A burning question: The spatial response of woodland caribou to wildfire in northeastern Alberta

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Ecology

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### Abstract

The Canadian Federal Recovery Strategy for woodland caribou classifies areas burned by wildfire in the last 40 years as disturbed habitat for woodland caribou. This delineation of fire disturbance has major economic and social implications across Canada. Caribou have been shown to avoid burned areas, but our understanding of the implications of burned habitats on survival is unclear. Previously, studies used coarse mapping techniques that failed to delineate unburned residual patches within the burn complex, which have recently been proposed to provide undisturbed habitat for caribou. To assess the importance of burns and unburned residual patches, we examined the multi-scale resource selection of these two landcovers and the implications of using burns to adult survival of caribou for 201 individuals dispersed among six Alberta caribou populations. We found that caribou avoided both the burn complex and unburned residual patches in all seasons. However, increased use of burned habitats did not influence survival, while use of uplands significantly decreased survival. Collectively, these results suggest that burns and the corresponding residual patches are indeed low-quality habitat for caribou; however, a negligible survival effect suggests the classification of burned habitat as disturbed may be overstated by current recovery strategy recommendations. This study provides important information for herd-level management decisions and defining critical habitat under the federal mandates.

# Preface

This thesis is an original work by Sean Konkolics. No part of this thesis has been previously published.

### Acknowledgements

Thank you to my supervisor, Dr. Stan Boutin, for taking me on as a graduate student and giving me the opportunity to advance my skills in research and pursue ecology as a career path. The research, ideas, and outlook you provided at the University of Alberta have been exceptional and I am thankful for all the opportunities. I would also like to thank my committee member Dr. Scott Nielsen for his guidance and feedback on my thesis. I also thank collaborators Dr. Rob Serrouya, Mel Dickie and Dave Herviuex for their perspective and support from which my thesis has greatly benefited.

Funding and in-kind support for the development of this research project was provided by the National Science and Engineering Research Council of Canada's CREATE- Environmental Innovation initiative, Regional Industry Caribou Collaboration, Alberta Biodiversity Monitoring Institute's Caribou Monitoring Unit, and Alberta Environment and Parks. Thank you to Alberta Environment and Parks, specifically Dave Hervieux, for providing me with the exhaustive caribou GPS and mortality data that took hundreds of hours to collect.

Thank you to Mike Peers, Yasmine Majchrzak, Zac MacDonald, Clayton Lamb, Ainsley Sykes, the Boutin lab, the Merrill lab, the Boyce lab, the Bayne lab and a countless number of graduate students and friends for their support through this process. Specifically, I would like to thank Melanie Dickie for her help on this project. Mel has been irreplaceable during my time at the university. I cannot thank her enough for always lending a hand with updates, budgets, reports, presentations, results, R-code, drafts and life.

Finally, thank you to my friends and family back home. Without your support none of this would have been possible.

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### Introduction

Natural disturbance events have wide-ranging effects on species ecology and evolution (Menge & Sutherland 1987). Natural disturbance disrupts the structure of an ecosystem and changes resource availability or the physical environment, opening opportunities for individuals of the same or different species to use them (Townsend & Hildrew 1994). The spatial heterogeneity created by disturbance influences ecological processes at multiple scales, with effects on species interactions such as interspecific competition and predator-prey dynamics (Connell 1978; Meffe 1984). The concepts of patch dynamics and disturbance regimes form a basic framework in which quantitative studies can develop sound mechanistic predictions about the relevance of disturbance to species persistence (Pickett & White 1985).

In the boreal forest, wildfire is the dominant natural process influencing forest structure, vegetation composition and habitat heterogeneity (Goldammer & Furyaev 1996). The sprucedominated forests of western Canada have a typical fire frequency of 80-100 years and single large fires (>100,000 ha) constitute much of the total area burned (Perera & Buse 2014). An excellent example of a species that is dependent on the boreal forest and encounters these firedisturbed habitats, is the boreal ecotype of woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)). Due to recent declines, woodland caribou are provincially and federally listed as threatened (COSEWIC 2002). Caribou declines are hypothesized to be primarily driven by habitat disturbance from humans (Dsuz 2001; Sorensen *et al.* 2008; Festa-Bianchet *et al.* 2011), which has been shown to decrease adult survival and calf recruitment facilitated by increased predator densities and hunting efficiency in human disturbed areas (McLoughlin *et al.* 2003; Whitmer 2005; Dickie *et al.* 2017). The increase of predators in human disturbed areas is largely attributed to the process of apparent competition (Holt 1977; DeCesare et al. 2010), where disturbances in caribou ranges increase the amount of early seral habitat, thereby attracting moose (Alces alces) and deer [Odocoileus spp.]. Increases in these primary prey species subsequently increase the density of predators which opportunistically predate caribou (Seip 1992; Bergerud 1996). Though human disturbance is the primary driver of population declines, areas recently burned by wildfire are also considered disturbed habitat for caribou under the federal recovery strategy (ECCC 2012). Like human disturbance, burned habitats create early seral habitat and are hypothesized to facilitate apparent competition (Serrouya *et al.* 2011; Courbin et al. 2013); therefore, caribou are generally thought to avoid these areas (Fritz et al. 1993; Joly et al. 2003; Barrier & Johnson 2012). Additionally, caribou depend on lichen as a food resource which is destroyed in wildfires (Shaefer & Pruitt 1991; Jandt et al. 2008; Joly et al. 2015) and can take over 40 years to recover in post-fire disturbance habitats (Dunford 2006; Anderson & Johnson 2014). Therefore, Environment Canada (2012) defined the total area of habitat within 500 meters of an anthropogenic feature or within the boundaries of a recent (< 40years) wildfire as disturbances within caribou ranges. Further, the federal recovery strategy suggests that for caribou populations to have a 60% probability of persistence as self-sustaining populations, disturbance must constitute < 35% (i.e. 65% undisturbed) of a woodland caribou range (ECCC 2011). Limiting range-level disturbance to less than 35% of the land base is the primary objective of population recovery strategies; however, the relative influence of human versus wildfire disturbance on caribou population persistence is unclear. With the projected increase of both human disturbance (Bogdanski 2008; Government of Canada 2009), and wildfire frequency (Finnigan et al. 2009), meeting 65% undisturbed habitat becomes increasingly difficult and has major land use and economic implications (Hebblewhite 2017).

