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Original Research

A Bayesian Approach to Characterizing Habitat Use By, and Impacts of Anthropogenic Features On, Woodland Caribou (*Rangifer tarandus caribou*) in Northeast British Columbia

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Abstract

Woodland caribou (*Rangifer tarandus caribou*) ranges in northeast British Columbia (BC) have been altered by industrial forestry and oil and gas development. In addition to numerical and functional changes in the predator-prey system, these habitat changes might be altering habitat use by caribou. Our objective was to understand impacts of anthropogenic disturbances and fire on the composition of woodland caribou home ranges to inform decisions about where, and to what extent, different habitats need to be restored to serve as effective caribou habitat. We used a non-parametric Bayesian analysis to model selection of habitats in their current condition, and then estimated selection in an hypothesized landscape without anthropogenic features and fire to identify potential areas for habitat restoration in the Parker woodland caribou range of northeast BC. Treed bogs and poor fens were selected by woodland caribou among all seasons analyzed (based on comparisons with a random dataset) and areas of high linear feature density were avoided, particularly in late fall and late winter. Unexpectedly, areas closer to early seral/immature forest habitats were selected. The slopes of selection curves were relatively shallow and model precision (i.e., proportion of correct predictions) was <60% for all seasons, suggesting that woodland caribou were not particularly discriminating in their selection of home ranges, at least with respect to the factors analyzed. Anthropogenic features and fires negatively affected 43-75% of the Parker range and selection of these areas by woodland caribou was 8-11% lower than expected compared to the hypothesized landscape without anthropogenic features and fire, depending on season. The models generated by the Bayesian approach were more intuitive than traditional parametric methods and provided a platform for generating predictions regarding the effectiveness of mitigation or restoration activities.

Key Words: Anthropogenic Disturbance, Bayesian Approach, Boreal Forest, Habitat Use, Woodland Caribou

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INTRODUCTION

Woodland caribou (*Rangifer tarandus caribou*) currently pose one of Canada's most significant conservation challenges. The species is in decline throughout most of its circumpolar distribution (Vors and Boyce 2009) and the Committee on the Status of Endangered Wildlife in Canada rated the boreal population as *Threatened* (COSEWIC 2002). The proximate threat to most woodland caribou local populations is hypothesized to be high predation rates resulting from human-caused habitat change. Changes have increased the abundance of other ungulates and consequently the abundance of predators (principally wolves [*Canis lupus*]), which have in turn affected woodland caribou survival (Seip 1992; Wittmer *et al.* 2005; Latham *et al.* 2011b; Environment Canada 2012). Climate change (Vors and Boyce 2009; Latham *et al.* 2011b), disease, nutrition, disturbance (Wasser *et al.* 2011), and hunting (Courtois *et al.* 2007) have also been identified as potential factors contributing to the species' decline.

In addition to the demographic impacts of habitat change, woodland caribou in the boreal forest alter their behaviour in the presence of linear features and forest harvesting, although results of studies have been inconsistent (e.g., Stuart-Smith *et al.* 1997; Dyer *et al.* 2001; Courtois *et al.* 2007; Proulx 2013; Johnson *et al.* 2015).

Habitat selection by woodland caribou and other wildlife species is usually estimated by modelling resource selection functions (Manly *et al.* 2002), using a series of candidate explanatory variables and model selection criteria (Burnham and Anderson 1998). Despite its popularity, we argue that this technique generates results that are difficult to interpret for management purposes, in particular when >1 model has support, when categorical variables are analyzed, or when inferences about absolute, rather than relative selection, are of interest. These are all important factors when considering the management implications of habitat selection studies.

We conducted a study of habitat use by woodland caribou in northeast British Columbia (BC) using radio-collar data to inform decisions about where, and to what extent, different habitats need to be restored to serve as effective caribou habitat. We present an analysis technique based on fitting habitat use data to non-parametric Bayesian networks. This method is conceptually simpler than many parametric alternatives and can be used to test hypotheses regarding the expected benefit of management actions.

STUDY AREA

Our study area was composed of 5, federally designated woodland caribou ranges in the northeast corner of BC (Figure 1; Environment Canada 2012). The landscape is a mosaic of deciduous and mixed-wood uplands, poorly drained low-lying peatlands, and riparian areas (DeLong *et al.* 1991). Common upland tree species include white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta*), trembling aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*). Low-lying peatlands are characterized by black spruce (*Picea mariana*) intermixed with stands of tamarack (*Larix laricina*). Terrain is predominantly flat to undulating (elevation range: 214-1,084 m) and the climate is northern continental, characterized by long, cold winters and short summers (Environment Canada 2015). Forest fire is a frequent natural disturbance with a mean fire interval of approximately 100 years (Johnstone *et al.* 2010).

MATERIALS AND METHODS

Wildlife capture and collaring

We deployed Iridium GPS radio-collars from 2 manufacturers (Advanced Telemetry Systems [ATS], Isanti, MN, model #2110E, and Lotek Wireless Inc., Newmarket, ON, model IridiumTrackM 2D) on 27 adult female (≥3 years old) woodland caribou in northeast BC, Canada. Each radio-collar was equipped with a release mechanism that either released the collar on remote command or low battery (ATS), or by a timed blow-off device (Lotek).

We captured caribou by net-gunning from a helicopter during December-March 2011 and 2012, following approved government and institutional animal care protocols (*BC Wildlife Act* Permits FJ12-76949 and FJ12-80090; University of Alberta Animal Use protocol # 748/02/13). We deployed collars programmed to obtain a GPS location (or fix) every 2 or 4 hours during the calving/post-calving season (15 April-15 July), and once per day otherwise.

Prior to data analyses, we removed all locations with low positional accuracy (i.e., non- 3-dimensional fixes; Lewis *et al.* 2007). We then excluded outlying locations that were beyond the range of biologically possible movement using the methods described in Bjørneraas *et al.* (2010). We also removed the first 2 weeks of fixes post-capture to reduce the effects of capture-related behavioural alterations (Morellet *et al.* 2009) and from 10:00-18:00 h on dates of aerial surveys to reduce behavioural effects associated with helicopter disturbance.

Environment variables for modelling

For characterizing habitat, we used Enhanced Wetlands Classification (EWC) GIS data (30x30-m pixel resolution) produced by Ducks Unlimited Canada (Ducks Unlimited, Inc. 2010), which we collapsed into 7 categories that were biologically meaningful to caribou (Table 1). Areas with little or no terrestrial vegetation (category "other"), except where captured in other map layers (see below), were not analyzed.

For rivers, lakes, major roads and forestry data (fires, cut blocks, and forestry roads), we used data sets from the BC Geographic Data Discovery Service (http://data.gov.bc.ca). We combined cut blocks and forest fires <50 years old to create a unified variable describing early seral and immature forest vegetation, which has been shown to be important in caribou habitat selection (Dalerum *et al.* 2007; Sorensen *et al.* 2008; Hins *et al.* 2009). For anthropogenic features such as well sites, pipelines, seismic lines (1996 to present) and petroleum development roads, we accessed data sets from the BC Oil and Gas Commission (http://www.

