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RESEARCH ARTICLE

Mixed evidence for disturbance-mediated apparent competition for declining caribou in western British Columbia, Canada

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Abstract

Understanding causal mechanisms of decline for species at risk is critical for effective conservation. Caribou (*Rangifer tarandus*) face threats from habitat loss and degradation due to human activities, and many caribou populations across Canada have experienced dramatic declines in recent decades. Disturbance-mediated apparent competition (DMAC) has been implicated in many of these declines, but its generality has been questioned, particularly for low-productivity caribou ranges. The DMAC hypothesis leads to the following predictions: 1) a vegetation productivity pulse after disturbance, 2) primary ungulate prey attraction to disturbed areas, 3) predator attraction to primary prey and disturbance, and 4) increased caribou predation risk due to overlapping habitat use with primary prey and predators. We tested these predictions for the declining Itcha-Ilgachuz caribou population, located in the low-productivity Chilcotin Plateau region of west-central British Columbia, Canada. We used a remotely sensed productivity index to examine vegetation recovery patterns after disturbance and used camera traps and Bayesian mixed effects negative binomial regression models to estimate the responses of primary prey, predator, and caribou relative abundance to landscape disturbances <40 years old, interacting species, and other habitat features. We identified a productivity pulse in harvested and burnt forest patches, but overall productivity was lower than in other caribou ranges where DMAC occurs. Primary prey, moose (*Alces alces*) and mule deer (*Odocoileus hemionus*), showed strong positive responses to burnt areas and weak positive responses to harvested forest. For predators, wolves (*Canis lupus*), black bears (*Ursus americanus*), and grizzly bears (*Ursus arctos*) were positively associated with primary prey species, while coyotes (*Canis latrans*) and Canada lynx (*Lynx canadensis*) were more strongly associated with snowshoe hare (*Lepus americanus*), and wolverines (*Gulo gulo*) were not associated with any focal prey species. Wolves, grizzly bears, and wolverines were not associated with habitat disturbance, but black bears, coyotes, and lynx responded positively to burned and harvested areas. Caribou did not have reduced relative abundance in harvested forests or burns, potentially increasing their overlap with predators. Overall, we found mixed support for DMAC for the Itcha-Ilgachuz caribou population, with stronger evidence for a pathway mediated by disturbance from forest fire, rather than forest harvest. We recommend further research and action on wildfire management for the recovery of this population, including monitoring population trends of caribou and interacting species in response to habitat management. Our results emphasize the context-dependency of mechanisms of decline for caribou and underscore the need for population-specific knowledge to effectively conserve threatened species.

KEYWORDS

camera trapping, habitat disturbance, moose, mule deer, primary productivity, species interactions, threatened species, wolves

Wildlife face a complex array of direct and indirect anthropogenic drivers of change (Young et al. 2016). This has resulted in a drastic decline in the global abundance of wild vertebrates (Díaz et al. 2019). Changing ecosystem conditions across time and space (Young et al. 2015) combined with varying species interactions (Parsons et al. 2019) and individual behaviors (Sih et al. 2011) often create context-dependency in the causal mechanisms behind observed impacts (Côté et al. 2016). For example, vulnerability of amphibians to disease caused by chytrid fungus varies not only by species, population density, and pathogen genotype but local environmental conditions like temperature (Doddington et al. 2013). This knowledge allows more accurate forecasting of risk for populations across space and time. Understanding mechanisms for a particular context is key for directing limited resources effectively (Cooke et al. 2023) and prioritizing management actions to protect and recover threatened populations.

In North America, woodland caribou (*Rangifer tarandus caribou*) – an ecologically, culturally, and economically important species – exemplify the challenge of interacting and context-dependent drivers of decline. Woodland caribou (hereafter caribou) populations are currently under threat, with populations units classified as threatened, endangered, or special concern because of widespread and often drastic population declines and extirpation across their range (Festa-Bianchet et al. 2011, Hebblewhite 2017). Almost half of boreal caribou populations are in decline (Hebblewhite 2017) and southern mountain caribou have declined in abundance by 50% since the 1990s, with 15 of 41 populations now functionally extirpated (Lamb et al. 2024). The ultimate cause of these declines is human activity, primarily habitat loss and degradation due to timber harvesting and oil and gas activities (McLoughlin et al. 2003, Festa-Bianchet et al. 2011, DeMars et al. 2023), which have accelerated in recent decades within many caribou ranges in western Canada (Nagy-Reis et al. 2021). A prominent hypothesis describing the mechanisms underlying caribou declines is habitat- or disturbance-mediated apparent competition (DMAC; Serrouya et al. 2021). This mechanism links habitat disturbance, as the ultimate cause of decline, to predation, which is the proximate driver of many caribou declines (Environment Canada 2014). Disturbance-mediated apparent competition is characterized by habitat disturbance within caribou ranges that creates early seral forage patches with abundant, high-quality forage for ungulates including moose (*Alces alces*), deer (*Odocoileus* spp.), and elk (*Cervus canadensis*; Franzmann and Schwartz 2007, Hebblewhite et al. 2007). This increased forage attracts primary prey into areas that previously would not have provided enough food or supports larger populations of primary prey than undisturbed habitat (Bergerud 1988). Predators including wolves (*Canis lupus*), bears (*Ursus* spp.), and cougars (*Puma concolor*) can then respond by immigrating into or increasing their population sizes in these disturbed areas because of increased densities of their preferred prey species (Kinley and Apps 2001, Latham et al. 2011*b*, Frenette et al. 2020). Caribou avoid predation primarily by spatially segregating from other ungulate species that are the primary prey of their shared predators (Bergerud et al. 1984, Seip 1992). In caribou ranges with high densities of habitat disturbance where populations of both primary prey and predators have increased, maintaining separation from these species becomes increasingly difficult. The result is increased encounters between caribou and predators and ultimately increased caribou mortality due to opportunistic predation (Whittington et al. 2011, Peters et al. 2013).

Evidence for DMAC as the cause of caribou declines has come primarily from populations in western Canada, more specifically in eastern British Columbia, and northern Alberta. In these regions, predation by wolves or cougars was found to be the primary cause of caribou mortality, and this risk was greater when and where caribou overlapped with primary ungulate prey including moose, elk (*Cervus canadensis*), and white-tailed deer (*Odocoileus virginianus*; Seip 1992, Kinley and Apps 2001, Wittmer et al. 2005, Latham et al. 2011*b*, Ehlers et al. 2016). This predation risk for caribou was further linked to areas with high levels of habitat disturbance (Kinley and Apps 2001, Wittmer et al. 2007, Ehlers et al. 2016), or increased after disturbance within caribou ranges (Latham et al. 2011*b*). Across 15 caribou populations in southeastern British Columbia (Wittmer et al. 2005) and 14 caribou populations in the western boreal forest (Serrouya et al. 2021), DMAC was supported as the cause of caribou decline over other potential mechanisms, including forage limitation and increased predator movement in disturbed areas. This evidence has led to DMAC being used as the theoretical framework for much of the current caribou management across Canada (Environment Canada 2014, 2020).

However, not all literature supports DMAC, particularly for caribou in portions of the northern boreal forest where primary productivity is low and forest fire, rather than industry, is the main source of disturbance (Mumma et al. 2018, DeMars et al. 2019, Neufeld et al. 2021, Superbie et al. 2022). For 5 boreal caribou herds in northeastern British Columbia, the direct spatial response of wolves to anthropogenic linear features caused an increased predation risk to caribou, rather than risk being mediated through the presence of an apparent competitor (Mumma et al. 2018). Linear features in disturbed areas, like roads and seismic lines, can serve as travel corridors for predators, particularly wolves, allowing them to increase their access across the landscape by moving both farther and faster (Dickie et al. 2017). In low-productivity forests, disturbance may not stimulate sufficient early seral vegetation growth to attract primary ungulate prey or allow their populations to increase, preventing the first step of the DMAC mechanism (DeMars et al. 2019, Neufeld et al. 2021). Neufeld et al. (2021) coined this the primary productivity hypothesis of DMAC. There is also evidence that natural disturbances such as forest fire function differently than anthropogenic disturbances, potentially not attracting primary prey to the same extent, and thus may be less detrimental to caribou (DeMars et al. 2019, Stewart et al. 2020, Superbie et al. 2022). In Alberta, declines of caribou populations were linked to increases in industrial disturbance over the last 30 years, rather than fire regimes with which caribou have historically coexisted (Stewart et al. 2020). Current management recommendations for disturbance thresholds in caribou ranges consider the combined footprint of industrial disturbance (with a 500-m buffer) and wildfire (Environment Canada 2020). However, caribou, apparent competitors, and predators may respond differently to different types of disturbance across different regions (Johnson et al. 2020).

