendix A for number of animals included in each season by range. Utilization distributions (UDs) map the intensity of caribou use, essentially creating density-contours of telemetry locations. Contours (or isopleths) smooth across individual animal locations, thereby reducing concerns over outliers and other issues regarding individual animal locations (Marzluff et al. 2004). UD identifies landscape areas that have been encountered by individuals, and areas within these mapped distributions can be classed into of high- versus low-probability of use of resources across a home range. We calculated individual seasonal kernel density estimates to determine UD for animals with ≥ 30 GPS locations within a season (≥ 50 locations in winter) (Millspaugh et al. 2006) using Geospatial Modelling Environment version 0.7.2.1 (Beyer 2012) with the “PLUGIN” bandwidth estimator to create 25 m raster cells. UD were bounded by the 99% isopleth and standardized.

Resource Selection and Hypothesis Testing

We consider resource selection as the act of using a resource if it is encountered, and the probability of resource selection as the probability that a resource unit (of some specified type) is selected, when encountered (Lele et al. 2013). We treated resource selection as season-specific within a range, but not year-specific, so we pooled data

across years within a season and range. To summarize overall use among all animals within a range we merged individual-based, seasonal UD maps within a range by overlaying the 16 ha hexagon grid and using the maximum UD value by season for any given hexagon. We equated areas of high-use as ‘selected’ by caribou and low-use as ‘not-selected’. Low-use includes those areas through which a caribou may traverse quickly to reach an area of high-use. We defined ‘selected’ as any hexagon where the value was within the 90th percentile of the UD within a season and range, and likewise ‘not-selected’ as below the 50th percentile. Values between the 50th and 90th percentile were not included in the analysis. Operationally, ‘not-selected’ was as an area of the landscape that at least one caribou had encountered in at least one season, but overall was rarely used by any caribou in the range for that particular season. We randomly sampled the UD maps to create a subsample of analysis units (hexagons), and then used logistic regression (with intercept) to estimate the resource selection probability function (RSPF). The intercept was included in the logistic regression model because the sampled analysis units identify areas in the landscape that were encountered and then either selected or not-selected; thus the models predict absolute rather than simply relative probabilities of selection (Boyce et al. 2002; Manly 2002; Lele and Keim 2006; Lele et al. 2013). Note that because analysis of “available” habitat is restricted to areas underlying the UD maps, the interpretation of selection also is technically restricted to those underlying areas. However, the mapped UD maps encompass 65% - 80% of the range, so selection coefficients should be a reasonable estimate for the entire range. To visually assess whether our modeled estimates of resource selection (i.e., use relative to availability) are consistent with resource availability throughout the range, we graphed relative proportional use of

environmental variables within UDs versus availability across entire range for each of the 6 ranges and 4 seasons.

During a preliminary assessment of analysis across 5 spatial scales (100, 500, 1 000, 5 000, and 10 000 ha spatial analysis units) we used Akaike's Information Criterion (AIC) selection procedures to select the spatial analysis scale at which the model was best supported, and found that patterns of selection were best supported at the broadest spatial extent (10 000 ha) for all ranges (Fig. 3). We used values from the 10 000 ha analysis scale to characterize environmental conditions for the landscape context, but used values at the 16 ha scale to characterize resource selection. So for example, a sampled 16 ha hexagon was identified as either selected or not-selected by caribou, and included in this data record were the landscape environmental variables assessed at the 10 000 ha scale. To avoid bias from arbitrary boundaries or placement of the 10 000 ha gridset, we performed spatial averaging equivalent to a 'moving-window' average.

