The Canadian Field-Naturalist

Estimated effects of clear-cuts and burns associated with habitat use by female Newfoundland Caribou (*Rangifer tarandus*)

Daniella J. Dekelaita[1, 2, *], **Paul R. Krausman**[1, 3], and **Shane P. Mahoney**[4, 5]

[1]Wildlife Biology Program, University of Montana, Missoula, Montana 59812 USA
[2]Current address: Bureau of Land Management, Sierra Front Field Office, Carson City, Nevada 89701 USA
[3]Current address: School of Renewable Natural Resources and the Environment, University of Arizona, Tucson, Arizona 85721 USA
[4]Department of Environment and Conservation, Government of Newfoundland and Labrador, P.O. Box 8700, St. John's, Newfoundland and Labrador A1B 4J6 Canada
[5]Current address: Conservation Visions, LLC., 354 Water Street, P.O. Box 5489, St. John's, Newfoundland and Labrador A1C 5W4 Canada
[*]Corresponding author: ddekelaita@blm.gov

Dekelaita, D.J., P.R. Krausman, and S.P. Mahoney. 2022. Estimated effects of clear-cuts and burns associated with habitat use by female Newfoundland Caribou (*Rangifer tarandus*). Canadian Field-Naturalist 136(4): 316–332. https://doi.org/10.22621/cfn.v136i4.2767

Abstract

The decline of Caribou (*Rangifer tarandus*) is mainly attributed to anthropogenic disturbance from resource development (i.e., logging, oil and gas extraction), which causes habitat loss and increased predation risk. Natural landscape disturbance, particularly from fire, can have similar effects, and cumulative effects from disturbance have been associated with lower neonate recruitment. Our objective was to evaluate the potential effects of land cover types on resource selection by females, with an emphasis on clear-cuts and fire, during the calving season (May–June) in three neighbouring herds (Middle Ridge, Gaff Topsails, and Pot Hill) on insular Newfoundland, Canada, and compare results with pre-existing information on calf recruitment. We applied a resource selection framework to analyze location data collected from global positioning system collars between 2007–2010 and estimate relative probability of use for different cover types. Recruitment was lowest in Pot Hill, where ≤10-year old clear-cuts were favoured, whereas recruitment was highest in Middle Ridge and Gaff Topsails, where females favoured burns, suggesting that burns could be more beneficial to Caribou fitness. Further investigation will be needed to more closely examine how anthropogenic versus natural disturbance affects Caribou fitness in Newfoundland and improve our understanding of important habitat for calving females.

Key words: Calving; clear-cuts; disturbance; fire; logging; Newfoundland; radio-collars; resource selection; spatial shifts; Caribou

Introduction

Birthing and rearing sites are an important aspect of reproductive ecology in ungulates because site selection can influence survival and success of neonates (Fox and Krausman 1994; Bangs *et al.* 2005; Gustine *et al.* 2006; Monteith *et al.* 2014) and recruitment may ultimately influence population dynamics in large herbivores (Gaillard *et al.* 1998). For Caribou (*Rangifer tarandus*), calving site locations are typically determined by distance from predators, food availability, hiding cover, and familiarity with the landscape (Bergerud 1996, 2000). Caribou commonly exhibit strong site fidelity to calving grounds (i.e., the geographical area used by most parturient females in a herd; Gunn and Miller 1986; Schaefer *et al.* 2000), although calving grounds may also shift spatially over time (Nagy *et al.* 2011; Gunn *et al.* 2012; Taillon *et al.* 2012). We speculate that such shifts could be a response to resource availability, predation risk, and human use.

Female Caribou on insular Newfoundland, Canada (hereafter Newfoundland) typically move from winter range to calving grounds during March and April and aggregate on calving grounds from May to June during the pre-calving, calving, and post-calving phases of their annual cycle (Bergerud 1974). In the Middle Ridge herd, females demonstrated southward shifts in their seasonal aggregations between 1987 and 1996, whereby the distribution in May–June shifted with increasing distance away from expanding clear-cuts across years (Chubbs *et al.* 1993; Schaefer and Mahoney 2005). By 2009–2010 the calving distribution appeared to be concentrated in an area that burned in 1986 (23–24 years earlier). Calf mortality in the Middle Ridge herd also increased between 1997 and 2003, which was attributed to an increase in predation by American Black Bear (*Ursus americanus;* Mahoney and Weir 2009; Lewis and Mahoney 2014). Clear-cuts are associated with increased predator density (Mahoney and Virgl 2003; Wittmer *et al.* 2007; Brodeur *et al.* 2008; Leblond *et al.* 2016) and predation risk may have increased as clear-cuts expanded, causing shifts in space-use. Logging is also associated with road construction, increased traffic and noise, and surface disturbance, similar to mining operations, and oil and hydroelectric development, to which female Caribou have demonstrated sensitivity and avoidance during calving (Cameron *et al.* 1992; Vistnes and Nellemann 2001; Mahoney and Schaefer 2002; Weir *et al.* 2007).

The decline of Caribou in Canada is attributed mainly to resource development and associated habitat loss and predation risk (COSEWIC 2014). Since 2000, the Boreal population, which occupies mature boreal forest and occurs throughout mainland Canada from the western to eastern seaboards, has been assessed as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2014). An estimated one-third of subpopulations comprising the Boreal population are projected to decline continually as a result of anthropogenic disturbance (COSEWIC 2014). The Boreal population faces increasing predation pressure by Gray Wolf (*Canis lupus*) that use linear features associated with resource extraction (e.g., roads, seismic lines; COSEWIC 2014). Additionally, logging in particular results in habitat conversion from old forest to early seral stands that attract opportunistic predators, such as Black Bear and Coyote (*Canis latrans*; Brodeur *et al.* 2008; Boisjoly *et al.* 2010) and can increase abundance of alternate prey species such as White-tailed Deer (*Odocoileus virginianus*) and Moose (*Alces americanus*), that, in turn, increase predator abundance (Mahoney and Virgl 2003; Wittmer *et al.* 2007). Natural fire disturbance can also contribute to functional habitat loss and higher predation in the same way as logging, and as such may be considered tantamount to human disturbance (Courtois *et al.* 2007; Wittmer *et al.* 2007; Sorensen *et al.* 2008).

The Newfoundland population, which occupies coniferous forest, barrenland, shrubland, and wetland complexes on insular Newfoundland, was assessed as Not at Risk in 2002 by COSEWIC, but the population thereafter declined by approximately 60% and was reassessed as Special Concern in 2014 (COSEWIC 2014). The decline was associated with high population density, harvest, and predation (COSEWIC 2014). Current projections, unlike those for the Boreal population, do not indicate this population is in peril (Randell *et al.* 2012; Weir *et al.* 2014). Caribou on insular Newfoundland are unique from mainland Caribou populations because they do not face predation pressure from wolves, which were extirpated from the island around 1922 (Allen and Barbour 1937). Black Bear and the recently recruited Coyote that colonized the island in 1985 (Mahoney and Schaefer 2002) are major predators (Lewis and Mahoney 2014; Mahoney *et al.* 2015). Moreover, the level of landscape disturbance within Caribou ranges in mainland Canada may be seven times higher, if not more, than that of insular Newfoundland (Sorensen *et al.* 2008; McCarthy *et al.* 2011; Natural Resources Canada 2020).

Recent studies on Caribou on Newfoundland have examined landscape disturbance and calf recruitment (McCarthy *et al.* 2011), predation and neonate survival (Mahoney *et al.* 2015; Rayl *et al.* 2015), effects of vegetation and predation risk (inferred from habitat characteristics) on resource selection by calving females (Bastille-Rousseau *et al.* 2015), and the influence of landscape heterogeneity on neonate mortality risk (Rayl *et al.* 2018). McCarthy *et al.* (2011) detected a negative correlation between calf recruitment and total landscape disturbance (i.e., from anthropogenic and natural factors including clear-cuts and fire) within calving and post-calving ranges. Mahoney *et al.* (2015) reported that predation by Black Bear and Coyote was the leading cause of mortality for Caribou calves from 2003 to 2012, which coincided with the period of population decline after a period of sustained growth between 1979 and 1997. Bastille-Rousseau *et al.* (2015) concluded that calving females selected calving grounds with greater access to forage, while avoiding predation risk in varying degrees across herds. Rayl *et al.* (2018) further revealed that neonate mortality risk from bear predation increased in areas with higher proportions of conifer scrub (i.e., stunted conifer forest) and water, presumably because conifer scrub provides dense cover that enables ambush tactics, and water may limit mobility and escape routes for young calves.

To our knowledge, the effects of fire and clear-cuts associated with resource selection by female Caribou during calving on Newfoundland have not yet been specifically addressed. Given the distribution shifts displayed by calving females in the Middle Ridge herd, we wanted to analyze selection of land cover types with an emphasis on clear-cuts and burns and compare our results with pre-existing information about calf recruitment in selected herds to expand the discussion on habitat selection, landscape disturbance, and calving. Thus, we examined resource selection by females during the calving season between 2007 and 2010 in three neighbouring Caribou herds (i.e., Middle Ridge, Pot Hill, and Gaff Topsails) that used ranges where progressive logging and natural fires occurred. These herds are considered subpopulations and occupy ranges that typically overlap year-round (COSEWIC 2014), although females aggregate by herd affiliation during the calving season and use separate calving grounds. We also visualized spatial shifts in Middle Ridge by comparing mean activity centres during the calving season across years. We hypothesized that negative effects associated with clear-cuts would trigger an avoidance response in calving females and we predicted that females would therefore have a low relative probability of use associated with clear-cuts compared to other available cover types in May and June. Although some studies equate logging to fire disturbance, suggesting burns have similar negative effects on Caribou (Wittmer *et al.* 2007; Sorensen *et al.* 2008; McCarthy *et al.* 2011; Lafontaine *et al.* 2019), researchers have also reported use of burns by calving females (Bergerud 1974; Skatter *et al.* 2017), and Skatter *et al.* (2017) concluded that burns with residuals (i.e., unburned patches) are important calving habitat for the mixture of food-security and safety they may provide. As such, we further hypothesized that burned areas could be variably important for calving females, and we predicted that selection for this cover type might vary across herds. We assumed that selection of land cover types on the calving grounds adequately characterized habitat use by calving females, and considered available cover types within the larger home range traversed by females in May and June to investigate third-order habitat selection (i.e., within the seasonal home range; Johnson 1980) and draw comparisons across herds.

