

RESEARCH ARTICLE



Linking woodland caribou abundance to forestry disturbance in southern British Columbia, Canada

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Abstract

The decline of many woodland caribou (*Rangifer tarandus caribou*) populations is thought to be linked with habitat disturbances resulting from industrial development, including timber harvesting and its network of haul roads. Defining a disturbance-abundance relationship offers a tool to assess and potentially manage for the influence of disturbance on caribou abundance. Defining this relationship is challenged by limited historical land use and abundance data, the choice of a disturbance measure, and variability in the relationship between subpopulations and across core versus matrix habitat. For 12 subpopulations of woodland caribou within the southern mountain population, we linked longitudinal caribou abundance data with historical forestry disturbances simulated from forest harvest data. We compared disturbance measures estimating the proportion of forested area commercially harvested with even-aged, regeneration treatments (cutblocks) and converted to roads for transporting timber within subpopulation-specific core and matrix habitats as predictors of caribou abundance. Non-linear mixed models provided evidence that disturbances in matrix habitats negatively influenced caribou abundance, with the effects in core habitat being variable between subpopulations. Of the disturbance types evaluated, the best predictors included roads buffered by 50 m (R50), cutblocks ≤ 80 years old, and the cumulation of cutblocks ≤ 80 years old plus roads buffered by 50 m. The top-ranked model was composed of R50 present in core and in matrix habitats.



This model predicted a 42% (95% CI = 33–51%) reduction in caribou abundance for every 1% increase in matrix R50 (holding core R50 constant). Given the lack of pre-forestry abundance data, we failed to directly derive critical disturbance thresholds; however, our models could be used to estimate subpopulation-specific habitat-disturbance thresholds necessary to achieve abundance targets. We recommend that in addition to existing protections of core habitat, few if any new roads should be built in core habitat, and that timber harvest in matrix habitat should be designed to minimize the establishment of associated roads.

KEYWORDS

landscape disturbance, land use simulation models, matrix habitat, *Rangifer tarandus caribou*, roads, wildlife conservation

The persistence of many woodland caribou (*Rangifer tarandus caribou*) populations remains uncertain, as ongoing population declines are intricately linked with industrial development, which includes oil and gas, mining, and commercial timber harvest activities, and all associated roads that serve these activities (Vors and Boyce 2009, Festa-Bianchet et al. 2011). Timber harvest can alter caribou habitat by increasing the amount of early-seral forest and linear features such as roads (collectively referred to as disturbances). Measures that quantify timber harvest and other industrial disturbances within caribou habitat are negatively correlated with caribou population trends (Sorensen et al. 2008, Johnson et al. 2015, Fryxell et al. 2020), survival, and recruitment rates (Wittmer et al. 2007, 2010; Johnson et al. 2020). The extent of industrial development that a landscape can sustain while also supporting viable caribou populations is a key management question that remains uncertain for several caribou populations (Wittmer et al. 2010).

Habitat loss and the functional and numerical responses of predators to disturbances are mechanisms thought to explain the negative effects of industrial disturbance on caribou abundance. Habitat loss is a direct result of industrial development and these impacts can extend several kilometers from a single disturbance feature (Polfus et al. 2011). A predator numerical response occurs when human disturbance features indirectly increase predator density by directly enhancing habitat for their prey (DeCesare et al. 2010). The increased proportion of early-seral forest resulting from timber harvest is thought to be beneficial to alternative prey species like moose (*Alces americanus*; Mumma et al. 2021), potentially increasing their fecundity. An increase in prey abundance can lead to a numerical response in predators such as wolves (*Canis lupus*), black (*Ursus americanus*) and grizzly bears (*U. arctos*), or cougars (*Puma concolor*), which further leads to increased predation on caribou (Seip 1992, Wittmer et al. 2005b, DeCesare et al. 2010, Apps et al. 2013). A predator functional response occurs when disturbances facilitate predator movement across a landscape (DeCesare et al. 2010). Linear disturbance features such as roads can help predators move farther and faster (Dickie et al. 2017, 2020), increasing encounter rates with caribou (Whittington et al. 2011) and potentially predation rates. Caribou are primarily regulated by predation (Seip 1992, DeCesare et al. 2010, Apps et al. 2013). Therefore, abundance of caribou is primarily driven by the effectiveness of predator avoidance strategies (Seip and Cichowski 1996), which can be disrupted by industrial disturbances (Beauchesne et al. 2013), necessitating disturbance management policies in caribou habitat. In addition, these relationships occur across large spatial and temporal scales (Apps et al. 2013, Johnson et al. 2015) making industrial disturbance management a complex land use problem.



The southern group of the southern mountain population of woodland caribou (SGSMC; Environment Canada 2014) is an ecologically distinct group that has experienced an estimated 50% loss in habitat and several sub-population extirpations (Wittmer et al. 2010, Festa-Bianchet et al. 2011). Habitat management to conserve these caribou has largely prioritized protection of areas occupied by caribou (i.e., core habitat); however, there is increasing evidence that these efforts may be insufficient to support stable caribou populations (Wittmer et al. 2007, 2010; Nagy-Reis et al. 2021). Apps et al. (2013) concluded that habitat conditions outside of core southern mountain population habitats can drive numerical and functional predator responses, suggesting that habitat management strategies are also needed for matrix habitats (i.e., habitats adjacent to core habitats). Although matrix habitat is rarely used by caribou, it acts as habitat for other ungulate species such as moose, elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*) that share the same predators as caribou, such as wolves, bears, and cougars, and thus may influence caribou predation in core habitat (Seip and Jones 2015). In general, the quality of matrix habitat has been shown to be an important indicator of animal persistence (Prevedello and Vieira 2010, Swift and Hannon 2010), given increased mortality risk in these habitats (Seip 1992, Apps et al. 2013). For example, Fahrig (2001) used a spatially explicit simulation model of population dynamics for a hypothetical organism to show that improving matrix habitat quality (including reducing mortality factors) could improve population persistence, despite substantial loss of core habitat. While SGSMC core habitat has largely been protected (Wittmer et al. 2010), matrix habitat may also need consideration as part of a disturbance management strategy for caribou.

Models that define the relationship between habitat disturbance and caribou abundance offer a tool to assess the implications of proposed habitat management regimes for caribou populations. Similar models have been developed for woodland caribou in boreal landscapes, where the amount of industrial disturbance buffered by 500 m in caribou habitat was a strong predictor of adult female survival (Johnson et al. 2020). Based on similar work, the woodland caribou recovery strategy for the boreal population recommended a maximum of 35% disturbed habitat in caribou ranges to achieve a sufficient probability of achieving self-sustaining subpopulations (Environment Canada 2011), with this threshold also proposed for some habitats of the southern mountain population (Environment Canada 2014).

