NRC Research Press

ARTICLE

Comparison of pre-fire and post-fire space use reveals varied responses by woodland caribou (*Rangifer tarandus caribou*) in the Boreal Shield

J.A. Silva, S.E. Nielsen, P.D. McLoughlin, A.R. Rodgers, C. Hague, and S. Boutin

Abstract: By regulating successional dynamics in Canada's boreal forest, fires can affect the distribution of the Threatened woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)). Caribou tend to avoid areas burned within the last 40 years; however, few studies have compared pre-fire and post-fire caribou observations. In this study, we used caribou GPS locations from the Boreal Shield of Saskatchewan, Canada, to assess the short-term response of caribou to areas that burned while they were collared (hereafter recent burns). We used a "before–after, control–impact" design to compare the overlap of pre-fire and post-fire seasonal home ranges to the overlap of year-to-year seasonal home ranges. Caribou rarely encountered recent burns and when they did, they adjusted their space use in variable and complex ways that were largely indistinguishable from regular, interannual variation. Caribou tended to reduce use of recent burns in summer–autumn and winter, but not during the calving season, in some cases shifting their home range to incorporate more burned habitat. We conclude that recently burned areas (<5 years) may provide habitat value to woodland caribou, particularly during the calving season, requiring a more flexible approach to interpret fire in habitat management strategies.

Key words: boreal forest, caribou, fire, habitat disturbance, home range, *Rangifer tarandus*, space use.

Résumé : En régulant la dynamique de succession dans la forêt boréale du Canada, le feu peut influer sur la répartition du caribou des bois (*Rangifer tarandus caribou* (Gmelin, 1788)), une espèce menacée. Si les caribous ont tendance à éviter les secteurs brûlés au cours des 40 années précédentes, peu d'études ont toutefois comparé les observations de caribous avant et après un feu. Nous utilisons des emplacements de caribous obtenus par GPS dans le bouclier boréal de la Saskatchewan (Canada) pour évaluer la réaction à court terme des caribous à des zones brûlées alors qu'ils étaient dotés d'un collier (des « brûlis récents »). Nous employons un schéma « avant–après, témoin–effet » pour comparer le chevauchement des domaines vitaux saisonniers avant et après le feu au chevauchement des domaines vitaux saisonniers d'une année à l'autre. La fréquence des rencontres de brûlis récents par des caribous est faible et, quand elles se produisent, les caribous ajustent leur utilisation de l'espace de manières variées et complexes qui sont difficiles à départager de la variation interannuelle normale. Les caribous ont tendance à moins utiliser les brûlis récents en été–automne et en hiver, mais non durant la saison de mise bas, déplaçant dans certains cas leur domaine vital pour y intégrer plus d'habitat brûlé. Nous concluons que les brûlis récents (<5 ans) pourraient accroître la valeur d'habitats pour le caribou des bois, particulièrement durant la saison de mise bas. Une approche plus souple à l'interprétation des feux dans les stratégies de gestion d'habitats est donc nécessaire. [Traduit par la Rédaction]

Mots-clés : forêt boréale, caribou, feu, perturbation de l'habitat, domaine vital, *Rangifer tarandus*, utilisation de l'espace.

Introduction

Global ecosystems are experiencing accelerated rates of change as the frequency, extent, and intensity of natural and human disturbance increases (IPBES 2019). Habitat disturbance is contributing to population declines in a wide array of species, including the Threatened woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)) in Canada's boreal forest (Festa-Bianchet et al. 2011). Woodland caribou have developed a unique ecology that makes them particularly vulnerable to habitat disturbance. Caribou evolved a specialized gut microbiome (Boertje 1990; Palo 1993) and nitrogen conservation strategies (Parker et al. 2009) to consume terrestrial lichens as the primary component of their diet (Thompson et al. 2015). Relying on lichens enables caribou to occupy unproductive mature coniferous forests and peatlands, spatially separating themselves from more productive deciduous and mixedwood forests that support higher densities of moose (*Alces alces* (Linnaeus, 1758)) and wolves (*Canis lupus* Linnaeus, 1758), the latter their primary predator (Rettie and Messier 2000). Terrestrial lichens are often completely consumed and slow to recover following the stand-replacing fires that typify the boreal forest (Morneau and Payette 1989; Silva et al. 2019), compromising caribou foraging habitat for several decades (Klein 1982). Human dis-

Received 19 June 2020. Accepted 13 August 2020.

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Published at www.nrcresearchpress.com/cjz on 8 October 2020.

turbance (e.g., forestry, oil and gas, mining) has expanded into the range of woodland caribou over the past century (Schaefer 2003) and can cause temporary or permanent habitat loss and fragmentation (Hins et al. 2009). Like fire, human disturbance increases the proportion of young forest on the landscape, which can increase the abundance of deciduous plants and support higher densities of moose and wolves (Seip 1992; Street et al. 2015). This facilitates the process of disturbance-mediated apparent competition, where caribou experience high wolf predation in disturbed landscapes (Rudolph et al. 2017). Invoking these mechanisms, numerous studies have documented a tendency of caribou to avoid burns and human disturbance (Joly et al. 2003; Vors et al. 2007; Faille et al. 2010; MacNearney et al. 2016; Lafontaine et al. 2019) and disturbance-mediated apparent competition has been implicated as the primary mechanism driving woodland caribou population declines across Canada (Courtois et al. 2007; Festa-Bianchet et al. 2011; Serrouya et al. 2019; Fryxell et al. 2020).

Given the importance of disturbance-mediated apparent competition in population declines, Environment and Climate Change Canada developed a recovery strategy for woodland caribou that aims to minimize the cumulative footprint of burns (<40 years old) and human disturbance on population ranges (ECCC 2012*a*). An empirical study determined a low probability of caribou population persistence when cumulative range-level disturbance exceeds 35% (ECCC 2012*a*). Keeping range-level disturbance below this 35% threshold or recovering habitat to achieve the threshold has become a focus of caribou conservation over the past decade. However, because woodland caribou occupy a broad geographic distribution across Canada, high regional variation in caribou ecology and disturbance history may make a generalized disturbance classification untenable (DeMars et al. 2019; Neufeld et al. 2020). For example, the Boreal Shield of northern Saskatchewan, Canada, has high fire (57%) but low human disturbance (3%), and the local caribou population is stable despite cumulative disturbance 1.7 times the recommended limit (Johnson et al. 2020). Johnson et al. (2020) found the negative effects of human disturbance on calf recruitment and adult survival were three to five times greater than the equivalent effects of fire. There is mounting evidence that fires do not have a strong influence on caribou demography (Dalerum et al. 2007; ECCC 2011; S. Konkolics, M. Dickie, R. Serrouya, D. Hervieux, and S. Boutin, unpublished data).