The Itcha-Ilgachuz caribou population in the Chilcotin Plateau region of west-central British Columbia provides an urgent and unique case to investigate DMAC as a mechanism of caribou decline and specifically test the primary productivity hypothesis of DMAC along with the relative impacts of fire compared to forest harvest. The Itcha-Ilgachuz caribou are a shallow-snow, terrestrial-lichen-eating population, classified as northern mountain caribou (Designatable Unit 7) by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2014). The range of the Itcha-Ilgachuz caribou has relatively low primary productivity for central British Columbia and has a history of widespread forest fire and forest harvest (Table S1; Maltman et al. 2024). This population has undergone a drastic decline since the early 2000s, with the estimated population size dropping from about 2,800 in 2003 to 358 in 2019, in part because of low calf recruitment from 2018–2019 (Shores 2019). This decline prompted the British Columbia government to begin a predator management program in the area to reduce wolf densities in winter 2019–2020 (Ministry of Forests, Lands, Natural Resource Operations and Rural Development [MFLNRORD] 2021) with the goal of reducing predation, which was identified as the primary cause of adult mortality (Shores 2019). A total of 216 wolves were removed from the Itcha-Ilgachuz herd range during winter removal efforts from 2019–2020 to 2022–2023, with estimated wolf densities in the treatment area ranging from 0.8–1.3 wolves/1,000 km^2 after removals (MFLNRORD 2021, British Columbia Ministry of Land, Water and Resource Stewardship 2022, British Columbia Ministry of Water, Land and Resource Stewardship 2023). Following the initiation of wolf reduction, the Itcha-Ilgachuz population increased for 2 years, but from 2021–2023 it has experienced an apparent plateau despite continued wolf reduction efforts (Gannon 2023). Understanding whether and how habitat disturbance is driving predation risk for caribou in low-productivity contexts is necessary for building effective long-term management.

We evaluated the evidence for DMAC relative to other potential mechanisms of decline for the Itcha-Ilgachuz caribou (Figure 1). The hypothesis that DMAC is the mechanism behind the observed decline of the Itcha-Ilgachuz caribou leads to a set of 4 testable predictions:

1. Disturbances to forest vegetation within caribou range, such as from timber harvest and wildfire, result in an increase in vegetation productivity, and thus high-quality forage for primary ungulate prey, in these early seral patches (productivity pulse).
2. Primary ungulate prey in the system respond positively to increased forage by increasing use or abundance in these early seral disturbed patches (prey attraction).
3. Caribou predators associated with primary ungulate prey also increase their use or abundance in these disturbed areas (predator attraction).
4. Caribou can no longer effectively spatially segregate from predators, leading to increased overlap of caribou and predators potentially resulting in increased predation on caribou (caribou predation risk).

We used camera trap sampling to test these predictions and characterize patterns of relative abundance and co-occurrence in this multi-prey, multi-predator system. We took advantage of the multispecies monitoring using cameras to investigate responses of all potential predators that could be involved in caribou decline. In addition to wolves, which have been the focus of much DMAC research, we included coyotes (*Canis latrans*), black bears (*Ursus americanus*), grizzly bears (*Ursus arctos*), Canada lynx (*Lynx canadensis*), and wolverines (*Gulo gulo*) in our analysis. While cougars are a prominent predator in DMAC research (Kinley and Apps 2001, Serrouya et al. 2015), they were rarely detected across our camera array and could not be included in analysis. Within the context of ongoing wolf reduction efforts for the Itcha-Ilgachuz caribou, it is especially important to consider the impacts of other non-dominant predators that may be able to increase their populations under lower competitive pressure from wolves

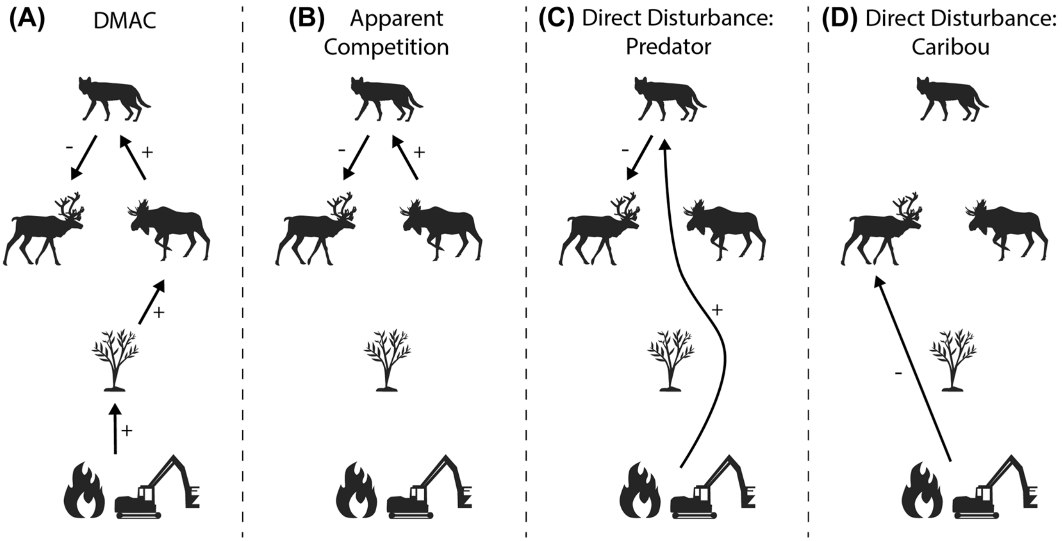

FIGURE 1 Conceptual models of competing hypotheses for the mechanism of decline for the Itcha-Ilgachuz caribou population in the Chilcotin Plateau of British Columbia, Canada, including disturbance-mediated apparent competition (DMAC). Symbols represent the following: wolf = all predators, moose = all primary prey, caribou = caribou, plant = early seral vegetation, feller buncher and fire = habitat disturbance.

or have compensatory predation on caribou with fewer wolves present (Prugh et al. 2009, Prugh and Arthur 2015). Relative abundance is an index that reflects a combination of the local abundance of a species and the movement patterns (use) of individuals around a site. While the DMAC hypothesis was formulated to explain changes in population abundances, we extend it to responses in relative abundance, under the assumption that animals change behaviors (e.g., habitat use, predator-prey interactions) as a mechanistic component of subsequent changes in population demography (e.g., survival, reproduction; Berger-Tal et al. 2011). We developed Bayesian mixed-effects regression models to test the degree of support for DMAC predictions compared to those from alternate hypotheses based on variation in camera trap detections of each focal species relative to disturbance features and detections of prey or predator species.

Alternatives to the DMAC hypothesis (Figure 1A) for explaining the Itcha-Ilgachuz caribou decline include apparent competition not mediated by habitat disturbance (e.g., increased overlap in habitat use due to changing vegetation or winter severity as a result of changing climate; Tape et al. 2016, Mallory and Boyce 2018, Laurent et al. 2021; Figure 1B), a direct response of predators to disturbance that results in increased caribou predation (e.g., increased predation efficiency due to road access; Dickie et al. 2017, Mumma et al. 2018; Figure 1C), a direct negative effect of habitat disturbance on caribou (e.g., through winter or summer forage limitation; Russell and Johnson 2019, Denryter et al. 2017; Figure 1D), or no relationship between disturbance and caribou with the observed decline being due to some other factor (e.g., parasites or disease; Hughes et al. 2009). The decline could also be caused by combinations of these pathways (e.g., direct negative effects of disturbance on caribou and DMAC).