Table 1. Classification of habitat types used to characterize woodland caribou habitat in northeast British Columbia. Habitat types were developed from Ducks Unlimited Enhanced Wetlands Classification data clipped to the study area (Ducks Unlimited, Inc. 2010).

Habitat Type	Enhanced Wetland Classification Class	Description
Treed bog	Treed bog, Open bog, Shrubby bog	Black spruce- and *Spaghnum* moss-dominated bogs with no hydrodynamic flow.
Nutrient Poor fen	Graminoid poor fen, Shrubby poor fen, Treed poor fen	Low nutrient peatland soils influenced by groundwater flows. Treed poor fens dominate, composed of black spruce, tamarack and bog birch, *Betula pumila;* 25-60% tree cover.
Nutrient Rich fen	Graminoid rich fen, Shrubby rich fen, Treed rich fen	Low nutrient peatland soils influenced by groundwater flows. Shrubby fens dominate, composed of bog birch, willow (*Salix* spp.) and alder (*Alnus* spp.).
Conifer swamp	Conifer swamp	Tree cover >60% dominated by black or white spruce. Occur on peatland or mineral soils.
Deciduous swamp	Shrub swamp, Hardwood swamp	Mineral soils with pools of water often present. At least 25% of tree cover is deciduous (paper birch and balsam poplar [*Populus balsamifera*]).
Upland conifer	Upland conifer	Mineral soils with tree cover >25%. Dominant tree species: black spruce, white spruce and pine.
Upland deciduous	Upland deciduous	Mineral soils with tree cover >25% and >25% deciduous trees. Dominant tree species: aspen and paper birch.
Other	Upland other, Cloud shadow, Anthropogenic, Burn, Aquatic	Uplands: mineral soils with tree cover <25%. Anthropogenic: urban areas, houses, roads and cut blocks. Burns: recent burns where vegetation is limited. Aquatic: includes a continuum of aquatic classes from low turbidity lakes to emergent marshes with aquatic vegetation (not analyzed).

bcogc.ca/public-zone/gis-data). We also used linear feature data from BC Terrain Resources Information Mapping that included all linear features visible on the landscape, regardless of type or age, from 1992 aerial photos (http://www.geobc.gov.bc.ca/base-mapping/atlas/trim/). To create a parsimonious linear feature data set for the study area, we merged all major roads, forestry roads, petroleum development roads, and seismic lines into one file and then integrated the resulting data at a scale of 10-m to eliminate redundancies among the original data sets. We converted linear features to a density metric (km/km^2) based on a 400-m radius moving window and rendered a map coverage at the same 30x30-m pixel resolution as the EWC mapping. Different types of linear features have been associated with different behavioural responses by woodland caribou and their predators (e.g., Dyer *et al.* 2001; Latham *et al.* 2011a) but density provides an overall index of landscape-level impact that has been correlated with woodland caribou demographic trends (Environment Canada 2008). Seismic lines currently account for approximately 65% of the area disturbed by linear features in northeast BC (BC Oil and Gas Commission 2013).

Analysis

We focused our analyses on the selection of home ranges by woodland caribou during late summer (13 August-12 September), late fall (21 October-30 November) and late winter (26 January-15 March; Nagy 2011) seasons within the 5 local population ranges. Although there is evidence that woodland caribou make habitat use decisions at multiple scales (e.g., Apps *et al.* 2001), we focused on the scale of the home range because this is most informative for management decisions. Because the movements of calving and post-calving adult females are restricted (DeMars *et al.* 2013), we omitted this season from our analysis and results are reported elsewhere (DeMars 2015).

To characterize boundaries of home ranges, we generated 80% kernel utilization distributions (UDs) from the GPS location data as described by Börger *et al.* (2006). The 80% utilization isopleth provides a better estimate of seasonal range size than minimum convex polygons for non-territorial species (Börger *et al.* 2006). UDs were estimated using the R package 'adehabitatHR' (The R Foundation, https://www.r-project.org) using the reference bandwidth smoothing parameter.

Because we were interested in the selection of home ranges in relation to the local population range (second-order selection; Johnson 1980), we generated 5,000 random locations within the bounds of the 80% utilization isopleth to characterize the composition of home ranges (DeCesare *et al.* 2012). We also generated corresponding sets of 5,000 random points within the larger local population ranges in which woodland caribou were collared to serve as sets of locations representing random use.

We modeled the difference between sets of locations generated within home ranges and sets of random locations generated within corresponding local population ranges using Bayesian networks (BNs) generated via machine learning. A BN is a graphical model that encodes relationships among variables. The probabilistic dependencies between variables (or "nodes") in a BN are represented by arcs and maintained in conditional probability tables associated with each node. These tables characterize the joint probability distribution of the data (Larrañaga and Moral 2011). In ecological applications, the topology of BNs and their associated probability tables are often derived from expert knowledge (*e.g.*, Marcot *et al.* 2006; McNay *et al.* 2006); however, these relationships can also be "learned" from data without any expert-based prior assumptions.

Because BNs analyze frequency distributions, all continuous variables were categorized into ordinal bins: 0, 0-2, 2-4, 4-8, >8 km/km^2 for linear feature density (to generate similar frequencies among bins); 0, 0-100, 100-500, >500 m for use of, or distance from, early seral/immature forest habitat and lakes; and 0-100, 100-500, and >500 m for distance from well sites and rivers. The 500-m upper limit was selected because distances from early seral/immature forest habitat and anthropogenic features at a 500-m scale have been inferred as important parameters for woodland caribou conservation (Sorensen *et al.* 2008; Environment Canada 2012).

To contrast home range and random datasets, we used the tree-augmented naïve Bayes classifier to learn network topology (i.e., maps predictor variables on a response variable). This method improves on the computationally simpler naïve Bayes classifier by accommodating dependencies among predictor variables (Friedman *et al.* 1997; Cheng and Greiner 1999). We determined the most parsimonious model structure using an information-theoretic criterion called Minimum Description Length (MDL; Lam and Bacchus 1994). MDL is used in artificial intelligence to estimate the number of bits required to represent a model as well as the data given the model. The metric balances network complexity by adding an arc between 2 variables only if the relation is strong enough to compensate (according to the MDL score) for the complexity added by the additional conditional probability table required to encode the relationship. Once the most parsimonious model topology was developed, we fit parameters using maximum likelihood estimation.