We used Bayesian logistic regression to calculate RSPFs and compare resource selection as defined under each hypothesis (outlined in Table 1) within each season and caribou range. Bayesian regression provides an efficient approach to testing whether a model developed for one range could be applied to the 2nd, paired range. We used the program BBR (Binary Bayesian Regression (Genkin et al. 2007) to specify variable coefficients for the first model as "priors" for the 2nd paired range, and allowed these to vary with new data. This allowed us to test if similar patterns of habitat selection were occurring in the 2nd range. We used a Laplace distribution as the form of both the general prior and the individual priors as this distribution is more conservative (parsimonious) than Gaussian for variable selection (Genkin et al. 2007). In each of the

model development ranges we randomly selected 20 000 of the 16 ha hexagons across selected and not-selected categories, stratified in proportion to use for each season. This resulted in 10 subsets of 2 000 data records to develop Bayesian logistic regression models using the train component of the BBR software and a supporting analysis interface called BBRI (Binary Bayesian Regression Interface) (Rempel 2013). Models for each hypothesis were created using each subset of data and the coefficients were averaged and used as priors in the final model. Models were then evaluated on the paired evaluation range for each region using a separate random sample of 5 000 data records.

We used area under the curve (AUC) of the resource operating characteristic (ROC) as well as sensitivity and specificity (Bonn and Schroder 2001) to determine model performance, including strength of model predictions. AUC is a threshold-independent approach to evaluating how well the data fits the model (Fielding and Bell 1997) and we considered models with $AUC > 0.6$ as having sufficient evidence to include in the plausible-model selection set. A threshold determines the minimum probability-of-selection that is classed as a 'predicted positive'. We used a tuned threshold that was determined by balancing the error rate between false positive and false negative predictions (Bonn and Schroder 2001). A threshold is required for evaluating sensitivity and specificity. Sensitivity is the conditional probability that any given case is correctly classified ($a/(a+c)$), while specificity is the inverse ($d/d+b$), where a = number of true positive observations, b = false-positives, c = false negatives, and d = true negatives (Fielding and Bell 1997).

We tested the validity of models by developing models in one range, and then applying and evaluating performance of the model in a paired adjacent range that was

physiographically similar. We used AUC to estimate model fit, and for this evaluation we expected a fairly strong fit with the data. A model was only considered successful if the AUC was ≥ 0.7 in the evaluation range, in which case the same model was applied to both ranges. If the model evaluation AUC was < 0.7 then a new Bayesian regression model was estimated, where model coefficients from the first model were set as individual priors and were permitted to vary.

We used informed Akaike's Information Criterion (AIC) model selection procedures to select among the five *a priori* hypotheses regarding resource selection for each range (Burnham and Anderson 2002). The best model has the lowest AIC value, but when alternative models have a $\Delta AIC < 2$, then this indicates relatively equal support among those models, and conversely, if $\Delta AIC > 2$ relative to the next closest model then this indicates substantial support for the top model (Burnham and Anderson 2002). The rank order of the AIC values indicates the rank order of support for the statistical hypothesis, while AIC model weight estimates the relative support for that model relative to all other candidate models.

Following model selection we re-estimated coefficients using z-deviates (data standardized to unit variance) to provide pseudo-standardized coefficients and estimates of effect size for each variable, allowing us to approximately rank the relative importance of each variable in the model (Menard 1995; Zar 1996).

Results

The global model, which integrates factors from the alternative hypotheses, was supported as the top hypothesis driving caribou habitat selection across all seasons and

ranges (20 seasonal RSPFs; Table 2). Other than models for the James Bay range, the global model had very high AIC model weights ranging from 0.98 to 1.0, and with ΔAIC values all > 20 (Appendix A), indicating little to no support for any alternative to this model. In the boreal shield regions, the next best hypothesis (either apparent competition or browse refuge) had a $\Delta\text{AIC} > 48$ (range 48.18 to 196.8; see Appendix A for full range of AIC values). Only in the in James Bay range did the alternative browse availability hypothesis gain some support, with a $\Delta\text{AIC} = 2.24$ and with model weights of 0.66 and 0.25 for the global model and browse availability hypothesis, respectively. The disturbance hypothesis consistently had the least amount of support across all ranges and seasons (Table 2).