STUDY AREA

We conducted this study in the range of the Itcha-Ilgachuz caribou population in the Chilcotin Plateau region of west-central British Columbia, Canada, located east of the Coast Mountains range and west of the Fraser River (52 to 53° latitude and −124 to −126° longitude; Figure 2). This area is characterized by large expanses of relatively

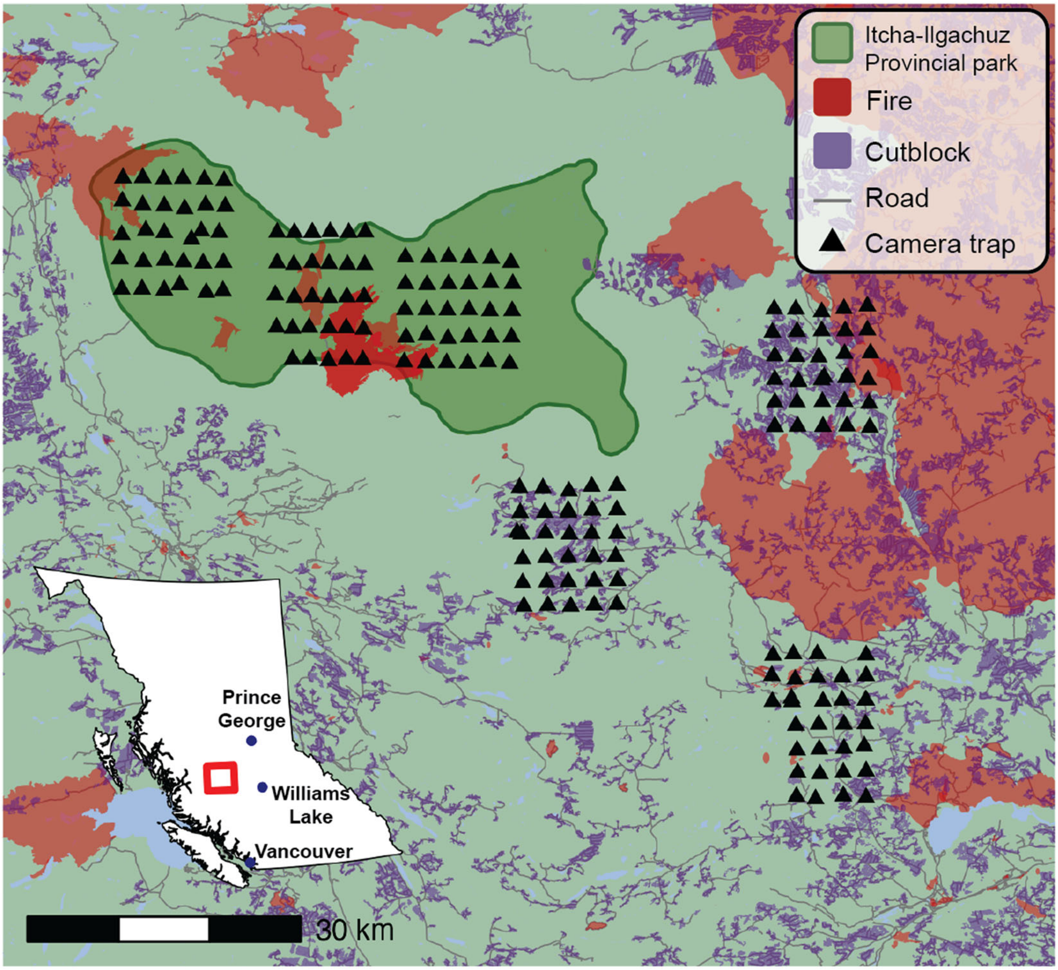

FIGURE 2 Study area and camera trapping grids in the Chilcotin Plateau of British Columbia, Canada, deployed 2020–2023. Camera traps are represented by triangles, the Itcha-Ilgachuz Provincial Park is in dark green, forest fires are in red, cutblocks are in purple, and roads are in grey.

flat terrain with smaller mountain ranges that include the Rainbow, Ilgachuz, and Itcha mountains, spanning elevations from 850 m to 2,410 m. The Chilcotin Plateau ecosystem has relatively low overall productivity, as it lies in the rain shadow of the Coast Mountain Range, making it dry (e.g., 342.8 mm annual precipitation at Puntzi Lake from 2010 to 2014), and experiences cold winters and cool summers (average temperature of 16°C in July and −10.5°C in January from 2020 to 2023; Government of Canada 2024). Low-elevation areas are characterized by Sub-Boreal Pine – Spruce and Montane Spruce biogeoclimatic (BEC) zones, with Engelmann Spruce – Subalpine Fir and Boreal Altai Fescue Alpine BEC zones at higher elevations (Ministry of Forests, Lands, Natural Resource Operations and Rural Development [MFLNRORD] 2018). Lodgepole pine (*Pinus contorta*) and hybrid Engelmann x white spruce (*Picea glauca x engelmannii*) are the dominant tree species, with trembling aspen (*Populus tremuloides*) also present in wetland patches. In the understory, willow (*Salix* spp.), common juniper (*Juniperus communis*), and soopalallie (*Shepherdia canadensis*) are the dominant shrubs, with kinnikinnik (*Arctostaphylos uva-ursi*), dwarf grouseberry (*Vaccinium scoparium*), twinflower (*Linnaea borealis*), and crowberry (*Empetrum nigrum*) making up a large portion of groundcover along with mosses and lichens. Common wildlife species in the study area include moose, mule deer (*Odocoileus hemionus*), caribou, black bears, coyotes, Canada lynx, snowshoe hares (*Lepus americanus*), and mountain goats (*Oreamnos americanus*) at high elevation. Grey wolves, grizzly bears, white-tailed deer, wolverine, American marten (*Martes americana*), fisher (*Pekania pennanti*), and cougar are also present but less common, and feral horses (*Equus caballus ferus*) are common in the southern region of the study area (British Columbia Ministry of Water Land and Air Protection Environmental Stewardship Division 2002, Smith et al. 2019; Figure S1).

The Itcha-Ilgachuz Provincial Park, established in 1995, encompasses the high-elevation calving and rutting range of the Itcha-Ilgachuz caribou and prevents forest harvest and other industrial development within this key habitat (British Columbia Ministry of Water Land and Air Protection Environmental Stewardship Division 2002). Wildlife habitat areas have been established within the range of the Itcha-Ilgachuz caribou, designating some areas as no-harvest, modified harvest, or enhanced conventional harvest, with the aim of maintaining mature forest and terrestrial lichen availability for caribou as timber is harvested (MFLNRORD 2011). The low-elevation summer range of the Itcha-Ilgachuz caribou is within a motor vehicle restricted area designed to limit disturbances associated with motorized recreational activities including hunting. There has been widespread forest harvesting across the low-elevation range of the Itcha-Ilgachuz caribou, with forestry activities peaking from about 1995 to 2005, resulting in 10.1% and 14.5% of low-elevation summer and winter range, respectively, having been harvested since 1960 (Table S1). There has also been widespread forest fire in the area, with 11.3% burned in the high-elevation calving area and 26.5% and 25.2% burned in the low-elevation summer and winter ranges, respectively, in the last century (Table S1). Approximately half of the area burned within the Itcha-Ilgachuz range was burned during high-intensity mega-fires in 2017, which covered 5,680 km^2. Matrix habitat surrounding the core seasonal ranges of the Itcha-Ilgachuz caribou has higher levels of habitat disturbance, with 23.6% harvested and 56.9% burned (Table S1). There have also been extreme mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the Chilcotin in the 1980s and early 2000s, with the most recent outbreak peaking in 2008, prompting widespread salvage logging and increasing fuel loads for fires (Alfaro et al. 2015, Maltman et al. 2024).