The output of the model was the probability that a location associated with a set of "evidence" (i.e., location-specific observations for habitat type, distance to lakes, distance to rivers, distance to early seral/immature forest habitat, distance to well sites, density of linear features) was drawn from the sample of points representing the empirically derived home ranges. For example, in a simple case of 2 habitat types where a woodland caribou home range is associated with a distribution of 75 points in habitat A and 25 points in habitat B, and random points are equally distributed in each habitat type, the probability that a point located in habitat A is drawn from the set of points representing the caribou home range is 75/(75+50) = 0.6 or 60%. Therefore, any probability of >50% indicates evidence of selection by woodland caribou. Conversely, probabilities of <50% indicate evidence of avoidance. This should not be confused with the definition of selection presented by Lele *et al.* (2013); specifically, "the act of using a resource unit if it is encountered" (page 1185). Note that the selection probabilities we report represent exact inferences from models and have no confidence intervals; however, results need to be interpreted in the context of model precision (i.e., proportion of correct predictions).

Because our focus was selection of habitats by woodland caribou for management purposes, we did not include individual adult females as a factor in our models. We acknowledge that individual variation might have reduced the fit of our models but maintain that variation among individuals has limited relevance for managers.

We assessed the generalizability of the best-fit seasonal models via k-fold (k = 10) cross-validation (Fielding and Bell 1997), examining the ratio of correct predictions to the total number of cases in resulting confusion matrices. All analyses were conducted in BayesiaLab 5.4 (Bayesia S.A.S., Laval, France).

We determined the independent contribution of each factor using "likelihood matching" (Conrady *et al.* 2014), which fixes the posterior probability distributions of variables related to the one being assessed. This allowed us to examine the effects of individual factors while holding others constant.

To demonstrate application of the models, we used them to infer selection of home ranges by woodland caribou found in the Parker local population range. The Parker caribou range is located west of the city of Fort Nelson, BC and covers 752 km^2 (Figure 1; Environment Canada 2012).

We ran data from a 30 x 30-m gridded representation of all input variables for the Parker caribou range through the seasonal BN models and mapped output as probabilistic surfaces of selection by woodland caribou. We then set anthropogenic features (*i.e.*, linear feature density, well sites, cut blocks) and early seral/immature forest habitat due to fire to minimums

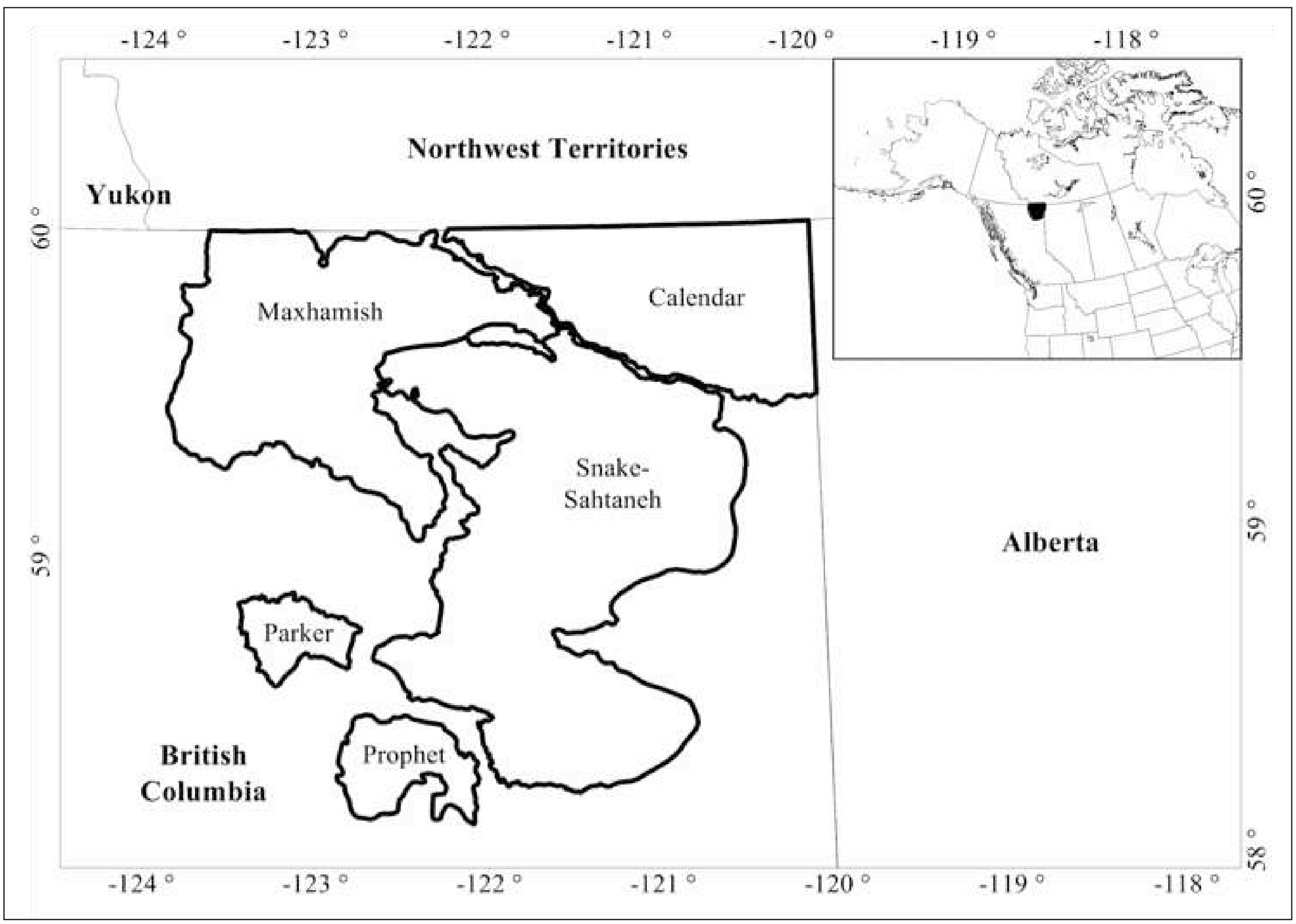

Figure 1. Woodland caribou local population ranges in northeast British Columbia, Canada (Environment Canada 2012).

and generated a second set of mapped probabilities to predict selection under the hypothesis of no anthropogenic features or fire.

RESULTS

Telemetry data were available to generate seasonal home ranges for 25 adult female woodland caribou during late summer, 27 for late fall, and 22 for late winter. Resulting BNs had the same topology for the different seasons (Figure 2). Total precision was similar among the 3 seasons but relatively low compared to what would be expected by random assignment (i.e., 50%): late summer 58.6%, late fall 58.9%, late winter 59.8%.

Woodland caribou selected treed bogs and poor fens, and avoided upland habitats and deciduous swamps in all seasons (Figure 3). Home ranges were more likely to be located at greater distances from rivers and lakes than random among all seasons, although this was most evident during late summer (Figures 4a, 4b).

Woodland caribou selected home ranges with low densities of linear features, but avoidance of areas with high densities was inconsistent among seasons (Figure 4c). Selection for areas closer to early seral/immature forest habitat was evident in all seasons (Figure 4d). There was no trend with distance to well sites in any season (Figure 4e).

