

# Moose, caribou, and fire: have we got it right yet?<sup>1</sup>

C.A. DeMars, R. Serrouya, M.A. Mumma, M.P. Gillingham, R.S. McNay, and S. Boutin

**Abstract:** Natural disturbance plays a key role in shaping community dynamics. Within Canadian boreal forests, the dominant form of natural disturbance is fire, and its effects are thought to influence the dynamics between moose (*Alces alces* (Linnaeus, 1758)) and the boreal ecotype of woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)). Boreal caribou are considered “threatened” and population declines are attributed, at least in part, to disturbance-mediated apparent competition (DMAC) with moose. Here, we tested a primary prediction of the DMAC hypothesis: that moose respond positively to burns within and adjacent to the caribou range. We assessed moose selection for  $\leq 25$ -year-old burns (when selection is predicted to be strongest) at multiple spatial scales and evaluated whether moose density was correlated with the extent of  $\leq 40$ -year-old burns (a time frame predicted to negatively affect caribou). Against expectation, moose showed avoidance and low use of  $\leq 25$ -year-old burns at all scales, regardless of burn age, season, and type of land cover burned. These findings mirrored the demographic response, as we found no correlation between  $\leq 40$ -year-old burns and moose density. By contradicting the prevailing hypothesis linking fires to caribou population declines, our results highlight the need to understand regional variation in disturbance impacts on caribou populations.

**Key words:** fire, natural disturbance, moose, *Alces alces*, caribou, *Rangifer tarandus*, boreal forest.

**Résumé :** Les perturbations naturelles jouent un rôle clé dans la dynamique des communautés. Dans les forêts boréales canadiennes, la principale forme de perturbation naturelle est le feu, dont les effets influenceraient la dynamique entre l’orignal (*Alces alces* (Linnaeus, 1758)) et l’écotype boréal du caribou des bois (*Rangifer tarandus caribou* (Gmelin, 1788)). Les cariboux boréaux sont considérés comme « menacés », et les baisses de leurs populations sont attribuées, en partie du moins, à la concurrence apparente modulée par les perturbations (CAMP) avec l’orignal. Nous vérifions une prédiction primaire de l’hypothèse de la CAMP, à savoir que les orignaux réagissent de manière positive à des brûlis au sein de l’aire de répartition du caribou ou jouxtant celle-ci. Nous évaluons la sélection par les orignaux de brûlis de  $\leq 25$  ans (quand il est prédit que la sélection est la plus forte) à différentes échelles spatiales et vérifions si la densité des orignaux est corrélée à l’étendue de brûlis de  $\leq 40$  ans (une période qui, selon les prédictions, devrait avoir une incidence négative sur les cariboux). Contrairement aux attentes, les orignaux font preuve d’évitement et d’une faible utilisation des brûlis de  $\leq 25$  ans à toutes les échelles, peu importe l’âge du brûlis, la saison ou le type de couvert brûlé. Ces constatations sont analogues à la réaction démographique puisque nous ne trouvons aucune corrélation entre les brûlis de  $\leq 40$  ans et la densité des orignaux. En contredisant l’hypothèse la plus courante reliant les feux aux baisses des populations de cariboux, nos résultats soulignent la nécessité de comprendre les variations régionales des impacts des perturbations sur les populations de cariboux. [Traduit par la Rédaction]

**Mots-clés :** feu, perturbation naturelle, orignal, *Alces alces*, caribou, *Rangifer tarandus*, forêt boréale.

## Introduction

Natural disturbance plays a key role in determining the abundance and distribution of organisms (Sousa 1984). Following disturbance, demographic and distributional changes occur because disturbance alters the quality and distribution of resources, creating spatial and temporal heterogeneity in the conditions necessary for growth, reproduction, and survival. In terrestrial systems, disturbance generally causes these effects by changing the structure and composition of vegetation, and such changes frequently result in cascading effects across higher trophic levels. With different species adapted to different successional stages, disturbance ultimately influences the structure and dynamics of communities by altering the intensity of processes such as competition and predation (Connell 1978; Meffe 1984; Halpern 1989).

In boreal forests of western Canada, forest fire is the dominant form of natural disturbance, and fire effects are thought to have opposing influences on its two primary ungulates, moose (*Alces alces* (Linnaeus, 1758)) and the boreal ecotype of woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788); hereafter, boreal caribou). Considerable research suggests that moose respond positively to the early seral conditions that result after fire. Throughout much of their distribution, moose have shown selection for early seral forests presumably because of the increased quality and quantity of preferred forage (e.g., young trees and shrubs; Maier et al. 2005; Lord and Kielland 2015; Joly et al. 2017). This forage mechanism has also been used to explain positive correlations between the extent of early seral forest and moose densities (Rempel et al. 1997; Serrouya et al. 2011), with increasing moose density resulting from increasing reproduction (Schwartz and Franzmann 1991).

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<sup>1</sup>Note that this title pays homage to Bergerud’s (1996) paper on caribou population dynamics.

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and (or) immigration (Peek 1974). Boreal caribou, in contrast, appear to be negatively impacted by fire. These animals are adapted to old-growth conditions and have shown avoidance of burned areas within their home ranges, particularly during winter, though fires may not necessarily result in range shifts or abandonment (Schaefer and Pruitt 1991; Dalerum et al. 2007; Faille et al. 2010). Avoidance of early seral forests has been attributed to lowered forage availability, primarily lichen (Schaefer and Pruitt 1991; Dunford et al. 2006), and to increased predation risk (Courtois et al. 2007; Courbin et al. 2013). Fire effects on caribou demography, however, have been equivocal. Although negative effects have been reported when fire is considered cumulatively with other types of disturbance (Environment Canada 2008, 2011; Sorensen et al. 2008; Rudolph et al. 2017), fire effects alone have been relatively weak or negligible (Dalerum et al. 2007; Environment Canada 2008, 2011).

Hypothesized dynamics among boreal caribou, moose, and fire are implicit in current management recommendations for boreal caribou. This ecotype is listed as “threatened” under Canada’s *Species at Risk Act* due to population declines throughout its distribution (Environment Canada 2008). The primary hypothesis for explaining population decline is a proximate increase in predation ultimately resulting from landscape disturbance and climate change (Bergerud 1996; Courtois et al. 2007; Sorensen et al. 2008; Festa-Bianchet et al. 2011). The disturbance–predation link has been primarily attributed to apparent competition (sensu Holt 1977; see Seip (1992), Festa-Bianchet et al. (2011), and Serrouya et al. (2015)). In this process, disturbances within and adjacent to caribou range increase the extent of early seral conditions, leading to numeric increases in moose (and deer (*Odocoileus* spp.)) and their predators, which opportunistically prey on caribou (Seip 1992; Bergerud 1996). Because of these effects, Canada’s federal recovery strategy for boreal caribou recommends limiting disturbance to  $\leq 35\%$  of the caribou range, a threshold that provides a 60% probability that a population will be self-sustaining (Environment Canada 2012). This threshold considers both human-caused disturbances (e.g., cutblocks and oil well pads) and burned areas  $\leq 40$  years after fire. Within this disturbance assessment, a key assumption is that all disturbances create favorable conditions for moose and other ungulate species (Environment Canada 2012, p. viii; see also Edwards (1954), Bergerud (1996), and Festa-Bianchet et al. 2011). This assumption, however, has rarely been tested within boreal caribou ranges and may not hold as ungulate response may depend on specific disturbance characteristics (e.g., disturbance type and time since disturbance; Maier et al. 2005) and regional variation in animal responses may limit extrapolating predictions across the wide distribution of boreal caribou (Whittingham et al. 2007).

In this study, we tested the prediction that moose respond positively to fires within and adjacent to boreal caribou ranges in western Canada. We evaluated the response of moose at multiple spatial scales and assessed whether such responses depended on time since fire (burn age) and (or) the type of land cover burned. For the former, research from Alaska suggests that moose response is time-dependent, with selection being highest for 11- to 30-year-old burns (Maier et al. 2005; Joly et al. 2017). For land cover  $\times$  fire interactions, field observations have suggested spatial variation in the quantity and quality of moose forage created after fire (C.A. DeMars, personal observation). For example, moose generally avoid low-lying peatlands presumably because peatlands have low abundances of forage (James et al. 2004). If the postfire trajectory of burned peatlands is a return to peatlands (Johnstone et al. 2010), then the amount of moose forage created after fire may be insufficient to alter moose spatial behaviour toward this land-cover type, which ultimately should result in minimal changes in moose densities as caribou ranges contain high proportions of peatlands (Stuart-Smith et al. 1997). This latter point — the linking of spatial behaviour to population changes — is critical

given that caribou declines are primarily attributed to disturbance-mediated apparent competition (DMAC; Festa-Bianchet et al. 2011). To that end, we used moose survey data from Alberta and British Columbia to evaluate whether moose densities were influenced by the spatial extent of burned areas  $\leq 40$  years after fire, the same age threshold used in the federal recovery strategy for boreal caribou (Environment Canada 2012).