METHODS

Camera trap sampling

We used a systematic sampling design to deploy 179 cameras (Reconyx Hyperfire 2, Holmen, WI, USA) across 6 grids of 30 cameras each (except one grid with 29 cameras) in the high-elevation calving and rutting range and adjacent low-elevation summer and winter ranges of the Itcha-Ilgachuz caribou (Figure 2; seasonal caribou ranges in Figure S2). Grids were located to span variation in the types and intensities of vegetation disturbances, seasonal caribou habitat use, and mammal community composition (Figure 2, Table S2). Each rectangular grid covered 200 km^2, with cameras evenly spaced approximately 2.6 km apart. There were 3 grids in the high-elevation range within the Itcha-Ilgachuz Provincial Park, 2 grids primarily in the low-elevation summer range, and 1 grid in the low-elevation winter range. The 5 grids in the high-elevation and low-elevation summer range were deployed in September 2020, with the grid in the low-elevation winter range deployed in October 2021. We completed data collection for this analysis in June 2023 for the low-elevation summer range grids, and October 2023 for the high-elevation and low-elevation winter range grid (see Figure S3 for activity periods of cameras).

We deployed cameras within 200 m of the center of each pre-defined grid cell when possible, targeting a forest service road, game trail, or other natural feature likely to maximize wildlife detections (e.g., alpine meadow, ridgeline). Cameras were attached to trees (or tripods in the high-elevation areas above the tree line) at a height of approximately 1 m, perpendicular to the expected path of travel for wildlife and 3–5 m away from the target feature to maximize detections of medium- to large-bodied mammal species. We did not use any lure or bait at camera sites. We set cameras to high sensitivity and one photo per motion trigger, with no delay between photos. Cameras also took a daily timelapse photo at noon to quantify camera effort in the absence of motion triggers. We used the machine learning model MegaDetector version 5 (Beery 2019, Microsoft 2022) to streamline image processing in instances where stations had large numbers of misfires not containing wildlife, humans, or vehicles due to moving vegetation or camera malfunction, but we still reviewed all images to ensure they had not been misidentified. Camera images containing humans and wildlife were manually classified to species by trained research technicians within a custom database, and these identifications were reviewed for quality control by project leads. To minimize the influence of repeat images of the same individuals during a short period, we grouped species detections into independent detection events using a threshold of 30 minutes between consecutive images of the same species at a site (Burton et al. 2015). We used the number of independent detection events of a focal species in a site-month as the response variable for all subsequent species modeling, and assumed it represented a measure of relative abundance in the area around each camera site (Tattersall et al. 2020). While not all use of an area would be detected by a camera (Burton et al. 2015), we standardized camera deployment features (e.g., camera model, height, distance to target feature) to minimize any differences in imperfect detections between cameras. We also focused on comparisons of species' responses to ecological factors, rather than direct comparisons of relative abundance between species, which may be influenced by differences in detectability across species due to variation in body size, movement patterns, and home range sizes (Devarajan et al. 2020). Based on these considerations, we assumed variation in detections reflected variation in relative abundance and chose not to treat variation as sampling error within a binary use–non-use response such as occupancy (Burton et al. 2015).

Analysis

Primary productivity

We used the remotely sensed enhanced vegetation index (EVI) as a measure of vegetation productivity to approximate the available deciduous forage for primary ungulate prey in disturbance patches (Neumann et al. 2015, Gagné et al. 2016). We compared this measure between the Itcha-Ilgachuz caribou range and 5 other caribou population ranges (Figure 3) in western Canada with varying ecosystem and disturbance conditions and levels of support for DMAC as the major cause of caribou declines (Table S3). We chose the Central and South Purcells

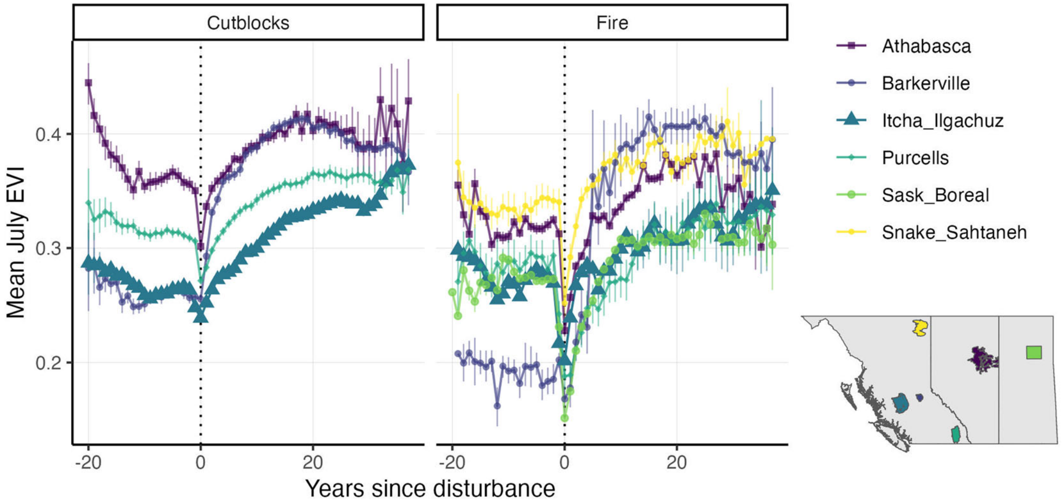

FIGURE 3 Trends in summer productivity from remotely sensed enhanced vegetation index (EVI; 2000–2022) across 6 caribou population ranges in western Canada before and after cutblock and fire disturbance that occurred from 1985–2020. Vertical lines on points represent 95% confidence intervals generated by bootstrapping.

(combined as Purcells hereafter) from southeastern British Columbia, Barkerville from east-central British Columbia, and the East and West Side Athabasca (combined as Athabasca hereafter) from east-central Alberta as ranges where DMAC has been supported (Kinley and Apps 2001, Wittmer et al. 2007, Latham et al. 2011*b*). In contrast, DMAC was not supported because of low primary productivity in a portion of the boreal caribou range in northern Saskatchewan (Neufeld et al. 2021) and has received mixed support in the Snake-Sahtaneh caribou range in northeastern British Columbia (contrast Mumma et al. 2018, and Serrouya et al. 2021).

We used moderate resolution imaging spectroradiometer (MODIS) vegetation indices (MOD13Q1) version 6 EVI data, which is summarized across 16-day periods at a resolution of 250 m (Didan 2021). We extracted EVI data in the month of July as a measure of peak summer productivity (Gagné et al. 2016, Serrouya et al. 2021) across disturbed areas in each caribou range from 2000 to 2022 using the MODISTools (Hufkens 2022) and terra (version 1.6-53; Hijmans 2023) R packages. We obtained disturbance data from the National Terrestrial Ecosystem Monitoring System (NTEMS) for Canada Forest Harvest 1985–2020 and Forest Fires 1985–2020 datasets (https://opendata.nfis.org/; Hermosilla et al. 2016). We converted the raster data to polygons for processing and excluded any polygons <0.25 km^2. We centered all EVI data relative to the year of disturbance to compare trends in EVI recovery after disturbance across the different caribou ranges. We excluded cutblock data for the Saskatchewan boreal and Snake-Sahtaneh ranges because of small sample sizes (3 and 35 cutblock polygons, respectively). We analyzed July EVI data for 3,572 cutblock and 2,341 fire polygons representing 1.06–11.05% and 2.03–35.73%, respectively, of the total caribou range area for these 6 caribou populations (Table S3). We used bootstrapping with 500 iterations to estimate 95% confidence intervals (CI) around the mean yearly EVI values for each range and disturbance type.