Study Area

The study area was between 49.4570°N and 47.6389°N, and 57.5167°W and 54.2806°W, spanning ~32 000 km^2 of land managed by the Government of Newfoundland and Labrador. This area encompassed ranges used by adult female Caribou during the calving season in the Middle Ridge, Pot Hill, and Gaff Topsails herds, from 1987 to 1996 and from 2007 to 2010. We refer to the calving season as the period 1 May–30 June, when females aggregate on calving grounds (Bergerud 1974).

The study area included the Long Range Barrens (Buchans Plateau subregion), Central Newfoundland Forest, and Maritime Barrens ecoregions characterized by a combination of rocky uplands, coniferous and deciduous forests, heaths, barrens, and bogs (Government of Newfoundland and Labrador 2020; Figure 1). The Long Range Barrens occurred within a portion of the range occupied by the Gaff Topsails herd, and Central Newfoundland Forest and Maritime Barrens occurred in all herd ranges. Elevations ranged from sea level to ~600 m. Common vegetation associated with the ecoregions included Balsam Fir (*Abies balsamea* [L.] Miller), Black Spruce (*Picea mariana* [Miller] Britton, Sterns & Poggenburgh), Tamarack (*Larix laricina* [Du Roi] Koch), birch (*Betula* spp. L.), Mountain Maple (*Acer spicatum* Lamarck), Trembling Aspen (*Populus tremuloides* Michaux), and alder (*Alnus* spp. Miller), commingled with lichen, moss, and Sheep Laurel (*Kalmia angustifolia* L.) dominated dwarf shrub plant communities. Common native mammal species included Black Bear, Canada Lynx (*Lynx canadensis*), Coyote, Red Fox (*Vulpes vulpes*), Northern River Otter (*Lontra canadensis*), Arctic Hare (*Lepus arcticus*), and Caribou. Moose, which are not native to Newfoundland, were also common and were the only other ungulate species present.

In the three ecoregions, summers (July–August) are mild and winters (December–March) are moderate to severe from the coast to inland areas, respectively (Bell 2002). In the Long Range Barrens, mean annual temperature is ~4°C, mean summer temperature is 12°C, and mean winter temperature is −4°C. Mean annual precipitation ranges from 1000 mm to 1400 mm (Bell 2002). In the Central Newfoundland Forest, mean annual temperature is ~4.5°C, mean summer temperature is 12.5°C, and mean winter temperature is −3.5°C. Mean annual precipitation ranges from 1000 mm to 1300 mm (Bell 2002). In the Maritime Barrens, mean annual temperature is ~5.5°C, mean summer temperature is 11.5°C, and mean winter temperature is −1°C. Mean annual precipitation ranges from 1200 mm to over 1600 mm (Bell 2002).

The study area also featured Routes 1 and 360, and the urban communities of Buchans and Badger, which occurred in the Gaff Topsails range. Towns close to the Pot Hill and Middle Ridge ranges included Howley, Grand Falls-Windsor, and Gander. Land-use consisted of logging, hunting, and recreation. In 2007, the Pot Hill and Gaff Topsails Caribou herds had an estimated 3066 and 2182 individuals, respectively, whereas the Middle Ridge herd had an estimated 8814 individuals in 2010, and the island wide population was estimated to be 38 241 individuals in 2008 (Randell 2019). Based on autumn herd composition surveys, average yearly calf recruitment ratios (calves:females) were ~7:100 for Pot Hill and ~19:100 for Gaff Topsails in 2005–2008 (McCarthy *et al.* 2011), and an estimated 18:100 for Middle Ridge in 2009–2010 (Ellington *et al.* 2020).

We note that between 1960 and 1966, herds occupied calving grounds that were different from each

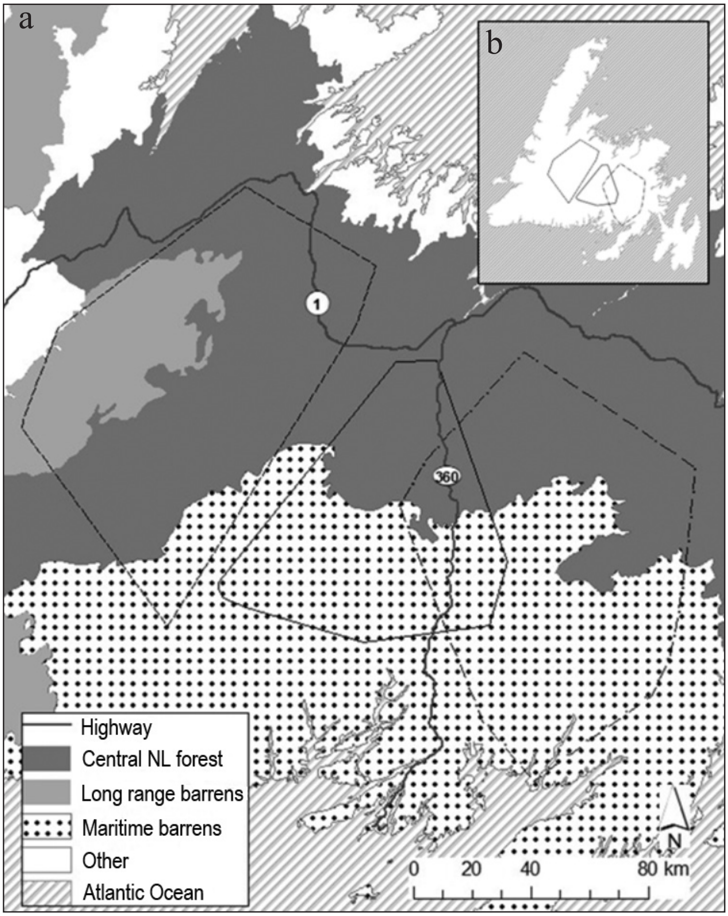

FIGURE 1. a. Delineations of the Gaff Topsails (dashed), Pot Hill (solid, black), and Middle Ridge (dash-dot) Caribou (*Rangifer tarandus*) herd ranges used from 1 May to 30 June in Newfoundland, Canada. Ranges were estimated with 100% minimum convex polygons using location data collected from adult females in 2007–2009 (Gaff Topsails and Pot Hill), and 1987–1996 and 2009–2010 (Middle Ridge). Ecoregions associated with herd ranges are also shown. b. Island of Newfoundland, Canada.

other in terms of cover characteristics (Bergerud 1974), and we therefore expected to find some variation in resource selection patterns across herds during our study. Bergerud (1974) reported that females in the Middle Ridge herd previously occupied areas with large marshes dominated by sedge (*Carex* spp. L.) during the calving season, whereas females in the Pot Hill herd occupied a bog complex with islands of closed-canopy spruce forest and females in the Buchans Plateau occupied open terrain consisting of sedge marshes and dry uplands that had burned 40 years prior.

Methods

Telemetry data

We used location data collected from adult female Caribou during the calving season in 2007–2010 to delineate calving grounds for each herd, which we identified as the area where the highest concentration of locations occurred in those years. We used additional May–June location data collected in 1987–1996 and 1993–1996, respectively, from adult females and calves in Middle Ridge to estimate earlier calving distributions. Adult female Caribou were net-gunned or darted from helicopter and collared on wintering grounds by the Newfoundland and Labrador Department of Environment and Conservation. Darted animals were chemically immobilized using a combination of Telazol (Zoetis, Parsippany-Troy Hills, New Jersey, USA) and xylazine (LGM Pharmaceuticals, Boca Raton, Florida, USA; 1.5 mg/kg Telazol + 0.75 mg/kg xylazine), etorphine hydrochloride (0.06 mg/kg), or Carfentanil (0.03 mg/kg;

Glenmark Pharmaceuticals, Mumbai, India). Calves were located by helicopter and captured at <5 days old without use of net-guns or chemical restraints. In Middle Ridge, females were fit with very high frequency (VHF) radio-collars (Lotek Engineering, Aurora, Ontario, Canada; Telonics, Mesa, Arizona, USA) monitored from 1987 to 1996. Calves were fit with expandable VHF radio-collars (Lotek Engineering; Telonics) in 1993–1996. Between 2007 and 2010, adult females from the three herds were fit with global positioning system (GPS) satellite-collars (Lotek Wireless, Newmarket, Ontario, Canada). Locations from VHF collars were obtained at altitude via fixed-wing aircraft approximately every 1–2 weeks. Location data from GPS collars were downloaded through an ultra-high frequency (Schwartz and Arthur 1999) modem or received through the Iridium satellite system (Iridium Communications, McLean, Virginia, USA). Locations from GPS-collars were recorded at varying intervals and we resampled data to achieve a standard frequency of five locations/day spaced 4–5 h apart for resource selection models.

Land cover covariates

We obtained spatial land cover data from the North American Land Change Monitoring System (NALCMS; https://www.mrlc.gov/data/north-american-land-change-monitoring-system, accessed 6 June 2020). The data were based on Landsat 7 satellite imagery with 30 m resolution collected in 2010 (Latifovic *et al.* 2017; CEC 2020). Land cover classifications were specified by NALCMS (Table 1; CEC 2020). We included four additional land cover classes: ≤ and >10-year clear-cut, 10-year burn, and 20-year burn. Twenty-year burns were the oldest burns in the available dataset while the oldest clear-cut was 37 years (see below). We differentiated between clear-cuts ≤ and >10 years old based on research in boreal forest ecosystems showing that vegetation trends in regenerating stands shift after 10 years following clear-cut logging (Archambault *et al.* 1998). Spatial clear-cut data were provided by the Newfoundland and Labrador Department of Natural Resources. We used the National Burned Area Composite from the Canadian Wildland Fire Information System (https://cwfis.cfs.nrcan.gc.ca/datamart, accessed 6 June 2020) to map historical burns retrospective to 1980.