Caribou evolved alongside fire and have developed strategies to respond to the shifting habitat mosaic, minimizing demographic effects (Klein 1982). Occupying large home ranges could allow caribou to redirect activity to unburned portions of their home range when they experience fire (Dalerum et al. 2007). Fires burn in a heterogeneous pattern across the landscape due to the complex interplay of fuel, weather, and topography (Johnson 1992). This results in a patchwork of burned and unburned forest within the fire perimeter (Kansas et al. 2016). Patches of unburned forest (i.e., post-fire residuals) may retain some habitat value to caribou (Schaefer and Pruitt 1991; Skatter et al. 2017) and slow tree recruitment in the surrounding burn complex (Gutsell and Johnson 2002) could temporarily improve predator detectability (Skatter et al. 2017). Studies suggest that there is a delay in the colonization of burns by moose and wolves (Ballard et al. 2000; Maier et al. 2005; Street et al. 2015; DeMars et al. 2019), meaning caribou may experience a refuge from predators within recently burned areas (<5 years). This could be particularly advantageous during the calving season (Skatter et al. 2017), when female caribou select habitat to minimize predation risk (Gustine et al. 2006; Viejou et al. 2018). As burns age, caribou may avoid such areas more strongly due to increased densities of moose and wolves (Bergerud 1974). Tree recruitment and deadfall accumulation in ageing burns may also promote range abandonment due to increased energetic costs of moving through the burn and reduced predator detectability (Schaefer and Pruitt 1991). The contemporary treatment of fire in habitat management strategies masks potential temporal variation in the response of moose, wolves, and caribou to fire.

In addition to varying temporally, the relative strength of the effect of fire on caribou demography may vary regionally (DeMars et al. 2019). In regions with high fire and low human disturbance, such as the Boreal Shield of Saskatchewan, coniferous forests cover a majority of the landscape and tend to self-replace after fire (Hart et al. 2019). Low productivity and poor edaphic conditions in northern boreal and taiga regions limit the extent of deciduous and mixedwood forests, keeping densities of moose and wolves low and negating disturbance-mediated apparent competition (Neufeld et al. 2020). In more productive areas, such as parts of northern Ontario, Canada, deciduous and mixedwood forests cover a larger proportion of the landscape and support higher densities of moose and wolves (Walker et al. 2020). Deciduous regeneration following fire may be more extensive in the southern boreal forest (Street et al. 2015), increasing the strength of disturbance-mediated apparent competition, which may be further enhanced by the presence of human disturbance in these regions (Fryxell et al. 2020).

The conflicting evidence of the effect of fire on woodland caribou has ignited debate surrounding its treatment in habitat management strategies. Understanding temporal, regional, and individual variation in the response of caribou to fire is required to decide how managers can best address fire in conservation actions. Most studies of caribou and fire assess selection of burns (<40 years old) but do not contrast pre-fire and post-fire space use to determine how individuals respond to fire (but see Dalerum et al. 2007). The lack of such evidence in the literature could lead to an incomplete description of the role of fire in caribou ecology, particularly in the immediate post-fire period (<5 years).

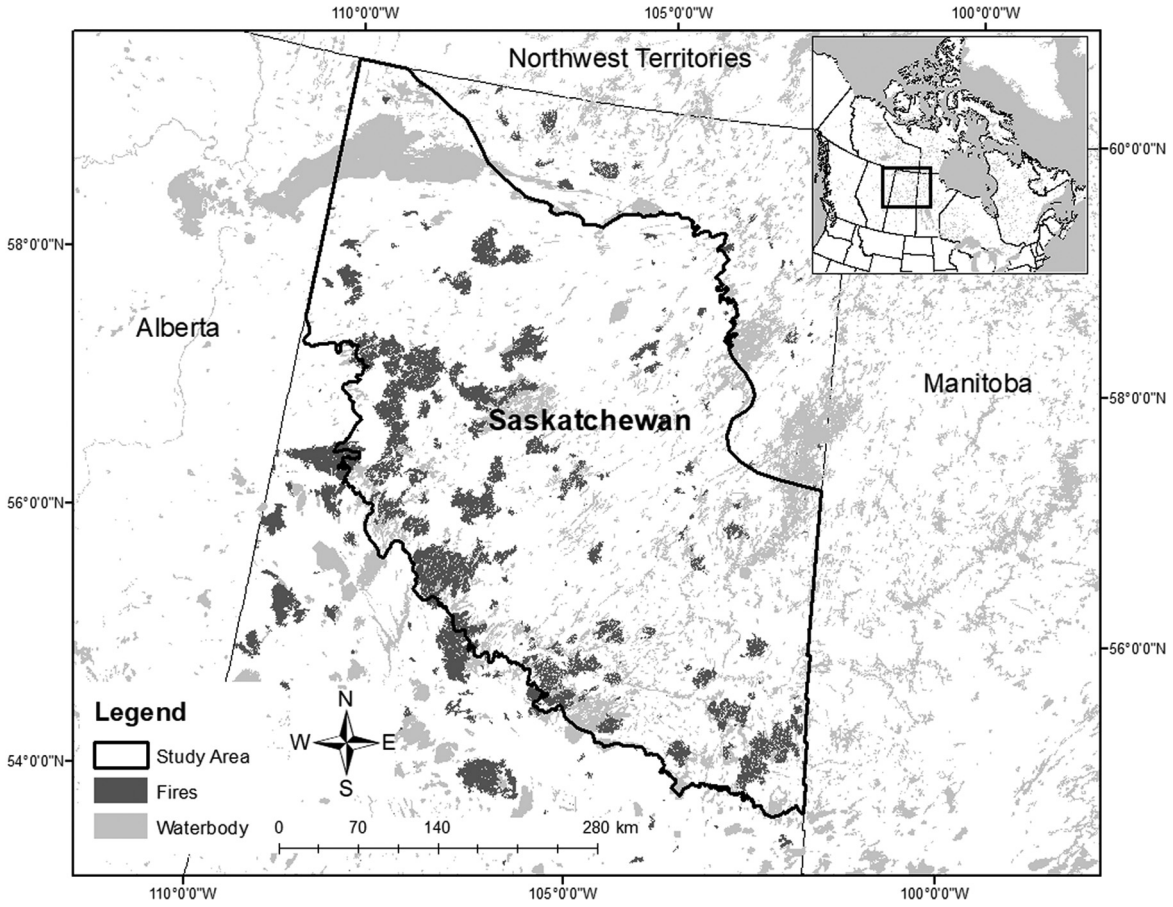
In this study, we observed changes in space use by woodland caribou in response to areas that burned while they were collared (hereafter recent burns) in the Boreal Shield of Saskatchewan. Woodland caribou demonstrate interannual fidelity to seasonal home ranges (Schaefer et al. 2000; Wittmer et al. 2006; Lafontaine et al. 2019). The degree of home range overlap between years is often used to assess fidelity to seasonal ranges and can be related to social or environmental conditions to study the drivers of space-use behavior (Peignier et al. 2019). For example, Faille et al. (2010) found caribou in heavily burned areas tended to demonstrate lower home range overlap, whereas Dalerum et al. (2007) found caribou did not shift their home range after large fires. Here we used a "before–after, control–impact" design (Stewart-Oaten et al. 1986) to compare the overlap of pre-fire and post-fire seasonal home ranges to the overlap of year-to-year seasonal home ranges. We contrasted the two groups to determine whether caribou adjusted their space use more strongly in response to fire than they typically would between years. We predicted caribou would reduce use of recent burns, resulting in lower overlap of pre-fire and post-fire seasonal home ranges compared with year-to-year seasonal home ranges. By characterizing the short-term response of caribou to fire, we seek to broaden the interpretation of fire in habitat management strategies.