Resource Selection Probability Functions

RSPFs revealed seasonal and range-based differences in habitat selection among the study regions; the top models for each season and range are mapped in Fig. 4. While there were substantive differences in environmental variable coefficients, we identified some trends that were consistent across all regions. Linear features had a negative association with resource selection across all regions as seasons, but the strength of this relationship differed by range. Water had a positive relationship with resource selection in spring, summer, and fall, but a negative relationship in winter. Deciduous and mixed forests generally had a negative association with resource selection across the ranges, and sparse forest generally had a positive association.

In the DBS region the spring model developed on the Nipigon range performed poorly on the Pagwachuan range ($\text{AUC}=0.65$), so a separate spring model was developed for Pagwachuan. The main differences between these two models were with the open

peatland, deciduous forest and mixed forest variables (Fig. 5A). Open peatland had a strong association with resource selection in Pagwachuan, but minimal effect in Nipigon; open peatland was 10 times more prominent on Pagwachuan than Nipigon (Fig. 6). The summer model was suitable for both ranges, with an AUC of 0.70 in Pagwachuan. Deciduous forest had a strong, negative association with resource selection, whereas eskers, coniferous forest, and sparse forest had a positive association with resource selection (Table 3). In contrast, the fall RSPFs for the Nipigon and Pagwachuan ranges were highly divergent (Fig. 5A). In Nipigon deciduous forest had a strong, negative association with resource selection, but in Pagwachuan this relationship was positive. Linear features had a small impact on the Nipigon model, but had a strong, negative association with resource selection in Pagwachuan. In both ranges, areas with a reduced density of linear features were selected relative to availability, but the effect was much stronger in Pagwachuan, where areas selected had a linear feature density approximately 15 times lower than the average density for the entire range (Fig. 7A). In winter the biggest differences between the two ranges were with mixed forest, natural disturbance and linear features (Table 3). Natural disturbance had a strong, negative association with resource selection in Nipigon, but in Pagwachuan there was a slight positive association. In Nipigon natural disturbance occurs on 8% of the range, whereas in Pagwachuan less than 1% of the range is affected by natural disturbance (Fig. 6), so selection varied according (Fig. S1).

In the UBS region the relationship between landcover variables and resource selection was similar between the Kinloch and Spirit Ranges. In spring, fall, and winter, the RSPFs developed in Kinloch were successfully evaluated on the Spirit range with

AUC values of 0.73, 0.72, and 0.78 respectively (Table A1). Treed peatland had a strong, positive association with resource selection and mixed forest had a strong, negative association. Deciduous and mixed forests as well as natural disturbance all had strong, negatively associations with resource selection and treed peatland had a positive association in all seasons (Fig. 5B, Fig. 7). In winter, natural disturbance and water were the top ranked variables and both had a negative association with resource selection (Fig. S2). In summer, the Kinloch model performed poorly on the Spirit range (AUC 0.63) so a separate summer model was developed for Spirit. In Spirit, open peatland had a strong, positive association with resource selection in summer, but in Kinloch open peatland had a weak and slightly negative association due to differences in use (Fig. S1). Natural disturbance had a moderately weak and negative relationship with resource selection in Nipigon and this relationship was stronger and positive in the Spirit range (Table 3). In Spirit, over 21% of the landscape was affected by natural disturbance, compared to 16% in Kinloch (Fig. 6).

In the HBL region the models were divergent between the Missisa and James Bay ranges and none of the models developed in Missisa performed well in the James Bay range. In spring, natural disturbance and linear features had strong, negative associations with resource selection in Missisa, but these variables had minimal impact on the James Bay model. Open peatland and coniferous forest both had a positive association with resource selection in Missisa, while in James Bay these associations were negative. In summer open peatland and mixed/deciduous forest had negative associations with resource selection in the James Bay range. In contrast, open peatland had a strong, positive association with resource selection in Missisa. Treed peatland, sparse treed, and

conifer forest also had strong, positive associations with resource selection in Missisa, but not in James Bay (Fig. 5C, Fig. 7). Treed peatland composed 35% of the landscape in Missisa and 47% of the landscape in the James Bay range (Fig. 6).