Caribou have evolved with wildfire, making them likely to have strategies to compensate for post-fire disturbance habitat shifts, suggesting the negative effects of fire may be overemphasized, particularly for population persistence (Bergerud 1974). One such strategy that caribou may employ is to take advantage of post-fire residual patches that have been left unburnt within the fire boundary (Skatter et al. 2017). As much as a third of the area in boreal fire events can be left unburned, retaining the pre-burn vegetation community and biomass (Eberhart & Woodard 1987; Andison & McCleary 2014; Araya et al. 2015), which are relatively unaffected compared to the physically burned area (burned complex) within the fire boundary (Cuesta et al. 2009, Ferster *et al.* 2016). However, the presence and ecological role of residual patches is rarely discussed in the caribou-fire literature, where most studies focus on the effects of wildfire extents (Perera & Buse 2014). Residual patches could serve as refugia that provide caribou with productive foraging and cover from predators (DeLong & Kessler 2000; Kansas et al. 2016). Yet, previous habitat selection studies have mapped fires using coarse polygons that do not delineate unburned residuals, precluding insight into their importance (but see Skatter et al. 2017). Currently, Environment Canada's (2012) estimate of total disturbance does not differentiate residual patches from the burn complex, potentially underestimating the amount of undisturbed habitat available to caribou.

Caribou are assumed to maximize fitness by avoiding burned habitats, however, the linkages between burned habitat associations and demography have been unclear. Although fire disturbed habitat has been shown to negatively affect demography when considered additively with human disturbance (ECCC 2008, 2011; Sorensen *et al.* 2008; Rudolph *et al.* 2017), the effects have been insignificant when fire disturbance is considered alone (Dalerum *et al.* 2007; ECCC 2008, 2011). Unproductive lowlands in the boreal forest (i.e. preferred caribou habitat)

often self-perpetuate following fire and may not show a dramatic increase in the amount of ungulate forage post-fire (James *et al.* 2004; Johnstone *et al.* 2010), leading to no numerical response from other ungulate species (Demars *et al.* 2019). Further, in the boreal forests of western Canada caribou populations are limited by predation rather than lichen availability (Rettie & Messier 1998; McLoughlin *et al.* 2003), suggesting that the loss of lichen due to fires may not affect caribou survival or reproduction. Therefore, forest fires may not facilitate apparent competition and their demographic effect on caribou may be overestimated under current recovery strategy guidelines.

Habitat use and demography are implicit in defining critical habitat under the federal recovery strategy and detailed research is needed to avoid incorrect prioritization of habitats (Battin 2004) and inefficient spending of limited recovery funds (Hebblewhite 2017). Here, we assessed the effects of wildfire on six Alberta caribou herds experiencing highly variable levels of wildfire disturbance. Caribou data were collected from 201 individuals and spans nearly 20 years, allowing us to test the spatial effects of burned habitats on caribou populations in western Canada. Specifically, we examined caribou habitat use and selection of unburned residuals using multi-scale resource selection functions and integrated effects of using burned habitat with adult survival through a Cox-proportional hazard survival model. A two-stage approach assessed broad- and fine-scale habitat selection patterns of caribou exposed to burned habitats and relate use and availability of burned habitat to adult female survival. Specifically, we ask the following: 1) Do caribou situate their annual ranges to avoid habitat that has recently burned? 2) Does caribou habitat selection differ between unburned residual patches and the burned complex? 3) Does increased exposure to, or use of, habitat created by recent fire disturbance affect adult female survival? This study aims to provide insight into the role of burns and unburned residual

patches to caribou ecology, offering important information for range-level management decisions and defining critical habitat under the federal recovery strategy. In addition, recognizing the potential importance of heterogeneity created by natural disturbance in ecological processes is important for promoting the recovery of Species at Risk in general.

### Methods

#### Study Area

The study area covers the ranges of six woodland caribou herds in northeastern Alberta (Figure 1): West Side Athabasca River (WSAR; 1,570,712 ha), East Side Athabasca River (ESAR; 1,311,902 ha), Richardson (RS; 707,390 ha), Cold Lake (CL; 672,586 ha), Slave Lake (SL; 151,623 ha) and Red Earth (RE; 2,470,203 ha). These ranges comprise 47.6% of the total area of caribou range in Alberta. The area is classified as the Boreal Plains ecozone (ECCC 2001) which consists of upland boreal mixed-wood forests. Common tree species are trembling aspen, (*Populus tremuloides*), jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), and tamarack (Larix laricina). Less common species are balsam poplar (Populus balsamifera), paper birch (Betula papyrifera), and balsam fir (Abies balsamea) (Lee & Boutin 2006). Tree cover in bogs seldom exceeds 35% and is dominated by black spruce (*Picea mariana*). The shrub cover features labradour tea (Ledum groenlandicum), bog cranberry (Vaccinium vitis-idaea), and small bog cranberry (Oxycoccus microcarpus). At these sites, most of the ground cover is mosses, Sphagnum fuscum, Sphagnum magellanicum, Sphagnum angustifolium, and Polystrichum strictum (Lee & Boutin 2006). Bradshaw et al. (1995) offers a description of typical caribou habitat in northeastern Alberta.

Well sites, industrial sites, mine sites, roads, trails, seismic lines and transmission lines are common sources of anthropogenic disturbance found in the region, primarily created by gas and oil development. Seismic lines are the most prominent anthropogenic disturbance with a mean density of 1.38 km per km<sup>2</sup> across the six herd ranges (AEP 2017). None of the six caribou ranges meet a threshold of 65% undisturbed habitat (ECCC 2012).

#### Caribou Data

We used GPS relocation data collected between 1998-2017 from 201 adult female caribou dispersed among the six herds (sample sizes; WSAR = 52; ESAR = 53; RS = 23; CL = 11; SL = 6; RE = 56). Data were collected by the Government of Alberta with the primary purpose of quantifying caribou-habitat associations and population trends. All animals were captured and handled using procedures developed under provincially or institutionally approved animal care protocols. No additional animals were captured for this study. GPS collars were programmed to obtain a relocation every two hours, and the mean monitoring times varied among the six herds (WSAR 403 days [range: 74-1101]; ESAR 548 days [range: 13-1442]; RS 498 days [range: 37-1273]; CL 597 days [range: 130-1067]; SL 682 days [range: 105-1421]; RE 504 days [range: 83-1490]). Prior to analysis, GPS data were cleaned to exclude locations beyond the feasible range and trajectory of caribou movement over the two-hour period (Bjørneraas *et al.* 2010).