## Materials and methods

### Study area

Our study area is broadly situated within the boreal forests of northeastern British Columbia, northern Alberta, and northeastern Saskatchewan, Canada (Fig. 1). Within this distribution, we accessed moose spatial data from three previously completed projects: two in northeastern Alberta (Cold Lake and Ft. McMurray) and one in northeastern British Columbia (NEBC). In each of these projects, moose global positioning system (GPS) radio-collars (hereafter referred to as “collars”) were deployed as part of separate studies evaluating predator–prey dynamics (McNay et al. 2014; Mumma et al. 2017; Neilson 2017). We also obtained estimates of moose density derived from aerial surveys conducted in northern Alberta and NEBC. Because of jurisdictional differences in available covariate data (see Environmental Covariates section), we analyzed data from Alberta separately from those from NEBC and Saskatchewan.

Across the study area, the landscape generally consists of a mosaic of upland forests, low-lying peatlands (i.e., fens and bogs), marshes, and other riparian features (DeMars 2015; Neilson 2017). Topography in the region is generally flat to undulating and the climate is northern continental. Moose and caribou are the dominant ungulates, although populations of white-tailed deer (*Odocoileus virginianus* (Zimmerman, 1780)) are expanding (Latham et al. 2011) and elk (*Cervus elaphus* Linnaeus, 1758) may occur along major river valleys and near agricultural areas. Dominant predators include wolves (*Canis lupus* Linnaeus, 1758), black bears (*Ursus americanus* Pallas, 1780), and, occasionally, grizzly bears (*Ursus arctos* Linnaeus, 1758). Coyote (*Canis latrans* Say, 1823), lynx (*Lynx canadensis* Kerr, 1792), and wolverine (*Gulo gulo* Linnaeus, 1758) are also present.

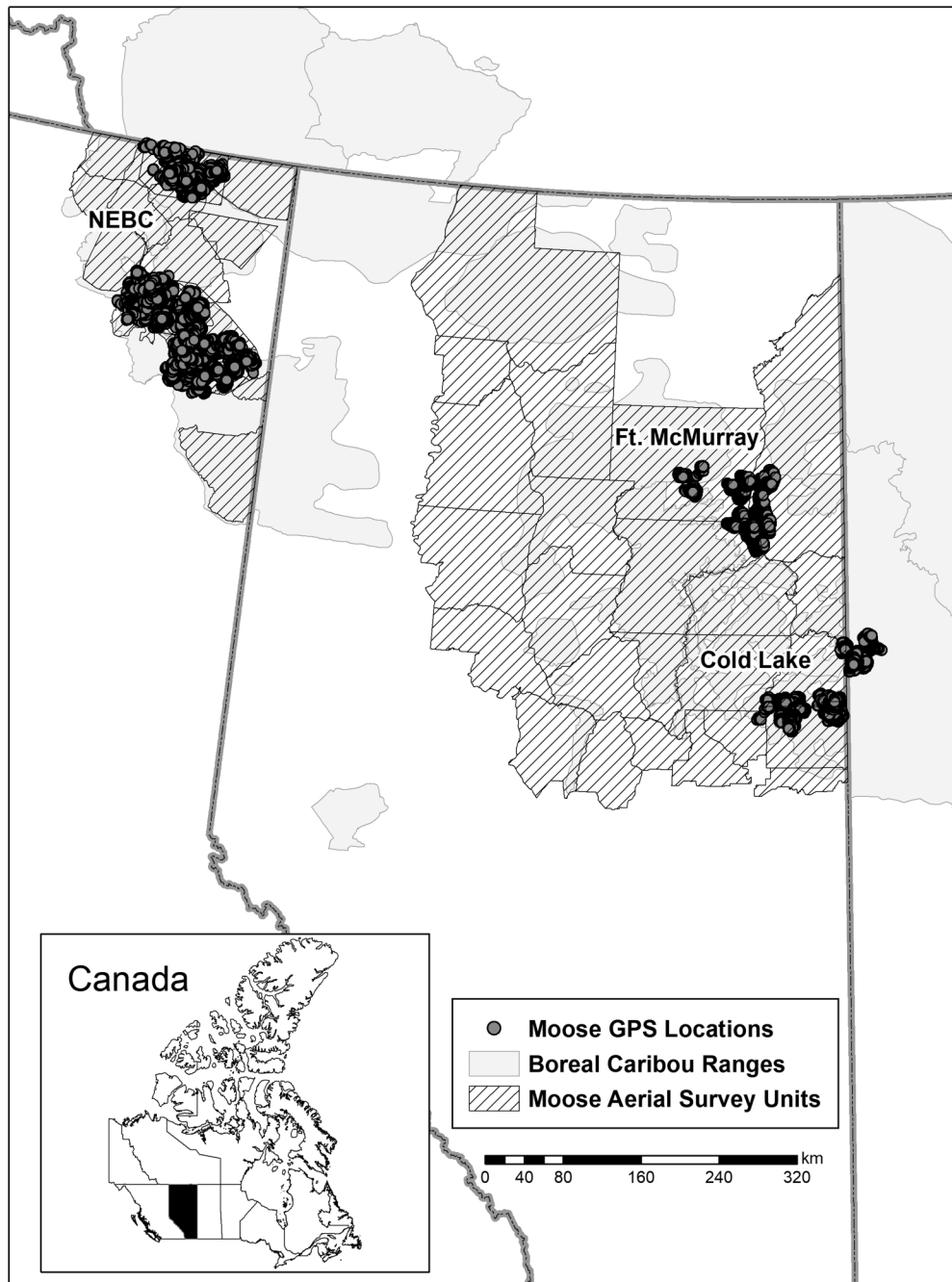
Fire is the dominant form of natural disturbance, with a mean return interval of  $< 100$  years (Larsen 1997; Johnstone et al. 2010), and analyses of Alberta’s fire history suggest that return intervals in uplands and peatlands are similar (Turetsky et al. 2004). Human-mediated disturbances are also prevalent and are primarily related to the extraction of natural resources. These disturbances include polygonal features (e.g., cutblocks, well sites, and oil sand mines) and linear features (e.g., roads, pipelines, and seismic lines). Of the two types, linear features are the most widespread and densities can exceed  $10 \text{ km} \cdot \text{km}^{-2}$  (Dickie et al. 2017; Neilson 2017; DeMars and Boutin 2018).

### Moose spatial data

We used GPS location data collected from 93 female moose distributed among the three study areas (Cold Lake,  $n = 23$ ; Ft. McMurray,  $n = 28$ ; NEBC,  $n = 42$ ). During these now-completed projects, individual moose were captured by aerial net-gunning in winter (January–March) and fitted with a collar. All capture and handling procedures followed provincial- and institution-approved animal-care protocols (McNay 2016; Mumma and Gillingham 2017; Neilson 2017; note that no additional animals were captured for the present study).

Moose in Cold Lake were captured in 2013 ( $n = 6$ ), 2014 ( $n = 9$ ), and 2015 ( $n = 8$ ), and we used data extending to 5 November 2015. Cold Lake collars had varying fix rates (i.e., rates of GPS location acquisition), ranging from every 5 min to twice per day depending on the collar and season. The mean monitoring interval per Cold Lake collar was 417 days (range, 117–1021 days). Moose in Ft. McMurray were captured in 2010 ( $n = 25$ ) and 2012 ( $n = 3$ ), and we used data

**Fig. 1.** Moose GPS locations were collected from three project areas (Cold Lake, Ft. McMurray, and NEBC) all located within and adjacent to boreal caribou ranges in northeastern British Columbia, northeastern Alberta, and northwestern Saskatchewan, Canada. Estimates of moose density were obtained from aerial surveys conducted within 24 survey units in Alberta and 17 survey units in northeastern British Columbia. [Base map of Canadian provincial boundaries from ESRI Canada (source of information: ©2003. Government of Canada with permission from Natural Resources Canada). Shapefiles of boreal caribou ranges were provided by provincial governments. Shapefiles of moose survey units were provided by the Alberta government and the British Columbia Boreal Caribou Research and Effectiveness Monitoring Board.]



extending to 28 October 2012. All Ft. McMurray collars acquired fixes every 3 h, and the mean monitoring interval per collar was 672 days (range, 61–968 days). NEBC collars were deployed in 2015 ( $n = 34$ ) and 2016 ( $n = 27$ ) and had a fix rate of every 12 h. Data extended to 31 March 2018, but because fire data were limited to 1985–2015, we used NEBC data extending to 14 May 2016. Within this truncated period, the mean monitoring interval per collar was 253 days (range, 23–422 days).

Prior to analyses, we subsampled the Cold Lake and Ft. McMurray down to a 12 h fix rate — equivalent to the NEBC data — to

facilitate comparisons across moose. We then screened the data for potential errors, removing all locations with low positional accuracy (i.e., two-dimensional fixes with positional dilution of precision values  $>5$ ; Lewis et al. 2007) and excluding outlying locations beyond the range of possible moose movement (Bjørneraas et al. 2010). We also removed GPS locations that fell outside the prespecified fix rate to ensure a regular sampling interval. For NEBC moose, we excluded locations occurring in the Northwest Territories due to a lack of environmental covariate data in this area (removal of one moose depending on the seasonal analysis,

described later). We also excluded one NEBC moose with a low rate of fix success (<22%) due to collar malfunction. Following these procedures, the mean per-collar rate of fix success was 90% (range, 62%–99%) for Cold Lake, 93% (57%–100%) for Ft. McMurray, and 87% (67%–98%) for NEBC.

