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Vulnerable caribou and moose populations display varying responses to mountain pine beetle outbreaks and management

Laura L. Griffin[1,2] | Laura Finnegan[3] | Julie Duval[3] | Simone Ciuti[4] | Virginia Morera-Pujol[4] | Haitao Li[1] | A. Cole Burton[1,2]

[1]Department of Forest Resources Management, University of British Columbia, Vancouver, British Columbia, Canada

[2]Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia, Canada

[3]fRI Research Caribou Program, fRI Research, 1176 Switzer Drive, Hinton, Alberta T7V 1V3, Canada

[4]Laboratory of Wildlife Ecology and Behaviour, School of Biology and Environmental Sciences, University College Dublin, Dublin 4, Ireland

Correspondence

A. Cole Burton, Department of Forest Resources Management, University of British Columbia, Vancouver, British Columbia, Canada; Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia, Canada.
Email: cole.burton@ubc.ca

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Abstract

Rising global temperatures and changing landscape conditions have led to widespread mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in western North America. Pine beetle management is typically implemented to mitigate economic losses, but its effects on wildlife, particularly ecologically important species like caribou (*Rangifer tarandus*) and moose (*Alces alces*), warrant greater attention. We assessed the effects of early-stage pine beetle infestation, timber harvest, and fire on habitat selection by caribou (boreal and central mountain designatable units) and moose in west-central Alberta, Canada. Using global positioning system (GPS) collar data collected 3–5 years after infestation, we developed resource selection functions and functional response models. Caribou exhibited seasonally variable responses, generally avoiding pine beetle-affected areas in winter but selecting them in summer. They also avoided harvested and burned areas, though this avoidance depended on overall disturbance levels within their ranges. Moose displayed sex-specific responses to pine beetle infestations and associated management: females avoided pine beetle-affected areas but selected burned sites year-round, while males showed the opposite pattern. These findings suggest that pine beetle disturbances may negatively affect caribou and female moose winter habitat availability while simultaneously enhancing conditions for male moose. Further research is needed to disentangle the individual and cumulative effects of pine beetle management actions versus general timber harvests and wildfires, as these disturbances may be compounding rather than acting in isolation.

KEYWORDS

apparent competition, bark beetles, caribou conservation, forest pests, prescribed burning, salvage logging, wildfire, wildlife habitat management

Global biodiversity loss and wildlife population declines have prompted research into how different disturbance types affect natural systems (Pirotta et al. 2018, Brodie et al. 2021). Understanding how emerging disturbances influence newly exposed wildlife populations enables landscape managers to reduce and mitigate associated negative effects on vulnerable species (Lindenmayer et al. 2008). One emerging disturbance that is gaining attention is insect outbreaks, which have become progressively more common with climate change and forest homogenization (Ono 2004, Ayres and Lombardero 2018).

Mountain pine beetle (*Dendroctonus ponderosae*) is a bark beetle native to the pine forests of western North America. It periodically erupts into large-scale outbreaks, targeting large, mature pines and drastically altering forest ecosystems (Mitton and Ferrenberg 2012, Sambaraju and Goodsman 2021). The most recent pine beetle outbreak has spread beyond historical ranges (i.e., into higher latitudes and elevations), including into western Alberta, Canada (Howe et al. 2021, Sambaraju and Goodsman 2021). In response, management practices that aim to reduce the spread of pine beetles have been applied, including accelerated pine harvest, salvage logging, and prescribed burns (Alberta Sustainable Resource Development 2007, McClelland et al. 2023).

These management actions are largely reactive, aiming to protect local community livelihoods and reduce the negative economic impacts of pine beetles (DeFries et al. 2004). However, there is concern about how wildlife species are responding to novel pine beetle disturbance and these associated management actions (Ono 2004, Saab et al. 2014, Steinke et al. 2020). Effective forest management should aim to minimize impacts to key wildlife species (Lewis 2008), but to do so, we must first unravel how these species respond to both the pine beetle itself and current management activities.

Large ungulates play a key role in forest ecosystems and may be directly affected by changes to forest structure (Boan et al. 2011). In western Canada, how forest disturbance affects woodland caribou (*Rangifer tarandus caribou*) is of particular interest, as caribou are federally and provincially listed as Threatened (Government of Canada 2018, Government of Alberta 2022). Moose (*Alces alces*) are also of interest, as they are integral to Indigenous food security (Priadka et al. 2022) and are a valued game species. Caribou and moose have different habitat requirements, so they may respond differently to the pine beetle and its management (Belovsky 1981, Webber et al. 2022). Caribou are habitat specialists; they are dietarily reliant on lichens in mature forests during winter, though they also eat vascular plants during summer (Nobert et al. 2020, Webber et al. 2022). Pine beetle infestations thin canopy cover, causing declines in lichen abundance as early as 3–5 years after infestation, though declines may not occur for 10–15 years depending on local environmental factors (Nobert et al. 2020, Cichowski et al. 2022). Pine beetle-killed trees may also begin to fall 3–5 years after infestation, potentially impeding ungulate movement (van Ginkel et al. 2021). Therefore, caribou may be negatively affected by pine beetle infestations, but this has not been assessed (Cichowski et al. 2022). While lichen cover may decrease soon after pine beetle infestation, the abundance and diversity of other understory vegetation generally increase (Seip and Jones 2008, Cichowski et al. 2022). Moose are generalist herbivores, feeding on a wider range of plant species year-round than caribou

(Belovsky 1981). Because pine beetles increase understory plant growth, infestations may have positive impacts on moose, but this also remains untested (Pappas et al. 2020, Steinke et al. 2020).

In terms of pine beetle management, caribou are sensitive to habitat disturbance and generally avoid areas recently harvested for timber or burned (Seip and Jones 2008, Finnegan et al. 2021). In contrast, moose typically select recently timber-harvested or burned areas, once early seral vegetation is regrowing (Wasser et al. 2011, Johnson and Rea 2023). However, this may be context dependent (Mumma et al. 2018, DeMars et al. 2019), and moose declines have also been documented in areas with increased habitat disturbance (Koetke et al. 2023).

In this study, we used global positioning system (GPS) collar data from caribou and moose to assess responses to pine beetle infestations and associated management activities. Pine beetle management may be cumulative to the effects of other forest disturbances (Cannon et al. 2017); therefore, we used general fire disturbance and all timber harvest disturbance within our study areas as proxies for these management actions. We predicted that, as mature forest specialists, caribou would 1) avoid areas with pine beetle infestations (3–5 years old) because of the associated impacts on understory vegetation (i.e., loss of lichens, increase of other vegetation species), 2) avoid areas with recent timber harvest and fires (≤20 years old) because caribou generally avoid disturbance that results in loss of forage and increased risk of predation in these areas, and 3) exhibit a functional response to disturbance. We predicted that caribou use of areas with pine beetles, timber harvest, and fire would decrease as that disturbance becomes more prevalent within an individual's home range. In contrast we predicted that, as generalists, moose would 1) select areas with more disturbance (i.e., pine beetle and management) and 2) increase their use of disturbed habitat when in home ranges with low levels of disturbance but that their use of disturbed habitat would become proportional to availability in home ranges with higher levels of disturbance.

STUDY AREA

The study area was in west-central Alberta, Canada (Figure 1), one of the initial entry points of pine beetles into the province in 2005 (Government of Alberta and Tyssen 2009). This area lies within the traditional territories, meeting grounds, and homes of many Indigenous Peoples, including the Aseniwuche Winewak, Danezaa, Métis, Nehiyawak, Simpcw, Stoney, and Tsuut'ina (best available information from Native-land.ca). We focused on 2 populations of woodland caribou: one boreal (Little Smoky [LS]) and one central mountain (Redrock-Prairie Creek [RPC]; Figure 1; Hervieux et al. 2013). The focal moose population overlaps with these caribou ranges (Figure 1).

The study area includes alpine, subalpine, upper foothills, and lower foothills natural subregions. It is characterized by coniferous forests, with lodgepole pine (*Pinus contorta*) being the primary host for the pine beetle in this area (Natural Regions Committee 2006, Dempster and Meredith 2021). Treed muskegs are also present, primarily in the LS range. In addition to disturbance from pine beetle, there is anthropogenic disturbance, including forest harvesting and oil and gas extraction, and natural disturbance, including wildfire and windthrow. Further details on the area are available in McClelland et al. (2023).

METHODS

Animal location data

We obtained GPS location data from female caribou collared by the Government of Alberta as part of long-term provincial monitoring programs. Capture and collaring are described in detail in Hervieux et al. (2013), and collars collected location information with a 1.5–4-hour fix rate (Lotek GPS1000, 2000, 2200, 3300, 4400 models; Lotek Engineering, Newmarket, ON, Canada). We kept boreal and central mountain caribou designatable units separate for analyses (Weckworth et al. 2018). Hereafter, whenever we refer to boreal caribou, we are specifically referring