#### Fire Mapping

All fires mapped were less than 40 years old and available to collared caribou (within annual home range boundaries) (Table 1). Remote sensing with satellite imagery is a commonly used tool to map and delineate wildfires (Lentile *et al.* 2006). In the simplest method, satellite images can be used to hand draw the outer fire boundary. To account for within burn complexity, a

common technique used is the Normalized Burn Ratio (NBR) (Kansas *et al.* 2016). The NBR is calculated using the near- and mid- infrared light on the electromagnetic spectrum. Near-infrared light is sensitive to vegetation greenness (Bands 4 and 7 of Landsat TM sensor) and mid-infrared light is sensitive to moisture (Band 5 and 7 of the Landsat OLI sensor). The NBR can be calculated as:

$$NBR = (B4_{near-infrared} - B7_{mid-infrared})/(B4_{near-infrared} + B7_{mid-infrared})$$

Pre- and post- fire images were overlaid to create a difference image or the Delta Normalized Burned Ratio (dNBR). dNBR reliably classifies surface imagery to quantify the complexity within the fire boundary (Key & Benson 2006, French *et al.* 2008), outperforming 12 remote sensing techniques for mapping fires using Landsat TM and ETM+ images in boreal interior Alaska (Epting *et al.* 2005). These methods have been described and tested many times (Guindon *et al.* 2017; Key & Benson 2006; Kansas *et al.* 2016). Updated dNBR fire images separated unburned residual patches from the burn complex within the outer fire boundary and were used for subsequent habitat selection analyses. See Appendix 2 for analysis details.

#### Habitat classification

Upland and lowland landcovers were classified with Alberta Biodiversity Monitoring Institute's (ABMI) Predictive Landcover 3.0 and ABMI wetland inventory. This is ABMI's high resolution data set for mapping wetland and lowland types at a 10 m resolution generated with a segmentation convolutional neural net algorithm that predicts patches of different lowland and upland types (Hird *et al.* 2017; DeLancey *et al.* 2019). ABMI's predictive landcover data was combined with fire maps and reclassified into six fire-habitat classes that were biologically

relevant to caribou (Table 2). Water was removed from analysis. From here on "burned habitats" are those areas which have burned in the last 40 years.

### Do caribou place their home ranges in areas with less burned habitat?

To evaluate whether burns influenced caribou selection of their annual home ranges, the proportion of burns within an individual's annual home range were compared to the proportion of burns within the herd range using selection ratios (2<sup>nd</sup> order selection, Johnson 1980; Manly et al. 2002). An annual home range was calculated for each caribou year using a 95% kernel UD, which was smoothed using the "reference bandwidth" parameter. To avoid poorly estimated ranges (Börger et al. 2006), animals that were not monitored for at least six months of the year were excluded. Then, we projected random locations at five-times the density of GPS locations for each animal within the KDE annual home ranges. Using ranges defined by Alberta Environment and Parks GPS and VHF collar data, the same range boundaries used in the federal and provincial recovery plans, we projected ten random locations per square kilometer. The proportion of the two sets of random samples within fire boundaries from the last 40 years was calculated. For broad-scale inference at this scale, burned habitat was considered any area within the boundaries of a burn, ignoring residual habitat. We accounted for varying caribou collaring dates by adjusting all fire ages to a "time-since-fire" value using the burn year and GPS location date. For caribou monitored for multiple years, the patterns were averaged for each individual, thus results are reported with individual caribou as the sampling unit. Individual responses were first summarized by reporting the proportion of individuals that selected or avoided burned habitat. To understand the herd-level response, the selection ratios across all individuals within each herd were averaged. All results are given as values with ninety-five percent confidence intervals calculated by bootstrapping with 2,000 permutations (Canty & Ripley 2015).

#### Do caribou avoid burns within their home range?

To examine if caribou seasonally avoided burned habitats within their annual home ranges, we used resource selection functions (RSFs) (Boyce and McDonald 1999, Johnson et al. 2004), which compared the proportion of a caribou's seasonal GPS locations within burned habitats to the proportion of that given habitat within an individual's annual home range (3<sup>rd</sup> order selection, Johnson 1980). To define availability, five random locations were generated for each used GPS location within each animal's 95% kernel UD annual ranges (described above). We defined used data as the GPS locations recorded during four biologically informed seasons based on Rettie and Messier (2000): Late Winter (January 1-April 14), Calving (April 15-June 30), Summer (July 1-October 31), and Early Winter (November 1-December 31). Individuals were removed that were monitored for less than two months of a given season (the length of our shortest season; early-winter) or did not have at least 1% of the burned habitat (e.g. residual-lowland) available. Locations were classified as falling in one of the six categories of burned habitat (Table 2). We estimated caribou habitat selection using resource selection functions (RSFs) and derived parameter coefficients using logistic regression. For each model, unburned bogs were set as the reference category, which is considered to be the highest quality habitat for caribou. To account for the influence of upland habitat on caribou selection, upland habitats were included in our models. However, on average 87.77 % [range; 30.2%-100%] of each caribou's seasonal GPS locations were classified as falling in lowland habitat types; therefore, we only report results on lowlands. For each burned habitat type, we report the proportion of individuals showing selection (i.e., a positive coefficient from individual model) or avoidance (i.e., a negative coefficient from individual model) relative to unburned bogs. For population-level inferences, selection coefficients were averaged across individuals and ninety-five percent confidence

intervals were calculated using a bootstrap analysis with 2000 permutations (Canty & Ripley 2015). The reason for not averaging across individuals using a weighted mean, as proposed by (Murtaugh 2007), can be found in Appendix 1.

### Do burns affect adult caribou survival?

We used a survival analysis to examine the demographic effects of exposure to burned habitat on caribou by using habitat conditions associated with known mortality events to characterize mortality risk. Specifically, we used a two-stage approach. First, we tested if the amount of burned habitat available in a caribou's annual home range influenced survival. Secondly, we tested if the amount of time a caribou spent within burned habitat influenced survival. We estimated semi-parametric Cox Proportional Hazards models within an information theoretic model selection framework, specifying herd as a random effect to account for between herd variation in survival (Cox 1972). Cox-models express the relationship between the hazard of an event, in this case death, and a set of variables, giving the hazard ratio or the instantaneous risk over a two-week period. A two-week period allows the majority of caribou monitoring data to be included in models while still allowing for the variation in time-dependent variables. In the first stage, we examined the influence of burned habitat within the annual home range on survival, using the proportion of a female's annual range attributed as recently burned habitat to predict mortality risk. In the second stage, we tested for short-term increases in mortality risk while using burned habitats through a female's seasonal and two-week proportional use of burned habitats, defined by the proportion of GPS locations within these habitats. We were unable to evaluate the underlying cause of mortality, so all mortality events were considered the same. Our candidate models were comprised of seven univariate and multi-variate models, each a combination of burn classes with landcovers known to affect adult caribou survival (Table 8)

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(McLoughlin 2005). We used Pearson's Correlation Coefficient to ensure no model covariates were collinear (coeff > .6) and satisfied the proportionality of hazards by sustaining a zero slope of Schoenfeld residuals (Fox & Monette 2008). Hazard ratios (HR) > 1 describe increased mortality risk with increasing use of associated variable. We used the survival package (Therneau 2014) and predict function in R software for modeling, calculating baseline survival and predicting survival metrics through time.