Materials and methods

Study area

Our study encompassed the SK1 woodland caribou range in northern Saskatchewan (Fig. 1). The study area is in the Boreal Shield West ecoregion, part of the traditional territories of the Cree, Dene, and Métis peoples. The Boreal Shield is characterized by a rolling topography of upland forest, peatlands, and numerous lakes. Dominant tree species include jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), with lesser amounts of trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marshall), and tama-

Fig. 1. Map of the study area in Saskatchewan, Canada. The study area encompasses the SK1 range of woodland caribou (*Rangifer tarandus caribou*). Only areas that burned while animals were collared are displayed. This figure was created using ArcMap version 10.5.1 (Esri, Inc. 2017) and assembled from the following data sources: study area (ECCC 2012*b*), fire polygons (CFS 2019), waterbodies (StatCan 2011; NRCan 2013), and territorial boundaries (NRCan 2013).



rack (*Larix laricina* (Du Roi) K. Koch). Lowland areas commonly support *Sphagnum* L. mosses and ericaceous shrubs (e.g., Labrador tea, *Rhododendron groenlandicum* (Oeder) Kron & Judd). Productive uplands support a moderate diversity of herbaceous plants and shrubs, whereas sandy or rocky uplands with shallow soils tend to be dominated by velvetleaf blueberry (*Vaccinium myrtilloides* Michx.) and terrestrial lichens (genus *Cladonia* Hill ex P. Brown). The climate is continental, with a mean annual temperature of –2.7 °C and mean annual precipitation of 503 mm (Fick and Hijmans 2017). Due to low fire suppression and a short fire cycle, the region experiences some of the highest annual area burned in Canada (Stocks et al. 2002; Parisien et al. 2004). The Boreal Shield of Saskatchewan has low human disturbance (3%) and high fire disturbance (~57%) (ECCC 2012*a*) and 8.4% of the study area burned during the study period (2014–2017).

GPS location data

We obtained GPS collar locations for 94 adult female caribou monitored from 2014 to 2018 as part of a research project led by the University of Saskatchewan (McLoughlin et al. 2019). Capture and collaring procedures were carried out following Canadian Council on Animal Care guidelines as approved by the University of Saskatchewan (protocol No. 20130127) and the Saskatchewan Ministry of Environment (permit No. 14FW037).

Seasonal home range estimation

Our objective was to characterize broad trends in space use in three biologically relevant seasons informed by McLoughlin et al. (2019): calving (1 May – 31 July), summer–autumn (1 August – 30 November), and winter (1 December – 31 March). To ensure consistency in the amount of data used to estimate home ranges, we rarefied GPS locations to a 5 h fix rate using the "amt" package in R version 3.6.0 (Signer et al. 2019; R Core Team 2019). We eliminated individual–seasons with a low rate of fix success (<66% of days) and individuals with insufficient collar life to facilitate interannual home range comparisons. We excluded GPS locations in April to minimize inflated home ranges because woodland caribou are known to exhibit directed, long-distance movements at this time of year when dispersing from their winter range to calving sites (Ferguson and Elkie 2004). The calving season approximates the calving and post-calving periods documented for caribou in Saskatchewan (McLoughlin et al. 2019).

We used the "adehabitatHR" package in R (Calenge and Fortmann-Roe 2019) to estimate seasonal home ranges as 95% utilization distributions (UDs) for each individual–year–season. We generated a 100% minimum convex polygon in ArcGIS version 10.5.1 (Esri, Inc. 2017) surrounding all seasonal home ranges to define the study area. We calculated Bhattacharyya's Affinity (BA) overlap for each individual's seasonal home range dyads (e.g., SK115-1-W to SK115-2-W). BA overlap describes the degree of three-dimensional similarity between two UDs (Fieberg and Kochanny 2005). Values range from 0 to 1 with higher values representing greater similarity in space use. Unlike overlap metrics that rely solely on home range boundaries, BA overlap incorporates intensity of use within the UD, providing a more detailed representation of space-use similarity between two home ranges (Fieberg and Kochanny 2005; Clapp and Beck 2015).

Table 1. Prediction, structure, and overall conclusion for statistical models used to assess the response of woodland caribou (*Rangifer tarandus caribou*) to areas that burned while they were collared in the Boreal Shield of Saskatchewan, Canada.