### Evaluating moose response to fire: general framework

We evaluated moose response to fire using resource selection analyses (RSAs) conducted at three spatial scales. In general, RSAs compare environmental variables (or “resources”) associated with observed (or “used”) locations or spatial domains with those associated with available locations or spatial domains (Johnson 1980; Manly et al. 2002). At each scale, we conducted RSAs specific to three biologically informed seasons: calving, summer–fall, and winter. Calving in western boreal forests generally occurs from mid-May to mid-June (Hauge and Keith 1981), so we defined calving as 15 May – 30 June, a period that also encompasses the first few weeks of the neonate period when calves have low mobility. The influence of snow on moose movement patterns and range use (Phillips et al. 1973) defined the remaining two seasons. Summer–fall extended from postcalving until the onset of the snow season (15 June – 31 October), while winter extended from 1 November – 14 May.

At the finest scale, we estimated step-selection functions (SSFs), which compare resources associated with each observed movement step (i.e., the Euclidean distance between successive GPS locations) with resources associated with a matched set of random steps (Fortin et al. 2005; Avgar et al. 2016). Although resource values can be averaged along each step, we compared resources at each step’s end point because the assumption of straight-line movements between GPS locations may not hold given our 12 h fix rate (Thurfjell et al. 2014). To generate random steps, we sampled step lengths and turning angles from a parameterized distribution of the animal’s empirical movement data (Forester et al. 2009). For each observed step, we generated 20 random steps to adequately characterize resource availability (Northrup et al. 2013; Supplementary material A<sup>2</sup>).

At the intermediate scale, we evaluated moose resource selection within their seasonal ranges by comparing the proportion of moose GPS locations within a given land-cover type with the proportion within an individual’s seasonal range (i.e., third-order selection; Johnson 1980). To delineate seasonal ranges for each individual, we used the 90% isopleth of utilization distributions (UDs; Börger et al. 2006), specifying the “reference bandwidth” as the smoothing parameter. Because UD’s are sensitive to the sampling regime (Börger et al. 2006), we only included individuals monitored over the entirety of a given season.

At the largest scale, we evaluated whether moose optimally situated their seasonal ranges to encompass burned areas. For this analysis, we compared the proportions of land-cover types, including burns, in seasonal ranges with those in a larger area surrounding each range. We delineated this available area by applying a minimum bounding box to the seasonal range and then buffering the range by the bounding box’s maximum dimensional extent (e.g., maximum length). In effect, this availability equates to the seasonal range plus a buffered area extending out one “seasonal range unit”. If moose were selecting for burns, the proportion of burns within observed seasonal ranges should be higher than the proportion within the available area.

### Correlation between fire and moose density

To determine if findings from moose resource selection scaled up to numeric changes in moose populations, we assessed whether the extent of ≤40-year-old burns influenced moose densities (number of moose per square kilometre) within 24 moose survey units in Alberta and 17 in NEBC (Fig. 1). In all units, moose

densities were estimated by aerial surveys. In Alberta, each unit (mean area = 8327 km<sup>2</sup>; range, 1916 – 26 146 km<sup>2</sup>) was surveyed by provincial government biologists once during 1993–2015, and survey methods were either stratified random block sampling ( $n = 21$ , all before 2014) or distance sampling ( $n = 3$ ; all after 2013). Both methods have been shown to produce similar estimates (Peters et al. 2014). In British Columbia, each unit (mean area = 3051 km<sup>2</sup>; range, 780–5248 km<sup>2</sup>) was surveyed sometime during 2010–2016, and all surveys were done by distance sampling (Thiessen 2010; McNay et al. 2013; Webster and Lavallee 2016). Two units received repeat surveys separated by 3 years, but because the spatial extents differed between surveys (the second survey was approximately twice as large in each case), we considered the two surveys as independent data points. In general, Alberta’s surveys had higher precision (mean coefficient of variation (CV) = 16%; range, 9%–41%) than those in British Columbia (mean CV = 31%; range, 12%–84%).

### Environmental covariates

We modelled moose resource selection using geographic information system (GIS) data characterizing land cover, historical forest fires, and anthropogenic disturbance. For land cover, we primarily used Enhanced Wetlands Classification data (EWC; 30 m resolution derived from Landsat imagery) from Ducks Unlimited Canada. These data classified the landscape into 29 land-cover types, which we reduced to five by combining types having small extents with other biologically similar classes (e.g., open bog (0.1%) and shrubby bog (1%) with treed bog (9%); Table 1). This reclassification maintained broad land-cover categories known to influence space use by moose (Hauge and Keith 1981; James et al. 2004; Osko et al. 2004). The EWC data also contained the land-cover type “burn”, which comprised burned areas where the underlying vegetation could not be discerned. Overlaying historic fire data (see later) on the EWC data suggested that these burns generally occurred within 3 years prior to the year of the Landsat imagery used to derive the EWC data. Because of our interest in evaluating differences between burned peatlands and burned uplands, we used Advanced Landcover Prediction and Habitat Assessment data (ALPHA; 10 m resolution) from the Alberta Biodiversity Monitoring Institute to backfill EWC-classified burns within the Alberta study areas. ALPHA data were unavailable outside Alberta; consequently, we conducted RSAs for moose in Alberta separately from those in NEBC and Saskatchewan. The ALPHA data have five land-cover classes: bog, fen, mineral wetlands, and open water. Concordance analyses suggested that the ALPHA peatland (bog and fen) and upland classes had reasonable predictive accuracy with the EWC peatland (bog and nutrient-poor fen) upland classes, respectively (peatland accuracy, 76%; upland accuracy, 80%). Note that because RSAs primarily focused on the collective effects of ≤25-year-old burns (see later), the proportion of burns that were backfilled was relatively small.

For all RSAs, we modelled fire and anthropogenic disturbances using Canada Landsat Disturbance data (CanLaD; 30 m resolution; Guindon et al. 2017; Fig. 2). These data identified areas affected by fires and harvest from 1984–2015 by applying a change detection method to Landsat mosaics developed from reflectance products produced by the United States Geological Survey. This method detects ~91% of harvested areas and 85% of burns and has a disturbance class attribution success rate of ~98%; however, because the method uses a 6-year moving window analysis for class identification, it may overestimate disturbed areas in the initial and final 2 years of the data’s time span. Given our objective of assessing fine-scale responses of moose to burns, the CanLaD data are advantageous over polygon data for depicting fire perimeters because the CanLaD data more accurately capture the heteroge-

<sup>2</sup>Supplementary materials are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2018-0319>.

**Table 1.** Classification of land-cover types used to model resource selection by moose in northeastern Alberta, northwestern Saskatchewan, and northeastern British Columbia, Canada.

Land cover	EWC class	Description
Bog	Treed bog, open bog, shrubby bog	Black spruce ( <i>Picea mariana</i> ) and <i>Sphagnum</i> moss dominated bogs with no hydrodynamic flow. Areal coverage: ~10%
Nutrient-poor fen	Graminoid poor fen, shrubby poor fen, treed poor fen	Low-nutrient peatland soils influenced by groundwater flows; treed poor fens dominate (25%–60% tree cover), comprised of black spruce, tamarack ( <i>Larix laricina</i> ), and bog birch ( <i>Betula glandulosa</i> ). Areal coverage: ~12%
Nutrient-rich fen	Graminoid rich fen, shrubby rich fen, treed rich fen	Low-nutrient peatland soils influenced by groundwater flows; treed fens dominate and shrub indicators consist of bog birch, willow ( <i>Salix</i> spp.), and alder ( <i>Alnus</i> spp.). Areal coverage: ~14%
Mineral wetlands (reference category)	Shrub swamp, conifer swamp, tamarack swamp, hardwood swamp, mixedwood swamp, emergent marsh, meadow marsh, mudflats, aquatic bed, open water, cloud, cloud shadow	Wetland areas and swamps that generally occur on mineral soils; cloud and cloud shadow (collectively <0.5% coverage) are included in this reference category. Areal coverage: ~17%
Upland	Upland deciduous, upland mixedwood, upland conifer, upland other, agriculture, anthropogenic, cutblock	Mineral soils in an upland environment with intact forested areas having tree cover >25%; disturbed areas have small extents (agriculture, <0.1%; anthropogenic, 3%; cutblock, <0.1%). Areal coverage: ~38%

Note: Land-cover types were developed from Ducks Unlimited Canada's Enhanced Wetlands Classification (EWC) data.

neous nature of burned landscapes (e.g., fire skips; Vermote et al. 2016).

For moose density analyses, limitations in the available land cover necessitated modelling Alberta separately from NEBC. In Alberta, we used the ALPHA data as it covered 23 of the 24 units, whereas EWC data only covered 10; in NEBC, we used EWC data. For modelling fire, the limited time span of the CanLaD data precluded their use for moose density analyses given our objective of evaluating moose response to  $\leq 40$ -year-old fires, the threshold used in the federal recovery strategy for caribou. We therefore used polygon data depicting historical fire perimeters available from provincial government repositories. After rasterizing these data (30 m resolution), the correlation with the CanLaD data was found to be high ( $r = 0.99$ ), at least for quantifying the proportion of  $\leq 25$ -year-old fires within moose survey units.