All analyses were completed in R, version 3.5.5.

### Results

#### Fire Mapping

Fires sizes ranged from 904 ha to 657,807 ha across 32 years from 1979 to 2011. The proportion of burned habitat < 40-years-old varied among herds (average across years; WSAR:  $3.42\% \pm 0.3$  95% CI, ESAR: 25.55% ± 0.10, RS: 72.77% ± 2.64, CL:  $30.32\% \pm 0.43$ , SL:  $45.06\% \pm 4.2$ , RE:  $33.13\% \pm 0.77$ ; Table 3). Across the six herds, average cumulative area burned was 1,994,302 ha equating to 28.9% of the total area within herd range boundaries (Table 3). Of dNBR mapped fire areas,  $35.71\% \pm 4.9$  and  $15.05\% \pm 4.8$  consisted of residual-lowland and residual-upland habitat, respectively, whereas  $30.99\% \pm 7.56$  and  $18.25\% \pm 5.9$  were burned lowland and upland habitat. However, the average proportion of burned habitat within the total area of caribou annual home ranges was lower, with  $19.89\% \pm 2.38$  made up of any burned habitat, of which  $7.75\% \pm 0.89$  consisted of residual lowland habitat,  $6.15\% \pm 0.72$  burned lowland habitat,  $2.36\% \pm 0.45$  residual uplands, and  $3.62\% \pm 0.63$  burned uplands (Table 4).

### Do caribou place their home ranges in areas with less burned habitat?

Of the 201 caribou annual home ranges analyzed, 55 (27.4%) had no burns in the last 40 years (Figure 2). The average proportion of burned habitat, corrected for collar year of sampling, within caribou annual home ranges was variable but generally low with the exception of caribou in RS and RE (WSAR:  $3.41\% \pm 1.84$ ; ESAR:  $11.13\% \pm 3.10$ ; RS:  $53.45\% \pm 10.35$ ; CL:  $8.98\% \pm 3.07$ ; SL:  $10.39\% \pm 5.61$ ; RE:  $37.14\% \pm 3.15$ ; Figure 3). Among herds, a large percent of caribou avoided burned habitat within the herd range (WSAR: 71%; ESAR: 79%; RS: 83%; CL: 100%; SL: 91%; RE: 48%; Table 5). With the exception of caribou in RE, average selection ratios for burned habitats were below one, indicating avoidance by caribou (WSAR: 0.845 [95% CI 0.451, 1.325]; ESAR: 0.541 [95% CI 0.366, 0.735]; RS: 0.686 [95% CI 0.506, 0.842]; CL: 0.275 [95% CI 0.159, 0.412]; SL: 0.248 [95% CI 0.159, 0.468]; RE: 1.077 [95% CI 0.952, 1.197]; Figure 4).

### Do caribou avoid burns within their home range?

A large proportion of individuals (22.8% [range: 1.69-35.36 %]) had no availability (defined as < 1%) of each of the burned habitat classes of interest (Table 6). We removed these animals in subsequent analyses. For the remaining animals, the proportion of locations across seasons found in residual- and burned-lowlands was generally low at 13.07% ± 1.26 and 5.99% ± 0.67, respectively (Figure 4). More caribou seasonally avoided residual-lowlands except in early-winter (Early Winter = 40.3 %; Late Winter = 71.9%; Calving = 62.3%; Summer = 54.6%; Figure 6) and burned-lowlands for all seasons (Early Winter = 51.7%; Late Winter = 90.3%; Calving = 77.8%; Summer = 66.7%; Figure 6). Seasonal RSF models showed caribou in our study generally avoided residual-lowlands (Early Winter:  $\beta$  = -0.141 [95% CI -0.375, 0.087]; Late Winter:  $\beta$  = -0.961 [95% CI -1.260, -0.616]; Calving:  $\beta$  = -0.430 [95% CI -0.707, -0.137]; Summer:  $\beta$  = -0.296 [95% CI -0.561, -0.035]; Figure 7) and consistently avoided burned-lowlands (Early Winter:  $\beta$  =  $\beta$  = -2.021 [95%

CI -2.300, -1.718]; Calving:  $\beta$  = -1.180 [95% CI -1.442, -0.905]; Summer:  $\beta$  = -0.577 [95% CI - 0.822, -0.035]; Figure 7). We removed individuals with no seasonal use of burns (i.e. perfect avoidance) from population-level analysis (see Appendix 1). The proportion of animals that were perfect avoiders can be found in Table 6. Individuals were more likely to select burns, particularly residual patches, as the availability of burns within their annual range increased during the calving and summer seasons (Figure 8).

### Do burns affect adult caribou survival?

Of 201 adult female caribou monitored, 51 (25.4%) had confirmed deaths within the study period. In the first stage, where we evaluated the effects of annual home range composition, explanatory variables did not predict survival as all models were within 2 AIC points of the Null model (Table 7). In the second stage, where we evaluated the effects of using burns more often, female survival was best predicted by a multivariate model describing proportional use of burned habitats and uplands during the previous two-week period (Table 7). Models with strongest support included only variables representing use of uplands and use of burns (Table 7). Model-averaged hazard ratios from these top models, however, indicated that use of burns had little influence on caribou mortality risk. The hazard ratios from the top model including use of uplands and burns, showed a significant increase in risk of mortality as two-week use of uplands increased (HR = 1.017, p = 0.029), equating to a 85% increase in mortality risk if an individual used upland 50% more over a 2-week period, and no change in risk as two-week use of burned areas increased (HR = 0.998, p = 0.850). The proportional hazard assumption was supported (p  $\geq$  .36 for scaled Schoenfeld residuals of each variable).

### Discussion

We found strong evidence that caribou avoided burns, but increasing proportional use of burned habitats did not affect survival among individuals. Though previous studies have shown caribou avoid burned habitat (Joly *et al.* 2003; Dalerum *et al.* 2007; Barrier & Johnson 2012) and habitat associations can influence survival (McLoughlin *et al.* 2005), we specifically describe avoidance of unburned residual patches and empirically demonstrate that increasing use of burned habitats does not decrease adult survival. These results offer information on the spatial response of caribou to wildfire for defining disturbed habitat under the federal recovery strategy.