Though various habitat-disturbance measures have been previously linked to caribou population responses (Wittmer et al. 2007, 2010; Sorensen et al. 2008; Johnson et al. 2020), their use in identifying critical disturbance thresholds is limited by several challenges (Swift and Hannon 2010). First, given limited monitoring funds, disturbance thresholds are often extrapolated across populations (Environment Canada 2014) and subpopulations that have different demographics (Rudolph et al. 2017) and life-history strategies, and are part of distinct ecological groups (Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2011), risking the implementation of incorrect disturbance regimes. Second, the correlative relationship between habitat-disturbance measures and caribou population responses have sometimes relied on small sample sizes (e.g., $n = 6$; Sorensen et al. 2008), limiting the variation of disturbed landscapes being sampled and thus the generalizability of this relationship (Sleep and Loehle 2010). Third, the lack of historical land use data forces studies to rely on sampling a gradient of disturbed landscapes from the current disturbance profile, thereby substituting space for time (Damgaard 2019). This problem negates the importance of subpopulation-specific trends in disturbance (Schrott et al. 2005) or sources of variation between subpopulations (Rudolph et al. 2017), potentially risking an ecological fallacy (Piantadosi et al. 1988). Lastly, disturbance analyses should distinguish between disturbances in the core habitat and disturbances within adjacent matrix habitat that can affect the predator-prey system (Andr n et al. 1997) because the disturbance relationships likely differ between these types.

Our objective was to quantify the relationship between habitat disturbance and caribou abundance for 12 subpopulations of SGSMC. We focused on forestry disturbance types because of the prevalence of these disturbances in the study area, their potential to influence numerical and functional predator responses, and our ability to exclusively model historical forestry activities. We tested whether trends

in historical forestry disturbances were negatively related to caribou abundance, and whether the effect differed by specific disturbance type (i.e., road, cutblock, and spatial buffers) and by habitat (core or matrix). We hypothesized that 1) forestry disturbance measures in core habitat would have a larger negative effect on caribou abundance than disturbances in matrix habitat, 2) cumulative disturbance measures that included both cutblocks and roads would be the best predictors of caribou abundance because they account for both numerical and functional responses of predators, 3) applying a 500-m spatial buffer on disturbances would be a better predictor of caribou abundance because caribou exhibit avoidance behavior with these disturbances, and 4) the magnitude of the disturbance effect would vary among subpopulations because of unaccounted variation in habitat conditions and predator-prey communities experienced by each subpopulation.

STUDY AREA

Our study area encompassed the current (as of 2021) range of the SGSMC, an endangered ecotype of woodland caribou that reside in mountainous landscapes in the southeastern portion of the province of British Columbia, Canada (COSEWIC 2011, Environment Canada 2014). Sixteen distinct herds or subpopulations (Environment Canada 2014) comprise SGSMC, of which 12 were included in this study (Figure 1) because of limitations with abundance data (described later). The SGSMC predominately resided in 3 biogeoclimatic zones: Alpine-Tundra at high elevations; Engelmann-Spruce Subalpine fir at mid elevations, and Interior Cedar Hemlock at lower elevations. Wittmer et al. (2005a) describe the flora and fauna in this area.

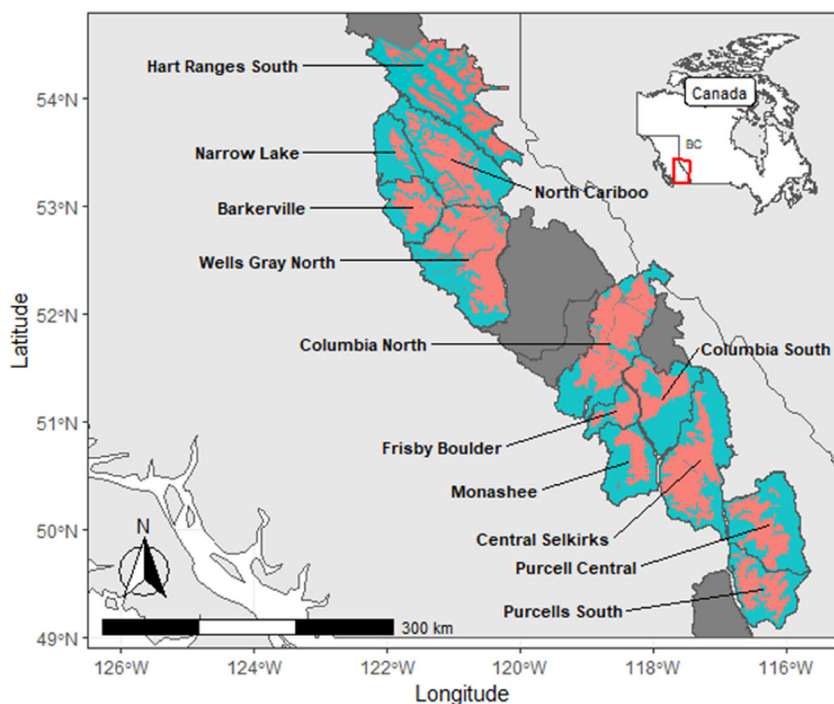


FIGURE 1 The distribution of the southern group of the southern mountain population of woodland caribou in British Columbia, Canada, 2020. Subpopulations analyzed in this study have their respective core (red) and matrix (blue) habitats delineated



The range of these subpopulations had a combined extent of 65,234 km² (73% forested; Table 1) and topography was highly variable; elevation ranged from 350 m to >3,500 m. Climate was also variable and heavily influenced by Pacific air masses. Mean annual precipitation averaged 1,213 ± 358 (SD) mm across the subpopulations, with most (>50%) occurring as snow (Wang et al. 2016). These cool, wet conditions have historically limited stand-replacing wildfires leading to landscapes dominated by older forest stands (Meidinger and Pojar 1991). These conditions allowed for large areas of commercial timber, which have been harvested extensively with even-aged, clear-cut regeneration methods and various levels of overstory retention such as seed tree prescriptions or other small reserves, referred to hereafter as cutblocks. Extraction of timber is typically preceded with building primitive haul roads. Between 1980 to 2021 (our study period), forestry-related disturbances on average made up 79 ± 8% (excluding roads) of the industrial disturbance (including roads, forestry, mining, and energy) footprint within SGSMC subpopulation ranges.

The SGSMC demonstrate distinct behavior related to their use of these landscapes that set them apart from other ecotypes (COSEWIC 2011). During winter, they tend to be found at high elevations where snowpack is 2–4 m, foraging for arboreal lichen, and in spring, some migrate to valley bottoms to forage on vascular plants. During summer, they return to high-elevation mountainous areas for calving and forage (Wittmer et al. 2005b). These seasonal altitudinal migrations were important factors for distinguishing habitat within caribou range (Seip and Jones 2015).

METHODS

Habitat delineation

Caribou biologists in the British Columbia Government classified habitat as core or matrix (Figure 1; British Columbia Provincial Caribou Recovery Program 2021). They defined core areas as those providing enough suitable habitat to support the life-history requirements of caribou across all seasons and to allow for movements on the landscape over time in response to disturbances. Biologists delineated core areas using subpopulation-specific information such as habitat models, telemetry data, biogeoclimatic zone, elevation, and forest type, when available. They defined matrix habitat as areas adjacent to core that had periodic or low known use by caribou but were used by primary prey and predators associated with caribou. They delineated matrix habitat using subpopulation-specific spatial buffers that ranged upwards of 30 km from core areas and further modified matrix areas based on data on local predator or prey distributions (where available), natural or topographic boundaries impeding predator movement (e.g., large water bodies, glaciers, human settlement), and expert knowledge.