### Data analyses

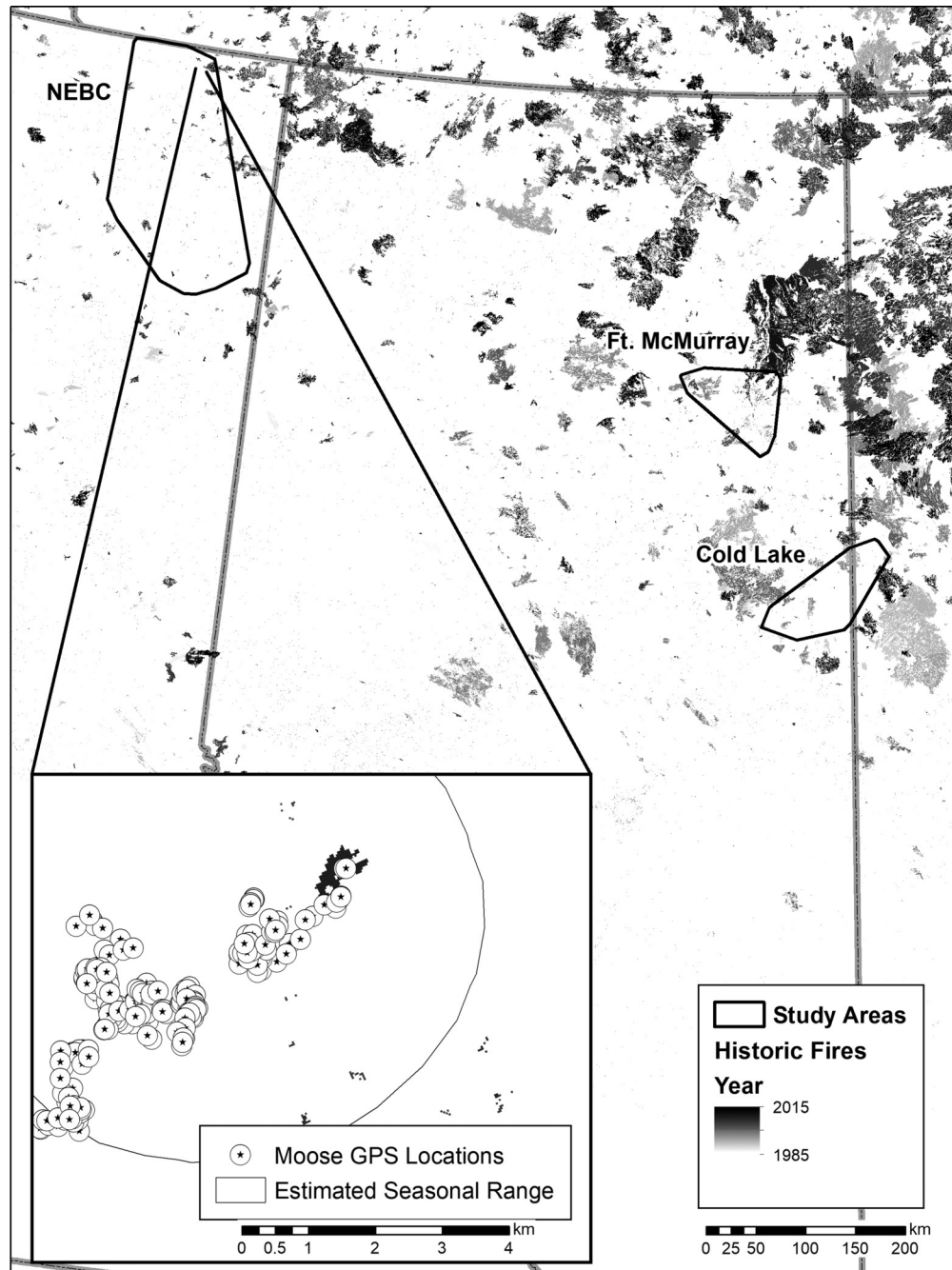
For fine-scale RSAs, we estimated SSFs for each individual moose using conditional logistic regression in a generalized estimating equation framework, which derives robust standard errors to account for potential autocorrelation among steps (Craiu et al. 2008; Oliveira-Santos et al. 2016). For all SSF analyses, we used only step lengths calculated from successive GPS locations (i.e., locations separated by 12 h; steps initiated or ending with a missing GPS fix were excluded). For all moose, we estimated the same model, which consisted of dummy variables representing various land-cover types, including those representing disturbed areas. In this formulation, variables representing fire  $\times$  land cover interactions were also coded as dummy variables; thus, each interaction variable (e.g., 1- to 5-year-old fire in uplands) became an additional land-cover type. Based on previous research evaluating moose responses to fire age (Maier et al. 2005; Joly et al. 2017), we considered the following age categories (i.e., time since fire) for fire  $\times$  land cover interactions: 1–5 years, 6–10 years, and 11–25 years. For all analyses, we set mineral wetlands as the reference category.

We derived population-level inferences by averaging parameter estimates across individual moose, weighting each estimate by the inverse of its variance (Murtaugh 2007). For each SSF, we evaluated predictive performance using  $k$ -fold cross-validation for conditional logistic regression (Fortin et al. 2009). This approach iteratively partitioned the strata (matched observed and random

steps) into five folds, using four folds for model estimation and then generating predictions for the withheld strata. Predictions were ranked within each stratum and then tallied into bins across strata. The correlation between bin rank and the associated frequency of predictions was assessed using Spearman's rank correlation coefficients for both observed ( $r_{S\_Obs}$ ) and random ( $r_{S\_Ran}$ ) steps. For estimating  $r_{S\_Ran}$ , one random step within each test stratum was randomly selected and the observed step was excluded from stratum ranking, a process that yields an  $r_S$  based on random expectation. We repeated this process 100 times for each SSF with increasing model performance equating to higher  $\bar{r}_{S\_Obs}$  relative to  $\bar{r}_{S\_Ran}$ .

For RSAs at the intermediate and largest scales, we estimated resource selection functions (RSFs) using logistic regression in a mixed-model framework. All models consisted of explanatory variables representing the proportions of the reclassified EWC land-cover types and the proportion of area burned. For the latter, fire data were "burned" into the land-cover raster; thus, burns became another land-cover type (i.e., all land-cover proportions summed to one). For models evaluating selection within seasonal ranges, the proportions of GPS locations occurring within each land-cover type for each moose season (i.e., the "used" component of the dependent variable, coded as 1) were compared with proportions within the individual's seasonal range for that year (i.e., the "available" component of the dependent variable, coded as 0). Proportions within seasonal ranges were derived by clipping the land-cover raster to seasonal ranges and then calculating the actual proportion of each land-cover type (i.e., availability was not sampled using random points). In this framework, each data row represents a single moose season and variance estimates therefore reflect moose season as the sampling unit. To account for moose having data spanning multiple years, we specified individual moose as a random intercept. We used the same approach for models evaluating seasonal range selection; that is, land-cover proportions within moose seasonal ranges were compared with proportions in the surrounding buffer. At both scales, we considered year as a random effect, but this formulation did not improve model performance (i.e., Akaike's information criterion (AIC) values increased by  $\sim 2$ ). For all RSF models, we evaluated performance using  $k$ -fold cross-validation, partitioning training and testing folds by animal (Boyce et al. 2002). Similar to SSF valida-

**Fig. 2.** The distribution of historic fires (1985–2015) in northern Alberta, northwestern Saskatchewan, and northeastern British Columbia, Canada. The extents of the three project areas were delineated by minimum convex polygons fit to the moose GPS location data. Inset shows the distribution of moose GPS locations in relation to small fires (<150 ha) in northeastern British Columbia. [Base map of Canadian provincial boundaries (2003) from ESRI Canada (source of information: ©2003. Government of Canada with permission from Natural Resources Canada). Fire data were from Guindon et al. 2017.]



tion, this process yields an  $\bar{r}_s$  (from 100 iterations) for each model, with higher values equating to better model performance.

We used linear regression models to evaluate the influence of fires on estimated moose densities. As with large-scale RSAs, we used explanatory variables characterizing the proportions of land-cover types and the proportion of area burned within a survey unit. We estimated models separately for Alberta and NEBC because of differences in the available land-cover data (see the earlier section Environmental covariates). We limited models to three or fewer explanatory variables because of small sample sizes and used a multistage model selection process to develop final

models. We discriminated among models at each stage using AIC corrected for small sample size ( $AIC_c$ ). In the first stage, we estimated univariate models with each non-burn land cover to identify the two types with the highest influence on moose density. We repeated this process to identify the most influential age class of burns. We considered age classes as specified for SSF models, as well as the cumulative influence of  $\leq 2$ -year-old burns and  $\leq 40$ -year-old burns. In the final stage, we combined the top land-cover and burn variables and evaluated all subsets of this three-variable model. From this final model set, we estimated model weights ( $\omega$ ) and calculated the relative importance of each vari-

able ( $\omega_+$ ; Burnham and Anderson 2002). For each top model, we evaluated performance by calculating a coefficient of determination ( $R^2$ ).