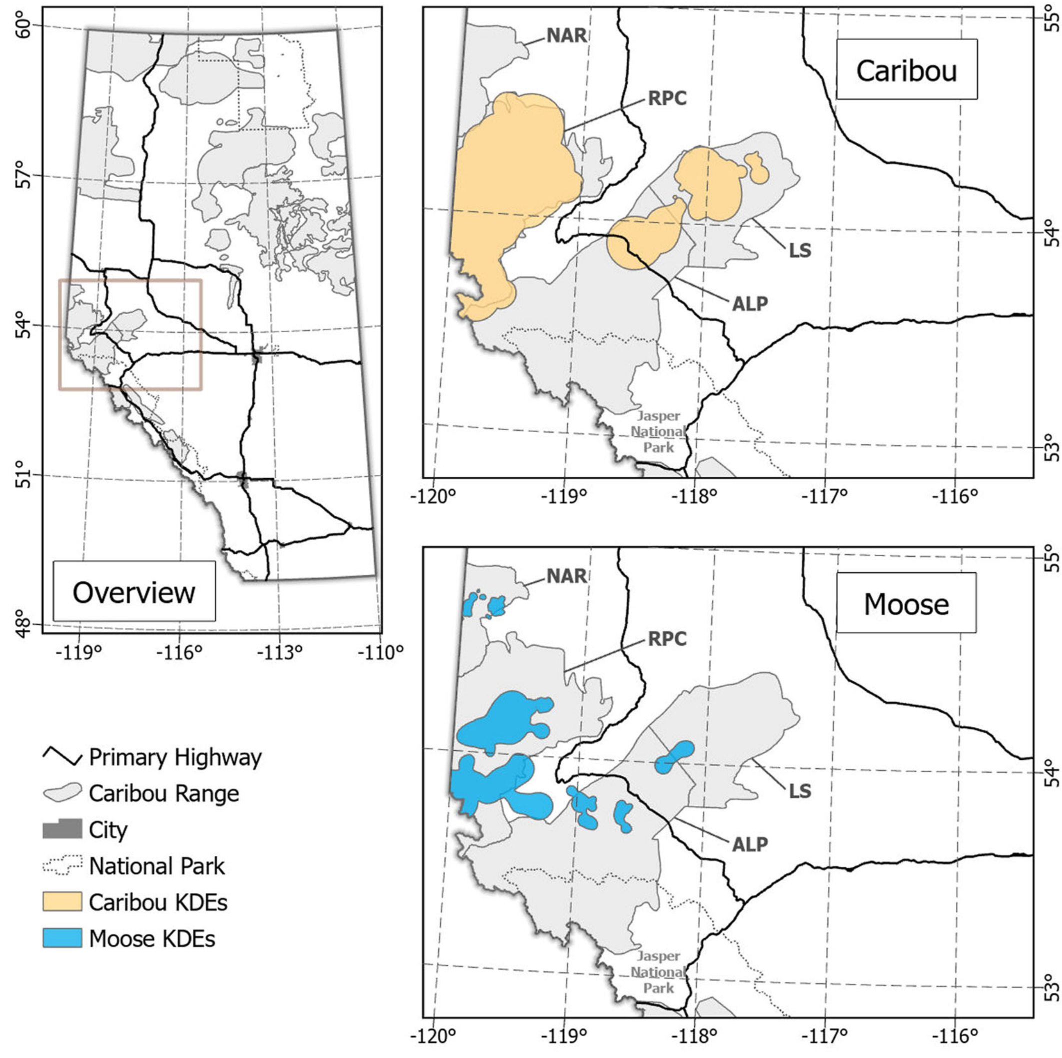

FIGURE 1 Caribou (orange) and moose (blue) home ranges (kernel density estimation [KDEs]) in west-central Alberta, Canada, used to assess responses to mountain pine beetle disturbance between 2008 and 2010. Home ranges are shown on a map of the overall province of Alberta (left), with the zoomed-in inlay represented by a grey square. Population ranges for the A La Peche (ALP), Little Smoky (LS), Narraway (NAR), and Redrock-Prairie Creek (RPC) caribou are outlined and labeled.

to the LS population, and whenever we refer to central mountain caribou, we are referring to the RPC population. We acknowledge that the results extracted from these populations may not be transferable to other populations of the same designatable unit, and do not wish to overextend interpretations, but have abbreviated to the designatable unit in places (e.g., figures and tables) to improve readability.

The focal moose population overlaps with these caribou ranges and extends into the Narraway and A La Peche central mountain caribou ranges (Figure 1). Male and female moose GPS collar data were originally collected as part of a study on moose habitat in west-central Alberta, and were obtained from Movebank for this study (2–4-hour fixes; ATS G2000 GPS collars, Advanced Telemetry Systems, Isanti, MN, USA; www.movebank.org; Peters et al. 2013).

We performed data handling and analyses in R version 4.3.2 (R Core Team 2023). Location data for both species were collected from 2008-2010, 3–5 years after pine beetle infestations first occurred. We focused on this early period of pine beetle infestation as it marks when changes to forest and vegetation structure may first occur, and when initial management responses may be implemented. We removed locations with high dilution of precision values (DOPs: >12 for caribou and >5 for moose) or that occurred outside of a 2–4-hour fix interval. Caribou data were pre-cleaned to a DOP > 12, and further information on DOP and the number of satellites were not provided. For moose data, we removed 2-dimensional points and points with a DOP > 5 (*sensu* Lewis et al. 2007). We also removed individual caribou and moose with a fix-rate success of <90% (*sensu* Hebblewhite et al. 2007, Frair et al. 2010), and removed locations with an incoming and outgoing speed above the 99th percentile (Gupte et al. 2022; further details in Supporting Information S1).

For each dataset, we partitioned locations by individual, year, and season: winter (16 Oct–15 May) and summer (16 May–15 Oct; Peters et al. 2013). Hereafter, individual-year refers to individual-season-year combinations. We generated annual seasonal home ranges for each individual-year using kernel density estimation (95% adaptive kernel, default bandwidth) in the amt R package (Signer et al. 2019). We clipped home ranges and location data to exclude British Columbia and Jasper National Park, where pine beetle data were not available. We removed individual-year combinations without pine beetle infestations in their home range: 10 moose combinations (4 from winter, 6 from summer), 2 mountain caribou combinations (both from winter), 1 boreal caribou combination (summer). We also removed individual-year combinations with <200 locations (S1; Table S2). We generated 10 available locations for each used location within seasonal individual-year home ranges via amt (Signer et al. 2019). The final boreal caribou dataset included locations from 16 individual-years ($n = 9$ winter, $n = 7$ summer, based on 5 collared animals, all female; Figure 1; Table S2). The final central mountain caribou dataset included locations from 45 individual-years ($n = 32$ winter, $n = 13$ summer, based on 20 animals, all female; Figure 1; Table S2). The final moose dataset included locations from 24 individual-years ($n = 16$ winter [9 males, 7 females], $n = 8$ summer [4 males, 4 females]), based on 9 animals (5 males, 4 females; Figure 1; Table S2).

Predictor variables

We performed geoprocessing and extraction of predictor variables in ArcGIS Pro 3.1.2 (Esri, Redlands, CA, USA) and QGIS 3.32.1 (QGIS Development Team 2023). We extracted annual pine beetle survey data available from the Government of Alberta (Government of Alberta 2023). We combined these data to create annual 30×30-m rasters, with each cell depicting whether that area had been disturbed by pine beetles or not (Figure 2A; Table S3).

For timber harvest and fire, we used Landsat-derived 30×30-m rasters available from the National Terrestrial Ecosystem Monitoring system (NTEMS; Hermosilla et al. 2018, 2016; Figure 2B,C). We used disturbance by timber harvest and disturbance by fire as proxies for recent pine beetle management via timber harvesting or prescribed burning. Notably, salvage logging may be more intensive than regular timber harvesting activities (e.g., greater percentage removal, larger harvest areas), but data on salvage logging alone were not available across our study area. Previous studies have used clearcuts as proxies for salvage logging, which we considered; however, many salvage logging policies now include a greater percentage of tree retention, and it can be challenging to disentangle wildlife responses to cumulative, similar disturbance types, leading us to use all timber harvest activity (Peter and Bogdanski 2010, Thorn et al. 2018, Steinke et al. 2020). We subset timber harvest and fire rasters to only include recent (≤20-year-old) disturbances and then generated densities at 1-km and 5-km radii around each animal location. We focused on timber harvest blocks and fires <20 years old, as disturbed patches are dominated by vascular plants during this period, with potential implications for ungulate foraging behavior (Silva 2020, Finnegan et al. 2021, Lacerte et al. 2021). These distance radii are commonly applied in caribou and moose habitat selection models (Rudolph et al. 2019, Finnegan et al. 2023). Moose have been observed to move a mean distance of 1–5 km per day, depending on season and resource requirements (e.g., 1.2–4.6 km; Thompson et al. 1995). Caribou can traverse large distances, particularly during migration (e.g., 54 km a day; Rudolph and Drapeau 2012). Generally, however, their daily movement distances are documented to be within 0.9–2.5 km per day

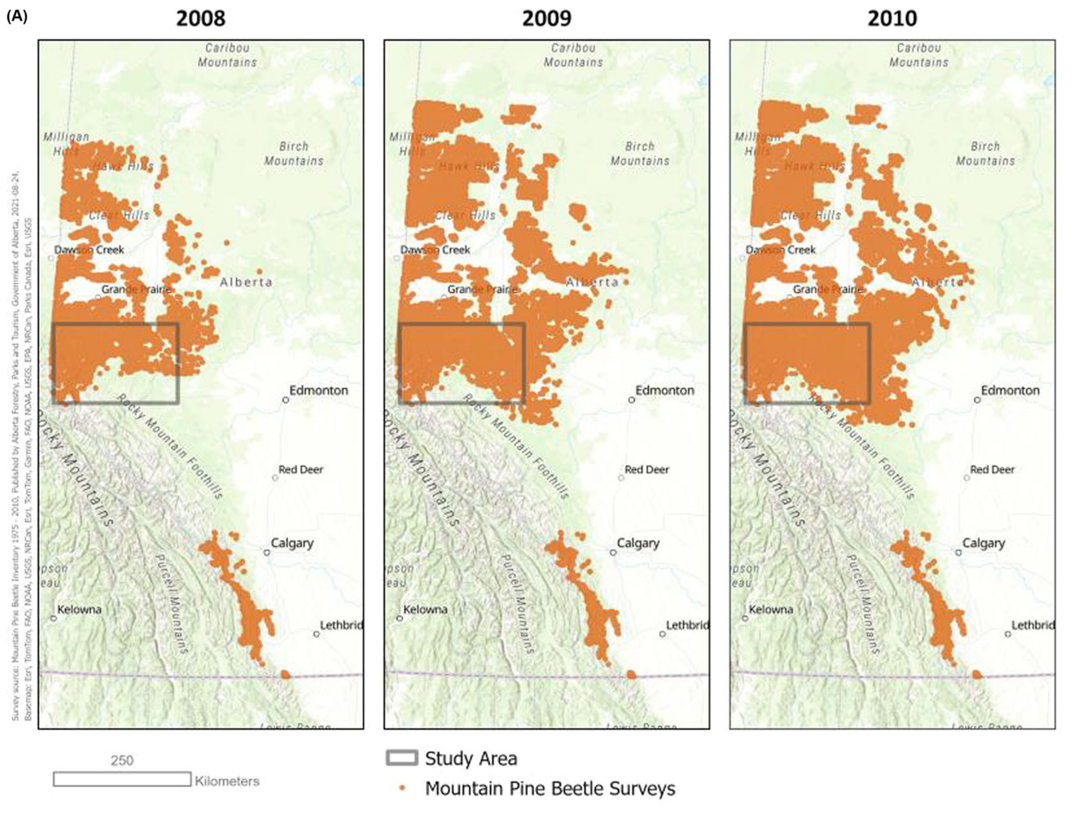

FIGURE 2 Area impacted by mountain pine beetles (A), ≤20-year-old timber harvest (B), and ≤20-year-old fire (C) in west-central Alberta, Canada, over the years of our study (2008–2010). Mountain pine beetle point locations represent 30×30-m areas where beetle damage was detected by annual aerial surveys, including locations from both that year and previous years, that had not been removed by fires or harvest. Disturbance polygon color varies with time since disturbance. The grey square highlights our study area, one of the initial entry points of pine beetles into Alberta (Panels B and C are on the following pages).