Forestry disturbance

Although several landscape-level disturbances (i.e., fire, other industrial activity) are related to caribou population demographics, we focused on forestry-related disturbances. Empirical forestry cutblock data provided harvest year and cutblock perimeters (British Columbia Ministry of Forests Lands Natural Resource Operations and Rural Development [FLNRORD] 2017), thus, we could estimate cutblock development over time and space. Road data lacked a development year and industrial use; thus, we used the caribou and land-use simulator (CLUS) model (<https://github.com/bcgov/clus>) to estimate the location and timing of forestry-road development by spatially associating roads with cutblocks (Figure 2). The CLUS used the R package SpaDES (Chubaty and McIntire 2018) to develop a reproducible 2-phase model, where an initiation phase estimated road paths, and a simulation phase attributed cutblock development with roads, through time.

TABLE 1 Total area, forested area, and the range (min.–max.) of forestry disturbance measures (i.e., percent of forested area that are roads buffered by 50 m [R50], cutblocks ≤80 years old [C80], or the cumulation of C80 and R50 [C80R50]) estimated within core or matrix habitat for subpopulations of the southern group of the southern mountain population of woodland caribou in British Columbia, Canada, 1980–2020

Subpopulation	Core			Matrix						
	Total (km ²)	Forest (km ²)	R50 (%)	C80 (%)	C80R50 (%)	Total (km ²)	Forest (km ²)	R50 (%)	C80 (%)	C80R50 (%)
Barkerville	1,562	1,384	3.6–5.1	10.1–13.8	12.6–17.0	1,497	1,312	7.9–10.5	26.2–36.7	30.6–41.7
Central Selkirks	3,935	2,361	2.3–3.0	4.8–6.4	6.2–8.1	4,311	2,674	5.3–7.5	9.5–16.2	13.1–20.4
Columbia North	4,806	2,813	4.0–5.4	10.2–13.3	12.3–16.0	3,245	2,052	6.1–8.0	14.7–19.6	18.3–23.8
Columbia South	1,978	1,121	2.8–3.8	4.9–6.8	6.9–9.2	2,873	1,325	3.7–4.3	8.1–9.5	10.3–12.0
Frisby Boulder	885	578	3.8–4.5	12.0–13.9	13.6–15.6	794	442	9.8–12.5	18.7–25.9	25.2–33.2
Hart South	3,414	1,865	0.4–0.4	1.1–1.1	1.4–1.4	4,564	3,922	5.6–6.1	23.1–26.1	25.9–28.9
Monashee	1,095	665	1.4–1.8	3.3–4.3	4.1–5.3	2,700	2,492	6.5–7.9	14.8–18.2	18.8–22.8
Narrow Lake	345	333	1.3–1.6	7.7–8.5	8.3–9.2	2,074	1,873	9.1–10.6	49.5–58.0	52.8–61.0
North Cariboo	2,831	1,727	0.6–0.7	4.4–4.9	4.6–5.2	3,865	2,782	6.3–7.1	28.0–32.4	31.0–35.4
Purcell Central	2,306	1,310	0.3–0.5	0.5–1.0	0.7–1.3	3,845	2,769	5.0–5.8	9.0–11.4	12.8–15.5
Purcells South	2,029	1,766	3.8–5.0	10.6–14.7	12.8–17.2	2,132	1,886	6.3–8.9	11.6–19.0	16.1–24.5
Wells Gray North	4,760	3,172	1.4–1.9	4.1–5.7	5.0–6.7	3,389	2,802	6.4–7.4	21.5–24.7	24.9–28.6

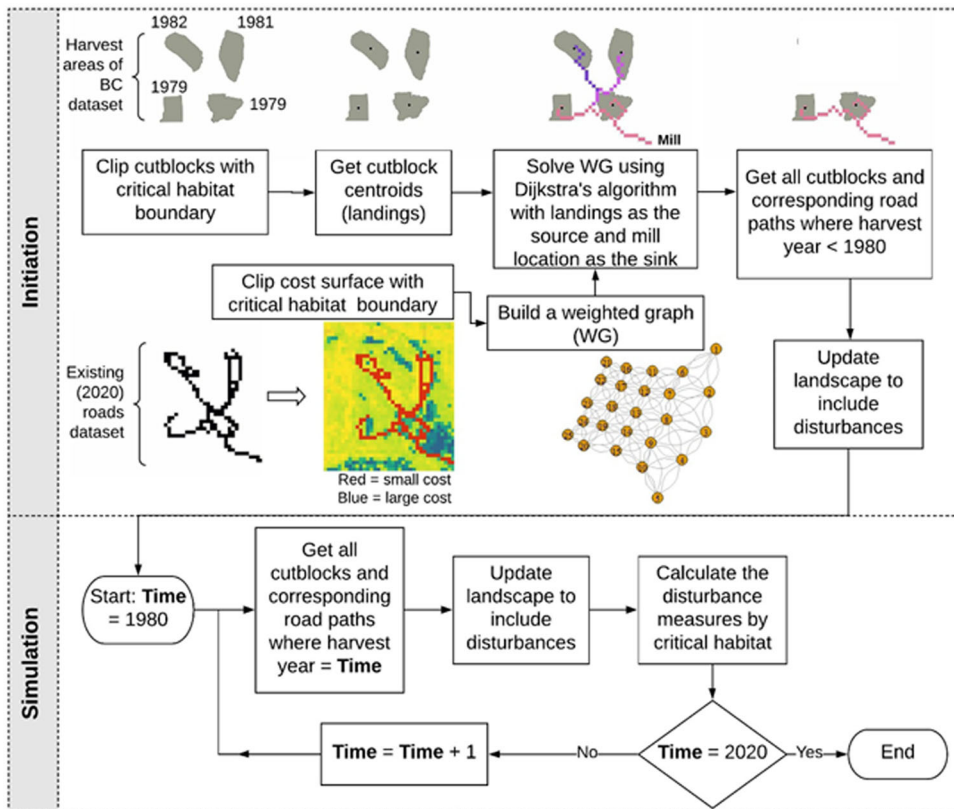


FIGURE 2 Flow chart illustrating the analytical approach used to estimate historical forestry disturbance profiles within the habitat of the southern group of the southern mountain population of woodland caribou in British Columbia, Canada, 1980–2020

During the initiation phase, we simulated least-cost paths between the centroid of each cutblock (assumed as a landing for a deck of logs) intersecting the subpopulation range (i.e., core and matrix habitat) and the closest forestry mill location (Figure 2). We used Dijkstra's algorithm via the R package *igraph* (Csardi and Nepusz 2006) to simulate the least-cost paths by solving a weighted graph. We used a cost surface to set the weights in the weighted graph, which we estimated using a combination of the existing (as of 2020) road network data and road construction cost estimates (required for connecting non-road areas between the landing and existing road network). We constructed the existing road network by amalgamating the forest road tenure (FLNRORD 2018) and digital road atlas (Data BC 2018) datasets. We buffered all road paths by 50 m, rasterized to a 1-ha resolution, and assigned the smallest cost (i.e., 0.01) to coerce the least-cost algorithm to follow the existing road paths and thereby reproduce the spatial location of roads observed in the data. The road construction costs depended on biogeoclimatic zone, timber supply area, topography, and linear crossings (e.g., pipelines, rivers) following the Interior Appraisal Manual (FLNRORD 2011). The outcome of the initiation phase was a set of road paths that corresponded to each cutblock.