All analyses were performed in R, version 3.5.0 (for the specific packages and functions used and the associated references, see Supplementary material B).<sup>2</sup>

## Results

### Fine-scale use and selection

Across all seasons and in all study areas, moose showed low use of burns regardless of burn age and land-cover type (Table 2). In Alberta, the number of individual moose with at least one observed step ending in a given burn class (age by land cover) rarely exceeded 25%. For NEBC and Saskatchewan, this finding was even more pronounced, with most burn classes having no GPS locations or use by only a single individual. In all cases, the number of individuals exhibiting complete avoidance of a burn class (i.e., burn classes with available step end points but no used step end points) was higher than the number of individuals exhibiting use. Consequently, at the population level, burns were generally avoided relative to the reference category (i.e., mineral wetlands), and among land-cover types, those depicting burns consistently had the lowest ranking. Across individual moose, SSF models generally performed better than random expectation (calving,  $\bar{r}_{S\_Obs} = 0.13$ ,  $\bar{r}_{S\_Ran} = 0.01$ , mean difference = 0.10 (range, -0.14, 0.55); summer-fall,  $\bar{r}_{S\_Obs} = 0.14$ ,  $\bar{r}_{S\_Ran} = -0.02$ , mean difference = 0.16 (range, -0.15, 0.70); winter,  $\bar{r}_{S\_Obs} = 0.20$ ,  $\bar{r}_{S\_Ran} = -0.02$ , mean difference = 0.21 (range, -0.16, 0.50)).

### Use and selection within seasonal ranges

The lack of moose response to burned areas was also evident when analyzing moose habitat use and selection patterns within their seasonal ranges. Across 142 moose calving seasons, 107 calving ranges contained  $\leq 25$ -year-old burns, yet 86 of these ranges had no moose GPS locations falling within burns (Fig. 3). Availability of burns, however, was generally limited, as only 16 ranges had burns covering  $> 5\%$  of their total area. Similar patterns occurred within summer-fall and winter ranges. Across 131 moose summer-fall ranges, 118 contained  $\leq 25$ -year-old burns, but 80 of these had no moose GPS locations within burns and only 11 ranges had burns exceeding 5% of their area. Where burns exceeded 20% of the summer-fall range, moose appeared to show stronger selection for burns (Fig. 3). Among 66 winter ranges, 61 contained  $\leq 25$ -year-old burns, 40 had no moose GPS locations within burns, and only 10 had burns exceeding 5% of their area. Because of the lack of burns or their small extent in moose seasonal ranges, we focused all subsequent analyses above the fine scale on  $\leq 25$ -year-old burns and did not consider land cover  $\times$  burn interactions.

RSF models estimated within the seasonal-range scale showed avoidance of burns by moose relative to the reference category of swamps, marshes, and aquatic areas (Table 3). Among seasons, moose selection for burns was highest during the summer-fall, ranking third among the seven land-cover types. During calving and winter, burns were ranked fourth. Model prediction was generally good across all seasons (all  $\bar{r}_s \geq 0.67$ ).

### Seasonal range selection

Burns did not have a strong influence on moose selection of seasonal ranges. Across all seasons, moose did not situate seasonal ranges to encompass a higher proportion of  $\leq 25$ -year-old burns than the surrounding landscape (Fig. 4; univariate analyses: calving,  $\beta = -1.70$ , standard error (SE) = 1.64,  $p = 0.30$ ; summer-fall,  $\beta = -0.97$ , SE = 1.61,  $p = 0.55$ ; winter,  $\beta = -8.27$ , SE = 3.82,  $p = 0.03$ ). RSFs estimated at this scale, which account for the effects of other land-cover types, further supported the low influence of burns on range selection. Relative to the reference category of swamps, marshes, and aquatic areas,  $\leq 25$ -year-old burns were avoided in all seasons, and among the seven land-cover types, burns were

ranked sixth in calving, third in summer-fall, and last in winter (Table 4). High variation in moose selection of seasonal ranges resulted in relatively low prediction across all seasonal models ( $\bar{r}_s \leq 0.66$ ).

### Correlation between fire and moose density

The extent of burns had minimal influence on the estimated density of moose within survey units in both Alberta and north-eastern BC (Fig. 5). In both areas, we only considered  $\leq 40$ -year-old burns for final models, though 6- to 10-year-old burns had similar effects (i.e.,  $< 1 \Delta AIC_c$ ) and was the best variable among those partitioning burns into smaller age intervals. For land-cover effects, we considered the proportions of mineral wetlands and uplands for final model building in Alberta and the proportions of mineral wetlands and bogs for NEBC. One survey unit in Alberta had to be excluded from final modelling as land-cover data were not available across its entirety.

The top model for Alberta described the influence of  $\leq 40$ -year-old burns and mineral wetlands (Table 5). The coefficient for burns was negative and marginally significant ( $\beta = -0.26$ ,  $p = 0.10$ ), and this model ( $R^2 = 0.36$ ) was only slightly better than models describing just land-cover effects (all within  $< 1 \Delta AIC_c$ ). Across all model subsets, the model-averaged estimate for burns was also negative ( $\beta = -0.19$ ), and the importance of burns was lower relative to land-cover effects (burns,  $\omega_+ = 0.36$ ; mineral wetlands,  $\omega_+ = 0.66$ ; uplands,  $\omega_+ = 0.51$ ). In NEBC, none of the candidate models performed better than the null model. Similar to Alberta, the model-averaged estimate for burns was negative ( $\beta = -0.31$ ), and burns had low relative importance (burns,  $\omega_+ = 0.21$ ; mineral wetlands,  $\omega_+ = 0.33$ ; bogs,  $\omega_+ = 0.44$ ).

## Discussion

For species with large geographic distributions, habitat selection can vary regionally as animals respond to different biotic and abiotic conditions (Whittingham et al. 2007; Nimmo et al. 2012). Failure to account for such variation can negatively impact the effectiveness of management plans applied uniformly over broad spatial scales (Whittingham et al. 2007). In this study, we observed moose responses to fire in boreal forests of western Canada that differed markedly from those reported elsewhere within the North American distribution of moose (e.g., Peek 1974; Maier et al. 2005). Our results also do not support fire as a contributing factor in the DMAC hypothesis for explaining declines in boreal caribou populations, at least in this region where moose are considered the primary alternate prey. Our findings, however, do provide a possible mechanistic understanding as to why previous analyses have reported relatively weak effects of fire on caribou demography, especially in western ranges (Dalerum et al. 2007; Environment Canada 2008, 2011).

Although the prevailing paradigm has been that moose respond positively to fire (Crête 1988; Fisher and Wilkinson 2005; Maier et al. 2005; Joly et al. 2017), our study is not the first to report negligible or opposite effects. In Newfoundland, Jung et al. (2009) reported that moose used burned forests in proportion to their availability during late winter. Similarly, Gillingham and Parker (2008) reported weak selection for deciduous burns during summer, fall, and early winter but no selection during late winter and calving. Neither study quantified moose response by burn age, which may influence selective behaviour due to temporal changes in forage quality and quantity after fire (e.g., avoidance of  $< 5$ -year-old burns and selection of 11- to 30-year-old burns; Maier et al. 2005; Street et al. 2015; see also Mumma et al. 2018). Our findings, however, did not support an effect of burn age on moose selection of burns, at least at a fine scale. Other studies have also suggested that fire severity may influence moose behaviour toward burns, though variation in severity generally did not correlate with moose avoidance of burns per se (Lord and Kielland 2015; Brown et al. 2018). Although we did not consider fire severity due to such

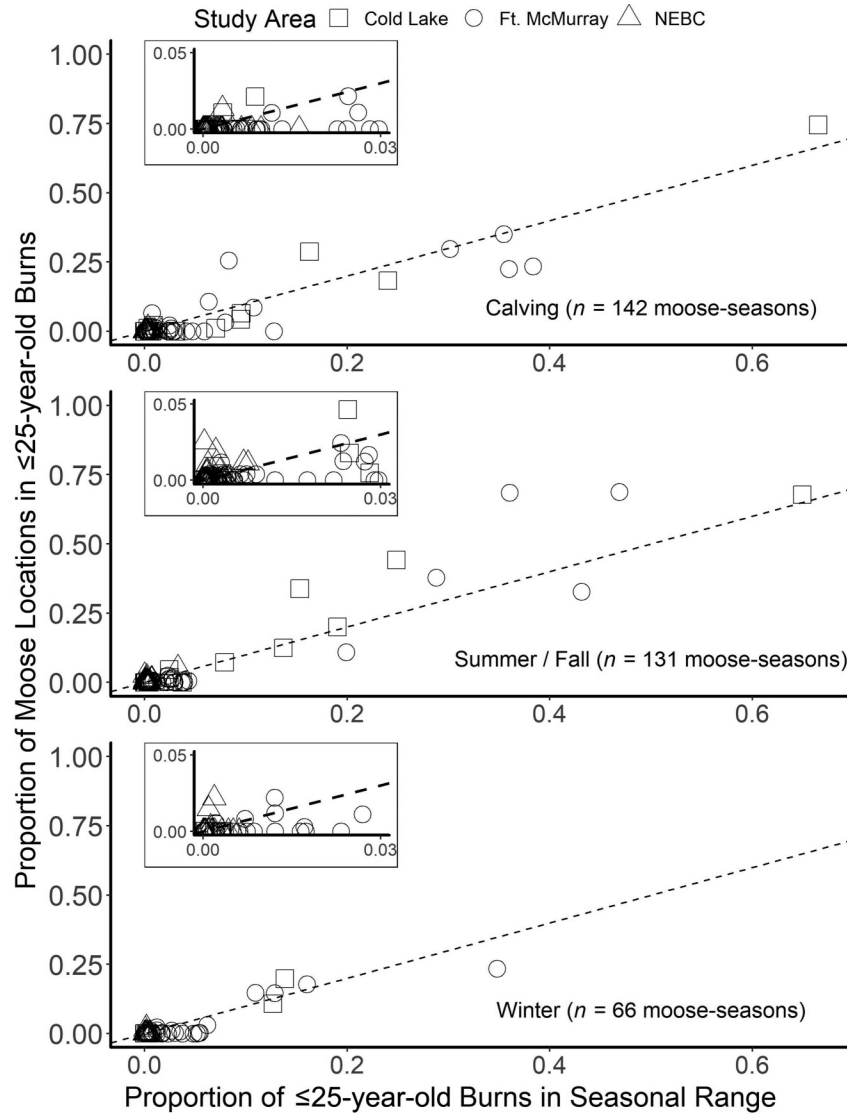
**Table 2.** Population-level parameter estimates ( $\beta$ ) and 95% confidence intervals (95% CI) from step selection functions fit to individual moose monitored for various periods between 2010 and 2015 in (a) Alberta and (b) British Columbia and Saskatchewan, Canada.