(Ferguson and Elkie 2004), and they have been seen to avoid areas within 5 km of disturbance (Reimers and Colman 2006), making 1 km and 5 km 2 key distances for them ecologically.

To account for other landscape characteristics that affect habitat use, we also included land cover (NTEMS), elevation, and slope (digital elevation model; Natural Resources Canada 2011). We recategorized land cover into forested and open locations (Table S3).

Resource selection function (RSF) models

Before fitting resource selection function (RSF) models, we screened variables for collinearity ($|r_p| < 0.7$; Dormann et al. 2013), grouping 1-km density variables together and 5-km density variables together (i.e., 12 collinearity tests; Figure S4). Timber harvest density at the 5-km scale was collinear ($r = -0.7$) with elevation in moose data during summer (and borderline in winter, $r = -0.6$). Therefore, we dropped timber harvest from moose RSF models but retained it for caribou models.

We fit each RSF as a binomial (used or available) generalized linear mixed effect model (GLMM) in lme4 (Bates et al. 2015), including animal ID-season-year as a random effect, and using the bobyqa optimizer (Hedlin and

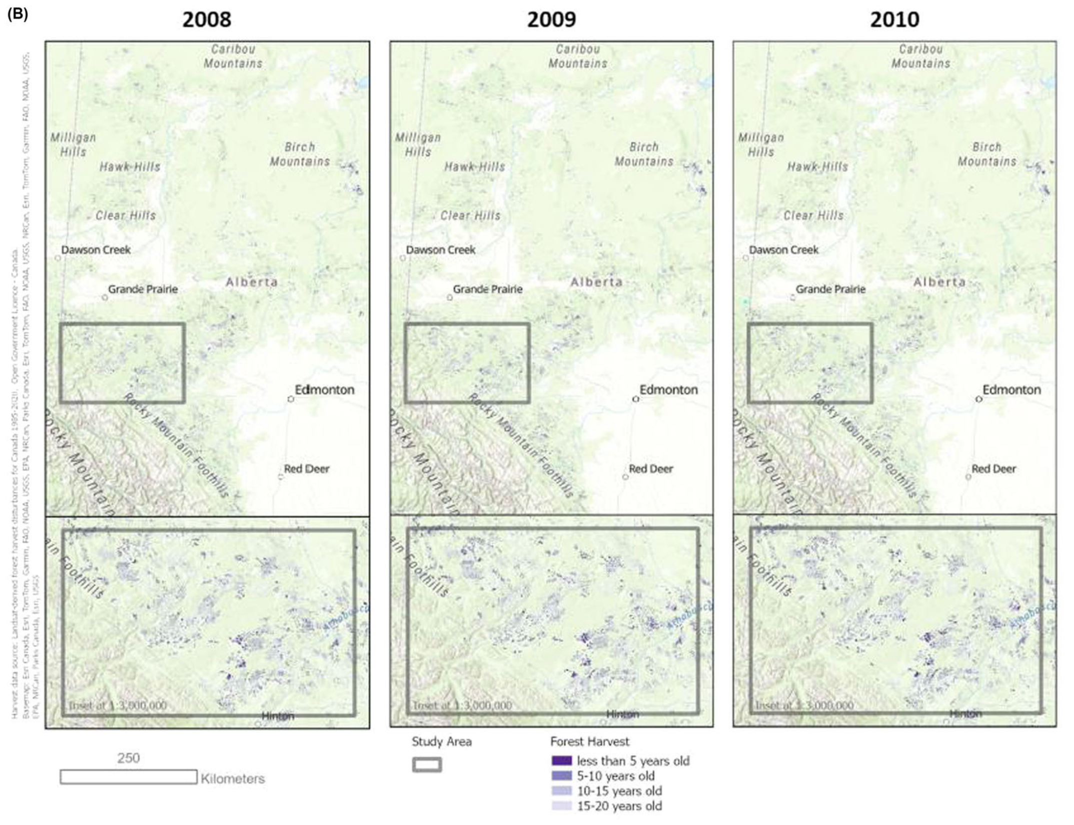

FIGURE 2 (Continued)

Franke 2017). We $\log_e$-transformed and scaled the numerical variables to improve model convergence and included them as single and quadratic terms, to allow for non-linear patterns. We then extracted the coefficients of the model and inserted them into the exponential form of the RSF, back-transforming them for plotting to aid interpretation (Boyce et al. 2002). We included sex as a 2-way interaction with pine beetle density and with fire density (both as a linear and quadratic term), allowing us to determine whether there was any variation in habitat selection between males and females. We did not include these interactions in caribou models, as data were only available on females. We built models using disturbance densities at the 1-km and 5-km scales for each of the 6 datasets (one dataset for each population and season, i.e., 12 models; Table S5). We used Akaike's Information Criterion (AIC) to identify the most parsimonious scale for models, i.e., retaining the scale with the lowest AIC value (Sakamoto et al. 1986; Table S5).

We used variograms to check for spatial autocorrelation in model residuals, with none being flagged (Roberts et al. 2017; Figure S6). We assessed model prediction using 5-fold cross-validation, partitioning data into 80% training data and 20% testing data (Boyce et al. 2002). We computed Spearman rank correlations (r_s) between frequencies of area-adjusted cross-validation locations and then calculated a rank for each cross-validated model. Better predictive performance is indicated by a strong positive correlation value, demonstrating that model predictions match actual observations (Smith et al. 2022).

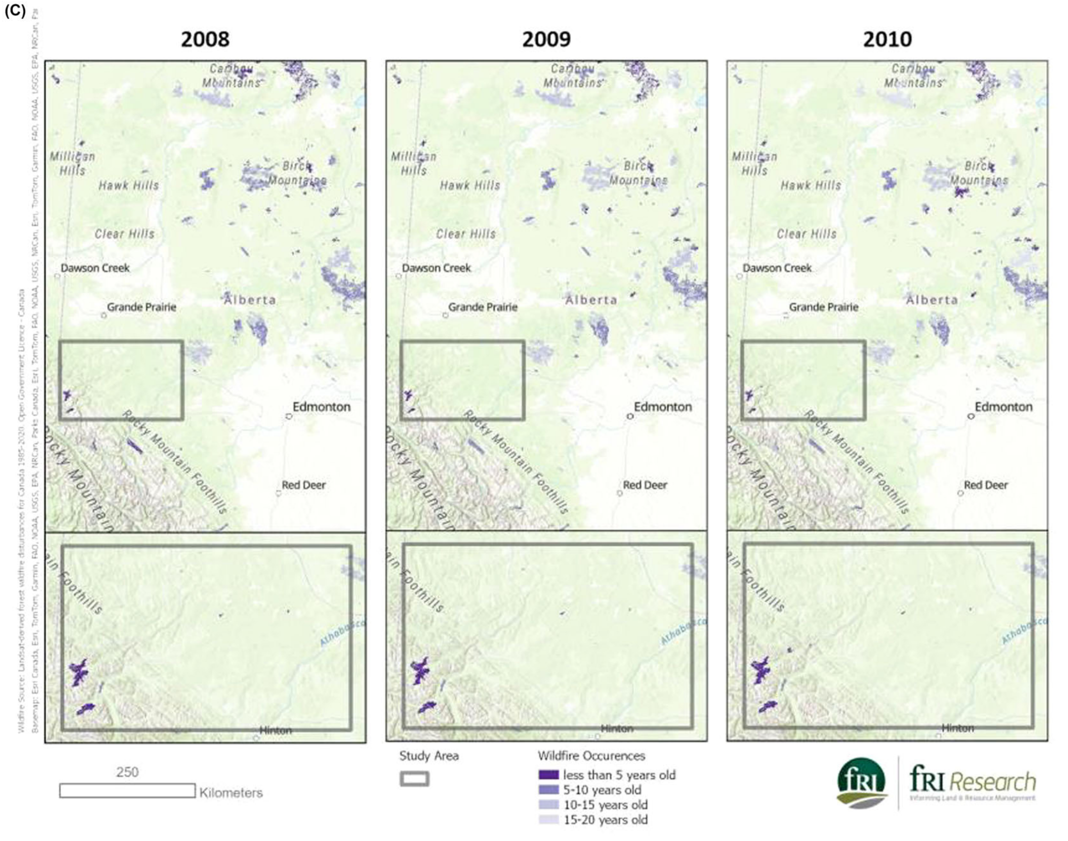

FIGURE 2 (Continued)

Functional response models

We generated functional response models on the multiplicative scale, as recommended by Holbrook et al. (2019). This allowed us to assess how habitat use changed relative to availability across home ranges (Mysterud and Ims 1998). The null hypothesis posits that habitat use is a constant multiplicative function of habitat availability, meaning that the $\log_e$-transformed ratio of use:availability remains constant, with deviations indicating a functional response in habitat selection (Holbrook et al. 2019).

We used base R (R Core Team 2023) to fit linear and quadratic models for each disturbance variable (i.e., pine beetle, timber harvest, and fire) to each of the 6 datasets (excluding timber harvest from moose models) at the 5-km scale. We opted to assess the moose population as a whole, rather than subdividing by sex, to provide a population-wide perspective that could inform broader management recommendations. This approach allowed for a more general assessment of moose behavior while also avoiding constraints associated with reduced sample sizes. We used $\log_e$-transformed mean disturbance density for each individual-year's used locations as the response variable and $\log_e$-transformed mean disturbance density for each individual-year's available locations as a fixed effect. We determined if linear or quadratic models best fit the data using likelihood ratio tests via lmtest (Zeileis and Hothorn 2002; Table S7). We exponentiated the predictions for visualization and interpretation, and visualized results in ggplot2 (Wickham 2016). We considered the overall trend in the relationship and the associated confidence intervals in assessments.

TABLE 1 Estimated β coefficients, standard errors (SE), lower and upper 95% confidence intervals, *Z*-values, and *P*-values for models of boreal caribou habitat selection during winter and summer in west-central Alberta, Canada, during 2008–2010. The reference category for land cover was forest. Harvest refers to timber harvesting. We $\log_e$-transformed and scaled the numerical variables to improve model convergence and included them as single and quadratic terms to allow for non-linear patterns. Disturbance metrics (pine beetle, fire, harvest) represent the percent of area disturbed within a 5-km radius.