Clear-cuts >10 years old had a median age of 24 years in Middle Ridge (range 11–37 yr), 17.5 years in Pot Hill (range 11–24 yr), and 18 years in Gaff Topsails (range 11–25 yr), whereas clear-cuts ≤10 years old in all ranges had a median age of 5.5 years (range

TABLE 1. Land cover types classified in the North American Land Change Monitoring System spatial data layer, which we used to analyze habitat use by adult female Caribou (*Rangifer tarandus*) during the calving season (1 May to 30 June) in Newfoundland, Canada, 2007–2010.

Land cover type	Description
Barrenland	Areas characterized by bare rock, gravel, sand, silt, clay, or other earthen material, and vegetation generally accounts for less than 10% of total cover
Lichen–moss barren	Areas dominated by a mixture of bare areas with lichen and moss that typically account for at least 20% of total vegetation cover
Lichen–moss grassland	Areas dominated by grassland with lichen and moss typically accounting for at least 20% of total vegetation cover
Lichen–moss shrubland	Areas dominated by dwarf shrubs with lichen and moss typically accounting for at least 20% of total vegetation cover
Mixed forest	Generally taller than 3 m and more than 20% of total vegetation cover, neither needleleaf nor broadleaf tree species occupy more than 75% of total tree cover, but are co-dominant
Subpolar broadleaf deciduous forest	Generally taller than 3 m and more than 20% of total vegetation cover, greater than 75% of tree crown cover represented by deciduous species
Subpolar grassland	Areas dominated by graminoid or herbaceous vegetation, generally accounting for greater than 80% of total vegetation cover
Subpolar needleleaf forest	Generally taller than 3 m and more than 20% of total vegetation cover, tree crown cover contains at least 75% of needle-leaved species
Subpolar shrubland	Areas dominated by woody perennial plants with persistent woody stems less than 3 m tall and typically greater than 20% of total vegetation
Urban	Areas that contain at least 30% or more of urban constructed materials for human activities (cities, towns, roads)
Water	Areas of open water, generally with less than 25% cover of non-water cover types and consistently covered by water
Wetland	Areas dominated by perennial herbaceous and woody wetland vegetation with the water table at or near surface over extensive periods of time (includes marshes, swamps, bogs)

1–10 yr). We removed used and available locations associated with clear-cuts that overlapped both age classes during the study. Burns were classified as 10 years and 20 years old (10-year and 20-year burn were ~ages whereby 10-year represented burns 8–12 years old and 20-year represented burns 18–24 years old, 24 years being the oldest burn for which there were data). We modified the NALMCS land cover layer to accommodate clear-cut and burn polygons using ArcGIS 10.5 (Esri 2016), such that clear-cut and burn classifications replaced other cover types identified by NALCMS in those areas.

Visualizing distribution shifts in Middle Ridge

To examine apparent shifts in calving distributions in Middle Ridge, we applied the kernel density tool in ArcGIS 10.5 (Esri 2016) to all May–June location data collected from VHF collars in 1987–1996 and from GPS collars in 2009–2010. We used a 98% contour to delineate the area where most use occurred for each year, based on fixed kernels with reference bandwidth (Worton 1995; Seaman and Powell 1996; Börger *et al.* 2006). We then visualized distribution shifts using locations within the 98% contours to calculate weighted centroids representing mean centres of activity for each year. (Note: we used a 98% contour to conservatively estimate calving ground boundaries, such that a single area with the highest concentration of use was defined, and outlier locations were excluded. The location data captured using a 95% versus 98% contour were essentially the same, but the 98% contour allowed for a continuous boundary around the entire area, whereas the 95% contour resulted in several smaller areas containing the same location data.)

Evaluating resource selection

We used a resource selection framework to evaluate habitat selection, whereby we compared sampling proportions of used and available units to analyze relative use (Manly *et al.* 2002). We used a logistic regression model with a *logit link* function following the *log-linear resource selection* function (RSF) for fixed-effects as defined by Manly *et al.* (2002: 100):

$$\hat{w}(x) = \exp(\hat{\beta}_1 x_1 + \hat{\beta}_2 x_2 + \cdots + \hat{\beta}_n x_n) \quad \text{(Equation 1)}$$

where $\hat{w}(x)$ is the predicted relative probability of use and $\hat{\beta}_1,\ldots,\hat{\beta}_n$ are coefficients for covariates $x_1,\ldots, x_n$. To account for individual variation and unequal sampling among individuals, we added a random intercept (γ_0) to equation 1 for each individual and included the intercept β_0 as per Gillies *et al.* (2006), whereby the individual animal is specified as the sample unit, yielding the following mixed effects model:

$$\hat{g}(x) = \exp(\hat{\beta}_0 + \hat{\beta}_1 x_{1ij} + \hat{\beta}_2 x_{2ij} + \cdots + \hat{\beta}_n x_{nij} + \gamma_{0j}) \quad \text{(Equation 2)}$$

which estimates the relative probability of use, $\hat{g}(x)$, at location i for animal j.

To obtain samples of available units, we applied 100% minimum convex polygons to all (i.e., non-resampled) May–June location data for each herd (we included VHF collar locations for Middle Ridge) and generated random points within polygons using ArcGIS 10.5 (Esri 2016). We assumed that a 100% minimum convex polygon encompassing all May–June locations from adult females within a given herd provided an accurate estimate of the area and resources available to those females during this period and represented the spatial extent of the herd home range traversed by females in May–June. For used units, we pooled all May–June GPS locations for each herd and study period and estimated calving ground boundaries using 98% fixed kernels with reference bandwidth (Silverman 1986). We assumed GPS locations outside of kernel boundaries were not representative of space-use by calving females at the herd level, and consequently identified them as potential outliers and removed those observations from the analysis.

To reduce location error, we excluded all GPS locations with 2D fix dimensions (i.e., if fewer than four satellites were used to obtain the fix) or dilution of precision >10, presumably yielding locations with low mean error (<30 m; Lewis *et al.* 2007; Ironside *et al.* 2017). We resampled locations such that individuals had five used units/day (unless data were missing because of location error or failed fixes), and we used a 1:5 ratio for used:available units to achieve large samples of available units (i.e., >10 000 locations) and ensure adequate sampling of land cover availability and convergence of coefficient estimates (Northrup *et al.* 2013). Finally, we projected used and available locations onto the land cover layer and extracted land cover types for all used and available locations using ArcGIS 10.5 (Esri 2016). We did not combine categorical levels of land cover types because we felt doing so would result in a loss of important information regarding use and could possibly bias results.

We evaluated relative use of all available cover types for each herd in separate analyses using the "lme4" package (version 1.1-23; Bates *et al.* 2020) in R version 3.6.3 (R Development Core Team 2020). We coded cover types as categorical variables (i.e., ≤ and >10-year clear-cut, 10-year burn, 20-year burn, and cover types identified in Table 1) and assigned water as the reference category because availability was similar across ranges; parameter estimates for cover types therefore represented apparent effects on relative use compared to the effect associated with water (i.e., fixed intercept). Each observation (i.e., data point) was mutually exclusive in terms of cover type. We removed cover types from the models if estimates did not converge because of too few or no used locations associated with them. Our final models estimated parameters successfully, and because the number of used observations was >800 times the number of parameters (9–12) in each model, theoretically the number of parameters we evaluated should not interfere with model performance. To examine multicollinearity among land cover covariates, we used the variance inflation factor (VIF) and interpreted VIF values <5 as indicative of low correlation between a given covariate and alternate covariates, values between 5–10 as indicative of moderate correlation, and values >10 indicative of high correlation (Wooldridge 2012; Vanhove 2019; Lüdecke 2020). We calculated VIFs using the "performance" package (Lüdecke 2020) in R (R Development Core Team 2020).

We compared relative odds of use for particular cover types compared to water to make inferences about selection strength and assessed general avoidance and selection of cover types based on proportional use versus proportional availability of samples (i.e., [number of used points associated with a particular cover type]/[total number of used points] versus [number of available points associated with a particular cover type]/[total number of available points]) for each herd. We concluded that animals were selecting a particular cover type if proportional use > proportional availability, and that animals were avoiding a particular cover type if proportional use < proportional availability (Johnson 1980). Lastly, we interpreted differences in selection of clear-cut and burn classes across herds by comparing relative odds of use if availability of a particular class was comparable across herd home ranges (i.e., <5% difference).

As a final step to verify and compare the importance of burns and clear-cuts on resource selection with respect to other cover types, we developed model sets containing other cover types with and without burn and clear-cut variables analyzed for each herd. We ranked models using AICc (Akaike 1973; Hurvich and Tsai 1989) with the "AICcmodavg" package in R (Mazerolle 2019; R Development Core Team 2020). We assessed the importance of the burn and clear-cut variables in our models for each herd by comparing their individual relative variable importance (sum of Akaike weights across all models in the set where variable *j* occurs; Burnham and Anderson 2010) to the grouped relative variable importance of the remaining covariates representing undisturbed land cover. We considered variables with values closer to one as most important (Burnham and Anderson 2010; Symonds and Moussalli 2011).

Model testing

Equation 2 assumes random effects were normally distributed with a mean of zero and unknown variance components (Breslow and Clayton 1993). We tested normality of random effects using normal quantile plots generated with the *qqnorm* function in R (R Development Core Team 2020). To evaluate goodness of fit we used the theoretical coefficient of determination (r^2) for binomial generalized linear mixed effects models as defined by Nakagawa *et al.* (2017), which we calculated using the "MuMIn" package (Barton 2020) in R (R Development Core Team 2020).

Results

Estimation of herd home ranges and calving grounds

To generate 100% minimum convex polygons for estimation of herd home range boundaries, and 98% kernels for estimation of calving ground boundaries, we used 19 080 GPS-collar locations from 24 adult females in Middle Ridge in May–June 2009 and 2010 (Tables S1 and S2) and 1145 locations from VHF collars on 52 females and 75 calves in May–June 1987 through 1996. For Pot Hill, we used 28 268 GPS-collar locations from 14 adult females in May–June 2007 through 2009 (Tables S1 and S2). For Gaff Topsails, we used 31 193 GPS-collar locations from 20 adult females in May–June 2007 through 2009 (Tables S1 and S2). Kernel density estimates captured >79% of GPS-collar locations for each herd (Figure 2).