Anthropogenic features and fire affected home range selection by woodland caribou over 75% of the Parker range in late summer, 75% in late fall, and 43% in late winter (Figure 5), and the average reduction in selection among seasons was 11%, 8% and 10%, respectively.

Focusing specifically on the effect of linear feature density in late winter when its effect was most evident, we found that selection of different habitat types differed considerably among density classes, with caribou selecting for some habitat types even if they were associated with relatively high linear feature densities (Figure 6). For example, woodland caribou selected treed bogs, even where linear feature density was as high as 8 km/km^2, but for rich fens only where linear feature density was <2 km/km^2.

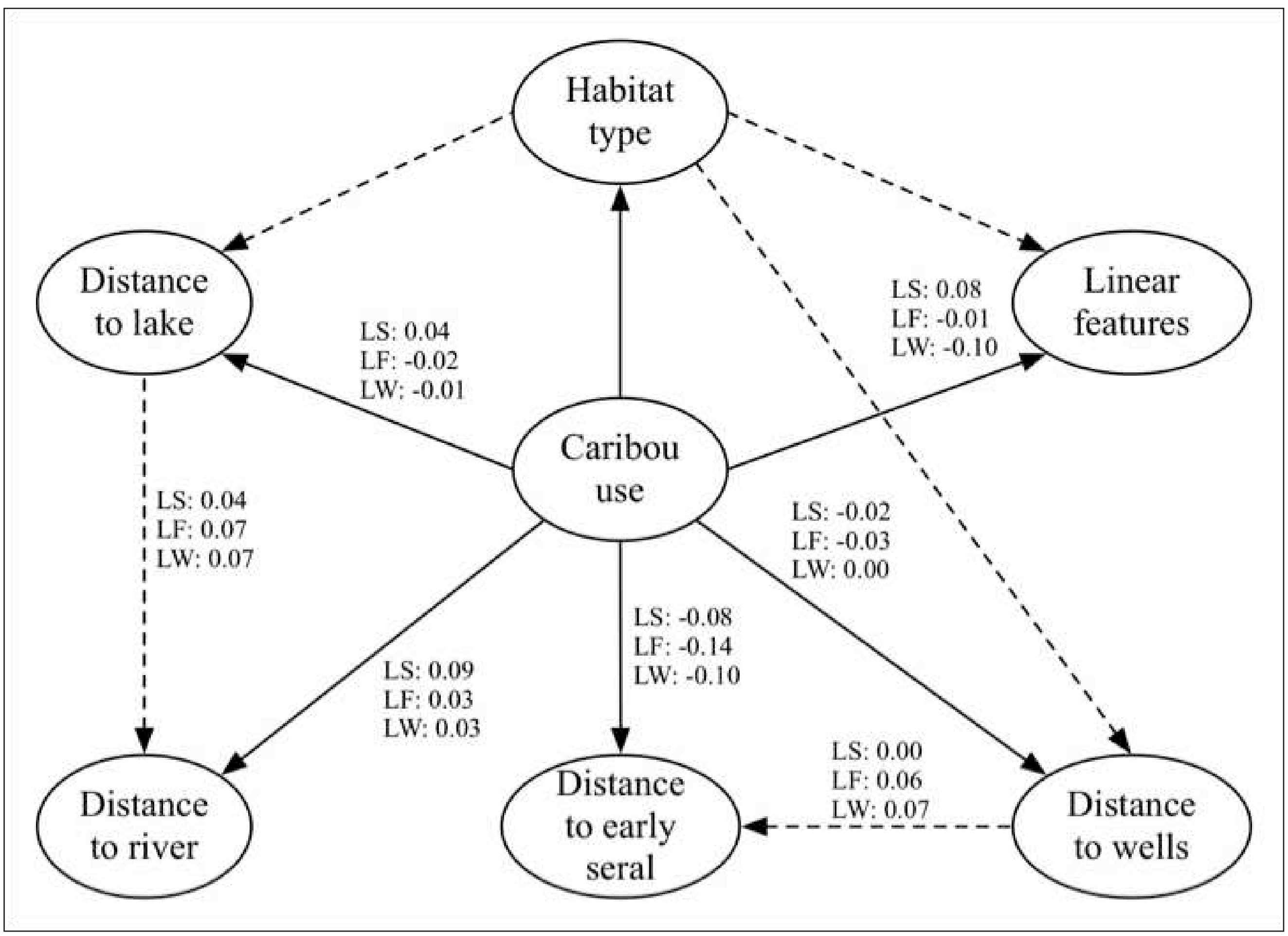

Figure 2. Network topology of the seasonal habitat models generated by the tree-augmented naïve Bayes classifier for late summer (LS), late fall (LF) and late winter (LW) seasons. Pearson correlations among variables for different seasons are presented for each relationship. Dotted lines denote relationships among predictor variables while solid lines denote relationships between predictors and the response variable. Naïve Bayes networks typically illustrate response variables pointing to predictor variables.

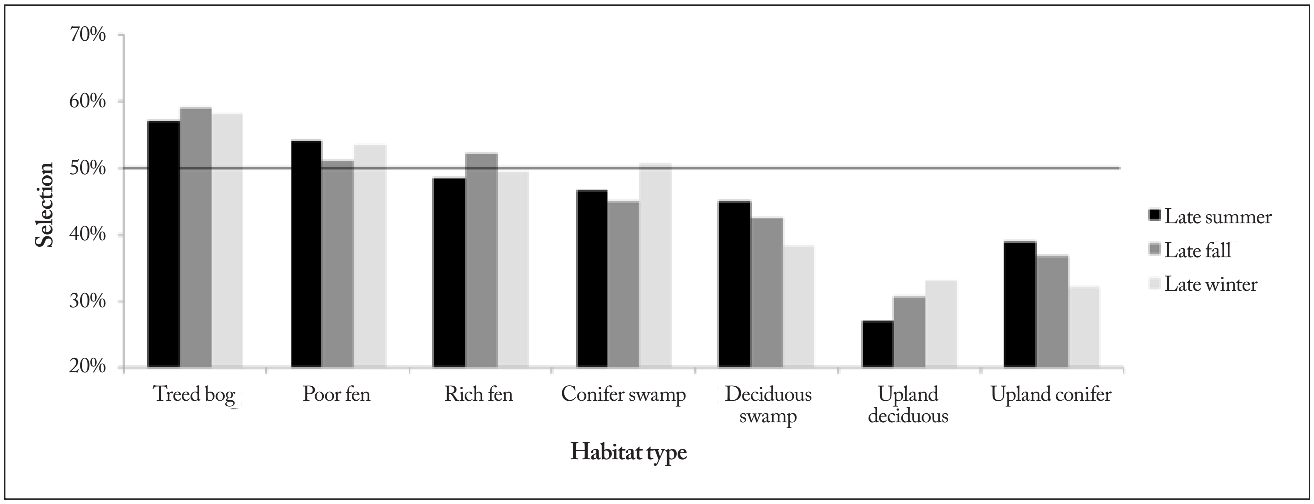

Figure 3. Selection for habitat types by woodland caribou in northeast British Columbia (see Table 1), by season. Bars above 50% indicate selection. Probabilities are exact inferences from the seasonal models.