Fixed effects	Estimate	SE	Lower 95% CI	Upper 95% CI	*Z*	*P*
Boreal caribou: winter						
Land cover (open)	−0.164	0.026	−0.216	−0.112	−6.235	<0.001
Elevation (m)	55.898	1.321	53.310	58.486	42.331	<0.001
Elevation^2 (m)	−56.592	1.327	−59.194	−53.991	−42.638	<0.001
Slope	0.105	0.0323	0.041	0.169	3.194	0.002
Slope^2	−0.434	0.036	−0.505	−0.363	−12.013	<0.001
Harvest	0.256	0.048	0.161	0.351	5.295	<0.001
Harvest^2	0.038	0.043	−0.047	0.122	0.869	0.385
Fire	0.016	0.050	−0.082	0.113	0.315	0.752
Fire^2	0.059	0.0480	−0.035	0.153	1.235	0.217
Pine beetle	−0.645	0.032	−0.708	−0.582	−19.962	<0.001
Pine beetle^2	0.286	0.030	0.227	0.344	9.605	<0.001
Boreal caribou: summer						
Land cover (open)	0.265	0.032	0.202	0.328	8.233	<0.001
Elevation (m)	−18.360	2.523	−23.306	−13.414	−7.276	<0.001
Elevation^2 (m)	19.213	2.522	14.269	24.156	7.617	<0.001
Slope	−0.375	0.041	−0.455	−0.294	−9.115	<0.001
Slope^2	−0.087	0.049	−0.183	0.010	−1.763	0.078
Harvest	0.789	0.062	0.667	0.911	12.685	<0.001
Harvest^2	−1.230	0.065	−1.337	−1.082	−18.544	<0.001
Fire	−3.057	0.199	−3.448	−2.666	−15.335	<0.001
Fire^2	3.368	0.191	2.994	3.742	17.643	<0.001
Pine beetle	0.717	0.090	0.541	0.894	7.983	<0.001
Pine beetle^2	0.067	0.076	0.083	0.217	0.879	0.380

RESULTS

Boreal caribou (LS)

The RSF models indicated that boreal caribou from the LS population avoided areas with higher densities of pine beetle disturbance during winter but selected them during summer (Table 1; Figure 3A,B, note that the table presents the summary of results from the GLMM, while the figures depict the relative probability of

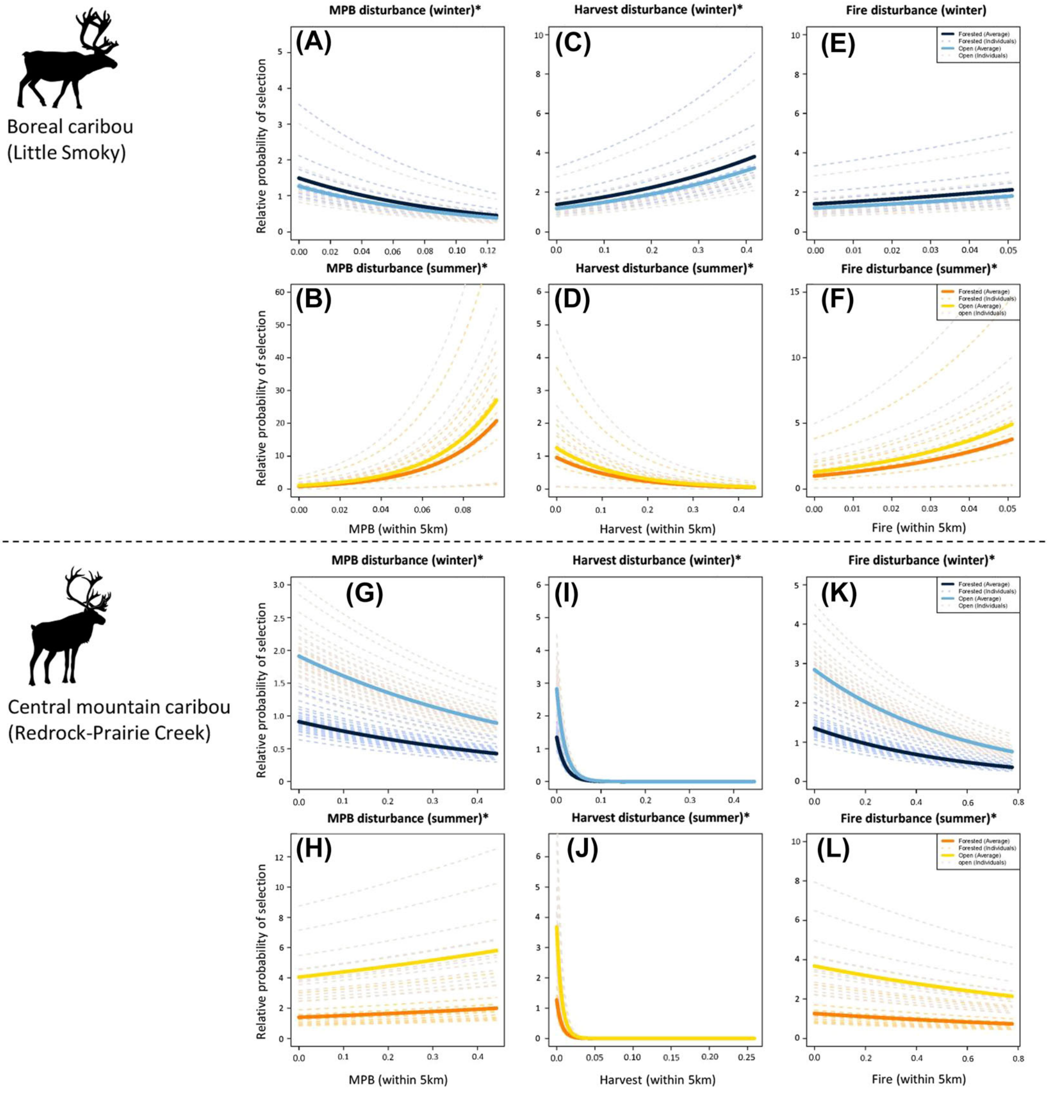

FIGURE 3 Relative probability of boreal caribou and central mountain caribou habitat selection in relation to mountain pine beetle (MPB), timber harvest, and fire during winter (blue) and summer (orange), in west-central Alberta, Canada, during 2008–2010. The relative probability of selection is depicted when the individual is locally (30×30 m) within forested or open land cover. All disturbance variables represent percent density at a 5-km radius. Dashed lines are estimates for each individual caribou. Scales for relative probability of selection on the *y*-axis have been adjusted to improve legibility. Significant variables are marked with an asterisk.

selection based on the RSF as described above). These caribou selected areas with higher densities of timber harvest during winter, and avoided timber harvest during summer (Table 1; Figure 3C,D). There was no response by these caribou to fire during winter, but they selected areas with higher densities of fire during summer (Table 1; Figure 3E,F), though notably fire was rare overall within home ranges in the LS population range (Table S3). Generally, these boreal caribou selected forested areas during winter and open areas during summer (Figure 3). They selected lower elevations during winter, higher elevations during summer, and flatter areas (lower slopes) year-round (Table 1; Figure S8). K-fold cross-validation demonstrated that both models

TABLE 2 Estimated β coefficients, standard errors (SE), lower and upper 95% confidence intervals, *Z*-values, and *P*-values (* denotes significant effects) for models of central mountain caribou habitat selection during winter and summer in west-central Alberta, Canada, during 2008–2010. The reference category for land cover was forest. Harvest refers to timber harvesting. We $\log_e$-transformed and scaled the numerical variables to improve model convergence and included them as single and quadratic terms to allow for non-linear patterns. Disturbance metrics (pine beetle, fire, harvest) represent the percent of area disturbed within a 5-km radius.

Fixed effects	Estimate	SE	Lower 95% CI	Upper 95% CI	*Z*	*P*
Central mountain caribou: winter						
Land cover (open)	0.739	0.015	0.711	0.768	51.058	<0.001*
Elevation (m)	−5.932	0.374	−6.665	−5.199	−15.861	<0.001*
Elevation^2 (m)	6.434	0.374	5.700	7.167	17.187	<0.001*
Slope	0.691	0.026	0.641	0.742	26.850	<0.001*
Slope^2	−1.275	0.027	−1.328	−1.221	−46.757	<0.001*
Harvest	1.146	0.028	1.090	1.201	40.452	<0.001*
Harvest^2	−2.295	0.049	−2.390	−2.199	−47.062	<0.001*
Fire	−0.120	0.018	−0.155	−0.084	−6.663	<0.001*
Fire^2	−0.022	0.018	−0.058	0.014	−1.209	0.226
Pine beetle	0.533	0.016	0.503	0.563	34.460	<0.001*
Pine beetle^2	−0.458	0.016	−0.489	−0.426	−28.408	<0.001*
Central mountain caribou: summer						
Land cover (open)	1.068	0.026	1.017	1.118	41.709	<0.001*
Elevation (m)	14.090	1.006	12.117	16.062	14.000	<0.001*
Elevation^2 (m)	−13.318	0.996	−15.270	−11.366	−13.375	<0.001*
Slope	0.943	0.052	0.841	1.046	18.044	<0.001*
Slope^2	−1.319	0.052	−1.319	−1.217	−25.341	<0.001*
Harvest	1.057	0.060	0.939	1.175	17.594	<0.001*
Harvest^2	−1.832	0.139	−2.104	−1.560	−13.196	<0.001*
Fire	0.298	0.031	0.238	0.358	9.750	<0.001*
Fire^2	−0.285	0.032	−0.347	−0.223	−8.995	<0.001*
Pine beetle	−0.198	0.026	−0.247	−0.149	−7.893	<0.001*
Pine beetle^2	0.186	0.028	0.132	0.240	6.766	<0.001*

had a high predictive performance, with a mean Spearman correlation of $r_s = 0.97$ for winter and $r_s = 0.96$ for summer (Table S9; Figure S10).

Contrary to expectations, boreal caribou did not exhibit a functional response to pine beetle disturbance during winter or summer, though there was a nonsignificant trend indicating reduced use of pine beetle areas in home ranges with higher pine beetle densities during winter (i.e., use less than proportional to availability; Figure 5A,B; Table S7). During winter, these caribou reduced proportional use of timber harvest when in home ranges with lower timber harvest densities, though this was largely proportional to availability (Figure 5C; Table S7). During summer, we did not find significant evidence of a response to harvesting, though there was a trend indicating reduced use at

TABLE 3 Estimated β coefficients, standard errors (SE), lower and upper 95% confidence intervals, *Z*-values, and *P*-values (* denotes significant effects) for models of moose habitat selection during winter and summer in west-central Alberta, Canada, during 2008–2010. The reference category was forest for land cover and female for sex. We $\log_e$-transformed and scaled the numerical variables to improve model convergence and included them as single and quadratic terms to allow for non-linear patterns. Disturbance metrics (pine beetle, fire) represent the percent of area disturbed within a 5-km radius.