Distribution shifts in Middle Ridge

We used 1034 locations from VHF collars on 46 females and 75 calves in May–June 1987 through 1996 (range 36–159 locations/year; median 121 locations/year) and 7416 resampled GPS-collar locations from 21 females in May–June 2009 and 2010 (4206 locations from 2009; 3210 locations from 2010) to calculate centroids for each year. Centroids indicated that yearly activity shifted southward away from clear-cuts between 1987 and 1996 (Figure 3). In May–June 2009 and 2010, females were clustered in a 20-year burn (Figure 3).

There were no documented range shifts from the other two herds. And, we do not have earlier collar data from these two herds.

Relative use, selection, and avoidance

Availability of some land cover types differed appreciably across herd ranges (Table 2, Figure S1). We analyzed resource selection by females on calving grounds based on 7416 locations from 21 females in Middle Ridge, 9274 locations from 13 females in Pot Hill, and 12 037 locations from 20 females in Gaff Topsails. Selection of land cover types varied among herds (Table S3, Figure S1), whereas individual variation was not appreciably different within each herd as indicated by low to no random intercept variance

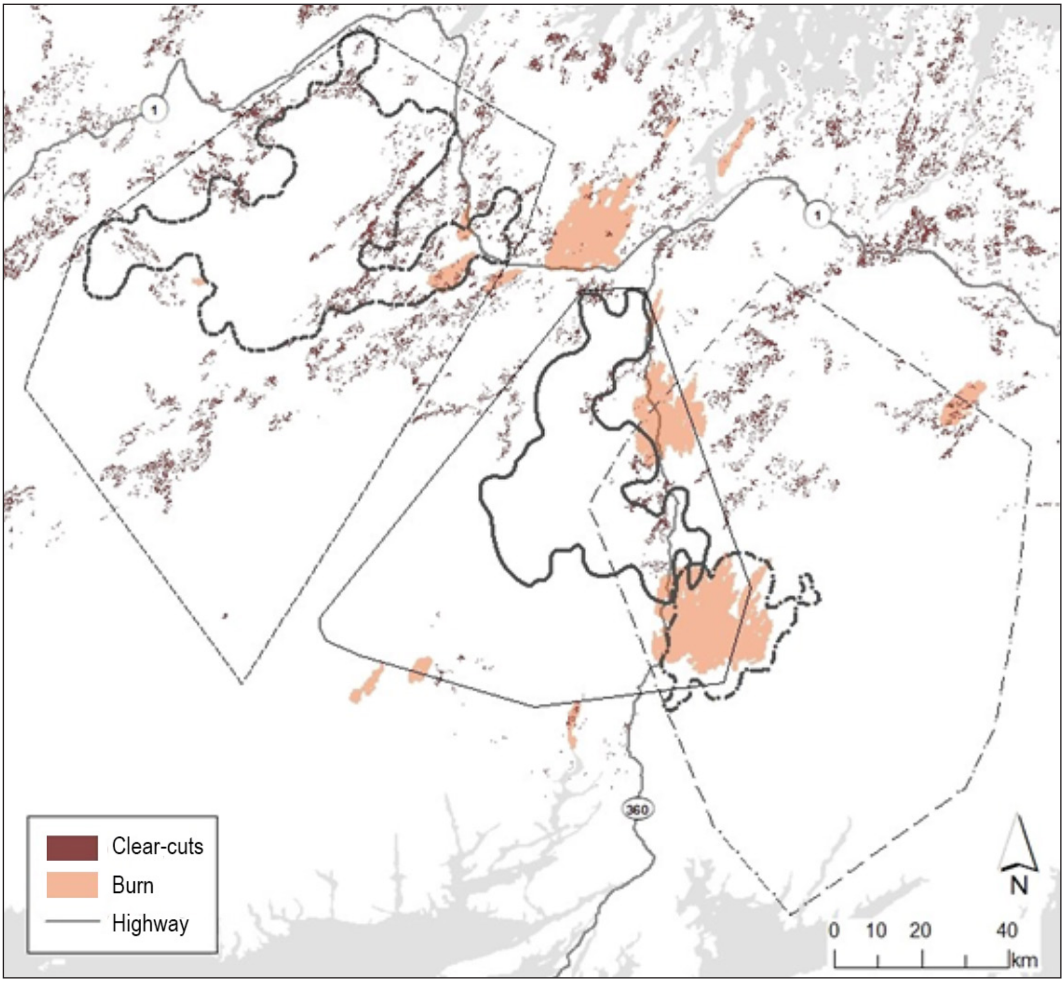

FIGURE 2. Delineations of the Gaff Topsails (dashed), Pot Hill (solid), and Middle Ridge (dash-dot) Caribou (*Rangifer tarandus*) herd ranges (black) and calving grounds (grey) based on location data collected from adult females from 1 May to 30 June in Newfoundland, Canada. Herd ranges were estimated with 100% minimum convex polygons applied to data collected in 2007–2009 (Gaff Topsails and Pot Hill), and 1987–1996 and 2009–2010 (Middle Ridge). We estimated calving ground boundaries using kernel density estimators with 98% contours to identify areas where the highest concentration of locations occurred in 2007–2009 (Gaff Topsails and Pot Hill), and in 2009–2010 (Middle Ridge).

(Middle Ridge: $\sigma^2_u = 0.016$; Pot Hill: $\sigma^2_u = 0.00$; Gaff Topsails: $\sigma^2_u = 3.25 \times 10^{-17}$). In Middle Ridge, 20-year burn was selected for and had the highest relative probability of use (β = 4.83, SE 0.09), while all other cover types were avoided (Table S3, Figures 4 and S1); clear-cuts and 10-year burn were not included in this analysis because these cover types did not occur within the calving grounds and therefore could not be evaluated. In Pot Hill, females selected for ≤10-year clear-cut, which had the highest relative probability of use (β = 2.98, SE 0.11). In Gaff Topsails, 10-year burn was more strongly selected (β = 2.89, SE 0.16) than >10-year clear-cut (β = 2.53, SE 0.12) and ≤10-year clear-cut (β = 2.35, SE 0.10).

In Middle Ridge, moderate collinearity was associated with 20-year burn. In Pot Hill there was high collinearity associated with needleleaf forest and moderate collinearity associated with subpolar shrubland. In Gaff Topsails, there was high collinearity associated with needleleaf forest and subpolar shrubland, and moderate collinearity associated with broadleaf deciduous forest and wetland.

Availability of ≤ and >10-year clear-cut was similar in all ranges. In Middle Ridge, ≤ and >10-year clear-cuts were not used at the herd level (i.e., these cover types did not occur on calving grounds

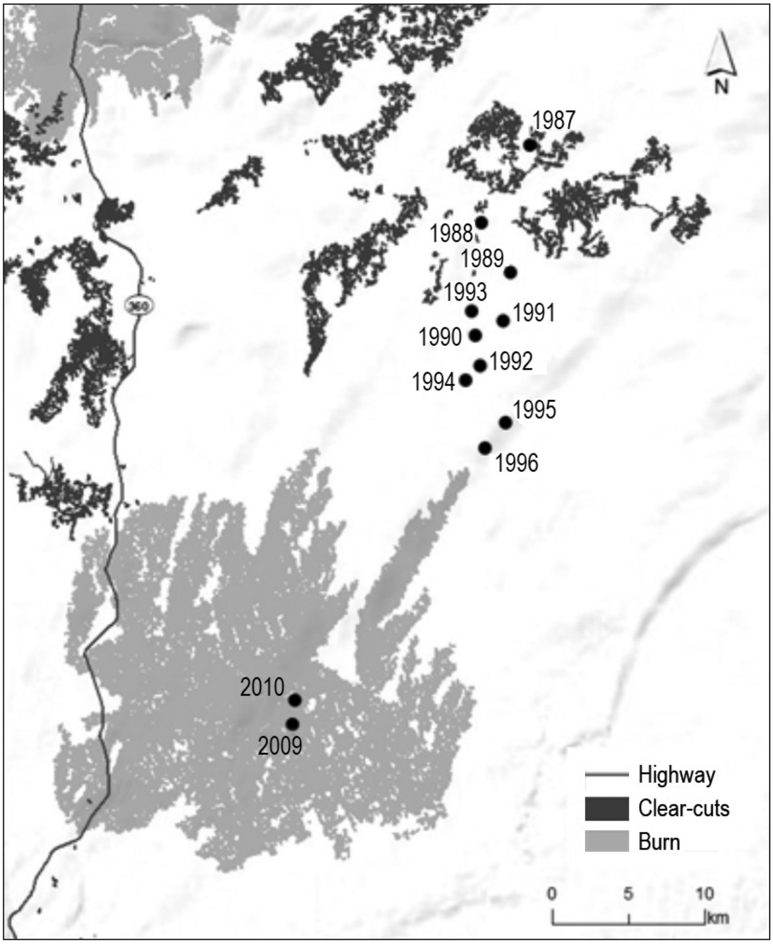

FIGURE 3. Weighted centroids representing yearly mean centres of activity based on calving distributions of adult female Caribou (*Rangifer tarandus*) in the Middle Ridge herd. Centroids were calculated from location data collected during the calving season (1 May to 30 June) in Newfoundland, Canada between 1987–1996 and 2009–2010.

and therefore could not be included in our analysis), whereas Pot Hill females selected for ≤10-year clear-cut, relative use being 19.60 (95% CI 15.96–24.29; Figures 4 and S1) times more likely based on relative odds compared to water, and appeared to avoid >10-year clear-cut as much as water (i.e., 95% CI overlapped 1; odds ratio = 0.60 , 95% CI 0.19–1.92). In Gaff Topsails, females selected for ≤ and >10-year clear-cut, with relative use 10.53 (95% CI 8.67–12.81) and 12.60 (95% CI 10.07–15.80) times more likely compared to water, respectively (Figures 4 and S1).

Availability of 10-year burn was comparable in Middle Ridge (0.2%) and Gaff Topsails (0.3%), and availability of 20-year burn was comparable in Middle Ridge (4.8%) and Pot Hill (7.5%). In Middle Ridge, 10-year burn was not used at the herd level, whereas in Gaff Topsails 10-year burn was selected for and females were 18.08 (95% CI 13.20–24.78) times more likely to use 10-year burn than water based on relative odds (Figures 4 and S1). In Middle Ridge, 20-year burn was selected for and females were 125.29 (95% CI 104.58–149.90) times more likely to use 20-year burn than water, whereas in Pot Hill, 20-year burn appeared to be avoided as much as water (odds ratio = 0.99, 95% CI 0.77–1.26; Figures 4 and S1).