DISCUSSION

The Bayesian approach developed for this study provides a number of advantages over resource selection functions (Manly *et al.* 2002). First, the analysis is non-parametric and free of the distributional assumptions of parametric tests that are commonly violated in ecological studies. Second, categorical factors do not need to be coded as dummy variables as they do for general linear models. This simplifies interpretation of selection for habitat types. Third, output is probabilistic and conceptually simpler to interpret than coefficients from general linear models.

A consistent result among the 3 seasons analyzed was the relatively little discrimination between points derived from woodland caribou home ranges and random locations generated within local population ranges, based on the factors examined. This limited the predictive power of the resulting models but was an important result in itself, suggesting that home range selection by woodland caribou in northeast BC is relatively indiscriminate with respect to factors of interest to managers. Analyses at finer spatial scales might reveal selection or avoidance of specific features, although Polfus *et al.* (2011) reported avoidance of human infrastructure by mountain caribou to be greatest at the second-order scale.

The affinity of woodland caribou for lowland bog and peatland habitats is well known (e.g., Bradshaw *et al.* 1995; Stuart-Smith *et al.* 1997; Anderson 1999; Rettie and Messier 2000; Schneider *et al.* 2000; Proulx 2013). These habitats are associated with abundant terrestrial lichens, which serve as a primary food source, particularly in winter (Dzus 2001; Thomas and Gray 2002). Inhabiting these low productivity environments also allows woodland caribou to segregate from other ungulates and their predators (Seip 1992; Cummings *et al.* 1996; Dzus 2001; Latham *et al.* 2011b). Our study suggests that caribou make differential use of these lowland habitats during different seasons.

There was evidence that woodland caribou located their home ranges away from lakes and rivers. This may indicate a response to predation risk because wolves follow natural linear features like shorelines, where travelling may be easier and primary prey abundance higher (Latham *et al.* 2011a).

The relatively high selection by woodland caribou for early seral/immature forest habitats, and areas close to these habitats, was an unexpected result and is contrary to results reported in most previous studies (Thomas and Gray 2002). Early seral habitats can provide abundant forage and visibility for predator detection (Schafer and Pruitt 1991; Dussault *et al.* 2012). Additionally, there is evidence that the creation of edge can cause caribou to aggregate near anthropogenic features (Fortin *et al.* 2013); however, whether this is occurring or whether it is an artefact of either mapping or analysis methods requires further investigation.

Comparing the current condition of the Parker range to that expected under an hypothesis of no anthropogenic features or fire suggested that home range selection by woodland caribou over large portions of the range had been affected by human-related activities and wild fire (43-75%, depending on season); however, the average reduction in selection was relatively small (8-11%, depending on season). This was a consequence of the low precision of the models; if woodland caribou are not particularly discriminating, then habitat changes result in relatively small changes in habitat selection. This does not necessarily correlate with demographic trends because factors other than habitat selection (e.g., distribution and abundance of predators and their primary prey) affect the system (Warren *et al.* 1996; Wittmer *et*

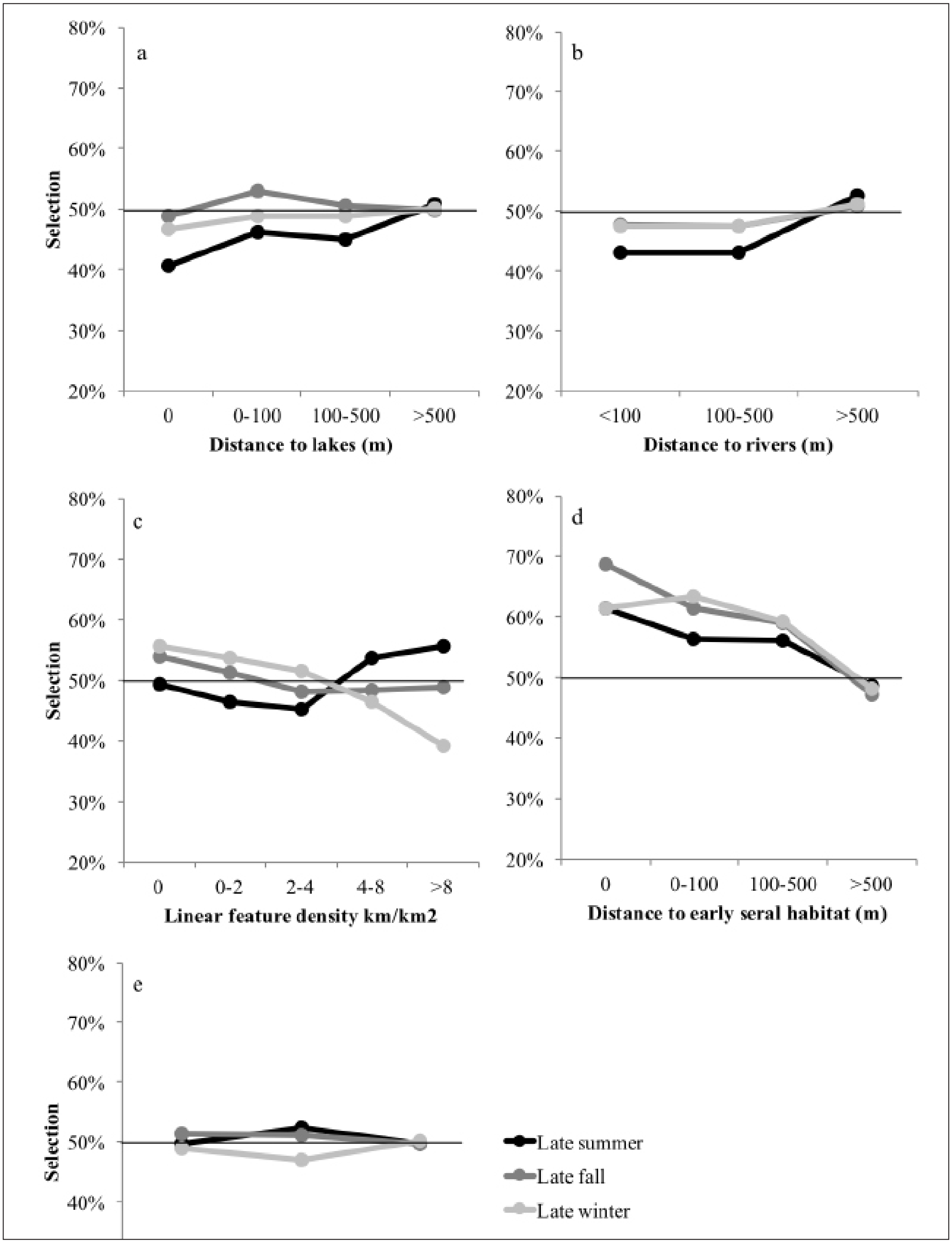

Figure 4. Selection by woodland caribou for habitat based on: a) distance to lakes; b) distance to rivers; c) linear feature density; d) distance to early seral/immature habitats; and, e) distance to well sites in northeast British Columbia, by season. Points above 50% indicate selection. Probabilities are exact inferences from the seasonal models. Lines between data categories are provided for illustrations purposes.

al. 2005).