Prediction	Model	Response variable	Predictor variable	Model type	Prediction supported
Overlap of pre-fire and post-fire home ranges < year-to-year home ranges	A	BA overlap	Home range comparison (0 = year-to-year; 1 = pre-fire and post-fire)	Beta	Refuted
Lower overlap of pre-fire and post-fire home ranges when more heavily affected by a fire	B	BA overlap	Pre-fire prop. use of burn	Beta	Refuted
Greater change in use of the burn when more heavily affected by a fire	C	Δ Prop. use of burn	Pre-fire prop. use of burn	Beta	Partially supported
Decreased use of the burn when more heavily affected by a fire	D	Increase (0 = constant or decrease; 1 = increase)	Pre-fire prop. use of burn	Logistic	Partially supported

Note: Models were fitted separately for each season (calving, summer–autumn, winter). Bhattacharyya's Affinity (BA) overlap is an index of space-use similarity between a pair of seasonal home ranges. "Prop. use of burn" is based on the proportion of GPS locations within an area that burned while caribou were collared.

Table 2. Beta coefficient (β), standard error (SE), and p value for statistical models used to assess the response of woodland caribou (*Rangifer tarandus caribou*) to areas that burned while they were collared in the Boreal Shield of Saskatchewan, Canada.

			Calving			Summer–Autumn			Winter		
Model	Response variable	Predictor variable	β	SE	p	β	SE	p	β	SE	p
A	BA overlap	Home range comparison (0 = year-to-year; 1 = pre-fire and post-fire)	−0.171	0.243	0.484	−0.408	0.340	0.230	−0.005	0.248	0.984
B	BA overlap	Pre-fire prop. use of burn	0.671	0.678	0.323	1.424	1.567	0.363	1.348	0.688	0.050
C	Δ Prop. use of burn	Pre-fire prop. use of burn	0.763	0.705	0.279	3.165	0.607	<0.001	4.027	0.560	<0.001
D	Increase (0 = constant or decrease; 1 = increase)	Pre-fire prop. use of burn	0.648	2.078	0.755	−17.423	9.319	0.062	−37.843	18.670	0.043

Note: Bhattacharyya's Affinity (BA) overlap is an index of space-use similarity between a pair of seasonal home ranges. "Prop. use of burn" is based on the proportion of GPS locations within an area that burned while caribou were collared. Random effect estimates are presented in Table 3.

Identifying caribou that interacted with recent burns

To determine whether individuals interacted with recent burns, we first rasterized provincial fire polygons (CFS 2019) and waterbodies (NRCan 2017) to a 30 m pixel size. All areas within the fire perimeter, excluding waterbodies, were classified as burned. We created a raster with cell values representing waterbodies, areas that burned prior to caribou being collared, and areas that burned while caribou were collared (i.e., recent burns). We used the "raster" package in R (Hijmans 2019) to assign cell values from the raster to the caribou GPS locations and summarized the proportion of GPS locations within recent burns for each individual–year–season.

We deemed an animal interacted with recent burns when ≥5% of the GPS locations for a single individual–year–season were within a recent burn. Individuals that did not meet this criterion were considered control cases for the purposes of comparison and the overlap of their seasonal home ranges represents year-to-year variation. We identified pre-fire and post-fire home range dyads for animals that interacted with recent burns based on the fire's start and end dates (CFS 2019). Our subsequent analyses are based on pre-fire and post-fire (n = 82) and year-to-year (n = 398) seasonal home range dyads for 70 individual caribou.

Statistical modelling

We fit a set of statistical models (Table 1) separately to each season to quantify the response of caribou to recent burns using the "glmmTMB" package in R (Magnusson et al. 2020). Hereafter, we refer to the proportion of pre-fire GPS locations within the burn as an index of how heavily affected an individual was by a fire. We predicted caribou would demonstrate lower BA overlap of pre-fire and post-fire seasonal home ranges than year-to-year seasonal home ranges (model A). We expected individuals would demonstrate lower overlap of pre-fire and post-fire seasonal home ranges when more heavily affected by a fire (model B). We also predicted caribou would exhibit greater change in use of the burn (model C) and would be more likely to decrease use of the burn (model D) when more heavily affected by a fire. Where appropriate, proportion response variables were transformed to exclude values of 0 and 1 (Cribari-Neto and Zeileis 2020). All models included a random effect for animal ID and a random effect for the years in the dyad (Peignier et al. 2019). Fixed effects, considered significant at α = 0.05, are reported in Table 2 and associated random effects are reported in Table 3. Due to lack of normality, we used median and 95% median confidence intervals (Le Boudec 2016) as a measure of central tendency for year-to-year BA overlap of seasonal home ranges (hereafter population median).

Results

Fire occurrence

Despite a significant portion of the study area burning while caribou were collared, caribou rarely encountered recent burns, suggesting it is rare for a large part of a caribou's home range to burn. Caribou had no GPS locations within recent burns in 44% of individual–seasons and <5% of GPS locations within recent burns in 71% of individual–seasons (Fig. 2).

Home range overlap

Overall, we found negligible differences in BA overlap of pre-fire and post-fire vs. year-to-year seasonal home ranges (Fig. 3). In all seasons, there was no significant difference in the BA overlap of pre-fire and post-fire vs. year-to-year home ranges (Table 2; model A). The overlap of pre-fire and post-fire home ranges did not decrease when caribou were more heavily affected by a fire in any season (Table 2; model B).