### Do caribou place their home ranges in areas with less burned habitat?

Across herds, caribou avoided burned habitats through annual home range placement except for the Red Earth range. Our results support previously described caribou responses to fire disturbed habitats (Fritz *et al.* 1993; Joly *et al.* 2003; Barrier & Johnson 2012). These findings are likely due, in part, to the two predominate hypotheses explaining caribou-fire avoidance responses. First, caribou could be avoiding areas with low lichen abundance and lichen is destroyed by fires (Schaefer & Pruitt Jr 1991; Dunford *et al.* 2006). Second, caribou could be attempting to spatially separate from increased wolf densities, facilitated by apparent competition (Serrouya 2011; Robinson *et al.* 2012; Courbin *et al.* 2013). Although we did not test these mechanisms directly, our findings suggest that, in general, caribou view burned areas as suboptimal habitat and attempt to limit their exposure to such areas when establishing a home range.

In the Red Earth range, 47% of the fire disturbance was 30-40 years old and caribou data were centered around two fires that burned in 1979 and 1981. Potentially, these fires were old enough that the negative habitat features associated with burned habitats (e.g., low lichen

abundance; high browse for other ungulates) have diminished and caribou have begun to reoccupy the area. Additionally, Dalerum *et al.* (2007) hypothesized that caribou can compensate for habitat lost in wildfires by occupying large home ranges, increasing their use of unburned portions within the home range rather than changing its placement. In our study, Red Earth caribou had the second largest home range sizes of the populations studied, possibly allowing these individuals to compensate for the effects of burned habitat through avoidance within the home range.

### Do caribou seasonally avoid burns within their home range?

Measured differences in the magnitude of avoidance between the burn complex and residuals suggests caribou avoid residuals less strongly, possibly due to the retention of lichen forage and predator cover in residuals that increase their habitat value (DeLong & Kessler 2000; Kansas *et al.* 2015). Skatter *et al.* (2017) proposed that it may be appropriate to consider residual patches as undisturbed habitat based on observations of female caribou selecting residuals when they were inside the boundaries of a burn. We describe the same result in this study, as residual patches are avoided less strongly than the burn complex, but it is important to emphasize that this is only when an animal is within the boundary of a burn. When compared to unburned habitats, residual patches are avoided, suggesting that, although residual patches retain pre-fire forest structure, their efficacy as habitat is decreased by the surrounding burn complex.

The proportion of an individual's annual range that was burned was a strong predictor of increased selection for residual-lowlands in the calving and summer seasons. We suggest that individuals that have a large proportion of their home range burned start to select for residual-lowlands to meet their habitat needs. Although we have described an overall trend of strong avoidance of residuals, this explains why there are individuals that do select these habitats. This

selection response pattern suggests residual habitats could be significant for caribou space-use if fire intervals drastically decrease over time (Flanigan *et al.* 2009), creating fire mosaics in which caribou cannot avoid burned habitat.

These results are not the first to report avoidance of burned habitats in both summer and winter (Dalerum *et al.* 2007). Although more individuals selected for residual-lowlands in early-winter the difference was negligible and averaged population estimates still implied avoidance of residual-lowlands during this season. Avoidance may be strongest during the late-winter because increasing snow depth and deadfall in burned habitats can reduce mobility (Metsaranta & Mallory 2007), and increase the effort needed to crater for lichen or access alternative forage.

### Do burns effect adult caribou survival?

Given that burned areas are generally low-quality caribou habitat and the assumption that animals are maximizing fitness through habitat selection or avoidance (Morris 2003), we predicted that selecting burned habitats would be associated with negative impacts on demography. Contrary to this prediction, we found adult female survival did not correlate with the proportion of home range burned or using burned habitat more frequently. The lack of relationship among burns and adult female survival supports past studies that found negligible demographic effects when fire disturbance was considered alone (Dalerum *et al.* 2007; ECCC 2008, 2011), rather than cumulatively with human disturbance (Sorensen *et al.* 2008; Rudolph *et al.* 2017). In this study, the proportion of the home range burned was highly variable amongst individuals (2.6%-80.2%), yet there was no measurable effect of burned habitat on mortality risk. Many of the highly burned home ranges were from animals in the Richardson herd, which is also characterized by low human disturbance (AEP 2017), supporting the hypothesis that fire disturbance alone does not drive adult survival. This hypothesis is also supported by caribou populations in Saskatchewan's boreal shield, where, despite caribou experiencing a high occurrence of burns, the SK1 range is one of the few stable populations of boreal caribou (ECCC 2012). However, caribou using burned habitats may have negative impacts on other important demographic parameters which were not specifically tested in this study, such as increased calf mortality via increased predator densities in burns.

Mechanisms for explaining caribou response to burned habitats have primarily focused on disturbance-mediated apparent competition (Serrouya et al. 2011; Courbin et al. 2013). However, these results challenge this theory, as females that used heavily burned areas did not experience an increased risk of mortality. We also observed no decrease in the risk of mortality for caribou that used burned habitats, suggesting the potential for residual patches to provide forage and predator cover is limited. One possible explanation for a lack of increased mortality risk in burned habitats, is that the disturbance-mediated apparent competition hypothesis has been primarily described in productive temperate systems (Kinley & Apps 2000; Whittmer 2007; Serrouya et al. 2011) where disturbances drastically increase moose forage (Meidinger & Pojar 1991). Our results support the increasing evidence that this process has not been fully described in low productivity boreal systems (Brown et al. 2018; DeMars et al. 2019). Other mechanisms have been suggested as potential negative influences of fire on adult survival, such as bottom-up effects from a decrease in lichen availability (Schaefer & Pruitt Jr 1991; Dunford et al. 2006) and an increase in white-tailed deer and, subsequently, wolves, the primary predator of adult caribou (Latham et al. 2011; Dawe et al. 2014). However, we suggest it is unlikely that these mechanisms play a major role given the overall limited effect of burned habitat on adult survival.

Similar to McLoughlin *et al.* (2005), we found that increased use of uplands significantly increased risk of mortality. However, the baseline survival over a 2-week period was high at .996

and caribou used uplands infrequently, average use of uplands over 2-weeks was 9.69 % [range; 0%-89.6%], suggesting the strong mortality risk associated with this short two-week survival window is unlikely to lead to strong negative yearly survival effects. Increased mortality of caribou in uplands is likely explained by increased predator densities, as upland habitats are preferred habitat for moose and white-tailed deer, the primary prey of wolves (James *et al.* 2004, McLoughlin *et al.* 2005). However, this is only speculative, as we did not know if predation was the direct cause of mortality.