Discussion

In this study, we contrasted caribou habitat selection patterns that exhibited important differences across 3 regions varying both in the amount of anthropogenic disturbance and dominant landform. The patterns of habitat selection consistently supported the global model, suggesting that caribou select habitat in response to multiple stressors. Caribou select habitat by minimizing apparent competition, selecting high browse availability, and avoiding disturbance across all seasons. While the global model used a common set of variables, in most cases the coefficients associated with the model were range specific. Our models provide support for the theory of spatial segregation, whereby caribou avoid areas with high moose density and high predator encounter rates such as deciduous and mixed forests, naturally disturbed areas, and linear features (James et al. 2004; Courtois et al. 2008; Fortin et al. 2008; Bowman et al. 2010; Avgar et al. 2015). Caribou select areas of 'refuge' such as peatlands and conifer forests to forage and minimize predation risk (Rettie and Messier 2000; McLoughlin et al. 2010). Our models can be used by biologists and land-use planners to identify areas of critical habitat that would benefit most from protection.

We integrated the advantages of individual UD maps derived from collar location data with Bayesian logistic regression to develop seasonal and range-specific RSPFs. Our logistic regression approach to calculating resource selection probability functions is based randomly sampling UD maps to estimate both selected (high-use) and not-selected

(low-use) categories. This approach avoided the bias associated presence/availability studies that pair collar locations (known-use, presence locations) with a set of availability data derived from randomly sampling a habitat map (unknown-use, available locations) (Boyce et al. 2002). The approach of dichotomizing the continuous utilization distribution into presence/absence categories may lose information relative to Poisson regression techniques that sample the continuous surface (Millspaugh et al. 2006), but we believe in this case the binary logistic regression approach facilitated the *a priori* model testing and better understanding of the factors driving caribou resource selection. By modeling areas of highest use versus lowest use, we increase our understanding of the habitat most critical to caribou. This approach may also be less sensitive to differences in the UD resulting from kernel algorithms or home-range analysis software. The coupling of Bayesian logistic regression with AIC informed model selection procedures allowed us to effectively define and test the 5 *a priori* hypotheses, while accounting for variability in the number of predictive variables associated with each hypothesis. Changes in both AIC and model weights allowed us to establish not just the rankings, but also the magnitude of support for alternative hypotheses. The multiple scale approach of assessing a hierarchical set of spatial analysis units allowed us to explore the most important spatial extents where resource selection occurred across the range. While a scale-integrated approach (as in DeCesare et al. 2012) may have permitted the investigation of finer scales, we were unable to complete this type of analysis due to the resolution of the telemetry data. Future studies may improve our understanding of caribou habitat selection in Ontario at finer spatial scales by integrating this type of approach (DeCesare et al. 2012).

Our results contrasted regional and temporal differences in caribou habitat selection across six ranges of interest. In the undeveloped boreal shield the landscape composition and structure was similar between the model development and evaluation ranges, and we were able to use a single RSPF to predict resource selection on both the Kinloch and Spirit ranges in 3 of 4 seasons. However, when landscape composition differed greatly due to environmental or disturbance gradients, we found that models less accurately predicted habitat selection from one range to another. This is consistent with recent studies by Moreau et al. (2012) and Johnson et al. (2015), which determined that the landscape context is necessary to understand regional differences in habitat selection by caribou. In addition to the differences in spatial structure, we also observed differences in caribou behaviour across the ranges. Spirit was the range with the highest disturbance (>20%), and here caribou appeared to select recently disturbed areas, suggesting that caribou may have some plasticity in their tolerance of natural disturbance (Moreau et al. 2012).