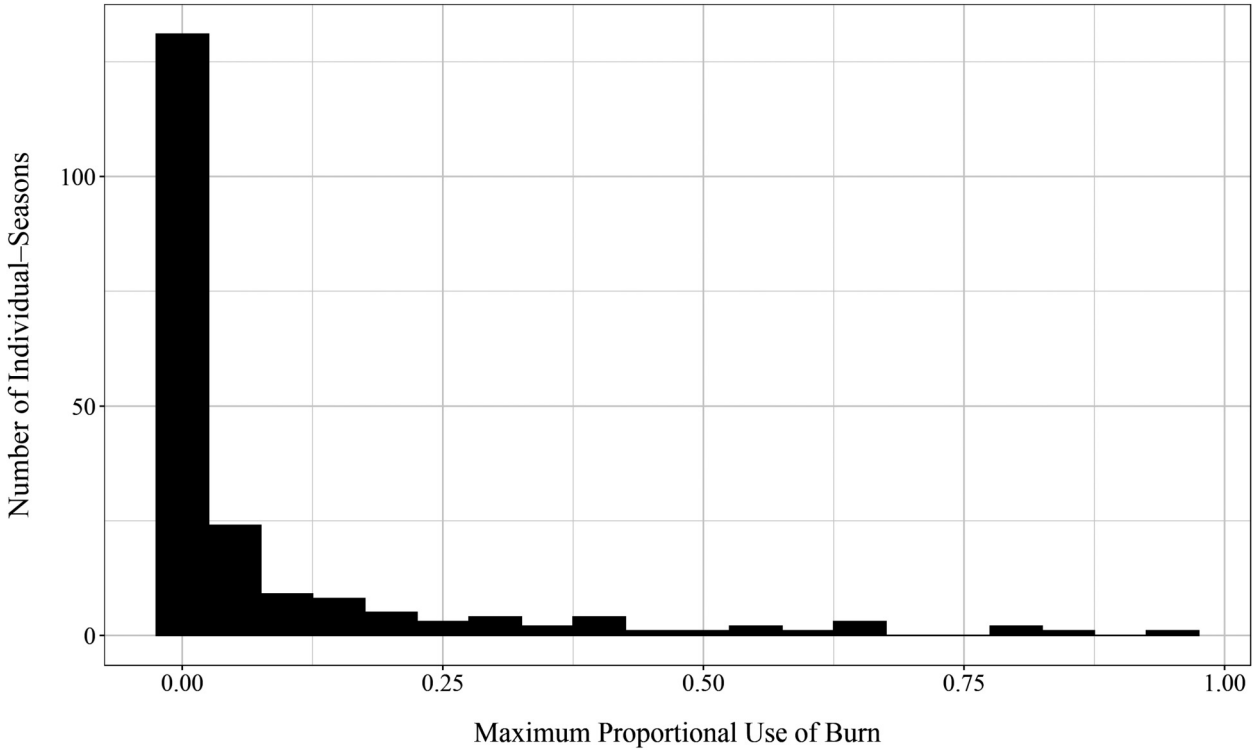
Caribou demonstrated high variation within and among individuals and seasons in their response to fire (Fig. 4). During calving, caribou often made small adjustments to use of the burn and

Table 3. Variance and standard deviation (SD) of random effects for statistical models used to assess the response of woodland caribou (*Rangifer tarandus caribou*) to areas that burned while they were collared in the Boreal Shield of Saskatchewan, Canada.

Model	Response variable	Predictor variable	Random effect	Calving (variance ± SD)	Summer–Autumn (variance ± SD)	Winter (variance ± SD)
A	BA overlap	Home range comparison (0 = year-to-year; 1 = pre-fire and post-fire)	Animal ID	0.511 ± 0.715	0.758 ± 0.871	0.343 ± 0.586
			Year	$1.297 \times 10^{-10} \pm 1.139 \times 10^{-5}$	0.031 ± 0.175	0.011 ± 0.103
B	BA overlap	Pre-fire prop. use of burn	Animal ID	0.032 ± 0.180	0.690 ± 0.831	0.091 ± 0.301
			Year	$2.467 \times 10^{-10} \pm 1.571 \times 10^{-5}$	0.087 ± 0.295	0.036 ± 0.190
C	Δ Prop. use of burn	Pre-fire prop. use of burn	Animal ID	0.027 ± 0.164	0.124 ± 0.353	$3.443 \times 10^{-10} \pm 1.855 \times 10^{-5}$
			Year	$1.861 \times 10^{-10} \pm 1.364 \times 10^{-5}$	0.025 ± 0.153	$9.871 \times 10^{-11} \pm 9.935 \times 10^{-6}$
D	Increase (0 = constant or decrease; 1 = increase)	Pre-fire prop. use of burn	Animal ID	0.266 ± 0.516	$1.517 \times 10^{-5} \pm 4.0 \times 10^{-3}$	$1.662 \times 10^{-9} \pm 4.077 \times 10^{-5}$
			Year	$5.940 \times 10^{-10} \pm 2.437 \times 10^{-5}$	$3.880 \times 10^{-8} \pm 1.970 \times 10^{-4}$	$2.440 \times 10^{-8} \pm 1.562 \times 10^{-4}$

Note: Bhattacharyya's Affinity (BA) overlap is an index of space-use similarity between a pair of seasonal home ranges. "Prop. use of burn" is based on the proportion of GPS locations within an area that burned while caribou were collared.

Fig. 2. Maximum proportional use of recent burns in a single individual–year–season for each individual–season (e.g., SK115-W; $n = 202$) for woodland caribou (*Rangifer tarandus caribou*) in the Boreal Shield of Saskatchewan, Canada. Recent burns are those that occurred while caribou were collared.



increased use of the burn in 42% of pre-fire and post-fire dyads. In several cases where caribou increased use of the burn, home range overlap was lower than the population median, suggesting that caribou shifted their home range to incorporate more burned habitat (Figs. 4 and 5*a*). In summer–autumn, caribou reduced use of the burn in 68% of pre-fire and post-fire dyads. BA overlap frequently fell below the median of the population, suggesting that caribou often made larger adjustments to their home range in response to fire than they typically would year to year (Fig. 4). In winter, many caribou that interacted with recent burns had similar BA overlap as the population median (Fig. 4). However, caribou reduced use of the burn in 63% of pre-fire and post-fire dyads (Fig. 5*b*), particularly when more heavily affected by a fire. When caribou were more heavily affected by a fire during the calving season, they did not strongly alter or reduce use of the burn (Table 2; models C and D). In summer–autumn, caribou demonstrated greater change in use of the burn but were not significantly more likely to reduce use of the burn when more heavily affected by a fire. Caribou altered use of the burn more strongly and tended to reduce use of the burn when their winter range was more heavily affected by a fire (Table 2; models C and D).

Discussion

Many fire ecology studies substitute space for time by studying burns already present on the landscape. Our study capitalizes on the temporal element of fire by comparing the overlap of pre-fire and post-fire seasonal home ranges. However, given GPS collars for woodland caribou are typically deployed for up to 4 years, our inference is restricted to the short-term effects of fire. The responses that we documented may differ from longer term impacts, as caribou must constantly adapt to the shifting habitat mosaic created by fire histories (Schaefer and Pruitt 1991). Caribou that interacted with recent burns in this study occurred on a

Fig. 3. Boxplots of Bhattacharyya's Affinity (BA) overlap for pre-fire and post-fire vs. year-to-year seasonal home ranges of woodland caribou (*Rangifer tarandus caribou*) in the Boreal Shield of Saskatchewan, Canada. BA overlap is an index of space-use similarity between a pair of seasonal home ranges. *n* is the number of seasonal home range dyads. Box limits indicate the 25th (lower) and 75th (upper) quartiles; whiskers indicate the last datum within 1.5 interquartile ranges of the box limits; solid circles beyond the whiskers indicate outliers; the solid horizontal line indicates the median.