Fixed effects	Estimate	SE	Lower 95% CI	Upper 95% CI	*Z*	*P*
Moose: winter						
Land cover (open)	−0.672	0.048	−0.767	−0.577	−13.877	<0.001
Sex (male)	−0.817	0.256	−1.318	−0.316	−3.194	0.001
Elevation (m)	9.883	0.753	8.406	11.359	13.121	<0.001
Elevation^2 (m)	−10.667	0.765	−12.150	−9.184	−14.100	<0.001*
Slope	−0.518	0.035	−0.587	−0.449	−14.714	<0.001*
Slope^2	0.304	0.039	0.229	0.380	7.878	<0.001*
Fire	−1.100	0.070	−1.234	−0.960	−15.730	<0.001*
Fire^2	1.105	0.056	0.994	1.215	19.612	<0.001*
Pine beetle	−0.506	0.146	−0.792	−0.220	−3.466	<0.001*
Pine beetle^2	0.225	0.175	−0.118	0.568	1.286	0.198
Land cover (open) × sex (male)	1.200	0.055	1.092	1.307	21.842	<0.001*
Fire × sex (male)	0.894	0.141	0.618	1.170	6.350	<0.001*
Fire^2 × sex (male)	−1.292	0.159	−1.604	−0.981	−8.141	<0.001*
Pine beetle × sex (male)	0.806	0.157	0.498	1.113	5.135	<0.001*
Pine beetle^2 × sex (male)	−0.396	0.181	−0.751	−0.040	−2.180	0.029*
Moose: summer						
Land cover (open)	−0.610	0.046	−0.701	−0.519	−13.159	<0.001*
Sex (male)	0.923	0.801	−0.646	2.492	1.153	0.249
Elevation (m)	0.139	1.117	−2.040	2.317	0.125	0.901
Elevation^2 (m)	−0.215	1.110	−2.390	1.961	−0.193	0.847
Slope	0.907	0.058	0.794	1.021	15.629	<0.001*
Slope^2	−1.040	0.060	−1.157	−0.922	−17.315	<0.001*
Fire	−1.271	0.207	−1.677	−0.865	−6.136	<0.001*
Fire^2	1.228	0.154	0.925	1.530	7.961	<0.001*
Pine beetle	−3.459	0.433	−4.308	−2.610	−7.984	<0.001*
Pine beetle^2	1.551	0.490	0.590	2.512	3.164	0.002*
Land cover (open) × sex (male)	0.604	0.060	0.486	0.722	10.010	<0.001*
Fire × sex (male)	2.147	0.236	1.684	2.611	9.084	<0.001*
Fire^2 × sex (male)	−2.274	0.212	−2.689	−1.859	−10.749	<0.001*
Pine beetle × sex (male)	2.696	0.436	1.841	3.551	6.180	<0.001*
Pine beetle^2 × sex (male)	−0.834	0.492	−1.798	0.130	−1.695	0.09

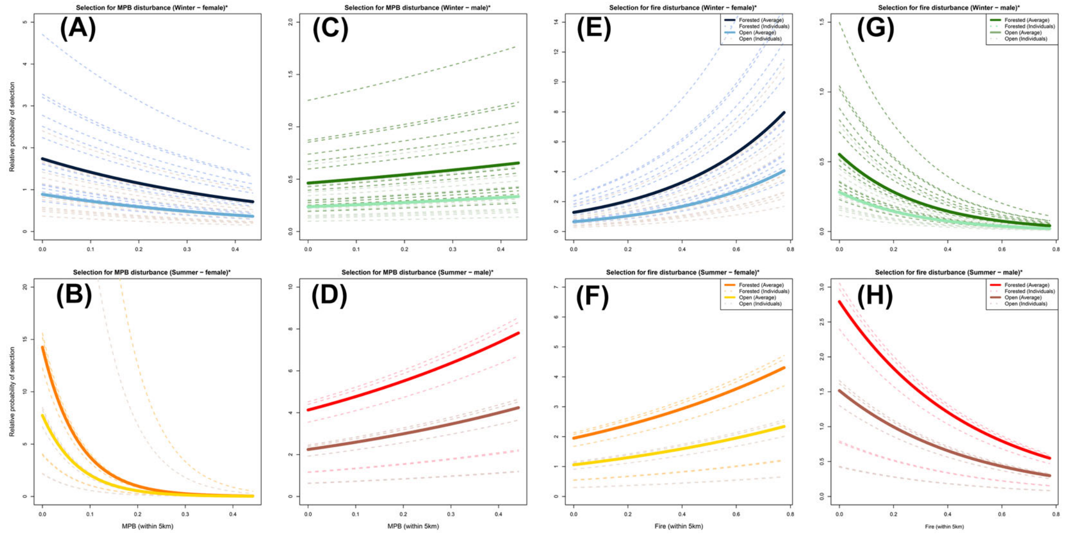

FIGURE 4 Relative probability of moose habitat selection in relation to mountain pine beetle (MPB) and fire in west-central Alberta, Canada, during 2008–2010. Females' responses during winter (blue) and summer (orange) and males' responses during winter (green) and summer (red) are depicted. The relative probability of selection is depicted when the individual is locally (30×30 m) within forested or open land cover. All disturbance variables represent percent density at a 5-km radius. Dashed lines are estimates for each individual caribou. Scales for relative probability of selection on the *y*-axis have been adjusted to improve legibility. Significant variables are marked with an asterisk.

higher densities (Figure 5D; Table S7). There was no functional response to fire during winter, but during summer they were more likely to use fire as densities increased across home ranges (Figure 5E,F; Table S7). Although we found moderate to strong evidence for non-linear effects of harvest during winter ($P = 0.023$), the limited sample size resulted in large confidence intervals, limiting the strength of inferences.

Central mountain caribou (RPC)

Central mountain caribou from the RPC population avoided areas with higher densities of pine beetle disturbance during winter and selected areas with pine beetles during summer (Table 2; Figure 3G,H). These caribou avoided areas with higher densities of timber harvest and fire during winter and summer (Figure 3I,J,K,L). They also selected open areas (Figure 3), high elevations in summer and all elevations in winter, and flatter slopes across winter and summer (Table 2; Figure S8). Both models had good to high predictive performance (mean winter $r_s = 1$, summer $r_s = 0.75$; Table S9; Figure S10).

During winter, central mountain caribou did not exhibit a functional response to pine beetle disturbance, though there was a nonsignificant trend indicating reduced use of pine beetle areas in home ranges with higher pine beetle densities (Figure 5G; Table S7). During summer, they displayed a functional response, with reduced use as pine beetle densities increased across home ranges (Figure 5H; Table S7). These caribou also displayed functional responses to timber harvest in both winter and summer, with reduced use as timber harvest densities increased across home ranges (Figure 5I,J; Table S7). Finally, these mountain caribou displayed a functional response to fire in winter, with use increasing as fire densities increased across home ranges (Figure 5I; Table S7; $P < 0.001$). There was no functional response to fire in summer (Figure 5L; Table S7).

Moose

Moose displayed inverse results, depending on sex. Females avoided areas with higher densities of pine beetle disturbance in winter and summer (Table 3; Figure 4A,B), whereas males selected them (Figure 4C,D). Conversely, females selected areas with greater densities of fire in both winter and summer (Figure 4E,F), whereas males avoided them (Figure 4G,H).

Both sexes selected forested areas in both seasons (Figure 4). They selected lower elevations and flatter slopes in winter. We did not find evidence of an effect of elevation in summer, and individuals selected flatter slopes at this time of year (Table 3; Figure S8). K-fold cross-validation demonstrated that both models had good predictive performance (mean winter $r_s = 0.83$, summer $r_s = 0.67$; Table S9; Figure S10). In terms of overall population responses, while non-linearity was detected in pine beetle functional response models, in general, moose use of pine beetle and fire was largely proportional to availability across home ranges (Figure 5M–P; Table S7).

DISCUSSION

Responses to pine beetles

As predicted, both boreal and central mountain caribou avoided pine beetles in winter. Our models also indicated that both caribou populations may have a functional response, decreasing proportional use as pine beetle densities increase across home ranges, but this was not significant. In contrast with our predictions, trends were reversed during summer, with both populations of caribou selecting areas with higher densities of pine beetle. However, our functional response models indicated that, at least for central mountain caribou, proportional use of pine beetle in summer was low compared to availability when in more disturbed home ranges. Moose responses were more complex than was initially anticipated. We expected moose to select for all disturbance types at all times of year, regardless of sex. However, we found that female moose avoided pine beetle disturbance in winter and summer, while male moose selected it across both seasons. Functional response models showed proportional use to availability, but both sexes were grouped for a population-wide assessment of trends in these models, highlighting how sex-specific responses may become masked.

In terms of the seasonal differences in caribou responses to pine beetle, it has been well documented that caribou display seasonal shifts in diet (i.e., ingesting lichen during winter, vascular plants during summer; Nobert et al. 2020, Webber et al. 2022). Thus, the avoidance of pine beetle we observed during winter may be due to loss of lichen cover soon after infestation (3–5 years; Cichowski et al. 2022). However, studies from the same area suggest lichen cover may not be affected by pine beetles even 10–15 years after infestation (Nobert et al. 2020). The avoidance of pine beetle areas we observed could be driven by other environmental factors that have been influenced by pine beetles. For example, increased snow depth under pine beetle-thinned canopies may negatively affect caribou access and movement (Cichowski 2010). Caribou might also be more vulnerable to predation in areas impacted by pine beetles and are adapting their behavior accordingly. For example, other ungulates, like deer, may use pine beetle areas because of increased availability of early seral forage (Pec et al. 2015), attracting shared predators of caribou (i.e., disturbance-mediated apparent competition; Neufeld et al. 2021). However, the exact mechanisms driving the caribou response we observed are currently unknown and warrant further investigation.

Caribou shifting from avoiding to selecting pine beetle-impacted areas in summer may reflect seasonal transitions to consuming vascular plants (Webber et al. 2022). Alternatively, whatever factor is driving avoidance in winter may no longer be limiting during summer. For example, snowmelt may make pine beetle-impacted areas more accessible during summer. Summer use of pine beetle-impacted areas by caribou suggests that it is not inaccessibility due to treefall driving avoidance during winter, as this would continue into summer (Lewis and Hartley 2006).