In Middle Ridge, the relative variable importance for 20-year burn was 1 and equalled the grouped relative variable importance of remaining available cover types. (Table S4). In Pot Hill, the relative importance of ≤10-year clear-cut, which had the highest selection, was 1 and equalled the grouped importance of remaining available cover types barring >10-year

Table 2. Proportions of used and available cover types estimated from female Caribou (*Rangifer tarandus*) and random locations in three herds (i.e., Middle Ridge, Pot Hill, Gaff Topsails) during the calving season (1 May to 30 June) in Newfoundland, Canada, 2007–2010.

Land cover type	Middle Ridge		Pot Hill		Gaff Topsails	
	Used (%)	Available (%)	Used (%)	Available (%)	Used (%)	Available (%)
Barrenland	0.00	0.27	0.03	0.02	0.05	0.30
10-year burn	0.00	0.23	—	—	0.59	0.33
20-year burn	79.17	4.81	1.07	7.50	0.05	0.16
≤10-year clear-cut	0.00	1.13	2.91	1.03	3.25	3.13
>10-year clear-cut	0.00	1.00	0.03	0.37	1.62	1.30
Lichen–moss barren	0.04	0.17	0.00	0.03	0.02	0.08
Lichen–moss grassland	0.23	2.78	0.66	0.78	5.16	3.69
Lichen–moss shrubland	—	—	—	—	0.02	0.01
Mixed forest	0.69	10.12	5.26	7.61	2.99	12.69
Subpolar broadleaf deciduous forest	2.47	8.98	4.41	4.78	9.55	9.34
Subpolar grassland	0.01	0.09	0.08	0.03	0.22	0.34
Subpolar needleleaf forest	3.83	23.24	53.13	37.20	29.97	32.43
Subpolar shrubland	7.42	26.82	21.64	19.31	35.32	19.65
Urban	0.00	0.04	0.00	0.09	0.02	0.24
Water	1.74	10.29	1.94	13.32	1.01	10.57
Wetland	4.41	10.04	8.84	7.93	10.18	5.75

clear-cut and 20-year burn, which had low relative variable importance (0.36 and 0.27, respectively). In Gaff Topsails, the relative importance of ≤ and >10-year clear-cut and 10-year burn was one and equalled the grouped importance of remaining available cover types barring 20-year burn, which had slightly lower relative variable importance (0.82).

Clear-cuts and burns were mostly good predictors of use across herds, although their estimated influence on selection varied. In Middle Ridge, females appeared to select most strongly for 20-year burn compared to other cover types evaluated. In Pot Hill, females appeared to select most strongly for ≤10-year clear-cuts compared to other cover types, including burn and older age clear-cuts. In Gaff Topsails, females appeared to select more strongly for 10-year burn compared to both classes of clear-cuts and 20-year burn.

Residual normality and model fit

Quantile plots indicated that the assumption of normality for the random intercept had been met in the Middle Ridge and Gaff Topsails analyses. The individual intercepts in the Pot Hill model were all equal such that the residuals were zero. The Middle Ridge model had the best fit ($r^2 = 0.48$), followed by Gaff Topsails ($r^2 = 0.20$) and Pot Hill models ($r^2 = 0.18$).

Discussion

The selection of clear-cuts and burns by females during the calving season varied across Caribou herds. In Middle Ridge, where females had shifted away from clear-cuts prior to our study, use of clear-cuts appeared nonexistent, while females appeared to select exclusively for a 20-year burn (clear-cuts and 10-year burn were not evaluated in our models because these cover types did not occur on the calving grounds although they occurred within the seasonal range). In Pot Hill, ≤10-year clear-cuts had the strongest selection compared to other cover types and >10-year clear-cuts were avoided along with 20-year burn. Females in Gaff Topsails appeared to select for both clear-cut classes and females showed even stronger selection for 10-year burn, which was not used in Middle Ridge although availability was comparable. We caution that a direct comparison of selection coefficients for all available cover types across herds can be misleading given differences in availability, which largely influence estimated effects with respect to relative use and can lead to changes in habitat use that reflect a direct or indirect functional response (Mysterud and Ims 1998; Holbrook *et al.* 2019).

Clear-cuts and burns are associated with increased predation risk because early succession growth provides quality forage that attracts omnivores, herbivorous prey species, and consequently specialist predators (Mahoney and Virgl 2003; Wittmer *et al.* 2007; Brodeur *et al.* 2008; Lafontaine *et al.* 2019). We hypothesized that negative effects associated with clear-cuts, including higher predation, would cause females to avoid them, which was not supported by

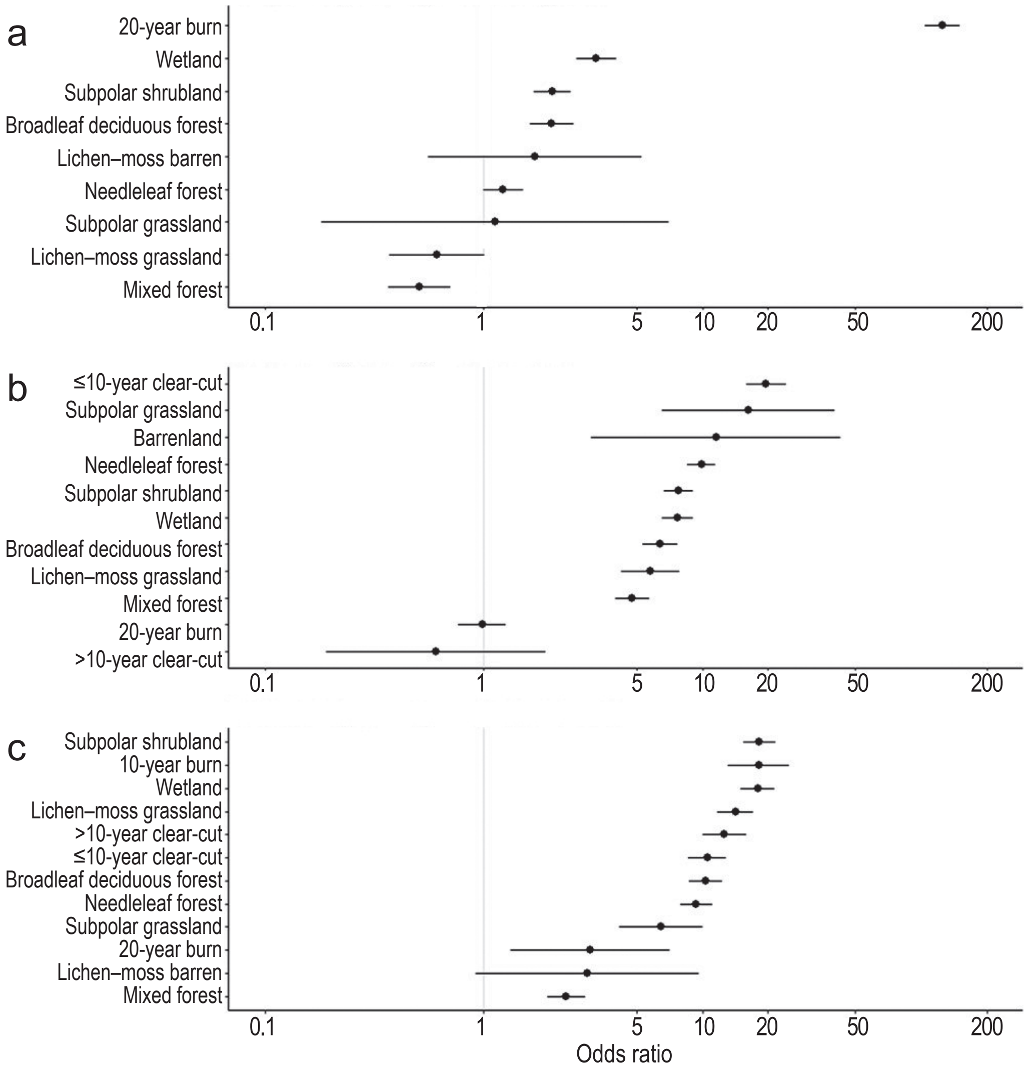

FIGURE 4. Relative odds ratios for use of cover types compared to water based on third-order resource selection by female Caribou (*Rangifer tarandus*) during the calving season (1 May to 30 June) in Newfoundland, Canada between 2007 and 2010. a. Middle Ridge herd; b. Pot Hill herd; c. Gaff Topsails herd. Relative odds of use were estimated using resource selection functions. A value of one indicates no effect (i.e., relative odds of use are equal to water).

our findings. We recognize that females may also trade off risk with foraging opportunities to meet nutritional demands (Barten *et al.* 2001; Gustine *et al.* 2006; Bastille-Rousseau *et al.* 2015), a strategy that could have contributed to differences in selection of clear-cuts and burns across herds. Our results provided support for our second hypothesis that burns could be important to calving female Caribou.

Clear-cut use by Caribou has been documented by other researchers and Caribou have demonstrated differing responses with respect to age of clear-cuts, associated predation risk, wildfire history, and availability (Courbin *et al.* 2009; Dussault *et al.* 2012; Leblond *et al.* 2016; Lafontaine *et al.* 2019). Courbin *et al.* (2009) indicated that female Caribou in the Boreal population (Côte-Nord region of Quebec, Canada) avoided recent (5 years) and later stage (5–10 years) clear-cuts in areas where wolf presence was strong and bear density was low, whereas Dussault *et al.* (2012) reported that female Caribou north of Québec City (Quebec, Canada) selected both classes during calving, with predation by bears being the main mortality factor for neonates in clear-cuts 5–20 years old, and no predation by wolves or bears detected in <5-year clear-cuts. Perhaps the absence of wolves in Newfoundland may partially explain the use of clear-cuts by female Caribou in the Pot Hill and Gaff Topsails Caribou herds, although predation by Black Bears was a major source of calf mortality during the study (Mahoney *et al.* 2015).