Together with changes in environmental conditions, patterns of resource selection, and changes in behaviour, our results provide evidence to support the delineation of these caribou management ranges in Ontario. In regions where environmental variables, landscape disturbance, or animal behaviour differ greatly, we recommend analysing seasonal patterns of habitat selection by range to elicit the relative impact of model parameters on selection. However, although the separation of models into seasonal and range specific versions increased the predictive power of the models within those divisions, it did mean sacrificing a more general model of the functional factors that drive caribou resource selection across regions and seasons. However, given

that caribou are managed at the range level in Ontario, and Environment Canada (2008) suggested this scale for determinations of critical habitat, we determined this to be the adequate unit to assess habitat needs. To facilitate application of the RSPF models for land-use planning and scenario analysis of alternative development options, we developed a graphical user interface based in the LSL programming environment to apply the range level models (Kushneriuk and Rempel 2011; Rempel and Elliott 2013).

Our study allows comparisons of habitat selection between lowland-dominated and boreal shield areas by integrating finer scale aspects with the broader patterns of selection (i.e., selection of high-use areas within a range or, between the first- and second-orders of selection (Johnson 1980). Through this assessment, the most important landscape features necessary to ensure a self-sustaining caribou population within a range can be identified. Linear features were selected against in all ranges and naturally disturbed areas were also largely avoided, regardless of location. However, the strength of selection differed across ranges and seasons, similar to differences in the zones of influence for central mountain caribou (Johnson et al. 2015). We also found that caribou selected treed peatlands, consistent with previous research (Dyer et al. 2002; Poley et al. 2014). However, there was both spatial and temporal variation in this relationship, whereby caribou selected treed peatlands in spring, summer and fall, but not winter on the shield, and only in spring and summer in the lowlands. The differences in this relationship across ranges could be explained by the differences in the availability of peatland complexes on and off the shield. In shield ranges, treed and open peatlands comprised 7-33% of the ranges, whereas in the lowlands, these peatland cover types composed over 60% of the landscape (Fig. 5). The differences in these relationships

across ecozones are consistent with previous work (Poley et al. 2014), and demonstrate the need for regional habitat models. Our results also showed temporal variation in selection of water, whereby caribou selected for lakes in ice-off seasons (spring, summer, and fall), but avoided water during the winter season. Ferguson and Elkie (2005) demonstrated that caribou select for lakes in winter due to lower snow accumulation and high predator detectability in these areas. However, Poley et al. (2014) reported that caribou did not select for lakes in winter. In a recent study within Kinloch and Nipigon Ranges, wolves were shown to select areas close to water, including shorelines, which could improve visibility of prey and provide travel corridors (Anderson 2012). This suggests that caribou could be avoiding these areas due to a perceived increase in predation risk during winter months.

We characterized environmental variables in relation to the probability of resource selection at 6 different spatial scales. Previous studies have shown that caribou avoid natural and anthropogenic disturbances at distances from 1 to 10 km (Dyer et al. 2001; Leblond et al. 2011; Rudolph 2011), and our results imply that habitat selection occurs at broad spatial scales (10 000 ha) with an analysis unit radius of 5.6 km. This has implications for land-use planning as broad landscape-scale patterns of disturbance (both natural and anthropogenic) can negatively influence caribou habitat selection.

Development of conservation strategies must consider broad-scale patterns of caribou habitat selection, such as preference for treed and open peatlands, avoidance of mixed and deciduous forests, and avoidance of both natural and anthropogenic disturbance. The impacts of linear features such as winter ice roads, all season roads, hydro-electric lines and railways, can be multiplicative by increasing predation risk (James and Stuart-Smith

2000; Whittington et al. 2011; Leblond et al. 2013) and functional loss of high quality habitat due to feature avoidance at broad spatial scales (Dyer et al. 2002; Schindler et al. 2006; Polfus et al. 2011). Road development near wetlands can have significant negative impacts on the biodiversity of plants, herptiles, and birds at both fine and broad spatial scales (Findlay and Houlihan 1997; Keddy 2010) by altering drainage patterns, interrupting water flow and changing the fire regime, which can lead to widespread changes on the landscape (Keddy 2010).