We caution that there are other factors likely influencing adult survival that we did not directly test, most notably human disturbance. The human footprint in Alberta caribou ranges is constantly changing and the historical spatial data associate with these features is limited. Therefore, due to the large temporal range of our caribou location data, we were unable to back cast the prevalence of human disturbance to test its effect on survival.

#### The implications of disturbed habitat classification

Fires create a mosaic of habitats of varying ages, and at any given point in time, a large portion of caribou herd ranges can consist of burns less than 40 years old. The range-level fire disturbance was quite variable, showing that caribou in the same region can be exposed to very different fire disturbance regimes. However, these results indicate that caribou in ranges with high fire disturbance did not necessarily have a large proportion of their home range burned, as explained by 2<sup>nd</sup> order avoidance. Dalerum *et al.* (2007) described slightly higher proportions of burned habitat within caribou home ranges then our study, although they were interested in pre-and post-fire differences and may have been biased to use caribou data from highly burned ranges.

Our results describe that about half of the area classified as burned within caribou ranges consisted of unburned residuals, suggesting, that if residual habitats were to be reconsidered as undisturbed for caribou under federal guidelines, there could be major shifts towards reaching the 65% undisturbed habitat threshold. For example, herd ranges in Alberta would experience a ~20% decrease in the percent of the herd range classified as disturbed (AEP current fire disturbance calculations); with up to 32% decrease in the area considered disturbed on the Richardson range. Although we found no evidence that caribou select unburned residuals, these numbers imply the importance of correctly defining whether residual habitat is disturbed for caribou.

Our results indicate higher proportions of unburned residuals within fire boundaries than other studies (Eberhart & Woodard 1987; Araya *et al.* 2015). Most notably Kansas *et al.* (2016) described that residuals in boreal caribou habitat of Saskatchewan consisted of 31.8% residual patches. The high proportion of residuals noted in this study may be determined by the prevalence of lowlands in caribou annual ranges ( $\bar{x} = 79.8\% \pm 1.34$ ), which have been shown to be a predominant landcover in the residual habitats of other boreal systems (Madoui *et al.* 2010). Additionally, we delineated any area mapped as unburned within the provincial fire boundaries as residuals, which may have led to fire adjacent habitat, such as peninsulas and area along the fire edge being misclassified as residuals (Andison & McCleary 2014). However, multiple studies have used this method for inferences on caribou recovery (Kansas *et al.* 2015; Skatter *et al.* 2017). Although our methods may have overestimated residuals, we were specifically interested in caribou response to unburned residuals overlooked by the federal recovery strategy, which were calculated using the provincial fire boundaries.

### Conclusion

Understanding how caribou respond to burned habitats is essential, as wildfires are predicted to increase in intensity and frequency with a changing climate. Across spatial scales, we describe limited use and avoidance of burned habitat, as well as unburned residual patches within the burn complex, by caribou in northeastern Alberta. We suggest unburned residual patches are not refugia for caribou and the potential for them to provide productive forage or cover from predators is limited. Therefore, there is no evidence to support modifying the current definition of fire disturbance by Environment Canada. However, the combination of limited fire prevalence within annual home ranges and negligible survival effects suggest the role of fire disturbance on caribou population persistence is likely overstated in the federal recovery strategy. This study supports Bergerud's 1974 hypothesis that caribou have evolved alongside wildfire and are able to adapt through plasticity in habitat selection to buffer against the effects of burned habitat. Other factors such as anthropogenic disturbance and the associated disruption of predator-prey relationships are more likely to be the primary drivers of population declines. Our results have implications for prioritizing the delineation and management of multiple disturbances by the federal recovery strategy. Effective delineation of disturbed habitat will require further research examining the cumulative effects of fire and anthropogenic disturbance and their mechanistic influence on predator-prey relationships.

Herd Range	Total	0-10yr	10-20yr	20-30yr	30-40yr
Richardson	13	5	6	3	3
WSAR	20	5	7	3	5
ESAR	15	3	5	3	4
Red Earth	19	2	10	1	6
Slave Lake	10	2	3	0	5
Cold Lake	8	1	4	2	1
Total Fire	85	18	35	12	24

**Table 1.** Number of fires mapped using the dNBR methods split into caribou herd range and thedecadal period of burn year from 1979-2011.

**Table 2.** Classification of burned habitats used to model resource selection and survival of adult female caribou in north-eastern Alberta, Canada. Landcover classes developed by the Alberta Biodiversity Monitoring Institutes ALPHA Predictive Landcover 3.0 data.

Habitat	Class	Description
Unburned Lowlands (UL)	Unburned Bog, Fen, Wetland	Unburned areas outside the fire perimeter in lowland areas with low nutrient peatland soils. Typically dominated by black spruce, Spagnum moss, tamarack, willow and bog birch.
Unburned Uplands (UU)	Unburned Upland conifer, Upland deciduous, Mixed-wood upland	Unburned areas outside the fire perimeter in uplands of any type. Typically dominated by spruce, pine, aspen and paper birch.
Residual Lowlands (RL)	Unburned residual Bog, Fen, Wetland	Unburned areas within the fire perimeter in lowland areas with low nutrient peatland soils. Typically dominated by black spruce, <i>Spagnum</i> moss, tamarack, willow and bog. birch.
Burned Lowlands (BL)	Burned matrix Bog, Fen, Wetland	Physically burned areas within the fire perimeter in lowland areas with low nutrient peatland soils. Typically dominated by black spruce, Spagnum moss, tamarack, willow and bog birch.
Residual Uplands (RU)	Unburned residual Upland conifer, Upland deciduous, Mixed-wood upland	Unburned areas within the fire perimeter in uplands of any type. Typically dominated by spruce, pine, aspen and paper birch.
Burned Uplands (BU)	Burned matrix Upland conifer, Upland deciduous, Mixed-wood upland	Physically burned areas within the fire perimeter in uplands of any type. Typically dominated by spruce, pine, aspen and paper birch.

Herd range	Total area (ha)	Avg. burned area (ha)	Burned habitat (%)
WSAR	1,570,712	53,718	<b>3.42</b> ± 0.30
ESAR	1,311,902	335,190	<b>25.55</b> ± 0.10
Richardson	707,390	514,767	<b>72.77</b> ± 2.64
Cold Lake	672,586	203,928	<b>30.32</b> ± 0.43
Slave Lake	151,623	68,321	<b>45.06</b> ± 4.20
Red Earth	2,470,203	818,378	<b>33.13</b> ± 0.77
Total	6,884,416	1,994,302	28.90

**Table 3.** Summary of the total area and average percent of habitat burned within the last 40 years among six herds in northeastern Alberta. Percentages were calculated for each caribou (i.e., time-since-fire) and are presented as the mean and 95% CIs.