The failure of woodland caribou to respond strongly to habitat changes such as the creation of linear features could ultimately have consequences for survivorship if predators use these features to access occupied caribou habitat (Environment Canada 2012); however, this hypothesis requires further investigation because the numerical response of primary prey and wolves to changing early seral and/or climate conditions could be resulting in higher predation pressure on caribou, regardless of linear feature density (Latham *et al.* 2011b).

MANAGEMENT CONSIDERATIONS

Woodland caribou habitat management has emphasized the effects of habitat alteration on predator-prey systems and subsequent demographic consequences for woodland caribou populations. This study suggests that habitat alteration can also affect home range selection by woodland caribou in boreal ecosystems, but that impacts of anthropogenic features and fire on selection are relatively small. This suggests that protection, mitigation or restoration of anthropogenic features will need to be extensive to alter woodland caribou habitat use significantly.

Seasonal models all identified treed bogs and poor fens as habitats selected by woodland caribou. These habitats might require less mitigation or restoration than other habitats in order to increase their use by woodland caribou.

The models developed for this study are intuitive and can be used to predict selection by woodland caribou for any combination of habitat characteristics, thus providing a platform for forecasting the relative benefits of mitigation efforts and restoration treatments.

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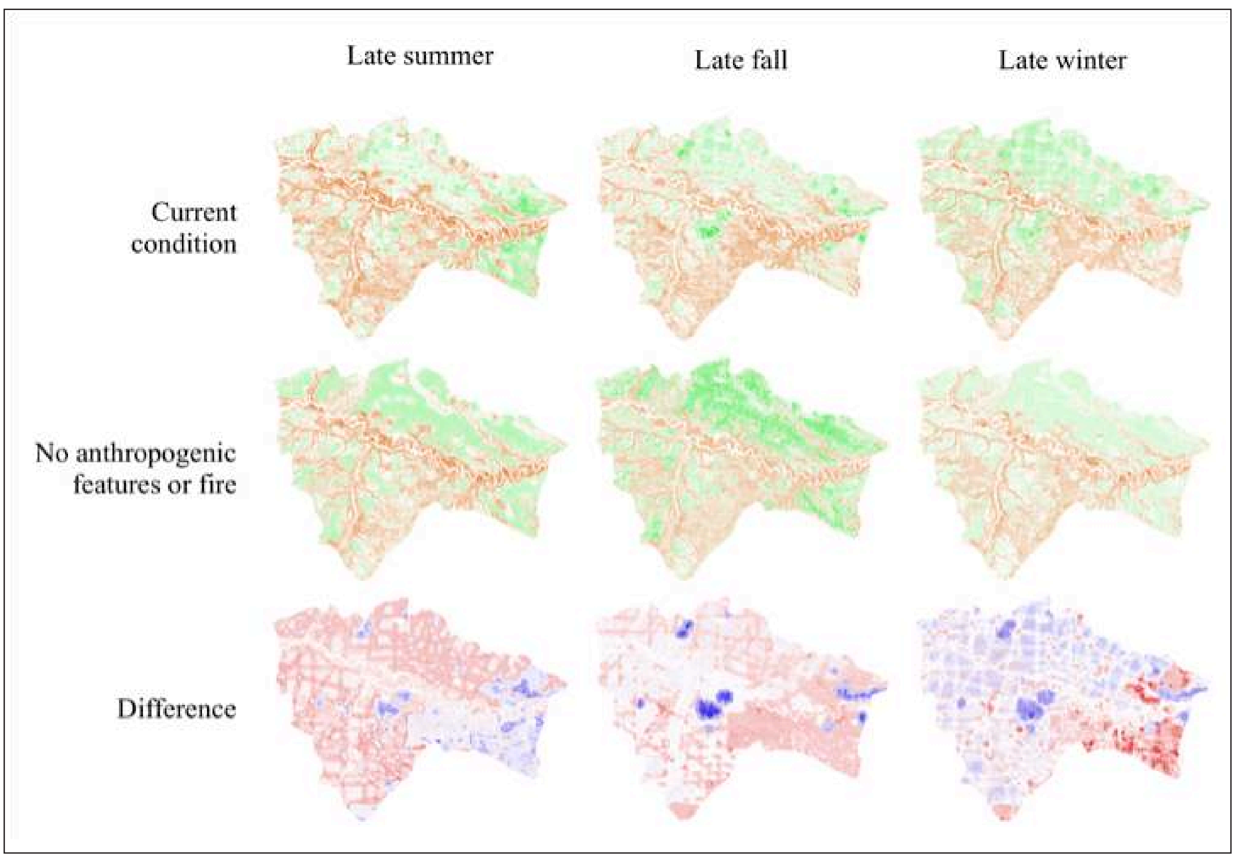

Figure 5. Selection probabilities by woodland caribou for the Parker range in northeast British Columbia. Greens indicate selection and oranges indicate avoidance. Reds indicate areas where the selection under current conditions was lower than expected under a landscape with no anthropogenic features or fire, while blues indicate areas where selection was higher than expected.