<b>(a) Alberta</b>									
Variable	Calving ( <i>n</i> = 42 moose)			Summer–fall ( <i>n</i> = 41 moose)			Winter ( <i>n</i> = 44 moose)		
	$\beta$ (95% CI)	Avail. ( <i>n</i> )	Use ( <i>n</i> )	$\beta$ (95% CI)	Avail. ( <i>n</i> )	Use ( <i>n</i> )	$\beta$ (95% CI)	Avail. ( <i>n</i> )	Use ( <i>n</i> )
Bog	-4.37 (-7.15, -2.10)	37	26	-6.13 (-9.57, -2.47)	40	29	-3.37 (-6.15, -1.56)	43	29
Nutrient-poor fen	-0.10 (-0.79, 0.29)	42	41	0.32 (-0.03, 1.00)	41	40	0.07 (-0.12, 0.26)	44	44
Nutrient-rich fen	0.39 (0.18, 0.56)	42	42	0.71 (0.17, 1.66)	41	40	0.37 (0.24, 0.51)	44	44
Upland	-0.06 (-1.40, 1.68)	42	40	0.30 (0.10, 0.52)	41	38	0.28 (-0.04, 0.63)	44	43
Harvested areas $\leq 25$ years old	-3.92 (-8.08, 0.51)	38	26	-0.81 (-2.09, 0.08)	39	30	-0.45 (-2.11, 1.12)	40	30
Fire $\times$ peatland $\leq 5$ years old	-9.77 (-15.08, -3.41)	10	4	-12.17 (-15.01, -7.02)	13	2	-14.45 (-16.55, -9.13)	15	1
Fire $\times$ upland $\leq 5$ years old	-14.05 (-16.15, -10.48)	13	2	-5.58 (-11.44, -2.01)	19	8	-10.37 (-15.26, -5.40)	20	4
Fire $\times$ other land cover $\leq 5$ years old	-8.54 (-15.07, -3.50)	12	4	-8.26 (-13.60, -3.70)	16	5	-13.22 (-15.75, -9.20)	20	3
Fire $\times$ peatland 6–10 years old	-14.24 (-15.87, -9.67)	7	2	-15.31 (-15.73, -14.75)	15	0	-15.33 (-16.42, -12.85)	15	2
Fire $\times$ upland 6–10 years old	-14.10 (-16.05, -9.76)	12	1	-14.66 (-15.47, -13.23)	20	4	-13.71 (-15.44, -9.68)	20	7
Fire $\times$ other land cover 6–10 years old	-12.09 (-15.45, -6.97)	13	2	-8.26 (-15.59, -13.35)	20	2	-14.32 (-15.75, -10.67)	19	6
Fire $\times$ peatland 11–25 years old	-7.48 (-13.21, -2.79)	12	5	-6.66 (-13.09, -2.99)	18	4	-6.47 (-11.45, -2.41)	17	9
Fire $\times$ upland 11–25 years old	-7.48 (-13.86, -3.03)	12	4	-6.76 (-12.80, -2.95)	21	7	-9.87 (-13.76, -5.62)	21	7
Fire $\times$ other land cover 11–25 years old	-11.48 (-14.50, -7.05)	20	6	-10.03 (-13.18, -6.12)	26	8	-11.82 (-14.06, -7.49)	26	13
<b>(b) British Columbia and Saskatchewan</b>									
Variable	Calving ( <i>n</i> = 43 moose)			Summer–fall ( <i>n</i> = 43 moose)			Winter ( <i>n</i> = 47 moose)		
	$\beta$ (95% CI)	Avail. ( <i>n</i> )	Use ( <i>n</i> )	$\beta$ (95% CI)	Avail. ( <i>n</i> )	Use ( <i>n</i> )	$\beta$ (95% CI)	Avail. ( <i>n</i> )	Use ( <i>n</i> )
Bog	-5.92 (-9.06, -3.04)	42	31	-2.55 (-4.66, -1.03)	43	37	-1.09 (-1.81, -0.61)	47	43
Nutrient-poor fen	-0.31 (-1.12, 0.16)	43	41	-1.11 (-2.69, -0.34)	43	42	-0.74 (-1.67, -0.31)	47	46
Nutrient-rich fen	-4.60 (-7.78, -1.55)	43	35	-0.76 (-2.12, -0.03)	43	41	0.25 (0.12, 0.37)	47	47
Upland	-0.94 (-2.05, -0.22)	42	38	-0.03 (-0.16, 0.07)	43	42	-0.23 (-0.36, -0.12)	47	47
Harvested areas $\leq 25$ years-old	-10.32 (-14.00, -6.71)	29	10	-4.46 (-7.65, -1.87)	41	24	-5.05 (-8.21, -2.57)	42	22
Fire $\times$ peatland $\leq 5$ years old	-15.24 (-15.95, -14.51)	4	0	-14.55 (-15.61, -12.45)	6	1	-14.89 (-15.25, -13.85)	9	0
Fire $\times$ upland $\leq 5$ years old	NE	0	0	-15.91 (-17.23, -13.81)	3	0	-14.30 (NE)	1	0
Fire $\times$ other land cover $\leq 5$ years old	-14.99 (-15.30, -14.11)	3	0	-13.38 (-15.60, -8.18)	6	2	-14.79 (-15.24, -13.95)	10	0
Fire $\times$ peatland 6–10 years old	-16.25 (-16.39, -15.33)	2	0	-10.21 (-14.21, 0.63)	3	1	-11.65 (-14.60, -7.08)	9	1
Fire $\times$ upland 6–10 years old	-14.84 (NE)	1	0	-13.25 (-13.43, -12.44)	3	0	-12.91 (-14.49, -8.54)	6	1
Fire $\times$ other land cover 6–10 years old	-16.39 (NE)	1	0	-12.79 (-15.51, -7.51)	5	1	-10.73 (-14.71, -4.75)	7	1
Fire $\times$ peatland 11–25 years old	-15.27 (-15.84, -14.24)	4	0	-14.01 (-15.63, -12.90)	7	0	-15.03 (-15.94, -13.97)	14	0
Fire $\times$ upland 11–25 years old	-16.13 (-16.80, -15.33)	4	0	-12.60 (-14.71, -8.71)	15	4	-14.84 (-15.74, -13.28)	10	0
Fire $\times$ other land cover 11–25 years old	-4.41 (-17.24, -1.00)	7	2	-9.50 (-15.28, -4.57)	17	2	-10.17 (-14.01, -5.98)	20	4

**Note:** Also presented are the number of moose where (i) the land-cover variable occurs at least once in the availability sample (Avail.) and (ii) at least one moose GPS location occurs within the land-cover variable (Use). Estimates from Alberta are presented separately from British Columbia and Saskatchewan due to slight differences in the data used to model land cover in these regions (see text). NE, not estimable.



**Fig. 3.** Univariate comparison of the proportion of moose GPS locations (i.e., use) in  $\leq 25$ -year-old burns and the proportion of these burns in the seasonal ranges (i.e., availability) of individual moose monitored for various periods between 2010 and 2015 within three project areas predominantly situated in northeastern Alberta and northeastern British Columbia, Canada. The dashed line indicates the threshold of random expectation: points falling above this line indicate selection for burns, while points below this line indicate avoidance. Insets show the distribution of points near the plot origin.