Species modeling

We developed Bayesian mixed effects negative binomial regression models for each focal species to determine if patterns of relative abundance—as measured by camera trap detection rates—were consistent with our predictions based on DMAC or competing hypotheses (Figure 1). Focal species for this analysis were moose and mule deer for primary prey, wolves, coyotes, black bears, grizzly bears, lynx, and wolverine for predators, and caribou. We used a negative binomial distribution for the response variables to account for a high proportion of zeros (i.e., overdispersion) from site-months with no detections of focal species. Models included nested random intercepts for camera station and grid to account for repeated sampling over time at stations and spatial clustering of stations within grids. We ran models in R software version 4.1.2 (R Core Team 2021) using the rstanarm package version 2.21.1 (Goodrich et al. 2020). We used weakly informative priors for all variables to stabilize computation (Lemoine 2019) using the default priors from rstanarm (Figure S4). We estimated all models with 4 chains, each with 2,000 iterations (including 1,000 warm-up iterations). We performed posterior predictive checks for all models to assess model fit, confirmed that R-hat values were below 1.05 for all models to ensure chain convergence, made visual assessment of chains to ensure mixing (Gelman and Rubin 1992), and ensured that no parameters had effective sample sizes <10% of the total sample size (Gabry and Modrák 2024). We present 50% and 90% credible intervals (CrI) of model parameter estimates throughout this analysis, as they are computationally stable (Gelman et al. 1995), and consider the weight of evidence based on the posterior estimate distributions. We considered a response to a predictor variable to be neutral when the 50% CrI of the posterior estimate distribution overlapped 0, weak when the 90% CrI, but not the 50% CrI, overlapped 0, and strong when the 90% CrI did not overlap zero.

We included spatial disturbance variables, prey variables for predator species, predator variables for caribou, environmental variables likely to affect relative abundance of focal species (disturbance, environment, prey, and predator variables), variables likely to affect species detectability (camera target [road or other], temperature), and camera effort in species models (Tables 1 and 2). We built models by first thinking about our hypothesized relationships based on DMAC and competing mechanisms and accounting for ecological factors that could affect

TABLE 1 Predictor variable descriptions and data sources for variables used in wildlife species models of camera trap data from the Chilcotin Plateau of British Columbia, Canada, 2020–2023. Asterisks (*) indicate rationales that are compatible with the disturbance-mediated apparent competition (DMAC) hypothesis.

Type	Variable name(s)	Description	Rationale	Data source
Disturbance	Cutblocks/roads	Proportion of area within a 500-m buffer of each camera site covered by cutblocks <40 years old. Highly correlated with road density ($r = 0.84$).	Increased forage availability for ungulates*; prey availability for predators*; ease of travel on associated roads (Dickie et al. 2017)	British Columbia Ministry of Forests - Forest Analysis and Inventory Branch (2022)
	Fire	Proportion of area within a 500-m buffer of each camera site covered by burnt areas <40 years old	Increased forage availability for ungulates*; prey availability for predators*	British Columbia Wildfire Service (2022)
Environment	Distance to water	Distance (km) from the camera site to the nearest lake or river	Access to drinking water; increased availability of preferred vegetation	Government of Canada (2022)
	Wetlands	Proportion of area within a 500-m buffer of each camera site covered by wetlands	Unique vegetation community with foraging opportunities for ungulates (Baker 1990)	GeoBC (2022)
	Mean EVI	Mean enhanced vegetation index (EVI) for each site, calculated within a 500-m buffer of each camera site	Measure of overall greenness and forage availability around a camera site (Neumann et al. 2015)	Didan (2021) Hufkens (2022)
	Canopy cover	Percentage of forest >2 m, representing canopy cover, averaged within a 500-m buffer of each camera site	Thermal regulation by providing shade or shelter from wind, providing cover from predators by reducing sightlines, affecting ease of travel (Mysterud and Østbye 1999)	Matasci et al. (2018); 2022 version provided by E. Muise, University of British Columbia
Prey	Moose, mule deer, white-tailed deer, caribou, feral horse, snowshoe hare, mountain goat[a]	Monthly count of detections of each prey species in each site-month	Availability of different potential prey at each camera site*	Camera data
Predators	Wolf, grizzly, black bear, coyote,[b] lynx wolverine[c]	Monthly count of detections of each predator species in each site-month	Measure of predator threat level for caribou at each camera site*	Camera data
Detectability	Camera target	Binary variable for whether a camera was targeting a road (value = 1) or other	Cameras on roads may be more likely to detect species if animals are	Camera deployment records

TABLE 1 (Continued)

Type	Variable name(s)	Description	Rationale	Data source
		habitat feature (e.g., game trail, ridge, meadow; value = 0)	preferentially using roads for travel	
	Mean monthly temperature	Mean monthly temperature at each camera site	Proxy for seasonal changes in wildlife activity (e.g., increased movement rate in summer; Leblond et al. 2010) and thus likelihood of detection	Temperature readings from camera for daily noon timelapse photos
Effort	Camera effort	Number of days per month that each camera was active, and its view of the target area was unobstructed	Account for variable effort due to camera failures, wildlife damage, obstruction due to snow, etc.	Camera data

[a] Only included for wolves and wolverine.

[b] Only included in low-elevation model.

[c] Only included in calving model.

species detections. Next, we reduced the variable sets for some species based on the amount of overlap between detections of a species and the predictor variable (e.g., calving caribou do not overlap with cutblocks or sufficient coyote detections). We used an age threshold of 40 years to quantify recent cutblocks and fire from the British Columbia Data Catalogue around each site (Table 1), consistent with caribou habitat disturbance described by Environment Canada (2014). We used a 500-m buffer around camera sites to summarize all variables, representing a third-order scale for spatial selection of the area and habitat features around the camera (Johnson 1980), within an animal's existing home range (e.g., 40 km^2 average seasonal home range for moose; Gillingham and Parker 2008). We assessed other possibilities of age thresholds and buffer sizes for disturbance variables using univariate model selection but did not find strong support for alternatives (see Supporting Information for details, Table S4). Roads are an important factor to consider in the causal mechanism of caribou decline (Mumma et al. 2018) but were not included directly in this analysis because of a high correlation between road density and cutblocks within the study area ($r = 0.84$ for proportion cutblocks and road density in a 500-m buffer). Forest harvest is the primary form of human activity in the study area, particularly in the low-elevation summer range where motor vehicle access is restricted for the public, so most roads were developed to access areas for harvest. We included only the proportion of cutblocks around a camera site in the models and consider this as the combined effect of cutblocks and roads. We included prey variables for predator species and predator variables for caribou as additive variables of the monthly detections of each relevant prey or predator species, which we found to perform best (see Supporting Information for details, Table S5). Because we examined observational data and co-occurrence trends of species, we recognize that these are not necessarily evidence of predator–prey interactions (Blanchet et al. 2020). We examined whether species associations are consistent with predictions from hypotheses of predator attraction or prey avoidance of a given species. We centered and scaled all continuous numeric variables by subtracting the mean and dividing by one standard deviation before modeling to allow direct comparison of estimated regression coefficients. We examined predictor variables for collinearity, and all final model variables had pairwise correlations <0.6 (Figure S5; Dormann et al. 2013).

Models for primary prey, moose and mule deer, included all disturbance and environmental variables (Table 2). Mule deer migrate to a winter range outside of the study area and were only detected 5 times from November

TABLE 2 Predictor variables included in models for each focal species in the Chilcotin Plateau of British Columbia, Canada, 2020–2023. We indicate model inclusion (+) for fixed effects and a nested random intercept of camera station within sampling grid (1 | grid, station ID).

	Predictor variable											
Species	Cutblocks/ roads	Fire	Prey	Predators	Distance to water	Wetland	Mean EVI[a]	Canopy cover	Mean monthly temp	Target	Effort	(1 | grid, station ID)
Moose	+	+			+	+	+	+	+	+	+	+
Mule deer	+	+			+	+	+	+	+	+	+	+
Wolf	+	+	+		+			+	+	+	+	+
Coyote	+	+	+		+			+	+	+	+	+
Black bear	+	+	+		+			+	+	+	+	+
Grizzly bear	+	+	+		+			+	+	+	+	+
Lynx	+	+	+		+			+	+	+	+	+
Wolverine	+	+	+		+			+	+	+	+	+
Caribou (calving)		+		+	+	+	+	+	+	+	+	+[b]
Caribou (low elevation)	+	+		+	+	+	+	+	+	+	+	+[b]

[a] Enhanced vegetation index.