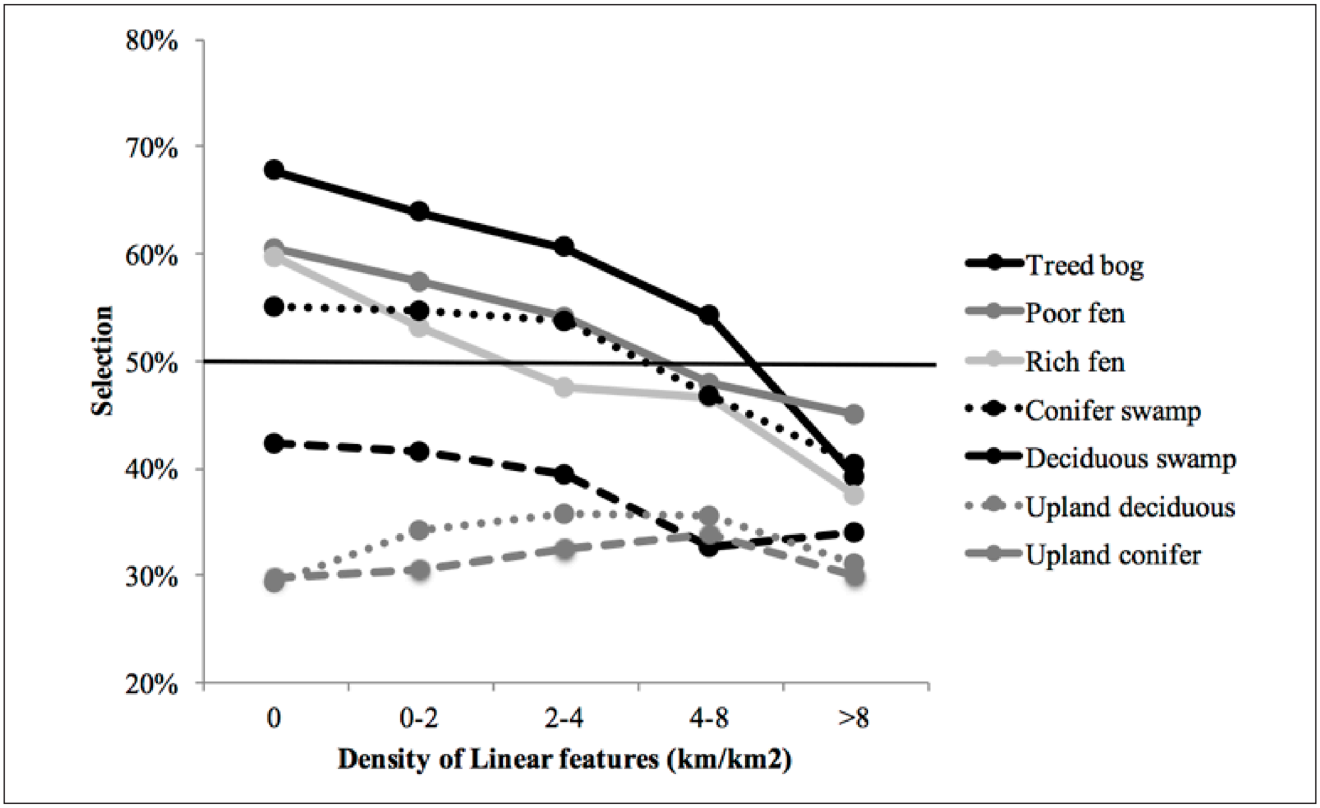

Figure 6. Selection by woodland caribou for linear feature densities (km/km²) in different habitat types in late winter. Points above 50% indicate selection. Probabilities are exact inferences from the seasonal models. Lines between data categories are provided for illustrations purposes.

Needlay, Lenny Tsakoza, Deirdre Leowinata, Brad Culling, Diane Culling and pilots of Qwest Helicopters in Fort Nelson for field assistance and logistical support.

LITERATURE CITED

Anderson, R. B. 1999. Peatland habitat use and selection by woodland caribou (*Rangifer tarandus tarandus*) in northern Alberta. MSc Thesis, University of Alberta. Edmonton, Alberta, Canada.

Apps, C. D., B. N. McLellan, T. A. Kinley, and J. P. Flaa. 2001. Scale-dependent habitat selection by mountain caribou, Columbia Mountains, British Columbia. Journal of Wildlife Management 65: 65-77.

BC Oil and Gas Commission. 2013. Oil and gas land use in northeast British Columbia. BC Oil and Gas Commission, Victoria, BC, Canada. http://www.bcogc.ca/node/12266/download. Accessed 28 May 2015.

Bjørneraas, K., B. Van Moorter, C. M. Rolandsen, and I. Herfindal. 2010. Screening global positioning system location data for errors using animal movement characteristics. Journal of Wildlife Management 74: 1361-1366.

Börger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari, and T. Coulson. 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75: 1393-1405.

Bradshaw, C. J. A., D. M. Hebert, A. B. Rippen, and S. Boutin. 1995. Winter peatland habitat selection by woodland caribou in northeastern Alberta. Canadian Journal of Zoology 73: 1567-1574.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Cheng, J., and R. G. Greiner. 1999. Comparing Bayesian network classifiers. Pages 101-108 *in* K. B. Laskey and H. Prade, editors. Proceedings of the fifteenth conference on uncertainty in artificial intelligence. Morgan Kaufmann Publishers Inc., San Francisco, California, USA.

Conrady, S., L. Jouffe, and F. Elwert. 2014. Causality for policy assessment and impact analysis. Bayesia S.A.S., Laval, France.

Courtois, R., J.-P. Ouellet, L. Breton, A. Gingras, and C. Dussault. 2007. Effects of forest disturbance on density, space use, and mortality of woodland caribou. Écoscience 14: 491-498.

COSEWIC. 2002. COSEWIC assessment – woodland caribou.

Committee on the Status of Endangered Wildlife in Canada. Ottawa, Ontario, Canada. http://www.sararegistry.gc.ca/document/default_e.cfm?documentID=228. Accessed 25 January 2015.

Cumming, H. G., D. B. Beange, and G. Lavoie. 1996. Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared predation. Rangifer Special Issue No. 9: 81-94.

Dalerum, F., S. Boutin, and J. S. Dunford. 2007. Wildfire effects on home range size and fidelity of boreal caribou in Alberta, Canada. Canadian Journal of Zoology 85: 26-32.

DeCesare, N. J., M. Hebblewhite, F. Schmiegelow, D. Hervieux, G. J. McDermid, L. Neufeld, M. Bradley, J. Whittington, K. G. Smith, L. E. Morgantini, M. Wheatley, and M. Musiani. 2012. Transcending scale dependence in identifying habitat with resource selection functions. Ecological Applications 23: 1068-1083.

DeLong, C., R. M. Annas, and A. C. Stewart. 1991. Boreal white and black spruce zone. Ecosystems of British Columbia. Pages 237-250 *in* D. Meidinger and J. Pojar, editors. Special Report Series 6, BC Ministry of Forests, Research Branch, Victoria, British Columbia, Canada.

DeMars, C. A. 2015. Calving behavior of boreal caribou in a multi-predator, multi-use landscape. PhD dissertation, University of Alberta, Edmonton, Alberta, Canada.

DeMars, C. A., M. Auger-Méthé, U. E. Schlägel, and S. Boutin. 2013. Inferring parturition and neonate survival from movement patterns of female ungulates: a case study using woodland caribou. Ecology and Evolution 3: 4149-4160.

Ducks Unlimited, Inc. 2010. Fort Nelson project enhanced wetlands classification user's guide. Ducks Unlimited, Inc., Rancho Cordova, California, USA.

Dussault, C., V. Pinard, J.-P. Ouellet, R. Courtois, and D. Fortin. 2012. Avoidance of roads and selection for recent cutovers by threatened caribou: fitness-rewarding or maladaptive behavior? Proceedings of the Royal Society B doi:10.1098/rspb.2012.1700. http://rspb.royalsocietypublishing.org/. Accessed 18 February 2015.