During the simulation phase, we quantified cutblock disturbances at a 1-ha spatial resolution on an annual basis between 1980 and 2020 (Figure 2). For each year, we simulated the corresponding road path for each harvested cutblock. Thus, we simulated only forestry roads connecting cutblocks to the developing road network. We assumed all road paths remained active on the landscape (no recovery). At the end of each simulation year, we calculated various disturbance measures (described later) as a percentage of the forested area, which we obtained



from forest inventory data (FLNRORD 2019), within core areas, matrix areas, and total range area (core + matrix; Table 1).

We designed the disturbance measures to capture possible effects of habitat loss (percentage of forest disturbed), functional responses of predators to linear features, avoidance behavior (though spatial buffers), and early-seral forest vegetation (0–40 yr) that may be selected by other ungulates (numerical responses of predators). We evaluated different combinations of models containing road and cutblock disturbance types as percentages of forested area within core areas, matrix areas, and total range area (core + matrix). Road disturbances included those buffered by 50 m (R50, the minimum spatial resolution of our data) or by 500 m (R500, as used by Sorensen et al. [2008] and Johnson et al. [2020]). Cutblock disturbances included 3 ages of cutblocks representing different stages of middle to early forest succession: ≤ 80 years old (C80), 10–40 years old (C10–40), and ≤ 40 years old (C40). We evaluated each road and cutblock disturbance type by themselves as individual models: core areas, matrix areas, and for the total range area (core + matrix). We further evaluated each of the 2 road disturbance types in combination with each of the 3 cutblock disturbance types as unique models, again for the core, matrix, and total range area. For models that combined R500 and cutblock disturbance types, we also included 500-m buffers around cutblock disturbance types. We calculated these combined disturbance measures with spatial overlap to avoid double counting in cases where pixels were both a cutblock and road. We opted to estimate road area instead of road density to account for caribou avoidance behavior as used in the proposed disturbance measure for the southern mountain population (Environment Canada 2014) and because road buffers provide a direct measure of the spatially explicit effects of roads that can otherwise be confounded with spatial scale when using road density estimates (Rowland et al. 2000).

Caribou abundance

We estimated caribou abundance from several sources of aerial survey data collected between 1993 to 2020 (Figure 3; British Columbia Ministry of Environment 2018). To maintain consistency, we strictly used surveys that corrected abundance for sightability through the resighting of telemetry-collared caribou. We derived corrected abundance and 95% confidence intervals (90% for Columbia North and Columbia South) from a joint hypergeometric maximum likelihood estimator using the NOREMARK software (White 1996). We set the lower confidence limit to the actual number of caribou seen during a survey when it was greater than the estimated lower confidence limit. When abundance was low, or collar information was lacking, we used a sightability correction factor (estimated as the proportion of sighted collars to the total number of known collars, averaged across survey years), following Wittmer et al. (2005a). The averaged sightability corrections were 0.709 (Barkerville), 0.830 (Frisby Boulder, Hart South, Monashee, Narrow Lake, North Cariboo), 0.813 (Purcell Central and Purcells South), and 0.857 (Wells Gray North).

Twelve SGSMC subpopulations provided >2 yearly surveys not confounded with population management involving maternity penning and wolf or moose reductions (Figure 3). We removed surveys from the sample when collected within 1 year of a moose reduction, given a lag effect was typically observed (Hervieux et al. 2014, Serrouya et al. 2017). An exception was the Hart Ranges subpopulation, which amalgamated Hart Ranges South and Parsnip locations. After recommendations from provincial biologists, we used only the Hart Ranges South abundance surveys and habitat boundary data because the Parsnip was considered distinct from Hart Ranges South. Overall, our analysis used 81 surveys from 12 subpopulations.

Analysis

We tested the effects of forestry disturbances on caribou abundance by fitting non-linear mixed effects models within the R package nlme (Pinheiro et al. 2017). A mixed modeling framework effectively captured the hierarchical

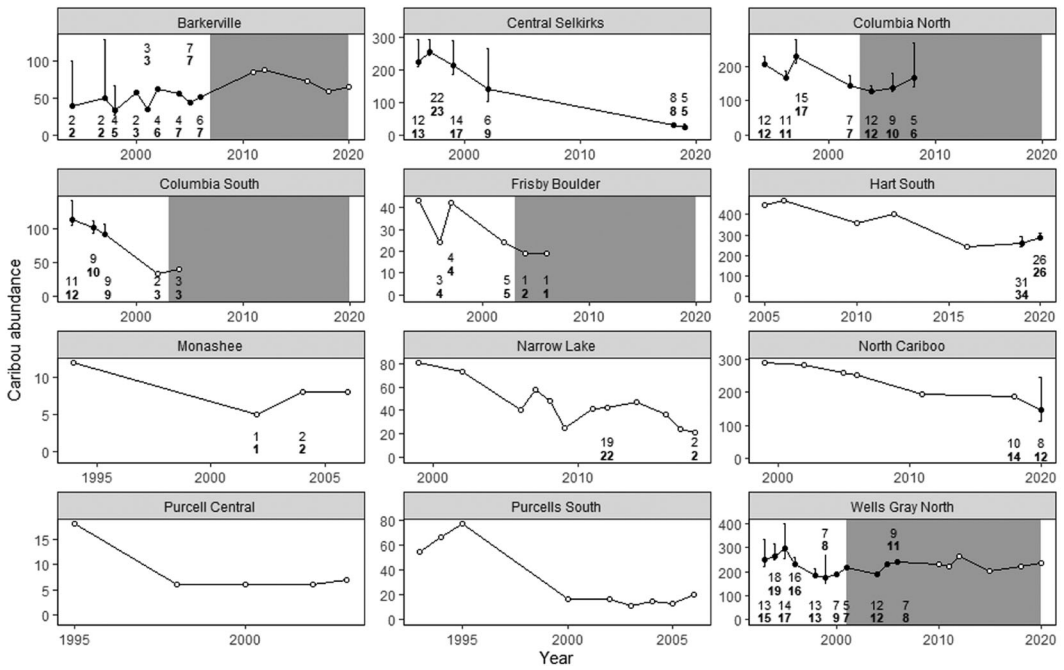


FIGURE 3 Corrected abundance estimates for subpopulations of the southern group of the southern mountain population of woodland caribou in British Columbia, Canada, 1993–2020. Labels correspond to the total (bolded) and sighted number of collared caribou during the survey. Solid circles represent estimates using a joint hypergeometric estimator with error bars representing 95% confidence intervals (90% for Columbia North and Columbia South). Open circles represent estimates that used a sightability correction factor. Shaded areas represent one or a combination of population management strategies, including maternity penning and wolf or moose reduction, that could affect caribou abundance (does not necessarily denote the exact timing of the strategy)

structure of our data, which was needed to estimate potential variation between subpopulations. We selected an exponential model, given its simplicity and biological relevancy to density-dependent population growth. While a logistic growth model would have been more realistic given potential resource constraints, or carrying capacity, our data had poor coverage of stable, high population estimates, which meant a carrying capacity could not be estimated. We included disturbance measures in the core and matrix separately (eq. 1) or together (eq. 2) as fixed effects and subpopulation as the random effects, the full models follow as:

$$N_{it} = \exp(\beta_0 + b_{0i} + (\beta_1 + b_{1i})Core_{it} + (\beta_2 + b_{2i})Matrix_{it}) + \varepsilon_{it} \quad (1)$$

$$N_{it} = \exp(\beta_0 + b_{0i} + (\beta_3 + b_{3i})Total_{it}) + \varepsilon_{it}, \quad (2)$$

where N is caribou abundance for the i th subpopulation at time t ; $Core$, $Matrix$, and $Total$ are the disturbance measures calculated in the respective areas or as an aggregated total for the entire subpopulation range; β_k are fixed parameters indexed by $k = 0...3$; b_{ki} are subpopulation-level random effects with $b_k \sim N(0, \sigma_{b_k}^2)$; ε is the within-subpopulation residual error with $\varepsilon_i \sim N(0, R_i)$, which is independent of b_k and where R_i is the error variance-covariance matrix for each subpopulation that was initially assumed as independent and identically distributed ($R_i = \sigma_R^2 I$), with a common σ_R^2 for all i . We fit models using maximum likelihood, using either the original or standardized scale of $Core$, $Matrix$, and $Total$ disturbance measures (Schielzeth 2010). We compared models using Akaike's Information Criterion with a small sample size correction (AIC_c ; Anderson et al. 2000).