[b] Grid + (1 | station ID).

through April, so we excluded data from this period for the mule deer model. We tested seasonal models for moose but found no significant differences in coefficient estimates between summer and winter models, so proceeded with a single year-round model. Predator models for wolves, coyotes, black bears, grizzly bears, lynx, and wolverine included disturbance and prey variables, and key environmental variables that would not primarily be mediated though prey availability (Table 2). We included distance to water sources and canopy cover but excluded mean EVI and wetlands from predator models, as we hypothesized that responses to these features would primarily reflect responses to prey availability, rather than the feature itself, and prey availability was included directly in the models. We included mountain goats as a prey species for wolves and wolverine only because they are the only predator species with frequent detections in the alpine areas where mountain goats were detected and have been reported as predators of mountain goats (Lofroth et al. 2007, Dulude-de Broin et al. 2020). We excluded winter data (November through April) for black and grizzly bears, as they are hibernating during these months (excluded 10 detections for black bears and 7 detections for grizzly bears). Caribou have distinct seasonal ranges with different available habitat and differing life-history strategies throughout the year, so we separated caribou data into calving and low elevation for modeling. Calving models contained data from the calving season (May to July) within the calving range in the 3 camera grids in the Itcha-Ilgachuz provincial park. We included predator variables for predator species with >20 detections in the calving grounds during the calving season (wolf, grizzly bear, wolverine, black bear, lynx) in the caribou calving models to assess caribou avoidance of predators. Investigating the occurrence of predators in the calving grounds was one of the motivating factors for this camera trapping project. The model for caribou at low elevation included data from the 3 grids in the low-elevation summer and winter ranges across all seasons to maintain an adequate sample size for modeling (150 detections across 2,623 station-months). We included wolves, coyotes, black bears, grizzly bears, and lynx as potential caribou predators for the low-elevation model but excluded wolverine, as they had <20 detections. We included camera grid as a fixed effect, rather than random, for caribou models because each model only included data from 3 grids, and we did not want to obscure potential insights from grid-level random effects (Gomes 2022).

RESULTS

Productivity pulse

Trends of productivity increase following disturbance were similar in the Itcha-Ilgachuz range to other caribou ranges, but July EVI in cutblocks was the lowest among caribou ranges with cutblock-type disturbance, and post-fire July EVI was among the lowest, similar to that of the Saskatchewan Boreal where DMAC was supported and Purcells where it was not (Figure 3). Across caribou ranges, we found that July EVI was stable or decreasing leading up to the time of disturbance and decreased sharply the year of disturbance, followed by a rapid increase in EVI over the next 5–10 years, with EVI values stabilizing or peaking around 20 years after disturbance at higher levels than pre-disturbance (Figure 3). The mean July EVI in cutblock and fire polygons was 0.27 (95% CI = 0.26–0.28) and 0.28 (95% CI = 0.27–0.28), respectively, in the Itcha-Ilgachuz caribou range in the 20 years before they were disturbed. This was similar to pre-disturbance productivity in cutblock polygons for Barkerville but 27% lower than in Athabasca at 0.37 (95% CI = 0.36–0.38) and 16% lower than the Purcells at 0.32 (95% CI = 0.31–0.33). Pre-disturbance productivity in fire polygons in the Itcha-Ilgachuz range was similar to the Saskatchewan Boreal and Purcells, 42% higher than in Barkerville, and 16% and 20% lower than the Athabasca and Snake Sahtaneh ranges, respectively. Twenty years post-disturbance, July EVI in the Itcha-Ilgachuz range had increased by 22% to 0.33 (95% CI = 0.33–0.34) in cutblocks and by 7% to 0.30 (95% CI = 0.27–0.33) in burnt patches relative to mean pre-disturbance levels. This was a similar increase to other caribou ranges except Barkerville, which ranged from an 11-16% increase 20 years after forest harvest and a 7-15% increase 20 years after fire. The Barkerville range had the highest increase in productivity after disturbance, with a 58% increase in July EVI 20 years after harvest and a 116% increase after fire.

Camera trapping

We analyzed data from >1.8 million camera images collected over 159,218 active camera trap days (mean of 28.4 active days per camera per month) from September 2020 to October 2023 (Figure S3). We had 8,778 independent detections (hereafter detections) of focal species, with moose, mule deer, and coyote being the most frequently detected with >1,500 detections each, followed by black bear and lynx with >800 detections each (Table 3). Caribou in the calving season and wolves were the next most detected, and caribou at low elevation, grizzly bears, and wolverine were detected the least frequently of the focal species (Table 3; see Figure S1 for complete species detections).

Primary prey attraction

Detections of primary prey were positively associated with disturbance features, as predicted by DMAC. Moose had a weak positive response to cutblocks (β = 0.146, 90% CrI = −0.068–0.370), and a strong positive response to fire (β = 0.334, 90% CrI = 0.136–0.521; Figure 4A). Using mean parameter estimates from the model, moose were predicted to have a 213% increase in monthly detections when proportion of burnt area around the camera (0.79 km^2) increased from 0 to 1, equivalent to approximately 2.7 more moose detections per year at a given station. We also found that moose responded positively to areas close to water sources (β = −0.267, 90% CrI = −0.451– − 0.079), wetlands (β = 0.358, 90% CrI = 0.182–0.542), and areas with higher canopy cover (β = 0.706, 90% CrI = 0.482–0.934; Figure 4A).

We found a weak positive response of mule deer to cutblocks (β = 0.098, 90% CrI = −0.117–0.325), and a strong positive response to fire (β = 0.513, 90% CrI = 0.313–0.724; Figure 4B), with a predicted increase in detections of 482% (5.3 more deer detections per year at a station) when proportion of burnt area increased from 0 to 1. Mule deer had a strong positive response to average site productivity (β = 0.777, 90% CrI = 0.383–1.18) and a weak positive response to distance to water sources (β = 0.094, 90% CrI = −0.095–0.277; Figure 4B). Moose and mule deer both had more detections in warmer months (moose: β = 0.592, 90% CrI = 0.534–0.655; mule deer: β = 0.664, 90% CrI = 0.581–0.750).

TABLE 3 Independent camera trap detections of focal species (30-minute threshold between images of the same species at the same camera station) in the Chilcotin Plateau of British Columbia, Canada, 2020–2023.

Species	Detections
Moose (*Alces alces*)	2,152
Mule deer (*Odocoileus hemionus*)	1,786
Caribou (*Rangifer tarandus*)	776 calving grounds 150 low elevation
Grey wolf (*Canis lupus*)	348
Coyote (*Canis latrans*)	1,520
Canada lynx (*Lynx canadensis*)	868
Black bear (*Ursus americanus*)	873
Grizzly bear (*Ursus arctos*)	174
Wolverine (*Gulo gulo*)	131

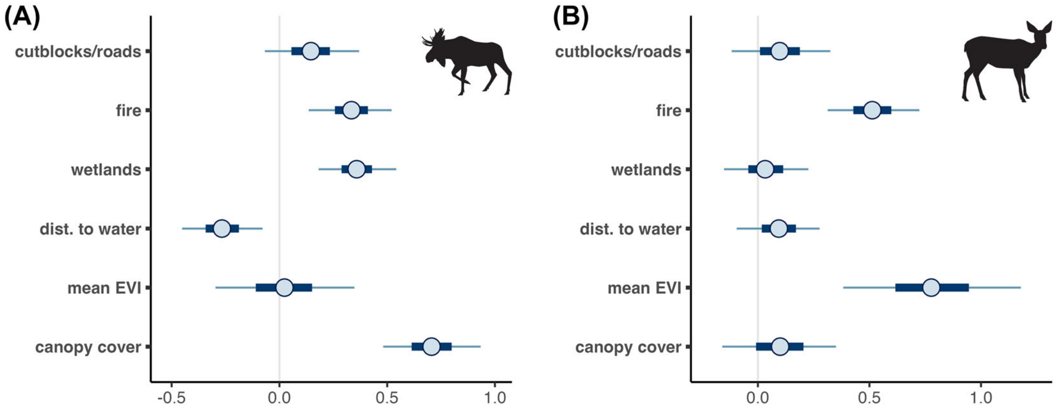

FIGURE 4 Standardized coefficient estimates and credible intervals (thin lines: 90%, thick lines: 50%) for disturbance and environmental variables of Bayesian negative binomial mixed effects models for detection of primary prey species A) moose and B) mule deer in the Chilcotin Plateau of British Columbia, Canada, 2020–2023 using camera trapping data. EVI = enhanced vegetation index and dist. = distance.