As development continues to push northwards, encroaching on previously undisturbed habitats to develop areas such as the Ring of Fire area in Ontario (Ontario Geological Survey 1997; Far North Science Advisory Panel 2010), we recommend that land-use planners utilize RSPF models for caribou, in an adaptive management framework, to assess the potential impacts and risk of alternative development options on general ecosystem condition (Johnson et al. 2004). In other parts of Canada, caribou populations are rapidly declining, due to a combination of factors including habitat loss due to industrial development (Festa-Bianchet et al. 2011; Environment Canada 2012). As the impacts of habitat loss can be magnified at a range scale due to the spacing out strategy caribou utilize to minimize predation risk (Festa-Bianchet et al. 2011), continued industrial development within caribou ranges could result in local extirpation of caribou populations (Johnson et al. 2015). As a result, landscape-level planning and habitat management on a range-level has been recognized as an urgent priority for recovery of boreal caribou (Environment Canada 2012). Environment Canada (2011) suggests that when more than 35% of the range is disturbed, the probability for sustained growth declines, increasing the extinction risk. This threshold provides a useful starting point,

but our models suggest the magnitude and threshold for disturbance effects likely differ among landscapes, which could alter the impact of development on caribou populations. Future work should focus on evaluating resource management and land-use planning policy scenarios as the human footprint increases and the impacts of climate change intensify across the Far North of Ontario.

Acknowledgements

We would like to thank the CNFER Northern Mammal Ecology Research Program and the Far North Caribou Conservation Program for sharing their caribou location data. Special thanks to Julie Elliott for writing LSL scripts, Rob Kushneriuk for supporting additions to the LSL programming language, Kevin Downing and Jevon Hagens for assembling GIS data, and Ian Smyth for assistance with disturbance data. We gained thoughtful insights through discussions with Art Rodgers, Bruce Pond, Darren Elder, Kevin Green, Gerry Racey, Jen Shuter and Cheryl Chetkiewicz. We also thank two anonymous reviewers for very helpful comments on the manuscript.

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Table 1. Hypotheses summarized with variables and predicted seasonal directionality of each relationship in brackets. We included 5 hypotheses in our analysis; Browse Availability (BA), caribou will select areas of high browse availability; Browse Refuge (BR), caribou (*Rangifer tarandus caribou*) will select areas of high browse availability and cover for refuge; Apparent Competition (AC), Caribou will avoid areas of high moose competition and select areas of low competition with moose; Disturbance (D), caribou will avoid areas of high road density and areas with high natural and anthropogenic disturbance; and the Global (G) hypothesis, which included all variables.

Variable	Hypothesis	Season			
		Spring	Summer	Fall	Winter
Conifer forest ¹	BA, BR, AC, G	+	+	+	+
Treed peatland ²	BA, BR, AC, G	+	+	+	+
Open peatland ²	BA, BR, G	+	+	+	+
Sparse treed forest ³	BA, BR, G	+	+	+	+
Eskers ⁴	BA, BR, G	+	+	+	+
Water ⁵	BR, G	+	+	+	-
Deciduous forest ⁶	AC, G	-	-	-	-
Mixed Forest ⁷	AC, G	-	-	-	-
Natural disturbance ⁸	D, G	-	-	-	-
Linear features ⁹	D, G	-	-	-	-

¹ (Fortin et al. 2008); ² (Bradshaw et al. 1995, Rettie and Messier 2000); ³ (Bradshaw et

al. 1995, Rettie and Messier 2000, Fortin et al. 2008); ⁴ (Racey et al. 1999); ⁵ (Neufeld

2006, Fortin et al. 2008, Semeniuk et al. 2012); ⁶ (Vors et al. 2007, Bowman et al. 2010);

⁷ (Vors et al. 2007, Fortin et al. 2008, Bowman et al. 2010); ⁸ (Dyer et al. 2002, Vors et al. 2007); ⁹(Vors et al. 2007, Bowman et al. 2010, Dussault et al. 2012)

Table 2. Ranked support for each hypothesis by season for the ranges where models were developed. Hypotheses were ranked based on AIC model selection (See Table A1). Seasons are spring (SP), summer (SU), fall (FA), and winter (WI).