More recently, Lafontaine *et al.* (2019) reported that female Boreal Caribou historically exposed to frequent wildfires in regions across Quebec were more likely to avoid clear-cuts than Caribou that had less evolutionary experience with fire disturbance, likely because of their heightened awareness to predation risk in regenerating habitat. They also reported that Caribou avoided older burn areas (6–20 years old), regardless of evolutionary experience with fire, and Caribou with more historical fire exposure avoided recent burns (0–5 years old), whereas naïve Caribou displayed selection for recent burns. In contrast, Skatter *et al.* (2017) reported that burned areas were important Caribou calving habitat in northern Saskatchewan and that females preferred residual unburned patches within burns. Skatter *et al.* (2017) concluded that residuals may act as island refuges and, given that residual unburned habitat patches can account for up to one-third of the area within a fire perimeter (DeLong and Kessler 2000; Kachmar and Sanchez-Azofeifa 2006), burns may provide a variety of resources that allow for safety and food-security. We suspect that patchiness in burns may have also influenced selection for burns among females in Newfoundland. We could not measure historical fire exposure prior to 1980 or the influence of fire on selection from an evolutionary perspective, but Chubbs *et al.* (1993) reported that female Caribou in Newfoundland avoided <5-year burns and Bergerud *et al.* (1974) observed females in Newfoundland using 8-year and 40-year burns during the calving season.

Differences in response to clear-cuts and burns across herds in our study may have contributed to differences in calving success. In Pot Hill, where selection for ≤10-year clear-cuts by calving females was strongest, average yearly recruitment was lowest compared to Gaff Topsails and Middle Ridge, where 10-year and 20-year burn were strongly selected for, respectively. Bastille-Rousseau *et al.* (2015) detected differences in the level of predation risk calving females were exposed to while selecting for habitat across herds in Newfoundland. Their study did not specifically evaluate clear-cuts and burns, but they noted that females in Pot Hill differed from all other herds by favouring open-canopy coniferous forest (we presume likely included ≤10-year clear-cuts), and in so doing were exposed to higher levels of predation risk compared to other herds. Evidently, vegetation density in regenerating boreal forest increases in the first 10 years after logging, subsequently decreasing (Archambault *et al.* 1998), and higher neonate mortality risk from bear predation is associated with dense vegetation that likely enables ambush tactics (Rayl *et al.* 2018). We speculate that recruitment may have been higher in herds where females favoured regenerating burns over clear-cuts (assuming vegetation density of regrowth was somewhat similar) because residual patchiness, likely absent from logging tracts, can potentially offset predation risk (Skatter *et al.* 2017), and burns may also lack the road networks of logging operations that potentially facilitate predator access (James and Stuart-Smith 2000).

Differences in selection of clear-cuts and burns across herds in our study, and in other studies, suggest that there may be situational factors influencing use of these cover types. The Caribou population in Newfoundland underwent a period of population growth (1979–1997) followed by a period of decline (2003–2012), which has been attributed to density-dependent food competition that resulted in lower adult and calf nutrition and ultimately higher rates of neonate mortality (Mahoney *et al.* 2015). If regenerating clear-cuts and burns offer good quality foraging opportunities, perhaps female Caribou in Newfoundland were more likely to select these cover types during the phase of population decline, when our study occurred. Furthermore, differences in selection of burns and clear-cuts across herds in our study may have been influenced by relative availability of those cover types. For example, the higher proportion of 20-year burn to 10-year burn in Middle Ridge, compared to Gaff Topsails, may have led to stronger selection for 20-year burn in Middle Ridge, even though availability of each class was comparable across ranges. We also acknowledge that social cues may have influenced selection. For example, the herd home range in Pot Hill encompassed much of the 20-year burn in Middle Ridge, and females in Pot Hill may have displayed a negative response to 20-year burn partially because they were distancing themselves from conspecifics in another herd (Bergerud 1992).

The amount of variance explained by models for each herd differed, and we suspect that other habitat components we could not control for (e.g., insect harassment, predation pressure, human presence; Bergerud 1974; James and Stuart-Smith 2000; Vistnes and Nelleman 2001; Courbin *et al.* 2009; Leblond *et al.* 2016) may have contributed to the differences. Accounting for these variables might have improved model fit but would not likely change our conclusions. The low variance associated with random intercepts in our models indicated that there was little variance among individuals within herds, which is what we would expect among females in the same herd, given the social nature of the species. Additionally, we note that strong correlations between covariates generally indicate a lack of independence but, for indicator variables with more than three categories, higher multicollinearity can result from a smaller proportion of observations in the reference category compared to other categories. In such cases, collinearity increases variance estimates but does not affect mean parameter estimates and can be safely ignored (Allison 2012; Vanhove 2019).

Caribou population decline is mainly attributed to anthropogenic disturbance (COSEWIC 2014), although anthropogenic and natural landscape disturbance are both associated with habitat loss and increased predation risk (Courtois *et al.* 2007; Wittmer *et al.* 2007), and cumulative effects of disturbance have been associated with lower neonate recruitment (Sorensen *et al.* 2008; McCarthy *et al.* 2011). Our study indicated that calving female Caribou on insular Newfoundland responded differently to two disturbance features, clear-cuts and burns, whereby two herds showed strong selection for different aged burn classes, apparently favouring them over clear-cuts, and another herd favoured clear-cuts over burns. Recruitment was higher in herds that favoured burns, suggesting that this land cover type could be more beneficial to calving females in terms of food-security and safety. We recognize that other cover types can influence calving success as well, and may have also contributed to observed differences in recruitment. McCarthy *et al.* (2011), for example, detected a negative correlation between calf recruitment and total landscape disturbance (i.e., from anthropogenic and natural factors including clear-cuts and fire) within calving and post-calving ranges, but also detected a negative relationship with total area of mixed forest. We further acknowledge that our study occurred during a population decline (associated with density-dependent regulation), when recruitment rates were low in general (Weir *et al.* 2014; Mahoney *et al.* 2015). We submit that differences in recruitment across herds may be less apparent during years when the population is less constrained by density-dependent processes.

Nevertheless, the distribution shifts away from clear-cuts and into a 20-year burn in Middle Ridge suggest that females may have perceived the burn as better habitat and begs the question of whether burns are beneficial to Caribou in terms of fitness, or if both disturbance features may ultimately act as ecological traps (Hale and Swearer 2016). Current projections indicate that the island-wide Caribou population in Newfoundland, unlike the Boreal population, is not endangered (Randell *et al.* 2012; Weir *et al.* 2014), presumably because of lower total landscape disturbance within Caribou ranges on the island. But we submit that negative effects associated with landscape disturbance may still have consequences for local herds. We suspect that spatial shifts, as demonstrated by females in Middle Ridge, reflect a dynamic process in an ever-changing landscape in which animals must make choices that ultimately influence their survival. As such, we conclude that protecting areas to ensure adequate resource options for Caribou over space and time may be important for the future success of the population, but further investigation will also be needed to more closely examine how anthropogenic versus natural disturbance affects Caribou fitness. Information from such studies can guide future management policy on sustainable levels of resource development in the context of Caribou conservation in Newfoundland, and potentially improve our understanding of important habitat for calving female Caribou.

Author Contributions

Writing – Original Draft: D.J.D.; Writing – Review & Editing: P.R.K., S.P.M., and D.J.D.; Conceptualization: S.P.M., P.R.K., and D.J.D.; Investigation: D.J.D., P.R.K., and S.P.M.; Methodology: D.J.D., S.P.M., and P.R.K.; Formal Analysis: D.J.D.; Funding Acquisition: S.P.M. and P.R.K.

Acknowledgements

We thank C.E. Soulliere, K.P. Lewis, J.N. Weir, K. Morgan, R.D. Otto, F. Dinn, T. Porter, B. Slade, T. Hodder, and others at the Newfoundland and Labrador Department of Environment and Conservation for technical assistance. We also thank C.J. Bishop, D.H. Pletscher, J.J. Millspaugh, T.E. Dilts, and K.M. Stewart who provided critical input and support. D. Lepitzki, the Associate Editor, and anonymous referees provided comments that enhanced our work—many thanks. This project was funded by the Government of Newfoundland and Labrador Department of Environment and Conservation, in partnership with the Institute for Biodiversity, Ecosystem Science, and Sustainability, the Safari Club International Foundation, University of Montana, and the Boone and Crockett Program at the University of Montana. Caribou were handled following protocol and guidelines approved by the Canadian Council on Animal Care (http://www.ccac.ca, accessed 4 March 2018) and established by the American Society of Mammalogists (Sikes *et al.* 2011). Data are available in Tables S5–S7.

Literature Cited

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *in* Proceedings of the Second International Symposium on Information Theory. *Edited by* B.N. Petrov and F. Csaki.

Akademiai Kiado, Budapest, Hungary. https://doi.org/10.1007/978-1-4612-1694-0_15

Allen, G.M., and T. Barbour. 1937. The Newfoundland wolf. Journal of Mammalogy 18: 229–234. https://doi.org/10.2307/1374474

Allison, P. 2012. When can you safely ignore multicollinearity? Statistical Horizons Blog. Accessed 4 September 2020. http://statisticalhorizons.com/multicollinearity.

Archambault, L., J. Morissette, and M. Bernier-Cardou. 1998. Forest succession over a 20-year period following clearcutting in balsam fir-yellow birch ecosystems of eastern Quebec, Canada. Forest Ecology and Management 102: 61–74. https://doi.org/10.1016/S0378-1127(97)00109-6

Bangs, P.D., P.R. Krausman, K.E. Kunkel, and Z.D. Parson. 2005. Habitat use by desert bighorn sheep during lambing. European Journal of Wildlife Research 51: 178–184. https://doi.org/10.1007/s10344-005-0098-8

Barten, N.L., R.T. Bowyer, and K.L. Jenkins. 2001. Habitat use by female caribou: tradeoffs associated with parturition. Journal of Wildlife Management 65: 77–92. https://doi.org/10.2307/3803279

Barton, K. 2020. MuMIn: multi-model inference. R package version 1.43.17. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Bastille-Rousseau, G., J.R. Potts, J.A. Schaefer, M.A. Lewis, E.H. Ellington, N.D. Rayl, S.P. Mahoney, and D.L. Murray. 2015. Unveiling trade-offs in resource selection of migratory caribou using a mechanistic movement model of availability. Ecography 38: 1049–1059. https://doi.org/10.1111/ecog.01305

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2020. lme4: linear mixed-effects models using 'eigen' and S4. R package version 1.1-23. Accessed 10 April 2023. https://CRAN.R-project.org/package=lme4.