Predator attraction

All predator species except wolverine had positive associations with one or more prey species and half responded positively to one or both disturbance types. Wolves had the strongest associations with snowshoe hares (β = 0.165, 90% CrI = 0.048–0.288) and mule deer (β = 0.083, 90% CrI = −0.049–0.205; Figure 5A). Counter to our expectations under DMAC, wolves did not show a response to cutblocks and roads (β = .004, 90% CrI = −0.355–0.351) and had a weak negative response to fire (β = −0.176, 90% CrI = −0.494–0.116; Figure 5A). Coyotes were associated with snowshoe hares (β = 0.095, 90% CrI = 0.048–0.147), caribou (β = 0.082, 90% CrI = −0.062–0.202), and moose (β = 0.056, 90% CrI = −0.030–0.146; Figure 5B). Coyotes also had positive responses to cutblocks and roads (β = 0.188, 90% CrI = −0.026–0.403) and fire (β = 0.181, 90% CrI = −0.040–0.395; Figure 5B). We found that black bears were associated with all large prey except mule deer, with the strongest associations with moose (β = 0.115, 90% CrI = 0.010–0.219) and caribou (β = 0.106, 90% CrI = −0.023–0.225; Figure 5C), and responded positively to both disturbance types (cutblocks and roads: β = 0.246, 90% CrI = 0.080–0.416; fire: β = 0.190, 90% CrI = 0.020–0.364). Grizzly bears were associated with moose (β = 0.272, 90% CrI = 0.138–0.411), feral horses (β = 0.070, 90% CrI = −0.057–0.194), and snowshoe hares (β = 0.068, 90% CrI = −0.052–0.191; Figure 5D), had a neutral response to cutblocks and roads (β = −0.001, 90% CrI = −0.354–0.363), and a weak negative response to fires (β = −0.146, 90% CrI = −0.450–0.152). Lynx were association with snowshoe hares (β = 0.108, 90% CrI = 0.063–0.156), had a weak negative association with caribou (β = −0.088, 90% CrI = −0.227–0.059), and a positive response to cutblocks and roads (β = 0.306, 90% CrI = 0.039–0.572) but not fire (β = 0.007, 90% CrI = −0.264–0.281; Figure 5E). Wolverines did not have a positive associations with any prey species and had weak negative associations with snowshoe hares (β = −0.211, 90% CrI = −0.407–0.004) and caribou (β = −0.085, 90% CrI = −0.299–0.099), and had a neutral response to cutblocks and roads (β = −0.047, 90% CrI = −0.569–0.452) and a weak negative response to fire (β = −0.393, 90% CrI = −0.863–0.033; Figure 5F).

Wolves (β = −0.565, 90% CrI = −0.948 to −0.206), grizzly bears (β = −0.679, 90% CrI = −1.11 to −0.304), lynx (β = −0.215, 90% CrI = −0.470–0.040), and wolverine (β = −0.667, 90% CrI = −1.22 to −0.178) responded positively to proximity to water sources. All predator species except wolverine had more detections at stations targeting roads compared to game trails or other natural features (wolf: β = 2.26, 90% CrI = 1.44–3.12; coyote: β = 1.12, 90% CrI = 0.655–1.62; black bear: β = 0.516, 90% CrI = 0.130–0.904; grizzly bear: β = 1.11, 90% CrI = 0.269–2.00; lynx: β = 0.800, 90% CrI = 0.226–1.41) and more detections at higher temperatures (wolf: β = 0.213, 90% CrI = 0.054–0.374; coyote: β = 0.497, 90% CrI = 0.422–0.573; black bear: β = 0.345, 90% CrI = 0.246–0.444; grizzly bear: β = 0.166, 90% CrI = −0.055–0.396; lynx: β = 0.512, 90% CrI = 0.432–0.592).

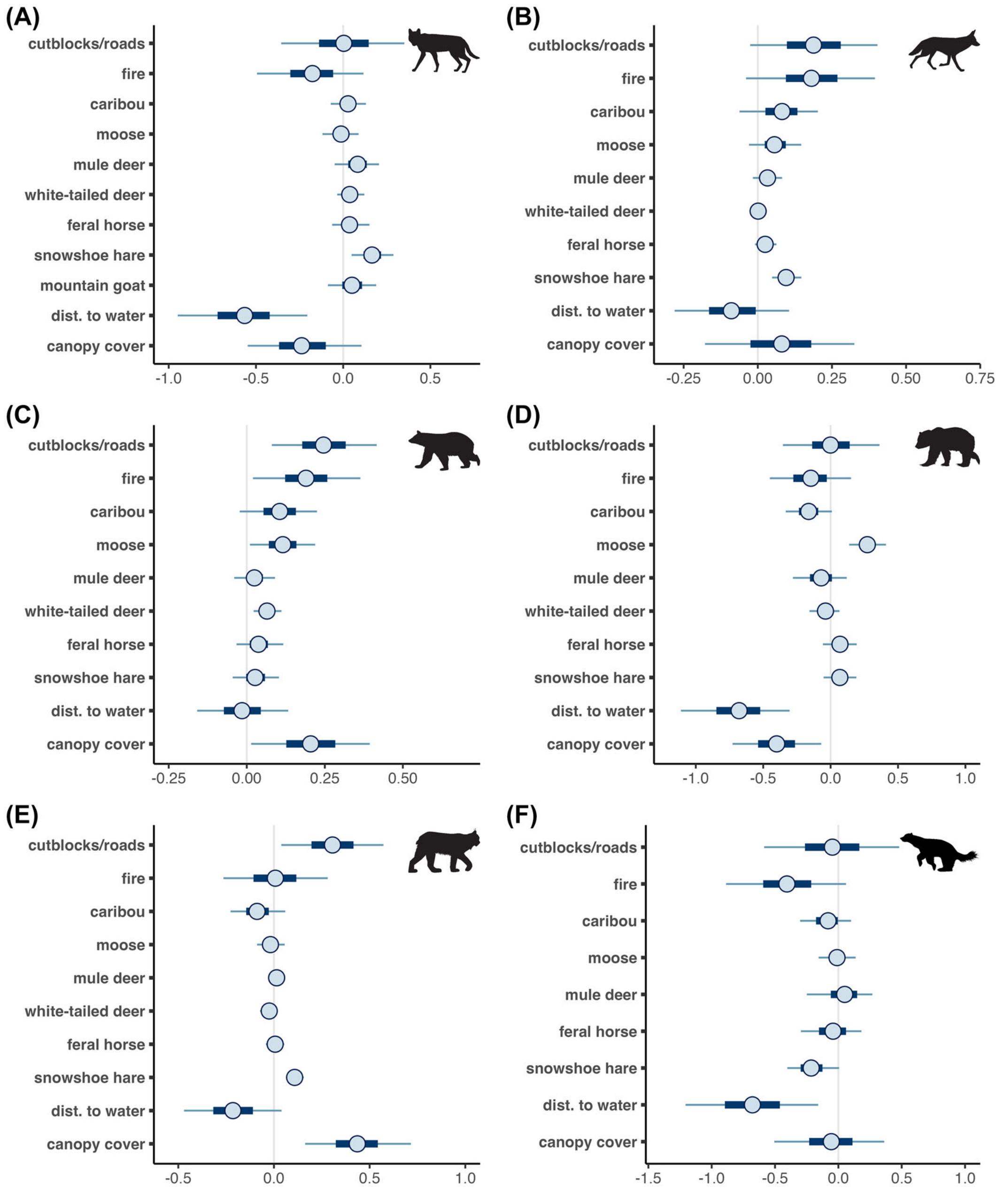

FIGURE 5 Standardized coefficient estimates and credible intervals (thin lines: 90%, thick lines: 50%) for disturbance, prey, and environmental variables of Bayesian negative binomial mixed effects models for detection of A) grey wolf, B) coyote, C) black bear, D) grizzly bear, E) Canada lynx, and F) wolverine in the Chilcotin Plateau of British Columbia, Canada, 2020–2023 using camera trapping data. dist. = distance.