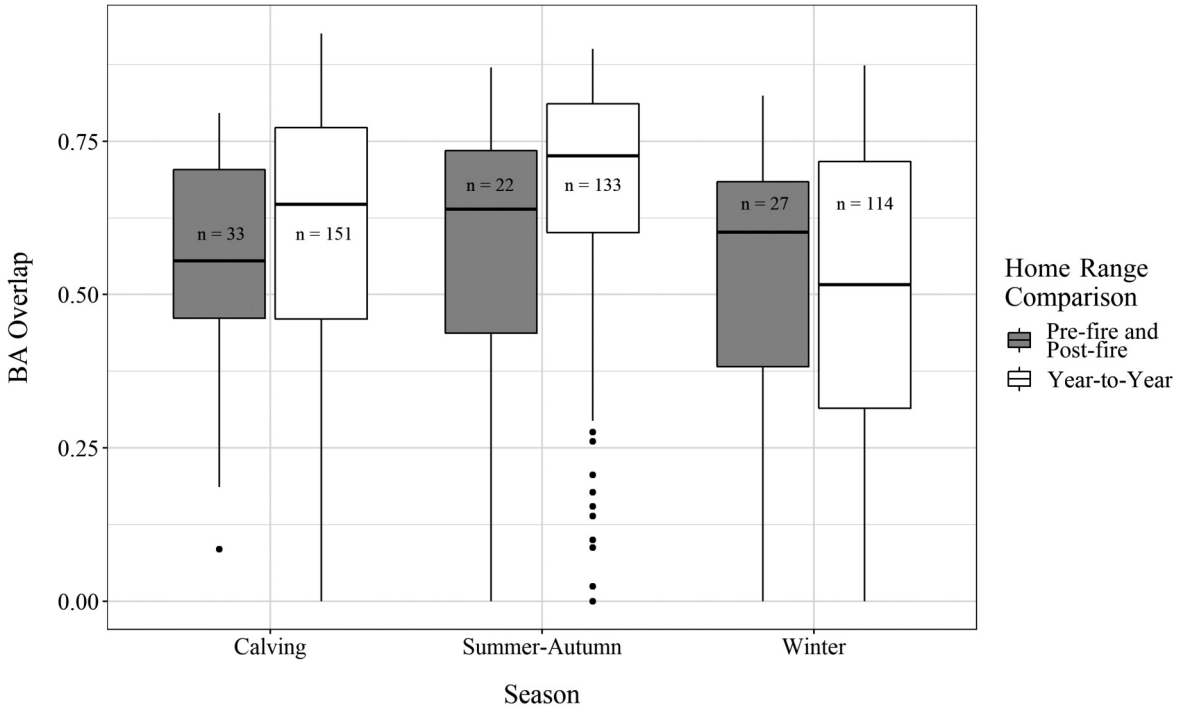


Fig. 4. Changes in seasonal space use by woodland caribou (*Rangifer tarandus caribou*) in response to areas that burned while they were collared in the Boreal Shield of Saskatchewan, Canada. Bhattacharyya's Affinity (BA) overlap is an index of space-use similarity between a pair of seasonal home ranges. "Change in use of burn" is the difference between the proportion of post-fire and pre-fire GPS locations within the burn. Each data point represents a single pre-fire and post-fire seasonal home range dyad. The size of data point corresponds to the proportion of pre-fire GPS locations within the burn. The horizontal line represents the median BA overlap of year-to-year seasonal home ranges, bound by 95% median confidence intervals.