Model selection followed an iterative approach similar to Wang et al. (2007) where we first determined which parameters would be considered as mixed effects (both fixed and random effects) versus only fixed effects, followed by specifying the variance–covariance structure ($\mathbf{R}_i$), and then choosing the disturbance measure. Because the third step may influence the second step, this process was iterative. In the model separated by core, matrix, or total range (eq. 1), initially we considered all 3 parameters as mixed effects; however, this full model was over parameterized. Thus, we fit our candidate models as reduced models with 2 mixed effects parameters (an intercept and a slope for either core, matrix, or total disturbance measures).

Given that the abundance data was hierarchical with repeated measures in time, there was strong evidence of heteroskedasticity and potential serial autocorrelation. To model the heteroskedasticity, we compared several variance functions (Pinheiro et al. 2017), with the best fit resulting from an exponential function using an indicator variable for subpopulation core habitat area as its predictor. We constructed this indicator variable from a natural break in the core habitat area–abundance relationship that classified subpopulations as those with large core habitat areas (>224,000 ha) or otherwise, yielding a model with 2 possible variance components. After modeling the variance this way and including 2 mixed effects for the intercept and slope, plots of the residual autocorrelation function provided no evidence of autocorrelation for the first, second, third, or fourth order, for all candidate models. The null model fit β_0 and b_{0i} , along with the exponential variance function described above and 2 autoregressive moving average parameters to deal with the serial autocorrelation.

RESULTS

Historical forestry disturbance

The simulated forestry disturbance profiles varied widely across caribou subpopulations (Table 1; Figure 4). Disturbance measures in core habitat were weak to moderately positively correlated with disturbance measures in the matrix habitat ($r < 0.37$). Cutblock and road disturbance types were moderate to strongly positively correlated within the corresponding habitat ($r > 0.68$, $P < 0.001$). Two road variables, R50 and R500, were strongly correlated at the total range level and within habitats ($r > 0.97$, $P < 0.001$). Across subpopulations, C80, R50, and C80R50 in the core ranged from 0.5–14.7%, 0.3–5.4%, and 0.7–17.2%, respectively. By contrast, values of C80, R50, and C80R50 in the matrix ranged from 8.1–58.0%, 3.7–12.5%, and 10.3–61.0%, respectively (Table 1). Frisby Boulder had the greatest percentage of matrix habitat disturbed by R50, whereas Columbia South had the smallest. Overall, the oldest cutblocks were in the matrix habitat and disturbance measures C80, R50, and C80R50 were on average 17.8%, 5.1%, and 20.4% greater in the matrix relative to the core (paired $t_{80} > 11.3$, $P < 0.001$).

Disturbance–abundance relationship

The best fitting models included a mixed effect for the intercept and a mixed effect for either the slope of the core disturbance measure (when disturbance measures were separated by habitat; eq. 1) or the slope of the total disturbance measure (eq. 2). Mixed effects disturbance models that considered core habitats only (eq. 1) consistently outperformed (lower AIC_c) those that considered matrix habitats only; thus, we do not describe the latter further. For models that separated disturbance by core and matrix habitats, the correlation between the random effects was strongly negative ($r > -0.83$), providing evidence that subpopulations with greater abundance (i.e., larger positive intercept) had a larger negative response to core disturbance (i.e., more negative slope). After scaling the disturbance measures (centering and dividing by SD), the correlation between the random effects was smaller ($r < -0.35$), yet the resulting trends were similar to the unscaled models.

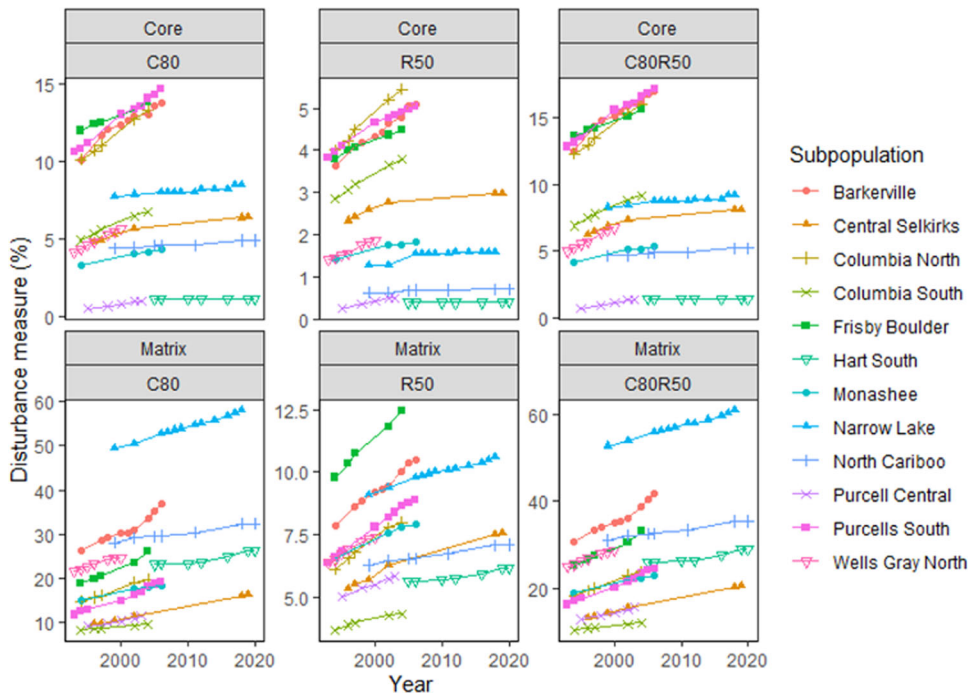


FIGURE 4 Disturbance measures by core or matrix habitat during the period of abundance surveys (each point represents a subpopulation abundance estimate) for subpopulations of the southern group of the southern mountain population of woodland caribou in British Columbia, Canada, 1993–2020. Disturbance measures shown include cutblocks ≤ 80 years old (C80), roads with a 50-m buffer (R50), and the cumulation of C80 and R50 (C80R50)

Road covariates were consistently included in the models with highest empirical support (model rank 1 and 2; Table 2). The next highest-ranked models (model rank 3, 4, and 5) included the C80R50 and C80 covariates. Thus, roads and to a lesser degree early to mature-seral forest were the best predictors of caribou abundance. Estimating separate disturbance coefficients for core and matrix habitat (eq. 1) consistently improved the top models (i.e., resulted in smaller AIC_c statistics; for example, the difference between the first versus second ranked models, third versus eighth ranked models, and fourth versus fifth ranked models).