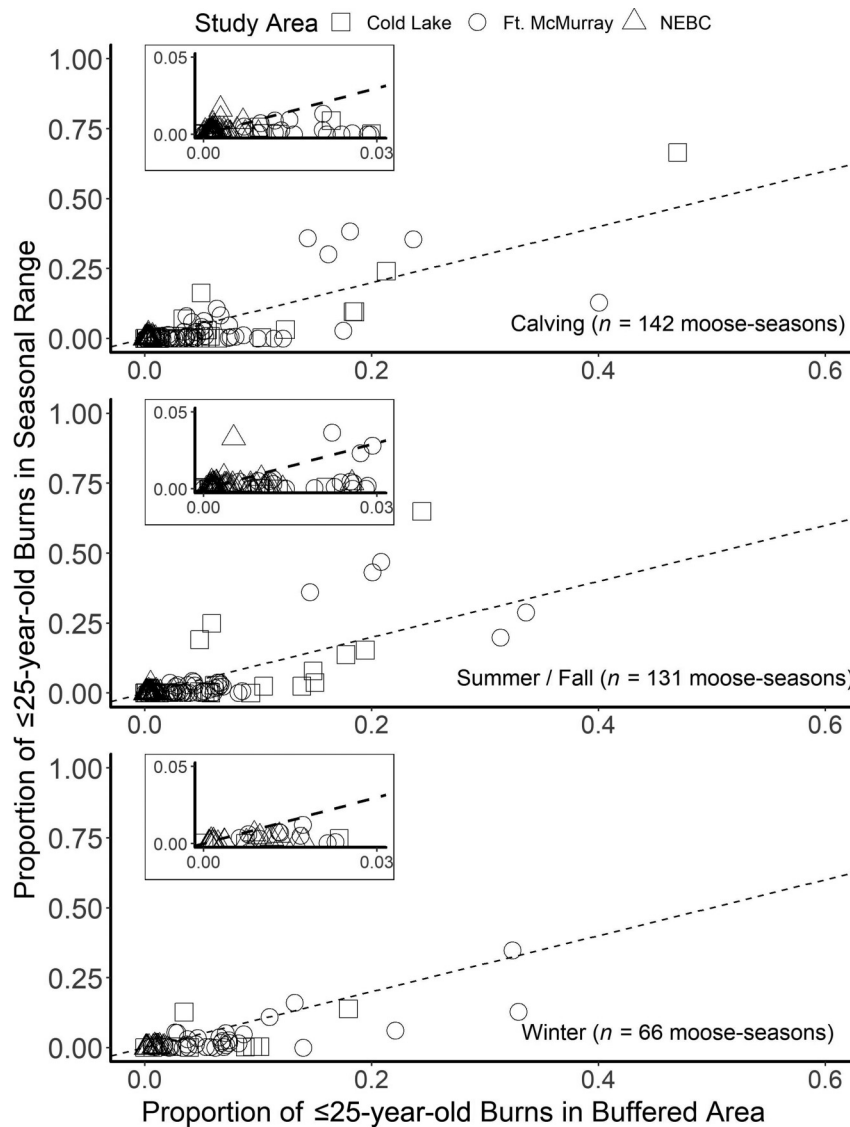
**Table 3.** Parameter estimates ( $\beta$ ) and standard errors (SE) from resource selection functions evaluating moose selection of burns, harvested areas, and various land-cover types within their seasonal ranges.

Variable*	Calving, $n = 142$ moose seasons (85 individual moose)			Summer–fall, $n = 131$ moose seasons (82 individual moose)			Winter, $n = 66$ moose seasons (52 individual moose)		
	$\beta$	SE	$p$	$\beta$	SE	$p$	$\beta$	SE	$p$
Proportion of rich fen	-1.60	1.07	0.135	-3.43	1.72	0.053	-0.57	2.66	0.829
Proportion of poor fen	-0.04	1.04	0.969	-7.23	1.82	<0.001	-10.61	2.89	<0.001
Proportion of bog	-5.82	1.43	<0.001	-13.89	2.81	<0.001	-10.09	3.47	0.003
Proportion of uplands	-2.87	0.97	0.003	-4.30	1.29	0.001	-4.11	1.99	0.039
Proportion of fires $\leq 25$ years old	-2.43	1.61	0.131	-3.73	1.46	0.011	-9.66	4.22	0.022
Proportion of harvested areas $\leq 25$ years old	-5.22	1.82	0.004	-6.68	1.99	0.001	-11.40	3.57	0.001
Model validation ( $\bar{r}_S$ )	0.67			0.77			0.69		

**Note:** Individual moose were monitored for various periods between 2010 and 2015 in three study areas predominantly situated in northeastern Alberta and northeastern British Columbia, Canada.

\*For all models, parameter estimates represent selection (positive  $\beta$ ) or avoidance (negative  $\beta$ ) relative to the reference category, presented as the proportion of mineral wetlands.

**Fig. 4.** Univariate comparison of the proportion of  $\leq 25$ -year-old burns in moose seasonal ranges (i.e., use) and the proportion of these burns in the surrounding landscape (i.e., availability), delineated by buffering each seasonal range by its maximal cross-sectional width. Moose seasonal ranges were estimated from GPS location data collected between 2010 and 2015 from three project areas situated in northeastern Alberta and northeastern British Columbia. The dashed line indicates the threshold of random expectation: points falling above this line indicate selection for burns, while points below this line indicate avoidance. Insets show the distribution of points near the plot origin.



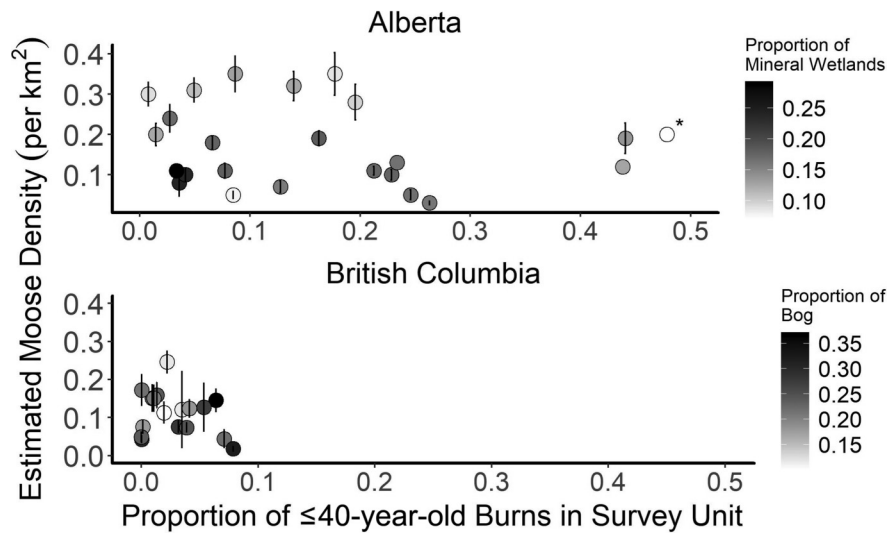
**Table 4.** Parameter estimates ( $\beta$ ) and standard errors (SE) from resource selection functions evaluating moose selection of seasonal ranges between 2010 and 2015 in three study areas situated in northeastern Alberta and northeastern British Columbia, Canada.

Variable*	Calving, $n = 142$ moose seasons (85 individual moose)			Summer-fall, $n = 131$ moose seasons (82 individual moose)			Winter, $n = 66$ moose seasons (52 individual moose)		
	$\beta$	SE	$p$	$\beta$	SE	$p$	$\beta$	SE	$p$
Proportion of rich fen	-1.39	1.46	0.341	-4.17	1.87	0.025	4.99	3.42	0.144
Proportion of poor fen	-3.47	1.56	0.026	-3.39	1.95	0.082	-2.56	3.22	0.426
Proportion of bog	-3.86	1.64	0.019	-5.40	2.27	0.018	3.12	3.54	0.379
Proportion of uplands	-2.87	1.34	0.033	-0.75	1.66	0.652	4.09	2.83	0.149
Proportion of fires $\leq 25$ years old	-4.17	1.92	0.030	-3.17	2.03	0.119	-8.84	4.44	0.047
Proportion of harvested areas $\leq 25$ years old	-4.38	1.81	0.016	-8.10	2.43	0.001	-2.08	3.58	0.561
Model validation ( $\bar{r}_S$ )	0.32			0.35			0.66		

**Note:** Seasonal ranges were estimated using 95% utilization distributions and availability was delineated by buffering each seasonal range by its maximal cross-sectional dimension.

\*For all models, parameter estimates represent selection (positive  $\beta$ ) or avoidance (negative  $\beta$ ) relative to the reference category, presented as the proportion of mineral wetlands.

**Fig. 5.** Univariate comparison of  $\leq 40$ -year-old burns and estimated moose density (with standard error bars where available) in survey units situated in northern Alberta ( $n = 23$ ) and northeastern British Columbia ( $n = 17$ ), Canada. For each region, the proportions of the land-cover variable with the highest influence on moose density are also shown (\*land-cover data were not available for one unit in Alberta). Units were surveyed between 1993 and 2015 in Alberta and between 2010 and 2016 in British Columbia.



**Table 5.** Parameter estimates ( $\beta$ ), log likelihoods ( $\log L$ ),  $AIC_c$  differences from the top model ( $\Delta AIC_c$ ), and model weights ( $\omega$ ) from the final candidate set of models considered for evaluating the influence of land cover and  $\leq 40$ -year-old burns on estimated moose within survey units situated in (a) northern Alberta ( $n = 23$ ) and (b) northeastern British Columbia ( $n = 17$ ), Canada.