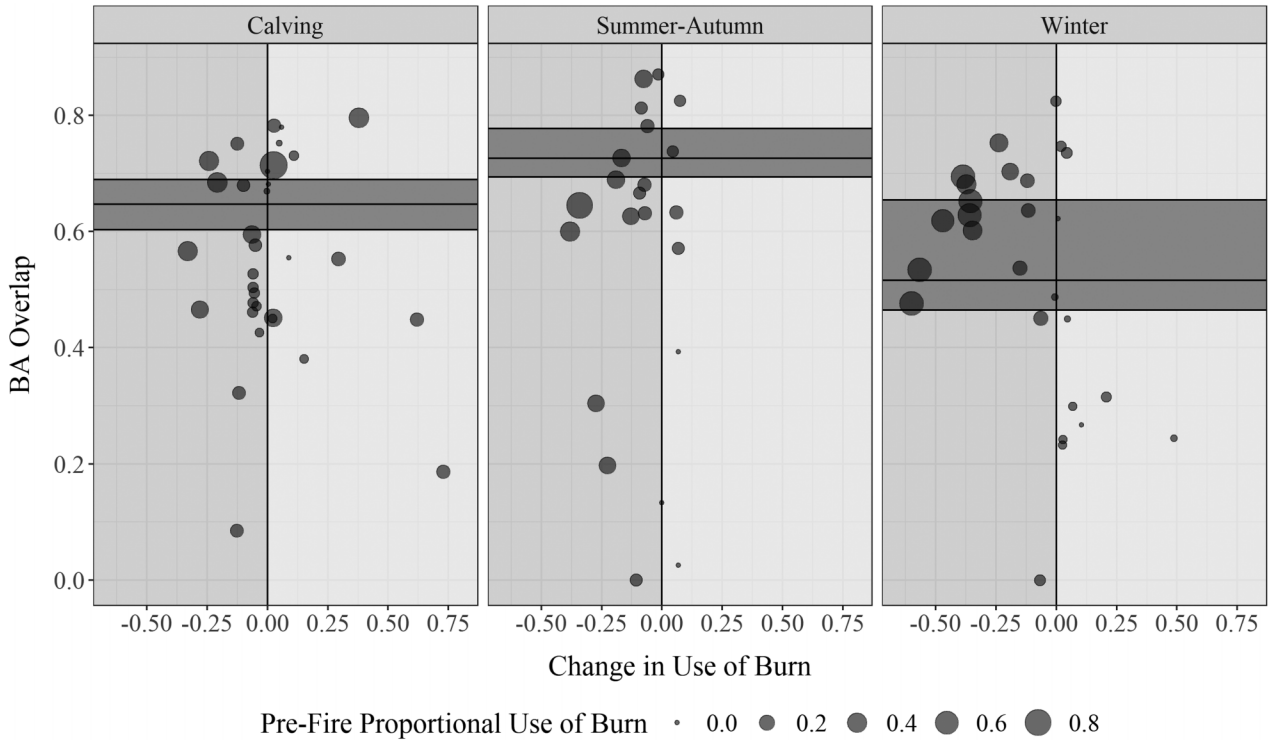
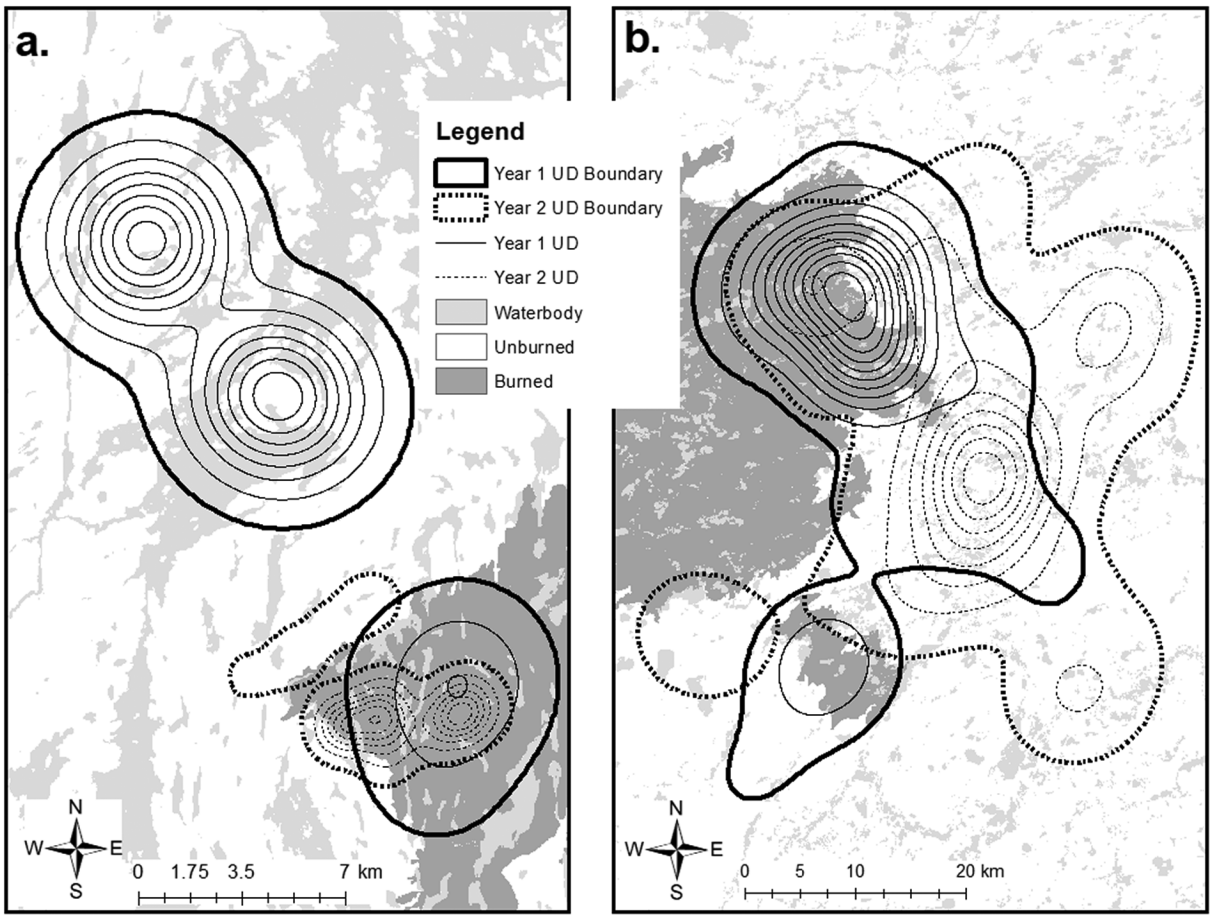


Fig. 5. Example comparisons of pre-fire and post-fire seasonal home ranges for woodland caribou (*Rangifer tarandus caribou*) in the Boreal Shield of Saskatchewan, Canada: (*a*) this individual substantially altered its home range among calving seasons (BA overlap = 0.19) to increase use of the burn post fire (14% pre-fire use → 87% post-fire use); (*b*) this individual reduced use of the burn post fire (65% pre-fire use → 8% post-fire use) but showed moderate overall similarity in home range boundaries among winters (BA overlap = 0.53). Bhattacharyya's Affinity (BA) overlap is an index of space-use similarity between a pair of seasonal home ranges. This figure was created using ArcMap version 10.5.1 (Esri, Inc. 2017) and assembled from the following data sources: fire polygons (CFS 2019) and waterbodies (NRCan 2017).



range with low human disturbance, conifer-dominated post-fire succession, and low densities of moose and wolves (Neufeld et al. 2020). The effects of fire on woodland caribou may differ in regions with high human disturbance, greater deciduous post-fire succession, and higher densities of moose and wolves (Wittmer et al. 2007). Therefore, we caution that managers must consider local range conditions to properly interpret fire in habitat management strategies.

Despite inhabiting boreal ecosystems with high fire frequency, our study suggests that it is rare for a large part of a caribou's home range to burn. Prevailing theory and policy predict that when caribou experience fire, they should shift their home range to avoid the affected area because burns have lower habitat quality compared with alternate, unburned ranges (Schaefer and Pruitt 1991; Joly et al. 2003). Home range fidelity should only be favoured if the current home range is of equal or higher quality than the alternate range (Switzer 1993). Therefore, we expected the overlap of pre-fire and post-fire seasonal home ranges to be significantly lower than the overlap of year-to-year seasonal home ranges. In all seasons, a caribou's response to fire was indistinguishable from regular, interannual variation in home range overlap. Many factors influence interannual home range fidelity including weather, body condition, reproductive status, social interactions, forage availability, predation, and disturbance (Wittmer et al. 2006; Faille et al. 2010; MacNearney et al. 2016; Lafontaine et al. 2017; Peignier et al. 2019). Our results indicate that recent burns do not cause adjustments to space use beyond these typical year-to-year variations.