Bell, T. 2002. Ecoregions of Newfoundland. Newfoundland and Labrador heritage web site project. Accessed 6 October 2020. https://www.heritage.nf.ca/articles/environment/ecoregions-newfoundland.php.

Bergerud, A.T. 1974. The role of the environment in the aggregation, movement and disturbance behaviour of caribou. Pages 552–584 *in* The Behaviour of Ungulates and its Relation to Management. *Edited by* V. Geist and F. Walther. International Union for Conservation of Nature and Natural Resources Publications New Series 24, Morges, Switzerland.

Bergerud, A.T. 1992. Rareness as an antipredator strategy to reduce the risk of predation for moose and caribou. Pages 1008–1021 *in* Wildlife 2001: Populations. *Edited by* D.R. McCullough and R.H. Barrett. Elsevier, London, United Kingdom.

Bergerud, A.T. 1996. Evolving perspectives on caribou population dynamics, have we got it right yet? Rangifer, Special Issue 9: 95–115. https://doi.org/10.7557/2.16.4.1225

Bergerud, A.T. 2000. Caribou. Pages 658–693 *in* Ecology and Management of Large Mammals in North America. *Edited by* S. Demarais and P.R. Krausman. Prentice-Hall Inc., Upper Saddle River, New Jersey, USA.

Boisjoly D., J.-P. Ouellet, and R. Courtois. 2010. Coyote habitat selection and management implications for the Gaspésie caribou. Journal of Wildlife Management 74: 3–11. https://doi.org/10.2193/2008-149

Börger, L., N. Franconi, F. Ferretti, F. Meschi, G. De Michele, A. Gantz, and T. Coulson. 2006. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. American Naturalist 168: 471–485. https://doi.org/10.1086/507883

Breslow, N.E., and D.G. Clayton. 1993. Approximate inference in generalized linear mixed models. Journal of the American Statistical Association 88: 9–25. https://doi.org/10.1080/01621459.1993.10594284

Brodeur, V., J.-P. Ouellet, R. Courtois, and D. Fortin. 2008. Habitat selection by black bears in an intensively logged boreal forest. Canadian Journal of Zoology 86: 1307–1316. https://doi.org/10.1139/z08-118

Burnham, K.P., and D.R. Anderson. 2010. Model Selection and Multimodel Inference: a Practical-theoretic Approach. Second Edition. Springer-Verlag, New York, New York, USA. https://doi.org/10.1007/b97636

Cameron, R.D., D.J. Reed, J.R. Dau, and W.T. Smith. 1992. Redistribution of calving caribou in response to oil field development. Arctic 45: 338–342. https://doi.org/10.14430/arctic1412

CEC (Commission for Environmental Cooperation). 2020. NALCMS (North American Land Change Monitoring System). Accessed 8 September 2020. https://storymaps.arcgis.com/stories/cb62207a38e1437f89165f5eac019f13.

Chubbs, T.E., L.B. Keith, S.P. Mahoney, and M.J. McGrath. 1993. Responses of woodland caribou (*Rangifer tarandus caribou*) to clear-cutting in east-central Newfoundland. Canadian Journal of Zoology 71: 487–493. https://doi.org/10.1139/z93-070

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2014. COSEWIC assessment and status report on the Caribou *Rangifer tarandus*, Newfoundland population, Atlantic-Gaspésie population and Boreal population, in Canada. COSEWIC, Ottawa, Ontario, Canada.

Courbin, N., D. Fortin, C. Dussault, and R. Courtois. 2009. Landscape management for woodland caribou: the protection of forest blocks influences wolf-caribou co-occurrence. Landscape Ecology 24: 1375–1388. https://doi.org/10.1007/s10980-009-9389-x

Courtois, R., J.-P. Ouellet, B. Laurier, A. Gingras, and C. Dussault. 2007. Effects of forest disturbance on density, space use, and mortality of woodland caribou. Ecoscience 14: 491–498. https://doi.org/10.2980/1195-6860(2007)14[491:EOFDOD]2.0.CO;2

DeLong, S., and W. Kessler. 2000. Ecological characteristics of mature forest remnants left by wildfire. Forest Ecology and Management 131: 93–106. https://doi.org/10.1016/S0378-1127(99)00203-0

Dussault, C., V. Pinard, J.-P. Ouellet, R. Courtois, and D. Fortin. 2012. Avoidance of roads and selection for recent cutovers by threatened caribou: fitness rewarding or maladaptive behaviour? Proceedings of the Royal Society B 279: 4481–4488. https://doi.org/10.1098/rspb.2012.1700

Ellington, E.H., K.P. Lewis, E.L. Koen, and E. Vander Wal. 2020. Divergent estimates of herd-wide caribou calf survival: ecological factors and methodological biases. Ecology and Evolution 10: 8476–8505. https://doi.org/10.1002/ece3.6553

Esri. 2016. ArcGIS Desktop: Release 10.5. Environmental Systems Research Institute, Redlands, California, USA.

Fox, K.B., and P.R. Krausman. 1994. Fawning habitat of desert mule deer. Southwestern Naturalist 39: 269–275. https://doi.org/10.2307/3671592

Gaillard, J.-M., M. Festa-Bianchet, and N.G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13: 58–63. https://doi.org/10.1016/S0169-5347(97)01237-8

Gillies, S.C., M. Hebblewhite, S.E. Nielsen, M.A. Krawchuk, C.L. Aldridge, J.L. Frair, D.J. Saher, C.E. Stevens, and C.L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75: 887–898. https://doi.org/10.1111/j.1365-2656.2006.01106.x

Government of Newfoundland and Labrador. 2020. Ecoregion brochures. Accessed 26 March 2023. https://www.gov.nl.ca/ecc/natural-areas/publications/#brochures.

Gunn, A., and F.L. Miller. 1986. Traditional behaviour and fidelity to caribou calving grounds by barren-ground caribou. Rangifer, Special Issue 1: 151–158. https://doi.org/10.7557/2.6.2.640

Gunn, A., K.G. Poole, and J.S. Nishi. 2012. A conceptual model for migratory tundra caribou to explain and predict why shifts in spatial fidelity of breeding cows to their calving grounds are infrequent. Rangifer 32: 259–267. https://doi.org/10.7557/2.32.2.2274

Gustine, D.D., K.L. Parker, R.J. Lay, M.P. Gillingham, and D.C. Heard. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. Wildlife Monographs 165: 1–32. https://doi.org/10.2193/0084-0173(2006)165[1:csowci]2.0.co;2

Hale, R., and S.E. Swearer. 2016. Ecological traps: current evidence. Proceedings of the Royal Society B 283: 20152647. https://doi.org/10.1098/rspb.2015.2647

Holbrook, J.D., L.E. Olson, N.J. DeCesare, M. Hebblewhite, J.R. Squires, and R. Steenweg. 2019. Functional responses in habitat selection: clarifying hypotheses and interpretations. Ecological Applications 29: e01852. https://doi.org/10.1002/eap.1852

Hurvich, C.M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76: 297–307. https://doi.org/10.1093/biomet/76.2.297

Ironside, K.E., D.J. Mattson, T.R. Arundel, and J.R. Hansen. 2017. Is GPS telemetry location error screening beneficial? Wildlife Biology 2017: 1–7. https://doi.org/10.2981/wlb.00229

James, A.R.C., and A.K. Stuart-Smith. 2000. Distribution of caribou and wolves in relation to linear corridors. Journal of Wildlife Management 64: 154–159. https://doi.org/10.2307/3802985

Johnson, D. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65–71. https://doi.org/10.2307/1937156

Kachmar, M., and G.A. Sanchez-Azofeifa. 2006. Detection of post-fire residuals using high- and medium-resolution satellite imagery. Forestry Chronicle 82: 177–186 https://doi.org/10.5558/tfc82177-2

Lafontaine, A., P. Drapeau, D. Fortin, S. Gauthier, Y. Boulanger, and M.-H. St-Laurent. 2019. Exposure to historical burn rates shapes the response of boreal caribou to timber harvesting. Ecosphere 10:e02739. https://doi.org/10.1002/ecs2.2739

Latifovic, R., D. Pouliot, and I. Olthof. 2017. Circa 2010 land cover of Canada: local optimization methodology and product development. Remote Sensing 9: 1098. https://doi.org/10.3390/rs9111098

Leblond, M., C. Dussault, J.-P. Ouellet, and M.-H. St-Laurent. 2016. Caribou avoiding wolves face increased predation by bears — caught between Scylla and Charybdis. Journal of Applied Ecology 53: 1078–1087. https://doi.org/10.1111/1365-2664.12658

Lewis, J.S., J.L. Rachlow, E.O. Garton, and L.A.Vierling. 2007. Effects of habitat on GPS collar performance: using data screening to reduce location error. Journal of Applied Ecology 44: 663–671. https://doi.org/10.1111/j.1365-2664.2007.01286.x

Lewis, K., and S.P. Mahoney. 2014. Caribou survival, fate, and cause of mortality in Newfoundland: a summary and analysis of patterns and causes of caribou survival and mortality in Newfoundland during a period of rapid population decline (2003–2012). Sustainable Development and Strategic Science, Technical Bulletin No. 009. Department of Environment and Conservation, Government of Newfoundland and Labrador. St. John's, Newfoundland and Labrador, Canada.

Lüdecke, D. 2020. performance: assessment of regression models performance. R package version 0.4.6. Accessed 10 April 2023. https://CRAN.R-project.org/package=performance.