**(a) Alberta**

$\beta$						
Intercept	Proportion of fires $\leq 40$ years old	Proportion of mineral wetlands	Proportion of uplands	$\log L$	$\Delta AIC_c$	$\omega$
0.39	-0.26	-1.13	—	25.20	0.00	0.24
0.03	—	—	0.31	23.70	0.04	0.24
0.33	—	-1.02	—	23.60	0.23	0.22
0.18	—	-0.63	0.20	24.77	0.86	0.15
-0.01	0.11	—	0.36	23.89	2.62	0.07
0.39	-0.27	-1.14	0.00	25.20	3.31	0.05
0.17	—	—	—	20.14	4.49	0.03
0.20	-0.17	—	—	20.65	6.13	0.01

**(b) Northeastern British Columbia**

$\beta$						
Intercept	Proportion of fires $\leq 40$ years old	Proportion of mineral wetlands	Proportion of bog	$\log L$	$\Delta AIC_c$	$\omega$
0.11	—	—	—	24.68	0.00	0.26
0.18	—	—	-0.32	26.16	0.04	0.25
0.01	—	0.37	—	25.73	0.90	0.16
0.09	—	0.33	-0.29	27.13	1.59	0.12
0.13	-0.59	—	—	25.30	1.76	0.11
0.18	-0.31	—	-0.28	26.33	3.18	0.05
0.04	-0.35	0.31	—	25.9	3.99	0.04
0.09	-0.05	0.32	-0.29	27.13	5.70	0.01

**Note:** Units were surveyed between 1993 and 2015 in Alberta and between 2010 and 2016 in British Columbia.

data being restricted to Alberta, it is unlikely that our results were strongly influenced by fire severity given the overall limited use and avoidance of burns by moose in our study areas.

Mechanisms for explaining moose responses to fire have primarily focused on the positive changes in forage that develop after fire (MacCracken and Viereck 1990; Weixelman et al. 1998; Brown et al. 2018). Our results may be explained by a similar mechanism. Ranges of boreal caribou are generally composed of high proportions of peatlands (Stuart-Smith et al. 1997) and the

postfire trajectory of this land-cover type may not generate substantial increases in preferred moose forage (e.g., willow (*Salix* spp.) and birch (*Betula* spp.); MacCracken and Viereck 1990; Brown et al. 2018). Indeed, burned peatlands were generally avoided by moose more than other burned land covers in our study. Negligible changes in forage quantity may also explain why we did not find an aggregative response of moose in burns (Peek 1974) and no significant relationship between  $\leq 40$ -year-old burns and moose density (c.f. Bangs and Bailey 1980; Maier et al. 2005).

Alternative mechanisms, however, could explain our findings. For example, after finding no aggregative response by moose to burns in central Alaska, Gasaway et al. (1989) suggested that traditional movement patterns prevented individuals from shifting home ranges to take advantage of burns. Selection of home ranges could also be influenced by predator and hunter avoidance, with moose becoming reluctant to spend increased time in the more open areas that result after fire (Courtois et al. 2002). In our study areas, discriminating among potential mechanisms will likely require further research such as conducting field site investigations within various burned land covers to estimate postfire forage changes.

In some respects, our findings might explain why moose, caribou, and fire have co-existed for thousands of years within North American boreal forests. Although other studies have shown increasing moose density in response to fire (e.g., Loranger et al. 1991; Maier et al. 2005), large increases in moose populations within and adjacent to caribou ranges after fire could lead to unstable caribou population dynamics. Bergerud (1996) suggested that caribou populations cannot persist when moose densities exceed 0.2–0.3 individuals·km<sup>-2</sup>, a threshold that in other systems may be exceeded for more than two decades after fire (Loranger et al. 1991). In our study, we did not quantify the expected change in moose densities following fire, but our results do not suggest increases of four- to six-fold as reported elsewhere (e.g., Minnesota, Peek 1974; Alaska, Loranger et al. 1991). Note that a substantial number of moose density estimates in our study are above Bergerud's (1996) threshold, indicating that other factors (e.g., climate change, human-mediated disturbances) are likely contributing to high moose populations within and adjacent to some caribou ranges. We further emphasize that our findings are restricted to western boreal forests. In other woodland caribou systems where moose are considered invasive, moose responses to fire may differ. For example, in the inland rain forests of south-central British Columbia where the southern mountain ecotype of caribou resides, fire and human-mediated disturbances have resulted in substantial increases in moose populations and subsequent caribou declines (Edwards 1954; Seip 1992; Serrouya et al. 2015). In these mountainous systems, disturbances have resulted in large increases in available moose forage (Serrouya et al. 2011).

The negligible response of moose to fire in our study does not preclude fire effects on caribou demography. Others have reported a negative correlation (Environment Canada 2008, 2011; Sorensen et al. 2008), and although this relationship has been primarily attributed to DMAC with moose (Festa-Bianchet et al. 2011), other mechanisms may be influential. For instance, caribou may be susceptible to increased predation risk if their avoidance of burns leads to an increasingly clumped spatial distribution that makes them more predictable on the landscape (Fortin et al. 2013; DeMars et al. 2016). Fires could potentially exert negative bottom-up effects on caribou demography by decreasing the availability and abundance of lichen (Schaefer and Pruitt 1991; Dunford et al. 2006), though evidence to date suggests that such effects are less influential in current population declines of woodland caribou (Wittmer et al. 2005; Dalerum et al. 2007). Caribou may also experience DMAC with ungulates other than moose. In Alberta's caribou ranges, white-tailed deer populations are expanding (Latham et al. 2011; Dawe et al. 2014), and the response of this species to postfire conditions may differ from that of moose. Fires may also affect the distribution and increase the abundance of black bears, which are primary predators of caribou neonate calves (Brodeur et al. 2008; Bastille-Rousseau et al. 2011). At present, the relative impacts of these various mechanisms on caribou demography have not been explicitly quantified.

Results of our study have direct implications regarding current management recommendations for boreal caribou. The relatively weak effects of fire on caribou demography (Environment Canada 2008, 2011) and the lack of support demonstrated here for its

primary hypothesized mechanism suggest that fire impacts may differ from those associated with other disturbances; consequently, considering all forms of disturbance as equal when determining disturbance thresholds in caribou ranges may be misguided (Environment Canada 2012). Previous research has demonstrated that linear disturbances impact caribou populations via different mechanisms (e.g., increased predator movement efficiency (Dickie et al. 2017) and increased caribou–predator spatial overlap (DeMars and Boutin 2018; Mumma et al. 2018)) than polygonal disturbances (e.g., apparent competition (Seip 1992)), and such differences may result in differing magnitudes of impact on caribou demography. Potential differential impacts among disturbance types have particular relevance to the Boreal Shield caribou range in Saskatchewan, which is 57% disturbed yet >96% of these disturbances are due to fire (Environment Canada 2012). Although the population trend of caribou within this range is currently unknown, findings from our study and others (e.g., Dalerum et al. 2007) would predict lower demographic impacts compared with other ranges with similar disturbance extents but predominantly different disturbance types (e.g., the Maxhamish Range in British Columbia, which is 58% disturbed with 98% of disturbances being anthropogenic; Environment Canada 2012). Going forward, understanding the differential impacts of various disturbance types should be a research priority to more effectively quantify habitat quality within caribou range.

Across spatial scales, our results consistently pointed to limited use and avoidance of burned areas by moose within western boreal forests. We suggest that these inferences may be conservative given that fix success rates on some moose collars were low (e.g., <90%), which generally results in a bias toward selection of more open land-cover types such as burns (Frair et al. 2010). We do caution, however, that our inferences are restricted to the ranges of the available data. For fires in particular, the proportion of burns within a given spatial extent rarely exceeded 20% (Figs. 2–4). Because of this limitation, we could not rigorously assess for potential functional responses in selection of burns by moose (Myserud and Ims 1998). Functional responses occur when resource use does not scale linearly with resource availability, and in the case of moose, use of burns may increase nonlinearly as the proportion of burns increases. With fires predicted to increase in extent and frequency within western boreal forests (Flannigan et al. 2009), further research may be necessary to understand the dynamics among moose, caribou, and fire in these changing landscapes.

## Conclusion

Population declines of boreal caribou have been primarily attributed to natural and anthropogenic disturbances, yet increasing evidence suggests that the magnitude of disturbance impacts, their mechanistic pathways, and the relative importance of disturbance types may vary regionally (Rudolph et al. 2017; Mumma et al. 2018). Our results support such regional variation as we found no evidence for an expected primary mechanism linking fire to population declines of boreal caribou within western Canada. If unaccounted for, regional variation in disturbance impacts can diminish the effectiveness and efficiency of management strategies aimed at recovering caribou populations (Whittingham et al. 2007). Currently, such strategies are primarily focused on habitat restoration (Environment Canada 2012), but the scale and cost of restoring caribou ranges necessitates prioritizing restoration efforts (Hebblewhite 2017). Effective prioritization will likely require further research to understand regional variation in disturbance impacts and to evaluate untested assumptions of potential mechanisms driving caribou populations across their distribution.

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