Dyer, S. J., J. P. O'Neill, S. M. Wasel, and S. Boutin. 2001. Avoidance of industrial development by woodland caribou. Journal of Wildlife Management 65: 531-542.

Dzus, E. 2001. Status of the Woodland Caribou (*Rangifer tarandus caribou*) in Alberta. Wildlife Status Report No. 30, Alberta Environment and Alberta Conservation Association, Edmonton, Alberta, Canada.

Environment Canada. 2008. Scientific review for the identification of critical habitat for woodland caribou (*Rangifer tarandus caribou*), boreal population, in Canada. Environment Canada, Ottawa, Ontario, Canada.

Environment Canada. 2012. Recovery strategy for the woodland caribou (*Rangifer tarandus caribou*), boreal population, in Canada. Species at Risk Act Recovery Strategy Series, Environment Canada, Ottawa, Ontario, Canada.

Environment Canada. 2015. National climate data and information archive: Fort Nelson, British Columbia. http://www.climate.weatheroffice.gc.ca. Accessed 25 January 2015.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24: 38-49.

Friedman, N., D. Geiger, and M. Goldszmidt. 1997. Bayesian network classifiers. Machine Learning 29: 131-163.

Fortin, D., P. L. Buono, A. Fortin, N. Courbin, G. C. Tye, P. R. Moorcroft, R. Courtois, and C. Dussault. 2013. Movement responses of caribou to human-induced habitat edges lead to their aggregation near anthropogenic features. American Naturalist 181: 827-36.

Hins, C., J.-P. Ouellet, C. Dussault, and M.-H. St-Laurent. 2009. Habitat selection by forest-dwelling caribou in managed boreal forest of eastern Canada: evidence of a landscape configuration effect. Forest Ecology and Management 257: 636-643.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65-71.

Johnson, C. J., L. P. W. Ehlers, and D. R. Seip. 2015. Witnessing extinction – cumulative impacts across landscapes and the future loss of an evolutionarily significant unit of woodland caribou in Canada. Biological Conservation 186: 176-186.

Johnstone, J. F., F. S. Chapin, T. N. Hollingsworth, M. C. Mack, V. Romanovsky, and M. Turetsky. 2010. Fire, climate change, and forest resilience in interior Alaska. Canadian Journal of Forest Research 40: 1302-1312.

Lam, W., and F. Bacchus. 1994. Learning Bayesian belief networks: an approach based on the MDL principle. Computational Intelligence 10: 269-293.

Larrañaga, P., and S. Moral. 2011. Probabilistic graphical models in artificial intelligence. Applied Soft Computing 11: 1511-1528.

Latham, A. D. M., M. C. Latham, M. S. Boyce, and S. Boutin. 2011a. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. Ecological Applications 21: 2854-2865.

Latham, A. D. M., M. C. Latham, N. A. McCutchen, and S. Boutin. 2011b. Invading white-tailed deer change wolf-caribou dynamics in northeastern Alberta. Journal of Wildlife Management 75: 204-212.

Lele, S. R., E. H. Merrill, J. Keim, and M. S. Boyce. 2013. Selection, use, choice and occupancy: clarifying concepts in resource selection studies. Journal of Animal Ecology 82: 1183-1191.

Lewis, J. S., J. L. Rachlow, E. O. Garton, and L. A. Vierling. 2007. Effects of habitat on GPS collar performance: using data screening to reduce location error: GPS collar performance. Journal of Applied Ecology 44: 663-671.

Manly, B. F. J., L. McDonald, D. L. Thomas, T. L., McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwere Academic Publishers, Norwell, Massachusetts, USA.

Marcot, B. G., J. D. Steventon, G. D. Sutherland, and R. K. McCann. 2006. Guidelines for developing and updating Bayesian belief networks applied to ecological modeling and conservation. Canadian Journal of Forest Research 36: 3063-3074.

McNay, R. S., B. G. Marcot, V. Brumovsky, and R. Ellis. 2006. A Bayesian approach to evaluating habitat suitability for woodland caribou in north-central British Columbia. Canadian Journal of Forest Research 36: 3117-3133.

Morellet, N., H. Verheyden, J.-M. Angibault, B. Cargnelutti, B. Lourtet, B. M. A. J. Hewison. 2009. The effect of capture on ranging behaviour and activity of the European roe deer (*Capreolus capreolus*). Wildlife Biology 15: 278-287.

Nagy, J. A. 2011. Use of space by caribou in northern Canada. PhD dissertation, University of Alberta, Edmonton, Alberta, Canada.

Polfus, J. L., M. Hebblewhite, and K. Heinemeyer. 2011. Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain woodland caribou. Biological Conservation 11: 2637-2646.

Proulx, G. 2013. Late-winter habitat use by boreal woodland caribou (*Rangifer tarandus caribou*) in Northwestern Saskatchewan. Canadian Wildlife Biology & Management 2: 11-22.

Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23: 466-478.

Schneider, R. R., B. Wynes, S. Wasel, E. Dzus and M. Hiltz. 2000. Habitat use by caribou in Northern Alberta, Canada. Rangifer. 20: 43-50.

Schaefer J. A., and W. O. Pruitt. 1991. Fire and woodland caribou in southeastern Manitoba. Wildlife Monograph 116: 1-39.

Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Canadian Journal of Zoology 70: 1494-1503.

Sorensen, T., P. D. McLoughlin, D. Hervieux, E. Dzus, J. Nolan, B. Wynes, and S. Boutin. 2008. Determining sustainable levels of cumulative effects for boreal caribou. Journal of Wildlife Management 72: 900-905.

Stuart-Smith, A. K., J. A. Corey, S. Boutin, D. H. Hebert, and A. B. Rippin. 1997. Woodland caribou relative to landscape patterns in north-eastern Alberta. Journal of Wildlife Management, 61: 622-633.

Thomas, D. C., and D. R. Gray. 2002. Update COSEWIC status report on the Woodland Caribou *Rangifer tarandus caribou* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa, Ontario, Canada.

Vors, L. S., and M. S. Boyce. 2009. Global declines of caribou and reindeer. Global Change Biology 15: 2626-2633.

Warren, C. D., J. M. Peek, G. L. Servheen, and P. Zager. 1996. Habitat use and movements of two ecotypes of translocated caribou in Idaho and British Columbia. Conservation Biology 10: 547-553.

Wasser, S. K., J. L. Keim, M. L. Taper, and S. R. Lele. 2011. The influences of wolf predation, habitat loss, and human activity on caribou and moose in the Alberta oil sands. Frontiers in Ecology and the Environment 9: 546-551.

Wittmer, H. U., A. R. E. Sinclair, and B. N. McLellan. 2005. The role of predation in the decline and extirpation of woodland caribou. Oecologia 144: 257-267.

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