Mahoney, S.P., K.P. Lewis, J.N. Weir, S.F. Morrison, J.G. Luther, J.A. Schaefer, D. Pouliot, and R. Latifovic. 2015. Woodland caribou calf mortality in Newfoundland: insights into the role of climate, predation and population density over three decades of study. Population Ecology 58: 91–103. https://doi.org/10.1007/s10144-015-0525-y

Mahoney, S.P., and J.A. Schaefer. 2002. Hydroelectric development and the disruption of migration in caribou. Biological Conservation 107: 147–153. https://doi.org/10.1016/S0006-3207(02)00052-6

Mahoney, S.P., and J.A. Virgl. 2003. Habitat selection and demography of a nonmigratory woodland caribou population in Newfoundland. Canadian Journal of Zoology 81: 321–334. https://doi.org/10.1139/z02-239

Mahoney, S.P., and J.N. Weir. 2009. Caribou data synthesis progress report. Sustainable Development and Strategic Science, Technical Bulletin No. 001. Department of Environment and Conservation, Government of Newfoundland and Labrador. St. John's, Newfoundland and Labrador, Canada.

Manly, B.F.J., L.L. McDonald, D.L. Thomas, T.L. McDonald, and W.P. Erickson. 2002. Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Second Edition. Kluwer Press, Boston, Massachusetts, USA. https://doi.org/10.1007/0-306-48151-0

Mazerolle, M.J. 2019. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). Accessed 10 April 2023. https://CRAN.R-project.org/package=AICcmodavg.

McCarthy, S.C., R.B. Weladji, C. Doucet, and P. Saunders. 2011. Woodland caribou calf recruitment in relation to calving/post-calving landscape composition. Rangifer 31: 35–47. https://doi.org/10.7557/2.31.1.1918

Monteith, K.L., V.C. Bleich, T.R. Stephenson, B.M. Pierce, M.M. Connor, J.G. Kie, and R.T. Bowyer. 2014. Life-history characteristics of mule deer: effects of nutrition in a variable environment. Wildlife Monographs 186: 1–56. https://doi.org/10.1002/wmon.1011

Mysterud, A., and R.A. Ims. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. Ecology 79: 1435–1441. https://doi.org/10.2307/176754

Nagy, J.A., D.L. Johnson, N.C. Larter, M.W. Campbell, A.E. Derocher, A. Kelly, M. Dumond, D. Allaire, and B. Croft. 2011. Subpopulation structure of caribou (*Rangifer tarandus L.*) in arctic and subarctic Canada. Ecological Applications 21: 2334–2348. https://doi.org/10.1890/10-1410.1

Nakagawa, S., P.C.D. Johnson, and H. Schielzeth. 2017. The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. Journal of the Royal Society Interface 14: 20170213. https://doi.org/10.1098/rsif.2017.0213

Natural Resources Canada. 2020. The state of Canada's forests. Accessed 23 February 2021. https://www.nrcan.gc.ca/our-natural-resources/forests-forestry/state-canadas-forests-report/16496.

Northrup, J.M., M.B. Hooten, C.R. Anderson, and G. Wittemyer. 2013. Practical guidance on characterizing availability in resource selection: population-level selection inference. Journal of Wildlife Management 70: 404–412. https://doi.org/10.1890/12-1688.1

R Development Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Randell, A. 2019. Newfoundland caribou population decline not alarming, provincial biologist. *In* The Telegram. Accessed 8 September 2020. https://www.thetelegram.com/news/local/newfoundland-caribou-population-decline-not-alarming-provincial-biologist-284405/.

Randell, H., J.N. Weir, J.G. Luther, and S.P. Mahoney. 2012. Population projections of Newfoundland caribou using population viability analysis. Sustainable Development and Strategic Science, Technical Bulletin No. 004. Department of Environment and Conservation, Government of Newfoundland and Labrador. St. John's, Newfoundland, Canada.

Rayl, N.D., G. Bastille-Rousseau, J.F. Organ, M.A. Mumma, S.P Mahoney, C.E. Soulliere, K.P. Lewis, R.D. Otto, D.L. Murray, L. Waits, and T.K. Fuller. 2018. Spatiotemporal heterogeneity in prey abundance and vulnerability shapes the foraging tactics of an omnivore. Journal of Animal Ecology 87: 874–887. https://doi.org/10.1111/1365-2656.12810

Rayl, N.D., T.K. Fuller, J.F. Organ, J.E. McDonald, R.D. Otto, G. Bastille-Rousseau, C.E. Soulliere, and S.P. Mahoney. 2015. Spatiotemporal variation in the distribution of potential predators of a resource pulse: black bears and caribou calves in Newfoundland. Journal of Wildlife Management 79: 1041–1050. https://doi.org/10.1002/jwmg.936

Schaefer, J.A., C.M. Bergman, and S.N. Luttich. 2000. Site fidelity of female caribou at multiple spatial scales. Landscape Ecology 15: 731–739. https://doi.org/10.1023/A:1008160408257

Schaefer, J.A., and S.P. Mahoney. 2005. Effects of progressive clearcut logging on Newfoundland caribou. Journal of Wildlife Management 71: 1753–1757. https://doi.org/10.2193/2005-479

Schwartz, C.C., and S.M. Arthur. 1999. Radiotracking large wilderness mammals: integration of GPS and Argos technology. Ursus 11: 261–274.

Seaman, D.E., and R.A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77: 2075–2085. https://doi.org/10.2307/2265701

Sikes, R.S., W.L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92: 235–253. https://doi.org/10.1644/10-mamm-f-355.1

Silverman, B.W. 1986. Density estimation for statistics and data analysis. Monographs on Statistics and Applied Probability. Chapman and Hall, London, United Kingdom.

Skatter, H.G., M.L. Charlebois, S. Eftestøl, D. Tsegaye, J.E. Colman, J.L. Kansas, K. Flydal, and B. Balicki. 2017. Living in a burned landscape: woodland caribou (*Rangifer tarandus caribou*) use of postfire residual patches for calving in a high fire — low anthropogenic Boreal Shield ecozone. Canadian Journal of Zoology 95: 975–984. https://doi.org/10.1139/cjz-2016-0307

Sorensen, T., P.D. McLoughlin, D. Hervieux, E. Dzus, J. Nolan, B. Wynes, and S. Boutin. 2008. Determining sustainable levels of cumulative effects for boreal caribou. Journal of Wildlife Management 72: 900–905. https://doi.org/10.2193/2007-079

Symonds, M.R.E., and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's Information Criterion. Behavioral Ecology and Sociobiology 65: 13–21. https://doi.org/10.1007/s00265-010-1037-6

Taillon, J., M. Festa-Bianchet, and S.D. Côté. 2012. Shifting targets in the tundra: protection of migratory caribou calving grounds must account for spatial changes over time. Biological Conservation 147: 163–173. https://doi.org/10.1016/j.biocon.2011.12.027

Vanhove, J. 2019. Collinearity isn't a disease that needs curing. Meta-Psychology 5. https://doi.org/10.31234/osf.io/mv2wx

Vistnes, I., and C. Nellemann. 2001. Avoidance of cabins, roads, and power lines by reindeer during calving. Journal of Wildlife Management 65: 915–925. https://doi.org/10.2307/3803040

Weir, J.N., S.P. Mahoney, B. McLaren, S.H. Ferguson. 2007. Effects of mine development on woodland caribou *Rangifer tarandus* distribution. Wildlife Biology 13: 66–74. https://doi.org/10.2981/0909-6396(2007)13[66:EOMDOW]2.0.CO;2

Weir, J.N., S.F. Morrison, J.G. Luther, and S.P. Mahoney. 2014. Caribou data synthesis — progress report 2: status of the Newfoundland population of woodland caribou. Sustainable Development and Strategic Science, Technical Bulletin No. 008. Department of Environment and Conservation, Government of Newfoundland and Labrador. St. John's, Newfoundland, Canada.

Wittmer, H.U., B.N. McLellan, R. Serrouya, and C.D. Apps. 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. Journal of Animal Ecology 76: 568–579. https://doi.org/10.1111/j.1365-2656.2007.01220.x

Wooldridge, J.M. 2012. Introductory Econometrics. Fifth Edition. South-Western College Publishing, Mason, Ohio, USA.

Worton, B.J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. Journal of Wildlife Management 59: 794–800. https://doi.org/10.2307/3801959

Received 26 March 2021
Accepted 7 March 2023
Associate Editor: G. Mowat

SUPPLEMENTARY MATERIALS:

TABLE S1. Radio-collar sample sizes and associated location data from Caribou (*Rangifer tarandus*) in three herds (i.e., Middle Ridge, Pot Hill, Gaff Topsails) during the calving season (1 May to 30 June) in Newfoundland, Canada, 1987–1996 and 2007–2010.

TABLE S2. Yearly location data from global positioning system-collars on adult female Caribou (*Rangifer tarandus*) in three herds (i.e., Middle Ridge, Pot Hill, Gaff Topsails) during the calving season (1 May to 30 June) in Newfoundland, Canada, 1987–1996 and 2007–2010, used for resource selection modelling.

TABLE S3. Parameter estimates from mixed effects resource selection models analyzing relative use of cover types by adult female Caribou (*Rangifer tarandus*) in three herds (i.e., Middle Ridge, Pot Hill, Gaff Topsails) during the calving season (1 May to 30 June) in Newfoundland, Canada, 2007–2010.

TABLE S4. Resource selection model sets evaluating relative use of land cover types by adult female Caribou (*Rangifer tarandus*) in three herds (i.e., Middle Ridge, Pot Hill, Gaff Topsails) during the calving season (1 May to 30 June) in Newfoundland, Canada between 2007–2010.

FIGURE S1. Proportions of used and available cover types estimated from actual and random locations used to analyze habitat use by adult female Caribou (*Rangifer tarandus*) in three herds (i.e., Middle Ridge, Pot Hill, Gaff Topsails) during the calving season (1 May to 30 June) in Newfoundland, Canada between 2007–2010.

TABLE S5. Resampled raw data used for resource selection analysis evaluating relative use of land cover types by adult female Caribou (*Rangifer tarandus*) in the Middle Ridge herd during the calving season (1 May to 30 June) in Newfoundland, Canada between 2009–2010.

TABLE S6. Resampled raw data used for resource selection analysis evaluating relative use of land cover types by adult female Caribou (*Rangifer tarandus*) in the Pot Hill herd during the calving season (1 May to 30 June) in Newfoundland, Canada between 2007–2009.

TABLE S7. Resampled raw data used for resource selection analysis evaluating relative use of land cover types by adult female Caribou (*Rangifer tarandus*) in the Gaff Topsails herd during the calving season (1 May to 30 June) in Newfoundland, Canada between 2007–2009.