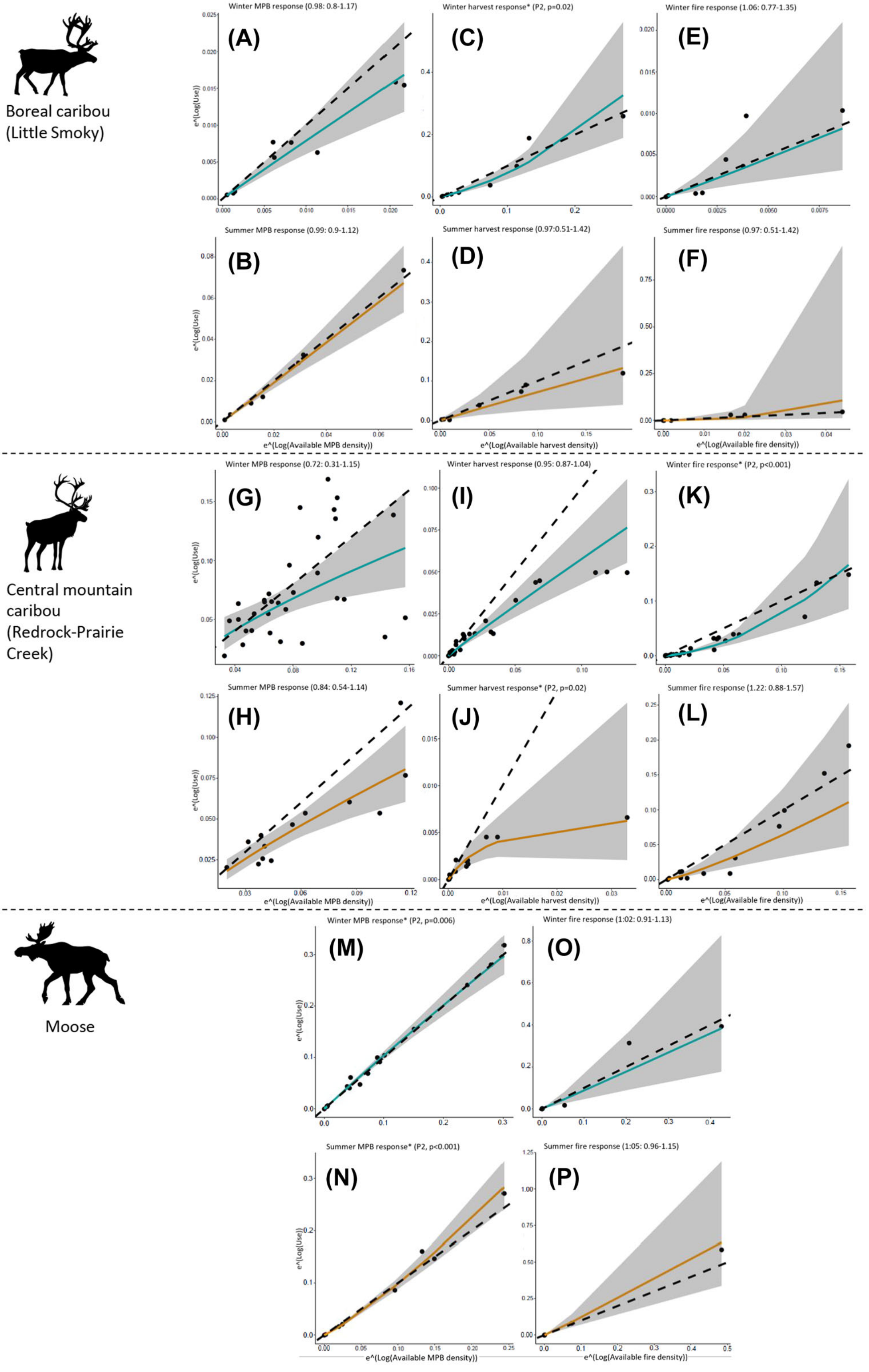

FIGURE 5 (See caption on next page).

While the RSF indicated selection for pine beetle-impacted areas during summer, while controlling for other factors, the functional response model indicated that pine beetle use was lower than expected given availability across mountain caribou summer home ranges. As RSF models showed that these caribou are using open areas and higher elevations (also in accordance with observed range contractions; MacNearney et al. 2016), the functional response we observed during summer may reflect the lower densities of pine beetle in alpine and subalpine areas (Sambaraju and Goodsman 2021). However, they did still avoid pine beetle in winter, so pine beetle infestations may contribute further to observed reductions in caribou winter habitat over time (Gibson et al. 2008, MacNearney et al. 2016).

We expected both male and female moose (as generalists) to display opposite responses to caribou (as specialists) towards pine beetle infestations. However, we found that female moose avoided pine beetle-impacted areas during summer and winter, while male moose selected them. Differences in selection between male and female moose have been reported previously and may be driven by their different ecological needs, body size, and reproductive status (Mumma et al. 2018, Joly et al. 2016, Finnegan et al. 2023). For example, female moose with calves prioritize forage quality (Francis et al. 2021). The time since pine beetle infestation in our analyses may be too recent to increase the availability of vascular plants in impacted areas, meaning that there is no high-quality forage to drive selection of these areas by female moose. Instead, this avoidance may simply reflect their preference for deciduous or riparian land cover types during this season (Timmermann and McNicol 1988). Winter avoidance by female moose may be due to greater snow depth in these areas, which calves may have difficulty traversing (Lima and Dill 1990). In contrast, it has been shown that herbaceous plant productivity rapidly increases within 5 years of pine beetle infestations, even when vascular plant growth does not (Pec et al. 2015). Male moose may prioritize consumption of large quantities of forage over quality, as outlined by the forage selection hypothesis (Main 2008), and may therefore be able to maximize on the forage available in pine beetle-infested areas during summer. In terms of their selection for these areas in winter, larger males are less likely to be impeded by deeper snow and may continue to select for the forage available in more open areas (Telfer and Kelsall 1979).

Responses to timber harvest and fire

We found that responses to our proxies for pine beetle management varied across species and populations. As predicted, central mountain caribou in the RPC population avoided areas with higher densities of timber harvest and fire, likely due to the risk of increased mortality and reduced lichen availability (Stevenson et al. 2024). Functional response models also showed that, as predicted, central mountain caribou increasingly avoided timber harvest as it became more available across home ranges (Schaefer and Mahoney 2007). This relationship was inverted for fire, with central mountain caribou easing avoidance of burned areas as they became more available across home ranges. This response may reflect an inability to avoid burned areas within their already restricted home ranges (density of fire was higher than density of timber harvest within home ranges for this population; Table S3; Figure 2; MacNearney et al. 2016).

Female moose displayed the opposite response to central mountain caribou, selecting areas with higher densities of fire (timber harvest was excluded from models). Previous research has shown that moose use fires, likely to access the forage available in burned areas (DeMars et al. 2019, Johnson and Rea 2023, Mumma et al. 2024). For female moose, the forage associated with burned areas, in comparison to pine beetle-infested areas

FIGURE 5 Functional responses in habitat use and selection by boreal caribou, central mountain caribou, and moose in west-central Alberta, Canada, during 2008–2010. Models included mountain pine beetle (MPB), timber harvest, and fire density across both winter (blue) and summer (orange). Dashed lines indicate proportional habitat use and black dots indicate individuals. Shaded areas are 95% confidence intervals. Asterisks indicate models that were best fit by quadratic formulae, with the *P*-value provided, whereas the range is provided for linear models. Significant functional responses are detected either by a quadratic model being the model of best fit or by a linear model significantly varying from proportional use after the confidence intervals have been considered.

(McClelland et al. 2023), may outweigh the risks associated with access (e.g., snow depth, predation; Francis et al. 2021). As previously outlined, the contrasting response by male moose may be driven by differing ecological needs across the year, and by body size. For example, as male moose are larger than females, they may struggle to thermoregulate in open, burned areas in summer (van Beest et al. 2012).

Boreal caribou from the LS population displayed more complex and variable relationships with our proxies for pine beetle management than central mountain caribou or moose. Boreal caribou did not respond to fire during winter but selected it during summer. However, the boreal population in our study (LS) had low densities of fire in its overall range (Figure 2; Table S3; Russell et al. 2016). Therefore, this selection may reflect a preference for forests where fires also occur, rather than selection for fire itself. Evaluating functional responses to fire relative to other characteristics of home ranges (e.g., % undisturbed, land cover type) might help to explain this result further, but it was beyond the scope of this study. Contrasting with previous research and central mountain caribou responses (Schaefer and Mahoney 2007, Finnegan et al. 2021), we found that these boreal caribou selected harvested areas during winter. Our functional response models indicated that individuals with lower levels of timber harvest in their winter ranges trended towards not using it, though results were broadly proportional to availability. These boreal caribou did, however, avoid timber harvest in summer. At the time of this study, the LS population had the highest level of anthropogenic disturbance of any boreal caribou population in Canada, with almost 90% of its range being disturbed (Semeniuk et al. 2012). Little Smoky caribou avoid timber harvest at the landscape scale (i.e., when selecting home ranges within their greater population range), but this effect is typically weakened at the home range scale, which we assessed (DeCesare et al. 2012). Seasonal dependency on old-growth pine forests for lichen during winter may be driving use of remaining mature forest stands within their home ranges, even if the surrounding 5-km-radius area is disturbed by timber harvest, making it seem like they are selecting for the timber harvest itself. Our winter functional response model supports this explanation, as individuals with less timber harvest in their home ranges displayed lower proportional use of timber harvest. This result highlights the importance of applying functional response models when interpreting patterns of habitat selection relative to disturbance, particularly in highly disturbed landscapes such as the LS range. In comparison, seasonal shifts in diet, reproductive status, and use of different land cover types likely drove avoidance of timber-harvested areas during summer. For example, caribou are not as reliant on lichen consumption in mature stands during summer months, and female caribou with young calves may reduce use of all heavily timber-harvested areas to avoid predation pressure (Viejou et al. 2018).

Limitations and further research

The limited GPS location data available during the initial stages of pine beetle infestation means that some of our estimated relationships in functional response models were uncertain. It also meant that we had to combine female and male moose into a single population model, which masked any sex-specific responses. Data collected across broader spatiotemporal scales might reveal more robust patterns, as would extending analyses to assess responses at the landscape scale (i.e., second order; Johnson 1980). Additionally, as stated, because there were limited data on pine beetle-specific management actions, we used available satellite data on timber harvest and fires as broad proxies for pine beetle salvage logging and prescribed burns. Larger GPS datasets may enable more complex and direct modeling of pine beetle management actions, for example by including the size and percent canopy removal of disturbances or by directly comparing different timber harvesting and fire types (wildfire vs. prescribed burns). The effects of timber harvest on moose also require further study, including disentanglement from the effects of elevation. Additionally, future studies could assess the responses of other species, particularly other generalist ungulates and predators, to unravel the potential role of predation risk as a driver in the patterns we observed (Curveira-Santos et al. 2024). Finally, while we assessed 2 designatable units of caribou (i.e., boreal and central mountain), we only assessed a single population from each. We, therefore, recommend that future research extend this analysis across other populations to determine the transferability of our results.