**Table 4.** Summary of the percent burned habitat within caribou annual ranges. Percentages were calculated for each caribou (i.e., time-since-fire) and averaged. Results reported as the mean and 95% CIs.

		Residual	Burned	Residual	Burned
Herd range	Total burn (%)	Lowland (%)	Lowland (%)	Upland (%)	Upland (%)
WSAR	<b>3.41</b> ± 1.84	<b>1.51</b> ± 0.75	<b>1.34</b> ± 0.63	<b>0.27</b> ± .25	<b>0.29</b> ± 0.29
ESAR	<b>11.13</b> ± 3.10	<b>4.73</b> ± 1.35	<b>3.87</b> ± 1.10	<b>0.97</b> ± 0.36	<b>1.55</b> ± 0.46
Richardson	<b>53.45</b> ± 10.35	<b>15.85</b> ± 3.20	<b>9.41</b> ± 1.70	<b>12.73</b> ± 2.80	<b>15.46</b> ± 3.33
Cold Lake	<b>8.89</b> ± 3.07	<b>2.76</b> ± 0.82	<b>3.58</b> ± 1.14	<b>0.98</b> ± 0.39	<b>1.66</b> ± 0.81
Slave Lake	<b>10.39</b> ± 5.61	<b>5.42</b> ± 2.98	<b>2.23</b> ± 1.18	<b>1.86</b> ± 0.82	<b>0.90</b> ± 0.89
Red Earth	<b>37.14</b> ± 3.15	<b>15.15</b> ± 1.26	<b>12.91</b> ± 1.27	<b>2.95</b> ± 0.50	<b>6.13</b> ± 1.28
All	<b>19.89</b> ± 2.38	<b>7.75</b> ± 0.89	<b>6.15</b> ± 0.72	<b>2.36</b> ± 0.45	<b>3.62</b> ± 0.63

**Table 5.** Summary of the total number of caribou analyzed using selection ratios among six herds. Selection ratios compared the proportion of annual range burned to the proportion of the herd range burned for each caribou. Table includes the number of caribou annual ranges that avoided or selected, defined by a selection ratio <1 being avoidance and >1 selection.

Herd Range	Total Caribou	Avoid	Select
WSAR	52	37	15
ESAR	53	42	11
Richardson	18	15	3
Cold Lake	11	11	0
Slave Lake	11	10	1
<b>Red Earth</b>	56	27	29

**Table 6.** The number and percent of caribou seasonal data with no burned habitats found in their annual home range or seasonal data with no GPS locations in burned habitats during the given season.

<b>C</b>	Dument habitat	Caribou		Caribou seasons in	
Season	Burned habitat	seasons	No habitat available	RSF models	No habitat used
Early-Winter	Residual-Lowland	191	47 (24.6%)	144	6 (4.1%)
	Burned-Lowland	191	50 (26.2%)	141	16 (11.3%)
Late-Winter	Residual-Lowland	236	4 (1.7%)	232	56 (24.1%)
	Burned-Lowland	236	9 (3.8%)	227	67 (29.5%)
Calving	Residual-Lowland	288	86 (29.8%)	202	34 (16.8%)
-	Burned-Lowland	288	90 (31.2%)	198	48 (24.2%)
Summer	Residual-Lowland	246	83 (33,7%)	163	15 (9,2%)
	Burned-Lowland	246	87 (35.4%)	159	25 (15.7%)

**Table 7.** Model selection of Cox-proportional hazard mixed-effects model on mortality events, with a mixed effect accounting for herd, showing the number of parameters (k), change in AIC<sub>c</sub> from best ranked model, and Akaike model weights (w) for the seven models for each survival stage.

Model Stage	Model	k	ΔAICc	W
Home Range				
Available	Null	1	0.00	0.23
	Burned Lowland	2	0.07	0.22
	Total Burn	2	0.90	0.14
	Upland	2	1.08	0.13
	Lowlands	2	1.84	0.09
	Burned Upland	2	1.97	0.08
	Total Burn + Upland	3	2.34	0.07
Second	Linland	2	0.00	0.24
Seasonal Use		2	0.00	0.24
	Total Burn + Upland	3	0.78	0.16
	Total Burn	2	0.89	0.15
	Burned Lowland	2	1.14	0.14
	Null	2	1.47	0.12
	Lowlands	2	1.61	0.11
	Burned Upland	2	3.30	0.05
2-week Use	Unland	2	0.00	0.42
	Total Burn + Unland		1 91	0.16
	I owlands	2	2 35	0.13
	Null	2	2.55	0.13
		2	2.57	0.12
	Burned Lowland	2	3.56	0.07
	Total Burn	2	3.78	0.06
	Burned Upland	2	4.57	0.04



**Figure 1.** Caribou herd ranges with dNBR fire boundary polygons in northeastern Alberta. Darker colors represent more recent fire events. For reference the outline of the study area and provincial boundaries are included.



**Figure 2.** Frequency distribution of caribou annual home ranges comprised of differing proportions of habitat burned in the last 40 years. The total proportion of burned habitat was calculated as the proportion of available locations classified as either burned or unburned within each caribou annual range (n = 201 caribou).



**Figure 3.** The average proportion of caribou herd and annual ranges considered burned habitat. The proportion of ranges considered burned was calculated for each caribou and then averaged across caribou. Error bars represent the 95% CIs of the mean. The number of caribou differed between herds (WSAR n = 52; ESAR n = 53, Richardson n = 18; Cold Lake n = 11; Slave Lake n = 11; Red Earth n = 56).



**Figure 4.** Caribou selection ratios (SR) and bootstrapped 95% CIs for burned habitat (including residuals) among the six herds. Individual SRs were calculated separately comparing the proportion of burned habitat within annual ranges to the proportion of burned habitat available within the herd range, then averaged for herd-level inferences. The number of caribou differed between herds (sample sizes; WSAR = 52; ESAR = 53, Richardson = 18; Cold Lake = 11; Slave Lake = 11; Red Earth = 56).



**Figure 5.** Percent of available and seasonally used caribou locations that were classified as either residual-lowland or burned-lowland. The proportion of available locations in each burned habitat class was calculated within each caribou annual range and the proportion of used locations was calculated for each caribou in each season. (sample sizes; RL: Early Winter = 144, Late Winter = 232, Calving = 202, Summer = 163; BL: Early Winter = 141, Late Winter = 227, Calving = 198, Summer = 159).