Boreal Shield	Nipigon				Pagwachuan				Kinloch (Spirit)				Spirit
Hypothesis	SP	SU	FA	WI	SP	SU*	FA	WI	SP	SU	FA	WI	SU ⁺
Global	1	1	1	1	1		1	1	1	1	1	1	1
Competition	2	3	2	2	4		4	2	2	3	2	2	2
Browse Refuge	3	2	3	4	2		2	3	3	2	3	3	3
Browse Availability	4	4	4	5	3		3	4	4	4	4	4	4
Disturbance	5	5	5	3	5		5	5	5	5	5	5	5
Lowlands	Missisa				James Bay								
Hypothesis	SP	SU	FA	WI	SP	SU	FA	WI					
Global	1	1	1	1	1	1	1	1					
Browse Refuge	4	2	3	2	3	3	3	2					
Competition	2	3	2	4	4	4	4	4					
Browse Availability	5	4	4	3	2	2	2	3					

Disturbance	3	5	5	5	5	5	5	5
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*Only 3 seasons modeled, Nipigon summer model evaluated with an AUC>0.7 so applied to Pagwachuan range

⁺ Only summer season modeled, Kinloch models evaluated (AUC>0.7) so applied to all other seasons.

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Table 3. Top model coefficients from Resource Selection Probability Functions as selected through AIC (see Table A1) for 6 ranges and 4 seasons. Models were based on standardized data, so magnitude of standardized coefficients approximately represents relative effect size¹.

Range	Open		Treed		Sparse		Natural		Linear	
	Water	Peatland	Peatland	Treed	Conifer	Deciduous	Mixed	Distrubance	Features	Eskers
Spring										
Nipigon	0.590	0.050	0.340	0.050	0.308	-1.374	0.518	-0.204	-0.175	0.329
Pagwachuan	0.188	1.183	0.205	0.114	0.308	-1.250	0.021	-0.859	-0.554	0.465
Kinloch	0.499	-0.060	0.720	0.377	0.275	-0.267	-0.539	-0.250	-0.329	0.001
Missisa	0.325	0.407	0.110	0.153	0.342		-0.028 ³	-1.102	-1.367	
James Bay	-						-0.222 ³			
	0.046	-0.780	0.387	0.122	-0.451			0.057	-0.013	
Summer										
Nipigon ²	1.381	0.315	0.388	0.652	0.854	-0.601	0.612	0.152	-0.176	0.439
Kinloch	0.685	0.008	0.866	0.221	0.569	0.198	0.130	-0.195	-0.254	0.066

Spirit	0.894	0.800	0.848	0.474	0.530	-0.472	0.131	0.812	-0.287	-0.175
Missisa	1.130	1.195	1.934	1.080	1.178		0.272 ³	-1.869	0.228	
James Bay	-						-0.417 ³			
	0.061	-0.728	0.315	0.052	-0.411			-0.065	-0.031	
Fall										
Nipigon	0.850	0.321	0.537	0.348	0.531	-1.311	0.510	-0.059	-0.001	0.211
Pagwachuan	0.160	1.167	0.838	0.133	1.099	0.939	-0.890	-0.625	-1.142	0.593
Kinloch	0.328	-0.374	0.409	-0.014	-0.102	-0.504	-1.099	-0.625	-0.268	0.117
Missisa	0.464	0.656	0.191	0.591	0.336		-0.570 ³	-0.301	-0.548	
James Bay	-						-0.148 ³			
	0.158	0.103	0.394	0.563	-0.526			-1.253	-0.410	
Winter										
Nipigon	-							0.559	-0.175	-0.023
	0.405	0.264	0.018	0.188	0.109	-0.365	-0.042			
Pagwachuan	0.143	0.326	0.201	0.564	0.015	-0.235	-0.718	0.290	-1.342	0.136
Kinloch	-	0.264	0.018	0.188	0.109	-0.365	-0.042	-0.559	-0.351	-0.023

	0.405							
Missisa	-					0.246 ³		
	0.003	1.563	0.003	1.492	-0.109		-1.305	0.546
James Bay	-					-0.032 ³		
	0.242	0.429	0.040	0.434	-0.465		0.041	-0.300

¹Data was z-deviate transformed and Bayesian logistic regression was used to develop models.