MANAGEMENT IMPLICATIONS

Pine beetles typically attack mature forests, which caribou are ecologically dependent upon and are used by moose during winter. It is, therefore, concerning that caribou and female moose avoided pine beetle-disturbed areas, particularly so soon after initial infestations. This indicates that insect infestations may further reduce habitat available to caribou and moose cumulatively to the impacts of human disturbance. Caribou also displayed complex and often avoidant responses towards timber harvest and burns. However, LS caribou showed positive responses to fire where fire occurrence was limited, suggesting that investigations into the benefits or impacts of fire management activities such as small-scale prescribed burning, Indigenous fire stewardship, or single-tree cut and burn may be useful. Given the accelerating impacts of climate change and compounding pressures faced by these species, our study highlights the need for effective early detection, response, and management of insect infestations like pine beetle, with the ultimate goal of ensuring sustainable outcomes for both wildlife and humans.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All data used in this study were previously collected for other projects, and appropriate permissions were obtained prior to use. Caribou collaring was performed under the Government of Alberta's Animal Care Protocol 008, and further detail is available in Hervieux et al. (2013). Moose collaring was performed under the University of Montana Animal Care and Use Protocol 056-56MHECS-010207 and 059-09MHWB122109, Alberta Sustainable Resource Development licenses no. 21803, 27086, 27088, 27090, and Parks Canada permit JNP-2007-952, and further detail is available in Peters et al. (2013).

DATA AVAILABILITY STATEMENT

Woodland caribou are listened as Threatened under federal legislation, are vulnerable to hunting and disturbance, and are the subject of multiple federal and provincial recovery programmes. As such, their GPS telemetry locations are kept confidential and any data sharing is made at the discretion of the Government of Alberta.

The moose data used in this study were requested and shared via Movebank (https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study178994931).

ORCID

Laura L. Griffin https://orcid.org/0000-0002-3501-3392
Virginia Morera-Pujol https://orcid.org/0000-0001-6500-5548

REFERENCES

Alberta Sustainable Resource Development. 2007. Mountain pine beetle action plan. Government of Alberta, Edmonton, Canada. https://open.alberta.ca/publications/9780778565420.

Ayres, M. P., and M. J. Lombardero. 2018. Forest pests and their management in the Anthropocene. Canadian Journal of Forest Research 48:292-301.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67(1):1-48.

Belovsky, G. E. 1981. Food plant selection by a generalist herbivore: the moose. Ecology 62:1020-1030.

Boan, J. J., B. E. McLaren, and J. R. Malcolm. 2011. Influence of post-harvest silviculture on understory vegetation: implications for forage in a multi-ungulate system. Forest Ecology and Management 262:1704-1712.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281-300.

Brodie, J. F., S. Williams, and B. Garner. 2021. The decline of mammal functional and evolutionary diversity worldwide. Proceedings of the National Academy of Sciences 118:e1921849118.

Cannon, J. B., C. J. Peterson, J. J. O'Brien, and J. S. Brewer. 2017. A review and classification of interactions between forest disturbance from wind and fire. Forest Ecology and Management 406:381-390.

Cichowski, D. 2010. Tweedsmuir-Entiako caribou project: effects of a mountain pine beetle epidemic on northern caribou habitat use: final report. Bulkley Valley Centre for Natural Resources Research and Management, Smithers, British Columbia, Canada.

Cichowski, D., G. D. Sutherland, R. S. McNay, and R. Sulyma. 2022. Direct and indirect effects of habitat disturbances on caribou terrestrial forage lichens in Montane Forests of British Columbia. Forests 13:251.

Curveira-Santos, G., S. Marion, C. Sutherland, C. Beirne, E. J. Herdman, E. R. Tattersall, J. M. Burgar, J. T. Fisher, and A. C. Burton. 2024. Disturbance-mediated changes to boreal mammal spatial networks in industrializing landscapes. Ecological Applications 34:e3004.

DeCesare, N. J., M. Hebblewhite, F. Schmiegelow, D. Hervieux, G. J. McDermid, L. Neufeld, M. Bradley, J. Whittington, K. G. Smith, and L. E. Morgantini 2012. Transcending scale dependence in identifying habitat with resource selection functions. Ecological Applications 22:1068-1083.

DeFries, R. S., J. A. Foley, and G. P. Asner. 2004. Land-use choices: Balancing human needs and ecosystem function. Frontiers in Ecology and the Environment 2:249-257.

DeMars, C. A., R. Serrouya, M. A. Mumma, M. P. Gillingham, R. S. McNay, and S. Boutin. 2019. Moose, caribou, and fire: have we got it right yet? Canadian Journal of Zoology 97:866-879.

Dempster, W. R., and S. Meredith. 2021. Growth and yield of lodgepole pine stands disturbed by mountain pine beetle in the Lower Foothills of Alberta. The Forestry Chronicle 97:65-77.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, and P. J. Leitao. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27-46.

Ferguson, S. H., and P. C. Elkie. 2004. Seasonal movement patterns of woodland caribou (Rangifer tarandus caribou). Journal of Zoology 262:125-134.

Finnegan, L., M. Hebblewhite, and K. E. Pigeon. 2023. Whose line is it anyway? Moose (*Alces alces*) response to linear features. Ecosphere 14:e4636.

Finnegan, L., S. Stevenson, C. Johnson, and T. McKay. 2021. Caribou, fire, and forestry. Literature Review prepared for the Alberta Regional Caribou Knowledge. fRI Research, Hinton, Alberta, Canada.

Frair, J. L., J. Fieberg, M. Hebblewhite, F. Cagnacci, N. J. DeCesare, and L. Pedrotti. 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2187-2200.

Francis, A. L., C. Procter, G. Kuzyk, and J. T. Fisher. 2021. Female moose prioritize forage over mortality risk in harvested landscapes. Journal of Wildlife Management 85:156-168.

Gibson, K., K. Skov, S. Kegley, C. Jorgensen, S. Smith, and J. Witcosky. 2008. Mountain pine beetle impacts in high-elevation five-needle pines: current trends and challenges. R1-08-020:1-32. U.S. Department of Agriculture Forest Service, Northern Region, Missoula, Montana, USA.

Government of Alberta. 2022. Wildlife Act. In Revised Statuses of Alberta. 2000. Chapter W-10. Alberta King's Printer. Government of Alberta, Edmonton, Canada.

Government of Alberta. 2023. Mountain Pine Beetle Inventory 1975-2010. Alberta Forestry, Parks and Tourism. https://geodiscover.alberta.ca/geoportal/rest/metadata/item/23ea7ff3fe2e4acdb39039ca40c912c3/html. Accessed 22 Feb 2024.

Government of Alberta, and B. Tyssen. 2009. Mountain pine beetle aerial overview 2005. Forestry and Parks. https://open.alberta.ca/publications/mountain-pine-beetle-aerial-survey-sites-map#detailed. Accessed 22 Feb 2024.

Government of Canada. 2018. Progress report on unprotected critical habitat for the woodland caribou (*Rangifer tarandus caribou*), Boreal population, in Canada - April 2018. https://www.canada.ca/en/environment-climate-change/

services/species-risk-public-registry/critical-habitat-reports/woodland-caribou-boreal-population-2018.html#toc7. Accessed 6 Mar 2024.

Gupte, P. R., C. E. Beardsworth, O. Spiegel, E. Lourie, S. Toledo, R. Nathan, and A. I. Bijleveld. 2022. A guide to pre-processing high-throughput animal tracking data. Journal of Animal Ecology 91:287-307.

Hebblewhite, M., M. Percy, and E. H. Merrill. 2007. Are all global positioning system collars created equal? Correcting habitat-induced bias using three brands in the central Canadian Rockies. Journal of Wildlife Management 71:2026-2033.

Hedlin, E., and A. Franke. 2017. An introduction to survival analysis using generalized linear mixed models. Pages 127–146 *in* D. L. Anderson, C. J. W. McClure, and A. Franke, editors. Applied raptor ecology: essentials from gyrfalcon research. The Peregrine Fund, Boise, Idaho, USA.

Hermosilla, T., M. A. Wulder, J. C. White, N. C. Coops, and G. W. Hobart. 2018. Disturbance-informed annual land cover classification maps of Canada's forested ecosystems for a 29-year landsat time series. Canadian Journal of Remote Sensing 44:67-87.

Hermosilla, T., M. A. Wulder, J. C. White, N. C. Coops, G. W. Hobart, and L. B. Campbell. 2016. Mass data processing of time series Landsat imagery: pixels to data products for forest monitoring. International Journal of Digital Earth 9:1035-1054.

Hervieux, D., M. Hebblewhite, N. J. DeCesare, M. Russell, K. Smith, S. Robertson, and S. Boutin. 2013. Widespread declines in woodland caribou (*Rangifer tarandus caribou*) continue in Alberta. Canadian Journal of Zoology 91:872-882.

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.

Howe, M., A. Carroll, C. Gratton, and K. F. Raffa. 2021. Climate-induced outbreaks in high-elevation pines are driven primarily by immigration of bark beetles from historical hosts. Global Change Biology 27:5786-5805.

Johnson, C. J., and R. V. Rea. 2023. Response of moose to forest harvest and management: a literature review. Canadian Journal of Forest Research 54:366-388.

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

Joly, K., M. S. Sorum, T. Craig, and E. L. Julianus. 2016. The effects of sex, terrain, wildfire, winter severity, and maternal status on habitat selection by moose in north-central Alaska. Alces 52:101-115.

Koetke, L. J., D. P. Hodder, R. V. Rea, C. J. Johnson, and S. Marshall. 2023. Landscape disturbance alters the composition and diversity of the diet of moose, a generalist herbivore. Forest Ecology and Management 530:120760.

Lacerte, R., M. Leblond, and M. H. St-Laurent. 2021. Determinants of vegetation regeneration on forest roads following restoration treatments: implications for boreal caribou conservation. Restoration Ecology 29:e13414.