In the top-ranked model, the fixed effect coefficient for R50 in matrix habitat was negatively related to caribou abundance ($P < 0.001$) where a 1% increase in matrix R50 resulted in a 42% (95% CI = 33 to 51) reduction in caribou abundance (holding core R50 constant). The fixed effect coefficient for R50 in core habitat was not statistically significant ($P = 0.680$; Table 3). There was, however, substantial variation in the slope for R50 in core habitat among subpopulations, with most subpopulations showing a negative relationship of R50 in core habitat with caribou abundance (Figure 5; Table A1). Columbia South had the most negative slope and Barkerville the most positive (Table A1).

Disturbance levels to achieve population abundance targets

Most caribou subpopulations did not have sufficient abundance data to estimate an asymptote at low disturbance levels. Such data would be useful to identify disturbance thresholds to achieve self-sustaining subpopulations. Instead, we used 3 of our top 4 models (model rank 1, 3, and 4) to estimate disturbance levels (i.e., thresholds)



TABLE 2 Comparison of forestry disturbance-abundance models for subpopulations of the southern group of the southern mountain population of woodland caribou in British Columbia, Canada, 1993–2020, including the number of parameters (K), Akaike's Information Criterion (AIC_c), difference in AIC_c from the best model (ΔAIC_c), and Akaike weight (w_i). Disturbance type refers to roads buffered by 50 m (R50) or 500 m (R500), cutblocks ≤ 40 years old (C40), 10–40 years old (C10–40), or ≤ 80 years old (C80), and combinations thereof

Model		K	AIC_c	ΔAIC_c	w_i	Model rank
Disturbance type	Habitat					
R50	Core, matrix	8	776.191	0.000	0.591	1
R50	Total	7	776.961	0.770	0.402	2
C80R50	Core, matrix	8	786.174	9.983	0.004	3
C80	Core, matrix	8	788.086	11.895	0.002	4
C80	Total	7	789.451	13.260	0.001	5
R500	Total	7	791.128	14.937	<0.001	6
R500	Core, matrix	8	791.538	15.346	<0.001	7
C80R50	Total	7	795.792	19.601	<0.001	8
C80R500	Core, matrix	8	799.511	23.320	<0.001	9
C10–40R50	Core, matrix	8	802.361	26.170	<0.001	10
C10–40R500	Core, matrix	8	804.403	28.212	<0.001	11
C10–40	Core, matrix	8	805.111	28.920	<0.001	12
C40R500	Core, matrix	8	809.716	33.525	<0.001	13
C80R500	Total	7	811.490	35.298	<0.001	14
C10–40R500	Total	7	815.233	39.041	<0.001	15
C40R50	Core, matrix	8	816.583	40.391	<0.001	16
C40	Total	7	816.661	40.470	<0.001	17
C40R50	Total	7	818.410	42.218	<0.001	18
Null	.	6	819.676	43.485	<0.001	19
C40	Core, matrix	8	819.868	43.677	<0.001	20
C10–40	Total	7	820.177	43.986	<0.001	21
C10–40R50	Total	7	827.514	51.323	<0.001	22
C40R500	Total	7	838.760	62.568	<0.001	23

necessary to achieve subpopulation-specific abundance targets, either based on the maximum observed abundance or by applying a density target of 0.04 caribou/km² as reported in Seip and Cichowski (1996). Given the majority of core habitat in each subpopulation has been protected from future forestry development and the importance of matrix habitat in influencing caribou predation rate, we opted to keep core habitat-disturbance estimates constant and calculate the necessary disturbance level in matrix habitat (i.e., a matrix disturbance threshold) to achieve an abundance target.

Narrow Lake, Frisby Boulder, and Barkerville had the largest matrix disturbance thresholds, while Central Selkirks, Purcell Central, and Columbia South had the smallest when using the top-ranked model (which only included the R50 covariate). Purcell Central and Purcell South had negative matrix disturbance thresholds when using the fourth-ranked model (which only included the C80 covariate), suggesting either the assumed abundance



TABLE 3 Top-ranked non-linear mixed models explaining abundance of the southern group of the southern mountain population of woodland caribou in British Columbia, Canada, 1993–2020, as an exponential function of forestry disturbance measures including roads buffered by 50 m (R50), cutblocks ≤80 years old (C80), and the combination of C80 and R50 (C80R50). Coefficient ($\hat{\beta}_0, \hat{\beta}_1, \hat{\beta}_2, \hat{\beta}_3, \{\hat{\sigma}_{b_k}\}$) values, standard errors (in parentheses), and standardized coefficients (labeled with superscript s) are provided; $\hat{\sigma}_{b_k}$ are the standard deviations of the random effects (b_k)

Model rank	Disturbance measure	$\hat{\beta}_0$	Core ($\hat{\beta}_1$)	Matrix ($\hat{\beta}_2$)	Total ($\hat{\beta}_3$)	b_k	$\hat{\sigma}_{b_k}$
1	R50	7.689 (0.714)	0.108 (0.248) 0.177 ^s (0.408)	−0.551 (0.076) −1.10 ^s (0.153)		b_0 b_1	2.141 0.691
2	R50	7.887 (0.857)			−0.728 (0.155)	b_0 b_3	2.601 0.454
3	C80R50	7.389 (0.949)	−0.109 (0.090) −0.553 ^s (0.458)	−0.093 (0.017) −1.295 ^s (0.238)		b_0 b_1	2.922 0.246
4	C80	7.140 (0.885)	−0.122 (0.110) −0.521 ^s (0.471)	−0.102 (0.019) −1.449 ^s (0.262)		b_0 b_1	2.797 0.283
19	Null	4.309 (0.306)				b_0	1.020