²In spring, fall, and winter, the Kinloch models were applied to the Spirit Range, and the Nipigon summer model was applied to the Pagwachuan range (AUC > 0.7 for evaluated models).

³In the Missisa and James Bay ranges, mixed and deciduous classes were combined to reduce collinearity.

Figure Captions

Figure 1. Regions and defined caribou range management areas in Ontario. Each of the 3 regions was comprised of two caribou (*Rangifer tarandus caribou*) ranges in the Hudson Bay Lowlands and the Boreal Shield (Developed/Undeveloped) Regions, Ontario. The stippled ranges were used for model development and the hashed regions were used to evaluate the models. The dashed line represents the northern limit of commercial forestry.

Figure 2. Current permanent roads, winter roads and proposed road corridors to access minerals (north-south and east-west), active mines, First Nation communities and caribou (*Rangifer tarandus caribou*) ranges located in the Ring of Fire area in the far north area of Ontario.

Imagery illustrates physiographic differences and similarities among range management areas. Hudson Bay Lowlands ecozone lies to the east and Boreal Shield to the west. Claims data was obtained on February 24, 2014 (Ministry of Northern Development and Mines 2014). ArcGIS imagery sources Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community.

Figure 3. An example of the preliminary analysis showing standardized coefficients at 6 different hexagon sizes for 4 selected variables within the global model for the Nipigon range in fall.

Dotted lines represent the standard error on the coefficient estimate.

Figure 4. Probability of habitat use for 6 caribou (*Rangifer tarandus caribou*) management ranges across 4 seasons in northern Ontario predicted using seasonal resource selection probability functions. Colour breaks represent a change of 1 standard deviation; lighter shades depict areas with no to minimal probability of use, whereas darker shades indicate areas with a higher probability of use.

Figure 5. Standardized coefficients for seasonal models for all variables in the top selected RSPFs. Circle size indicates effect size of the variable, with larger circles indicating larger deviance from 0, for (A) Nipigon and Pagwachuan in the Boreal Developed Region, (B) Kinloch and Spirit in the Boreal Undeveloped Region, and (C) Missisa and James Bay in the Hudson Bay Lowlands Region. Values for the model development range are in white for each region, dark grey indicates values for the model evaluation range and light grey indicates the same model was used both ranges in the region. A model was not developed for the central Ozhiski range because of low collaring effort (Berglund et al. 2014).

Figure 6. Relative proportion of environmental variables across 6 ranges of interest for caribou (*Rangifer tarandus caribou*) in northern Ontario, Canada. Cover types are expressed as relative proportion, linear features are expressed as $\text{km} \times \text{ha} \times 10^{-1}$.

Figure 7. Relative proportional use by caribou (*Rangifer tarandus caribou*) of environmental variables (within mapped utilization distributions) versus availability (across entire range), for each of the 6 ranges and 4 seasons, in northern Ontario, Canada, for (A) Linear Features, (B) Deciduous forest, (C) Coniferous forest, and (D) Treed Peatland. Cover types are expressed as relative proportion, linear features are expressed as $\text{m} \times \text{ha} \times 10^{-1}$. Note that the y axes are scaled to each variable for ease of interpretation. Figures S1 and S2 show remaining variables.

- Active Mines
- First Nations Communities
- Northern Limit of Forestry
- Proposed East-West Road
- Proposed North-South Road
- Railway
- Ring Of Fire Claims
- Caribou Management Ranges
- Provincial Parks

Ecozones

Ecozone Name

- Hudson Bay Lowlands
- Boreal Shield

Ontario Roads

National Road Class

- Expressway / Highway
- Secondary Highway
- Primary Roads
- Winter Roads