**Figure 6.** The percent of caribou seasons that avoided, selected or were neutral to burned habitats among the four seasons. Selection coefficients ( $\beta$ ) were calculated for each caribou in each season. Avoidance or selection were defined as a significant (p < 0.05)  $\beta$  estimate. Total caribou years differed between burned- and residual-lowlands between seasons (sample sizes; RL: Early Winter = 144, Late Winter = 232, Calving = 202, Summer = 163; BL: Early Winter = 141, Late Winter = 198, Summer = 159).



**Figure 7.** Caribou selection coefficients and bootstrapped 95% CIs of residual- and burnedlowlands among the four seasons. Individuals were modelled separately and then averaged for each burned habitat for population-level inferences. These results do not include individuals with zero GPS locations (i.e. perfect avoiders) in the habitats. The number of caribou used to average for each season differed between burned- and residual-lowlands (sample sizes, RL: Early Winter = 138, Late Winter = 176, Calving = 168, Summer = 148; BL: Early Winter = 125, Late Winter = 182, Calving = 150, Summer = 160).



**Figure 8.** The relationship between RSF modelled parameter estimates ( $\beta$ ) for residual-lowland and the proportion of annual range burned. Each parameter estimate ( $\beta$ ) was calculated for each caribou for each season and proportion was calculated for each caribou's annual range. (sample sizes, RL: Early Winter = 138, Late Winter = 176, Calving = 168, Summer = 148).

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### **Appendix 1**

We opted to obtain population-level selection inference by modeling individuals separately and then averaging estimates across individuals with a non-weighted mean and removing individuals that had no seasonal use data classified as our burned habitats of interest. Individuals with no seasonal use (i.e. perfect avoidance) have inflated negative selection coefficients and large standard errors. Though these negative values are biologically relevant, they are statistically inflated. Therefore, non-weighted population estimates are biased low with perfect avoiders included as these low values bias the estimate down (Figure A1). Commonly, a weighted population estimate is used to account for this; however, weighted averages are biased high as individuals that select burned habitats have more use data and inherently lower standard errors. Therefore, weighted population estimates are biased high through up-weighting individuals that selected (Figure A2). Consequently, for population-level inferences, we removed individuals with no seasonal use of burns (i.e. perfect avoidance) and used non-weighted averaging. We feel this interpretation best reflects the proportion of individuals that selected or avoided. The proportion of animals that were perfect avoiders can be found in Table 7.

### **Appendix 2**

Using Google Earth Engine (Gorelick *et al.* 2017) we compiled the highest quality pre-fire Landsat tiles from the summer preceding the fire and post-fire Landsat tiles from the summer after the fire. We used Landsat imagery exclusively from July and August scenes as they are optimal in terms of vegetation phenology in Canada (Guindon et al. 2014). Google Earth Engine's algorithm stacks Landsat tiles in order to account for tiles with missing data or cloud covered sections, creating continuous high-quality imagery at a 30 m resolution. Where multiple burns overlapped, we used Landsat imagery for the most recent fire as this would have been the burned habitat available to collared animals.

Fire images after 2013 were collected with the Landsat 8 OLI sensor, and the images from 1982-2013 were collected with the Landsat 4, 5 & 7 TM sensors. A few fires burned earlier than 1982 when available Landsat imagery consisted of Landsat 2's older sensor technology, which cannot be used to calculate dNBR. For these few older fires similar methods were used but replaced dNBR with dNDVI because this metric can be calculated with bands available onboard Landsat 2 sensors and has been shown to accurately define fire burn vs unburned matrix (Wessman 1997).

All dNBR images were clipped by the Alberta Government (2016) provincial fire polygon layer and classified any dNBR mapped unburned habitat within those boundaries as unburned residual patches. For our purposes, defining areas that were left unburned within fire boundaries was important for classify residual habitat that may remain productive for caribou. However, using dNBR, raster cells are simply considered unburned or burned and it is not until there is a defined fire boundary that areas can be classified as residual patches. The process of

delineating the outer boundaries of the fire can be difficult and requires a specific definition. Therefore, we used already available provincial fire boundary data provided by fire experts at Alberta Environment and Parks (AEP 2016). This classification of fire boundaries is appropriate, as we were interested in modelling caribou response to unburned residual habitat that has been understated by the federal recovery strategy, which used the provincial boundary data (ECCC 2011). However, this method may have misclassified unburned area along the fire edge or in peninsulas, which are connected to the fire boundary edge, as residual habitat. We suggest that this should not have effects on data because these burned habitat features do not make up a consistently large amount of the overall unburned habitat within fire boundaries.

Post-fire forest age is important in ecology, influencing the vegetation community and forest regeneration. Forest age is also considered in the federal recovery strategy. However, we did not include the post-fire forest age in this analysis. Burned habitats within boundaries of fires that burned in the last 40 years were considered the same, regardless of time-since-fire. For example, residual habitat that was created by a 30-year-old fire is considered the same as residual habitat created by a 10-year-old fire. Most of our caribou data (87%) is in low-productivity peatlands where vegetation regrowth is very slow, suggesting that the age difference between various post-fire regeneration times is likely not that different on a 40-year timeline. Additionally, patch metrics such as size, shape, and distance to fire edge may all be important aspects that make these habitats useful to caribou but we did not consider these in this study and all unburned areas classified by dNBR within fire boundaries were consider residual habitat regardless of size or shape of that feature.

**Figure A1.** Caribou selection coefficients and bootstrapped 95% CIs of residual- and burnedlowlands among the four seasons. Individuals were modelled separately and then averaged weighting by the inverse of the square of the variance for each burned habitat for populationlevel inferences. These results include individuals with zero GPS locations (i.e. perfect avoiders) in the habitats. The number of caribou used to average for each season differed between burnedand residual-lowlands (RL: Early Winter = 144, Late Winter = 232, Calving = 202, Summer = 163; BL: Early Winter = 141, Late Winter = 227, Calving = 198, Summer = 159).



**Figure A2.** Caribou selection coefficients and bootstrapped 95% CIs of residual- and burnedlowlands among the four seasons. Individuals were modelled separately and then averaged for each burned habitat for population-level inferences. These results include individuals with zero GPS locations (i.e. perfect avoiders) in the habitats. The number of caribou used to average for each season differed between burned- and residual-lowlands (RL: Early Winter = 144, Late Winter = 232, Calving = 202, Summer = 163; BL: Early Winter = 141, Late Winter = 227, Calving = 198, Summer = 159).