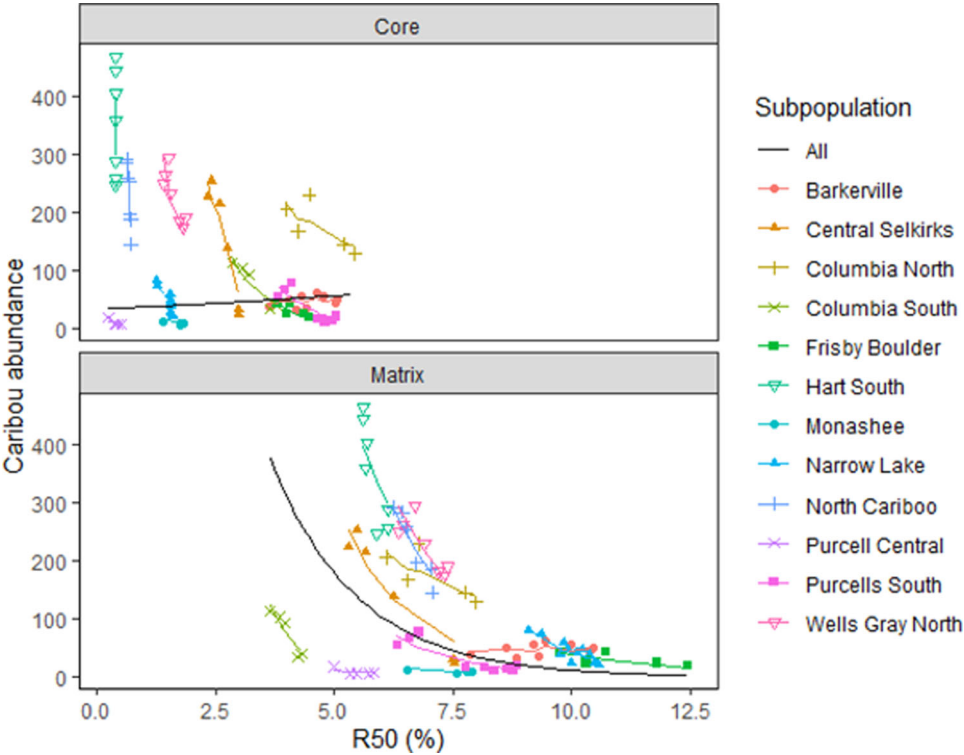


FIGURE 5 The disturbance-abundance relationship fitted with an exponential function of roads buffered by 50 m (R50) in core and matrix habitats for subpopulations of the southern group of the southern mountain population of woodland caribou in British Columbia, Canada, 1993–2020. All is the global-level model estimate (black line) and the respective subpopulation names correspond to the subpopulation-level model estimates



TABLE 4 Estimated caribou matrix habitat forestry disturbance thresholds needed to achieve 2 caribou abundance targets (the maximum observed abundance [N] in the subpopulation or a density of 0.04 caribou/km² within the core area [D]) using our top-ranked models (model rank in parentheses) predicting abundance of the southern group of the southern mountain population of woodland caribou subpopulations in British Columbia, Canada, 1993–2020. Forestry disturbance measures include roads buffered by 50 m (R50), cutblocks ≤80 years old (C80), and the combination of cutblocks and R50 (C80R50). Disturbance in the core habitat (Core %) was held static at the current (2020) level of disturbance

Subpopulation	Abundance targets		R50 thresholds (1)			C80R50 thresholds (3)			C80 thresholds (4)		
	N	D	Core (%)	Matrix (%)		Core (%)	Matrix (%)		Core (%)	Matrix (%)	
				N	D		N	D		N	D
Barkerville	88	62	5.1	9.5	10.1	17.0	33.9	37.7	13.8	29.3	32.7
Central Selkirks	254	157	3.0	5.0	5.9	8.1	6.8	12.0	6.4	3.1	7.8
Columbia North	230	192	5.4	7.1	7.5	16.0	18.4	20.3	13.3	14.7	16.4
Columbia South	114	79	3.8	2.6	3.2	9.2	1.9	5.8	6.8	0.1	3.7
Frisby Boulder	43	35	4.5	10.7	11.1	15.6	23.6	25.8	13.9	16.9	19.0
Hart South	488	136	0.4	5.2	7.6	1.4	23.2	37.0	1.1	21.0	33.5
Monashee	12	43	1.8	7.4	5.1	5.3	20.1	6.3	4.3	15.6	3.1
Narrow Lake	81	13	1.6	8.7	12.1	9.2	48.1	67.8	8.5	46.9	64.8
North Cariboo	291	113	0.7	6.2	7.9	5.2	29.2	39.4	4.9	26.9	36.1
Purcell Central	18	92	0.5	4.6	1.6	1.3	8.2	−9.4	1.0	4.8	−11.2
Purcells South	77	81	5.0	5.8	5.7	17.2	4.7	4.2	14.7	0.0	−0.5
Wells Gray North	295	190	1.9	6.3	7.1	6.7	22.7	27.4	5.7	19.8	24.1

target was unrealistic, or cutblock recovery (i.e., cutblocks reach >80 yr) would also be required in core habitat (Table 4).

DISCUSSION

We defined the historical forestry disturbance-caribou abundance relationship of SGSMC using best available abundance data and a simulation model to estimate spatial-temporal timber harvest and road development. This novel approach is useful for filling disturbance data gaps (specifically, the timing of haul road development) and provides an alternative to using satellite imagery (Johnson et al. 2020, Nagy-Reis et al. 2021). Using our approach, we reject our first hypothesis that caribou abundance is most negatively related to forestry disturbances in core habitat. In addition, we identified partial support for our second hypothesis that cumulative disturbance measures are the best predictors of caribou abundance. We failed to find support for our third hypothesis that including a 500-m buffer would improve model ranking. Instead, we identified support for our fourth hypothesis that the magnitude of disturbance effects differs by subpopulation. Overall, roads in matrix habitat with a minimal buffer had the greatest influence on caribou abundance.

Researchers have reported that in landscapes altered by humans, the quality of the matrix habitat is an important predictor of wildlife population dynamics (Prevedello and Vieira 2010, Swift and Hannon 2010, Beauchesne et al. 2014, MacNearney et al. 2016). Specific to caribou, Apps et al. (2013) showed that mortalities resulting from many predator species tended to occur at low elevations with higher road densities, which



characterizes SGSMC matrix habitat. In addition, Apps et al. (2013) reported that apart from roads, changes to core habitat had little effect on where caribou were killed by predators, suggesting disturbances in matrix may be a greater threat to caribou than disturbances in the core. Our results show that forestry disturbance in matrix habitat negatively influences caribou abundance, and thus should be a component of SGSMC habitat management policies.

Current habitat management policies for SGSMC are considering the use of cumulative, buffered disturbance thresholds designed for boreal woodland caribou ecotypes (Environment Canada 2014). Yet, we concluded the effect of roads on abundance was greater in matrix habitat, where caribou rarely occur; our model using unbuffered roads (R50) was better than a model with buffered roads (R500), suggesting the effects of displacement were less influential. Our results therefore provide further evidence of a significant functional response of predators to forestry disturbances in SGSMC caribou habitat. Linear features, including roads, have the potential to increase encounter rates between predators and caribou (Whittington et al. 2011, Dickie et al. 2017, Mumma et al. 2018), which could increase predation rates and have a significant influence on population dynamics of caribou because they are sensitive to predation (Seip and Cichowski 1996). Roads can also potentially increase the spatial overlap between humans and caribou, which can lead to displacement (Apps and McLellan 2006) and possibly increased mortality; however, direct human-caused caribou mortality related to vehicle collisions or poaching was historically low (Apps et al. 2013). Thus, we speculate that the simulated forestry roads in our study captured a network of travel corridors for predators, given that these roads directly connect cutblocks often favored by moose or deer. These roads connect the landscape at broad scales, including the connection of matrix habitat to core habitat areas. Predators such as bears tend to select for low use roads (Wielgus et al. 2002) like forestry roads, which have minimal traffic during the day, except for forestry workers, and almost no traffic at night. Wolves may also use these road networks; wolves select for roads in habitats of higher road density in boreal regions (Muhly et al. 2019).

Cutblocks also influence caribou abundance, although to a lesser degree than roads or the combination of cutblocks and roads. Cutblock disturbances aged ≤ 80 years old were the most related to caribou abundance, which suggests mechanisms related to habitat loss are persistent on the landscape and may not simply be due to early-seral forest providing forage for other ungulates. Conversely, Wittmer et al. (2007) reported that at broad scales, adult female caribou survival was negatively correlated with the proportion of early-seral (≤ 40 -yr-old) forest indicative of cutblock disturbances. Early-seral forest structure is generally favored by moose and deer because the open canopy allows for shrub growth (Lochhead and Comeau 2012), but not all cutblocks ≤ 40 years old provide the habitat necessary to elicit a density response in ungulate species (Mumma et al. 2021). For example, Fortin et al. (2017) reported that regions with higher forest productivity were associated with greater caribou survival and recruitment given the forest was able to transition into a mature state quicker. Therefore, a single early-seral cutblock age threshold may not be indicative of vegetation communities preferred by ungulates everywhere.