Lewis, D. 2008. Mountain pine beetle, wildlife habitat, and biodiversity: lessons learned and future challenges. Pages 24-32 *in* Mountain pine beetle: From lessons learned to community-based solutions conference proceedings. University of Northern British Columbia, 10-11 June 2008, Prince George, Canada.

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.

Lewis, K. J., and I. D. Hartley. 2006. Rate of deterioration, degrade, and fall of trees killed by mountain pine beetle. Journal of Ecosystems and Management 7:11-19.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640.

Lindenmayer, D., R. J. Hobbs, R. Montague-Drake, J. Alexandra, A. Bennett, M. Burgman, P. Cale, A. Calhoun, V. Cramer, and P. Cullen. 2008. A checklist for ecological management of landscapes for conservation. Ecology Letters 11:78-91.

MacNearney, D., K. Pigeon, G. Stenhouse, W. Nijland, N. C. Coops, and L. Finnegan. 2016. Heading for the hills? Evaluating spatial distribution of woodland caribou in response to a growing anthropogenic disturbance footprint. Ecology and Evolution 6:6484-6509.

Main, M. B. 2008. Reconciling competing ecological explanations for sexual segregation in ungulates. Ecology 89:693-704.

McClelland, C. J. R., B. Nobert, T. A. Larsen, K. E. Pigeon, and L. Finnegan. 2023. The impact of mountain pine beetle outbreaks and their treatment methods on the abundance of plant-foods important to caribou and grizzly bears. Forest Ecology and Management 532:120841.

Mitton, J. B., and S. M. Ferrenberg. 2012. Mountain pine beetle develops an unprecedented summer generation in response to climate warming. American Naturalist 179:E163-E171.

Mumma, M. A., A. R. Bevington, S. Marshall, and M. P. Gillingham. 2024. Delineating wildfire burns and regrowth using satellite imagery to assess moose (*Alces alces*) spatial responses to burns. Ecosphere 15:e4793.

Mumma, M. A., M. P. Gillingham, K. L. Parker, C. J. Johnson, and M. Watters. 2018. Predation risk for boreal woodland caribou in human-modified landscapes: evidence of wolf spatial responses independent of apparent competition. Biological Conservation 228:215-223.

Mysterud, A., and R. A. Ims. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. Ecology 79:1435-1441.

Natural Regions Committee. 2006. Natural regions and subregions of Alberta. Publication T/852. Government of Alberta, Edmonton, Canada.

Natural Resources Canada. 2011. Canadian Digital Elevation Model. https://ftp.maps.canada.ca/pub/nrcan_rncan/vector/index/html/geospatial_product_index_en.html. Accessed 24 Aug 2023.

Neufeld, B. T., C. Superbie, R. J. Greuel, T. Perry, P. A. Tomchuk, D. Fortin, and P. D. McLoughlin. 2021. Disturbance-mediated apparent competition decouples in a northern boreal caribou range. Journal of Wildlife Management 85:254-270.

Nobert, B. R., T. A. Larsen, K. E. Pigeon, and L. Finnegan. 2020. Caribou in the cross-fire? Considering terrestrial lichen forage in the face of mountain pine beetle (*Dendroctonus ponderosae*) expansion. Plos One 15:e0232248.

Ono, H. 2004. The mountain pine beetle: scope of the problem and key issues in Alberta. Pages 62–66 *in* T. L. Shore, J. E. Brooks and J. E. Stone, editors. Mountain Pine Beetle Symposium: challenges and solutions. Pacific Forestry Centre, 30-31 October 2003, Kelowna, British Columbia, Canada.

Pappas, G. S., D. B. Tinker, and M. E. Rocca. 2020. Understory vegetation response to mountain pine beetle disturbance in northern Colorado lodgepole pine forests. Plant Ecology 221:1293-1308.

Pec, G. J., J. Karst, A. N. Sywenky, P. W. Cigan, N. Erbilgin, S. W. Simard, and J. F. Cahill Jr. 2015. Rapid increases in forest understory diversity and productivity following a mountain pine beetle (*Dendroctonus ponderosae*) outbreak in pine forests. PLoS One 10:0124691.

Peter, B., and B. E. C. Bogdanski. 2010. The economics of salvage harvesting and reforestation in British Columbia's mountain pine beetle-affected forests. Pacific Forestry Centre, Victoria, British Columbia, Canada.

Peters, W., M. Hebblewhite, N. DeCesare, F. Cagnacci, and M. Musiani. 2013. Resource separation analysis with moose indicates threats to caribou in human altered landscapes. Ecography 36:487-498.

Pirotta, E., C. G. Booth, D. P. Costa, E. Fleishman, S. D. Kraus, D. Lusseau, D. Moretti, L. F. New, R. S. Schick, and L. K. Schwarz. 2018. Understanding the population consequences of disturbance. Ecology and Evolution 8:9934-9946.

Priadka, P., B. Moses, C. Kozmik, S. Kell, and J. N. Popp. 2022. Impacts of harvested species declines on Indigenous Peoples' food sovereignty, well-being and ways of life: a case study of Anishinaabe perspectives and moose. Ecology and Society 27:30.

QGIS Development Team. 2023. QGIS Geographic Information System version 3.32.1. Open Source Geospatial Foundation. https://qgis.org/en/site/

R Core Team. 2023. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reimers, E., and J. E. Colman. 2006. Reindeer and caribou (*Rangifer tarandus*) response towards human activities. Rangifer 26:55-71.

Roberts, D. R., V. Bahn, S. Ciuti, M. S. Boyce, J. Elith, G. Guillera-Arroita, S. Hauenstein, J. J. Lahoz-Monfort, B. Schröder, and W. Thuiller. 2017. Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography 40:913-929.

Rudolph, T. D., and P. Drapeau. 2012. Using movement behaviour to define biological seasons for woodland caribou. Rangifer 32:295-307.

Rudolph, T. D., D. MacNearney, and L. Finnegan. 2019. Lost in translation? Insights into caribou habitat selection from forest inventory data. Facets 4:531-550.

Russell, T., D. Pendlebury, and A. Ronson. 2016. Alberta's caribou: a guide to range planning, volume 2: Little Smoky. Canadian Parks and Wilderness Society, Edmonton, Alberta, Canada.

Saab, V. A., Q. S. Latif, M. M. Rowland, T. N. Johnson, A. D. Chalfoun, S. W. Buskirk, J. E. Heyward, and M. A. Dresser. 2014. Ecological consequences of mountain pine beetle outbreaks for wildlife in western North American forests. Forest Science 60:539-559.

Sakamoto, Y., M. Ishiguro, and G. Kitagawa. 1986. Akaike information criterion statistics. Springer, Dordrecht, The Netherlands.

Sambaraju, K. R., and D. W. Goodsman. 2021. Mountain pine beetle: an example of a climate-driven eruptive insect impacting conifer forest ecosystems. CABI Reviews 16:18.

Schaefer, J. A., and S. P. Mahoney. 2007. Effects of progressive clearcut logging on Newfoundland caribou. Journal of Wildlife Management 71:1753-1757.

Seip, D., and E. Jones. 2008. Response of woodland caribou to partial retention logging of winter ranges attacked by mountain pine beetle. FIA/FSP project #Y091010:9. Forest Science Program, Victoria, British Columbia, Canada.

Semeniuk, C. A. D., M. Musiani, M. Hebblewhite, S. Grindal, and D. J. Marceau. 2012. Evaluating risk effects of industrial features on woodland caribou habitat selection in west central Alberta using agent-based modelling. Procedia Environmental Sciences 13:698-714.

Signer, J., J. Fieberg, and T. Avgar. 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecology and Evolution 9:880-890.

Silva, J. 2020. Fire, lichens, and woodland caribou (*Rangifer tarandus caribou*) in Canada's Boreal Shield. Dissertation, University of Alberta, Edmonton, Canada.

Smith, A. F., S. Ciuti, D. Shamovich, V. Fenchuk, B. Zimmermann, and M. Heurich. 2022. Quiet islands in a world of fear: wolves seek core zones of protected areas to escape human disturbance. Biological Conservation 276:109811.

Steinke, J., A. C. S. McIntosh, L. Schroeder, and S. E. Macdonald. 2020. Understory vegetation responses to simulated mountain pine beetle attack and salvage logging in grey attack stage lodgepole pine stands. Forest Ecology and Management 474:118373.

Stevenson, S., L. Finnegan, C. Johnson, and T. McKay. 2024. Differential responses of woodland caribou to fire and forestry across boreal and montane ecosystems—a literature review. Forestry: An International Journal of Forest Research cpae053. https://academic.oup.com/forestry/advance-article/doi/10.1093/forestry/cpae053/7833417#489737993

Telfer, E. S., and J. P. Kelsall. 1979. Studies of morphological parameters affecting ungulate locomotion in snow. Canadian Journal of Zoology 57:2153-2159.

Thompson, M. E., J. R. Gilbert, G. J. Matula Jr., and K. I. Morris. 1995. Seasonal habitat use by moose on managed forest lands in northern Maine. Alces 31:223-245.

Thorn, S., C. Bässler, R. Brandl, P. J. Burton, R. Cahall, J. L. Campbell, J. Castro, C. Y. Choi, T. Cobb, and D. C. Donato. 2018. Impacts of salvage logging on biodiversity: a meta-analysis. Journal of Applied Ecology 55:279-289.

Timmermann, H. R., and J. G. McNicol. 1988. Moose habitat needs. Forestry Chronicle 64:238-245.

van Beest, F.M., B. Van Moorter, and J.M. Milner. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. Animal Behaviour 84:723-735.

van Ginkel, H. A. L., M. Churski, D. P. J. Kuijper, and C. Smit. 2021. Impediments affect deer foraging decisions and sapling performance. Forest Ecology and Management 482:118838.

Viejou, R., T. Avgar, G. S. Brown, B. R. Patterson, D. E. B. Reid, A. R. Rodgers, J. Shuter, I. D. Thompson, and J. M. Fryxell. 2018. Woodland caribou habitat selection patterns in relation to predation risk and forage abundance depend on reproductive state. Ecology and Evolution 8:5863-5872.

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

Webber, Q. M. R., K. M. Ferraro, J. G. Hendrix, and E. Vander Wal. 2022. What do caribou eat? A review of the literature on caribou diet. Canadian Journal of Zoology 100:197-207.

Weckworth, B. V., M. Hebblewhite, S. Mariani, and M. Musiani. 2018. Lines on a map: conservation units, meta-population dynamics, and recovery of woodland caribou in Canada. Ecosphere 9:e02323.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis. Springer, New York, New York, USA.

Zeileis, A., and T. Hothorn. 2002. Diagnostic checking in regression relationships. R News 2:7–10.

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