Caribou were least averse to recent burns during calving. Caribou showed similar overlap of pre-fire and post-fire and year-to-year home ranges during calving, and individuals more heavily affected by a fire did not strongly alter or reduce use of the burn. Caribou increased use of the burn in 42% of pre-fire and post-fire dyads, with some individuals appearing to shift their home range to incorporate more burned habitat. Following the logic of Switzer (1993), caribou should demonstrate these behaviors only if recent burns are of equal or greater habitat quality than alternate ranges.

There are several ways in which recently burned areas (<5 years) may provide habitat value to caribou during the calving season. Female caribou strongly emphasize minimizing predation risk when selecting habitat during calving (Gustine et al. 2006; Viejou et al. 2018). Caribou could experience lower predation risk in recently burned areas due to low deciduous forage abundance limiting or delaying recolonization of burns by moose and wolves (Ballard et al. 2000; Kittle et al. 2015; Street et al. 2015; DeMars et al. 2019; Neufeld et al. 2020). Females could compensate for the relatively low forage biomass at these sites by drawing from their body reserves (Parker et al. 1990) and consuming new, higher quality plant growth to help meet the high energetic costs of lactation (Oftedal 1985; Chan-McLeod et al. 1994; Gustine et al. 2006). In the Boreal Shield, it is common for ≥25% of the area

within a fire perimeter to consist of post-fire residuals (Kansas et al. 2016). Bogs and fens are particularly common as post-fire residuals (Silva 2018) because they are less prone to fire than uplands (Turetsky et al. 2004; Hart et al. 2019). Skatter et al. (2017) documented caribou calving in residual bogs and fens in burns in northern Saskatchewan; caribou could also calve on islands or peninsulas protected by fire breaks near lakes (Carr et al. 2011; Nielsen et al. 2016). Fires reduce the density of understory vegetation and could improve predator detectability when caribou use these features in recently burned areas (Skatter et al. 2017). Therefore, we infer recently burned areas (<5 years) could provide similar habitat value as alternate, unburned ranges during the calving season, primarily by affording caribou a refuge from predators. Maintaining fidelity to a burned calving range or shifting to calve in a recently burned area may be an adaptive strategy enabling caribou to spatially isolate themselves from conspecifics, other ungulate species, and predators in regions with high fire frequency to reduce predation on calves (Bergerud 1996; Walker et al. 2020).

In summer–autumn, BA overlap of pre-fire and post-fire vs. year-to-year home ranges was not significantly different. However, caribou reduced use of the burn in 68% of pre-fire and post-fire dyads. This suggests that caribou maintained relatively similar pre-fire and post-fire home ranges but adjusted their space use at a fine scale by decreasing use of the burn (Dalerum et al. 2007).

Female body condition reaches a low point in mid-summer due to the high nutritional demands of lactation, and caribou must quickly replenish their body reserves prior to winter to survive and reproduce (Parker et al. 2009). Calves are more mobile and less vulnerable to predators by summer–autumn (DeMars et al. 2013). This may allow female caribou to increase use of more productive habitats and take advantage of protein-rich vascular forage (Denryter et al. 2017), although lichens remain an important component of the summer diet (Thompson et al. 2015). As documented by Schaefer and Mahoney (2013), our study found that caribou maintained strong fidelity to their summer–autumn range, which Peignier et al. (2019) hypothesized is because forage is homogenously distributed and easily accessible at this time of year. By increasing heterogeneity, burns could promote caribou to increase use of unburned areas of their home range where the abundance of forage, especially lichens, is more predictable (Switzer 1993).

Because caribou rely heavily on lichens in winter (Thompson et al. 2015), we predicted caribou would be most averse to recent burns during this season. However, the overlap of pre-fire and post-fire vs. year-to-year home ranges in winter was not significantly different. Despite maintaining relatively similar home ranges, caribou reduced use of the burn in 63% of pre-fire and post-fire dyads, especially if they were more heavily affected by a fire.

The tendency of caribou to reduce use of burns in winter is consistent with unburned areas being of higher habitat quality (Switzer 1993), likely due to more predictable lichen availability (Joly et al. 2010). Caribou demonstrate low home range fidelity in winter (Schaefer et al. 2000; Wittmer et al. 2006; Lafontaine et al. 2017) because forage availability, snow conditions, and the location of social groups vary widely between years (Mayor et al. 2009; Peignier et al. 2019). Reductions in use of the burn reported here were achievable within this regular range of interannual variation in winter home range overlap.

Caribou did increase use of the burn in 37% of pre-fire and post-fire dyads, suggesting recently burned areas may retain some value as winter habitat. Schaefer and Pruitt (1991) observed caribou grazing lichens in upland post-fire residuals during winter. Graminoids (e.g., tussock cottongrass, *Eriophorum vaginatum* L.) can be plentiful in recently burned bogs and fens and serve as a relatively nutritious supplement to a caribou's winter diet (Klein 1982; Ballard et al. 2000). Caribou that increased use of burns in winter often demonstrated low BA overlap. Therefore, we hypothesize that caribou may opportunistically use habitats in recently burned areas when making large shifts in winter home ranges among years. In all seasons, additional research is required to verify the mechanisms of habitat selection by woodland caribou within recently burned areas.

Superficially, fire can appear to be a destructive disturbance for woodland caribou. However, there is growing evidence that fires have a weak influence on caribou demography, particularly in regions with low human disturbance, conifer-dominated post-fire succession, and low densities of moose and wolves (Johnson et al. 2020). In the present study, caribou rarely experienced fire and when they did, they adjusted their space use in variable and complex ways that were largely indistinguishable from regular, interannual variation. Our results suggest that recently burned areas (<5 years) may provide habitat value to woodland caribou, particularly during the calving season (Schaefer and Pruitt 1991; Skatter et al. 2017). These findings are consistent with calls for a regionally informed, flexible approach to interpret fire in habitat management strategies (DeMars et al. 2019; Neufeld et al. 2020).

Acknowledgements

J.A.S. was supported in conducting this research by a Natural Sciences and Engineering Research Council of Canada (NSERC) Canada Graduate Scholarship, the NSERC Collaborative Research and Training Experience program, and Domtar Dryden Forestlands. We thank our partners in Saskatchewan who collected the GPS collar data. Their work was supported by an NSERC Collaborative Research and Development Grant awarded to P.D. McLoughlin, J.F. Johnstone, and partners listed in McLoughlin et al. 2019. We also thank S. Konkolics, P. Walker, and M. Routh for your insights on this analysis. Lastly, we thank J.A. Schaefer and one anonymous reviewer for their thoughtful comments on an earlier version of the manuscript.

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