A key challenge with defining habitat-disturbance thresholds is accounting for regional variability in subpopulation responses (Mumma et al. 2018). Across the various non-linear models we tested in this study, the inclusion of subpopulation-level random effects confirmed that SGSMC subpopulations respond differently to core habitat disturbance. For instance, Seip (1992) attributed the lower predation rate of the Wells Gray subpopulation to greater access to refugia from predators. Researchers have reported that caribou will either increase matrix habitat use or spatially cluster within their home range in response to core habitat disturbance (Courtois et al. 2007, Beauchesne et al. 2014, MacNearney et al. 2016), making predation risk difficult to generalize. In addition, Rudolph et al. (2017) and Johnson et al. (2020) reported subpopulation-specific demographic structures and rates affect the vulnerability of caribou to disturbances. Further, differences in the sightability during abundance surveys of subpopulations can affect the quality of abundance estimates and contribute to between-subpopulation variability. An example being the low sightability and large confidence intervals around abundance estimates at relatively low disturbance levels for the Barkerville subpopulation, which might be a factor driving the positive response of this subpopulation to core disturbances. These subpopulation-level dependencies contribute to variation in the disturbance-abundance relationship and make the generalizability of this relationship difficult (Sleep and Loehle 2010, Mumma et al. 2018). We confirmed that SGSMC



recovery programs looking to implement habitat-disturbance management will need to consider subpopulation-specific effects of disturbances that will likely require establishing subpopulation abundance targets in caribou management plans.

Subpopulation abundance targets can be established from resource selection functions (Boyce and McDonald 1999, Serrouya et al. 2011), historical maximum observed abundance estimates, historical density estimates (Seip 1992), or possibly from research on caribou nutritional ecology in the study area. Once abundance targets are determined, our exponential models can be used to infer critical disturbance thresholds to achieve that target (Johnson 2013). For subpopulations where caribou abundance was generally >100 animals, the effects of core disturbances were more detrimental to caribou, suggesting the need for core habitat protection in these subpopulations. Where caribou abundance was generally <100 animals, our models should be used with caution given that predation rates on smaller populations may be density independent or even depensatory (McLellan et al. 2010). Furthermore, smaller populations are likely to be more vulnerable to extirpation (Fagan and Holmes 2006) resulting from random catastrophes, environmental stochasticity, skewed population age-structures, and inbreeding (Lande 1993, Wittmer et al. 2005b). Overall, model-based thresholds that extrapolate beyond the observed data should be used with caution and supplemented with additional information because the model does not account for all factors driving caribou abundance.

Our study linked habitat-disturbance measures and caribou abundance; however, there are several limitations to our approach. First, we kept the spatial delineation of caribou ranges static over time, which could lead to an under-estimation of the historical core habitat area. Although, range retraction or expansion is difficult to determine in the absence of long-term telemetry data. Second, the total influence of habitat disturbances on caribou abundance was likely underestimated given forestry disturbances were the sole focus of our study. Forestry disturbance was the principal industrial disturbance type in our study area, and Johnson et al. (2020) reported that the effects of natural disturbance (e.g., fire) on caribou survival were 5 times less than anthropogenic disturbances. Third, the disturbance measures assessed in this work did not holistically measure habitat quality in matrix and core habitats, which likely contributes to between-subpopulation variability. For instance, landscapes with high densities of arboreal lichen are selected by caribou (Johnson et al. 2015), but we did not account for this in our model. Future work could consider linking models of caribou abundance with multiple habitat quality measures, for example, derived from resource selection functions and nutritional relationships with habitat.

MANAGEMENT IMPLICATIONS

We found SGSMC abundance to be most sensitive to forestry roads and to a lesser degree the loss of mature forest (≤ 80 yr old), particularly in matrix habitats, and that these effects varied across subpopulations. We recommend habitat management policies focus on road management in matrix habitat by limiting new road development, offsetting new road development with road recovery, and recovering roads using various predator impedance techniques, possibly involving the use of post-harvest slash. This should supplement current habitat policies previously implemented by the British Columbia Government, which prioritized protection of core habitat areas. Our models offer the ability to assess the potential influence of hypothetical future forestry development scenarios in core and matrix habitat on SGSMC subpopulation abundance, and to help identify forestry disturbance regimes that achieve desirable caribou population targets. The linkages between empirical disturbance and caribou abundance did not necessarily identify disturbance levels needed to achieve stable caribou populations. Thus, long-term investment into robust caribou abundance monitoring will be required to assess the effectiveness of any habitat-based strategy.

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ETHICS STATEMENT

All capture and handling procedures were in accordance with the Standards for Components of British Columbia's Biodiversity (Number 32; Resource Information Standards Committee 2002).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the Government of British Columbia. Restrictions apply to the availability of these data, which were used under license for this study. Data are available (<https://www2.gov.bc.ca/gov/content/environment/plants-animals-ecosystems/wildlife/wildlife-data-information> and <https://www2.gov.bc.ca/gov/content/environment/plants-animals-ecosystems/wildlife/wildlife-conservation/caribou/recovery-program>) with the permission of the Government of British Columbia.

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APPENDIX A: RANDOM EFFECTS FOR SELECTED MODELS

TABLE A1 Random effects for the top-ranking models (rank in parentheses) predicting abundance for subpopulations of the southern group of the southern mountain population of woodland caribou in British Columbia, Canada, 1993–2020. We present the random intercept ($\hat{b}_0$) and slope ($\hat{b}_1$) of disturbance measures in core habitat, including roads buffered by 50 m (R50), cutblocks ≤ 80 years (C80), and the combination of C80 and R50 (C80R50)

Subpopulation	R50 (1)		C80R50 (3)		C80 (4)	
	$\hat{b}_0$	$\hat{b}_1$	$\hat{b}_0$	$\hat{b}_1$	$\hat{b}_0$	$\hat{b}_1$
Barkerville	−3.374	0.945	−4.363	0.380	−4.259	0.454
Central Selkirks	1.429	−0.387	1.212	−0.191	1.215	−0.269
Columbia North	−0.670	0.326	−0.563	0.129	−0.460	0.141
Columbia South	1.239	−0.840	0.917	−0.260	0.772	−0.343
Frisby Boulder	−1.499	0.663	−0.483	0.048	−0.441	0.035
Hart South	1.523	−0.450	1.250	−0.098	1.467	−0.126
Monashee	−2.484	0.636	−3.749	0.243	−3.438	0.209
Narrow Lake	2.493	−0.718	4.919	−0.265	4.205	−0.133
North Cariboo	1.686	−0.515	2.492	−0.178	2.685	−0.166
Purcell Central	−2.719	0.791	−3.979	0.293	−3.949	0.306
Purcells South	0.818	−0.303	1.334	−0.120	1.176	−0.148
Wells Gray North	1.558	−0.146	1.013	0.019	1.027	0.041