Caribou predation risk

In line with DMAC, caribou did not respond negatively to disturbance and did not have strong negative associations with predators during the calving season or at low elevation, potentially increasing their vulnerability to predators.

During calving season and within the calving grounds, caribou had a neutral response to fire (β = 0.030, 90% CrI = −0.276–0.342) and weak positive associations with black bears (β = 0.113, 90% CrI = −0.010–0.232) and wolverines (β = 0.083, 90% CrI = −0.080–0.244) but not other predator species (Figure 6A). In the calving season and range, caribou had a negative response to productivity (β = −0.569, 90% CrI = −0.908 to −0.234) and canopy cover (β = −0.234, 90% CrI = −0.582–0.105; Figure 6A).

At low elevation, we found that caribou had a weak positive response to cutblocks and roads (β = 0.356, 90% CrI = −0.058–0.801) but not fire (β = −0.101, 90% CrI = −0.516–0.325; Figure 6B). The model predicted a 319% increase in caribou detections (or an additional 0.3 caribou detections per year at a station) when the proportion of cutblocks around a station increased from 0 to 0.85. At low elevation, caribou did not have negative associations with predators but rather weak positive associations with wolves (β = 0.112, 90% CrI = −0.048–0.262), coyotes (β = 0.176, 90% CrI = −0.045–0.412), and black bears (β = 0.112, 90% CrI = −0.035–0.271; Figure 6B). Caribou at low elevation responded positively to wetlands (β = 0.338, 90% CrI = −0.045–0.731) and increased distances from water sources (β = 0.459, 90% CrI = 0.062–0.832; Figure 6B). Caribou had a positive response to monthly temperature during calving (β = 0.450, 90% CrI = 0.282–0.624) and at low elevation (β = 0.647, 90% CrI = 0.405–0.909).

DISCUSSION

In this study, we evaluated support for DMAC in the low-productivity, fire-prone, and extensively harvested range of the declining Itcha-Ilgachuz caribou herd. We found mixed support for DMAC as a putative cause of caribou decline. Specifically, we documented a productivity pulse after disturbance but overall low productivity; strong primary prey responses to burnt areas and weak responses to cutblocks; associations of wolves, coyotes, black bears, and grizzlies with primary prey, but mixed predator responses to disturbance; and higher relative abundance of caribou near cutblocks and associations with predators that could increase risk of predation for caribou. The hypothesis of direct responses of predators to disturbance (Figure 1C) warrants further investigation for the Itcha-Ilgachuz caribou, as we found that several predator species were associated with cutblocks and roads and detected more on roads than natural features, but we could not isolate the impact of linear features. We also found some

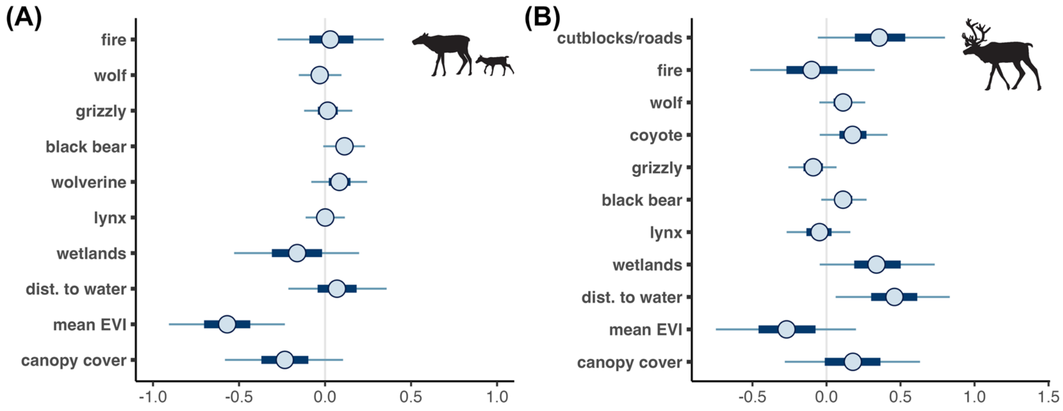

FIGURE 6 Standardized coefficient estimates and credible intervals (thin lines: 90%, thick lines: 50%) for disturbance, predator, and environmental variables from Bayesian negative binomial mixed effects models for detection of caribou A) in the calving range (grids in Itcha-Ilgachuz Provincial Park) and during the calving season (May-July) and B) at low elevation year-round in the Chilcotin Plateau of British Columbia, Canada, 2020–2023 using camera trapping data. EVI = enhanced vegetation index and dist. = distance.

responses consistent with the alternate hypothesis of apparent competition independent of disturbance (Figure 1B), with multiple predators responding positively to snowshoe hares and feral horses.

Productivity pulse

Testing the first prediction of DMAC, we documented an increase in vegetation productivity, measured using EVI, following forest harvest and fire in the Itcha-Ilgachuz range (Figure 3). However, overall productivity was lower compared to caribou ranges where DMAC has been documented as a driver of decline. The similarity in magnitude and trend of productivity after fire between Itcha-Ilgachuz and the Saskatchewan boreal forest, where DMAC was not supported because of low productivity (Neufeld et al. 2021), indicates that the boost in vegetation following habitat disturbance may be insufficient to yield increases in ungulate prey populations. In the Purcells caribou range, where the cause of decline was consistent with DMAC (Kinley and Apps 2001), productivity in cutblocks was substantially higher than for Itcha-Ilgachuz, although productivity after fire was similar. The Barkerville herd range had the most dramatic increase in productivity after disturbance, markedly more than Itcha-Ilgachuz, despite being the closest in proximity and latitude. The Itcha-Ilgachuz range lies in the rain shadow of the Coast Mountains, while Barkerville's location in the Columbia Mountains leads to much more annual precipitation. Pre-disturbance productivity was similar between Barkerville and Itcha in cutblock areas, and Barkerville had lower productivity than Itcha-Ilgachuz pre-fire, but the additional precipitation in this range, among other factors, allowed productivity to dramatically increase following disturbance. Overall, trends of post-disturbance productivity and faster recovery in cutblocks compared to burnt areas for Itcha-Ilgachuz were consistent with rates of forest recovery across Canada (e.g., White et al. 2022). Further research is needed to investigate the forage species composition in cutblocks and burnt areas to determine if the productivity pulse we found is sufficient to support increased primary prey populations for the DMAC mechanism, despite the lower overall productivity within the Itcha-Ilgachuz range.

Prey attraction

Our finding that moose and mule deer only had weakly increased relative abundance in cutblocks is contrary to predictions from DMAC, but we did see strong positive responses to fire from both species (Figure 4). This indicates that natural and industrial disturbances may be having different impacts on caribou in this system, as suggested for other caribou ranges by DeMars et al. (2019), Stewart et al. (2020), and Konkolics et al. (2021). DeMars et al. (2019) found that burns in the boreal forest did not increase moose site use, consistent with findings that burnt areas in the boreal forest did not support greater volumes of preferred moose forage (Neufeld et al. 2021). In contrast, our results suggest that both moose and mule deer respond positively to fire, and thus fire could be more detrimental for caribou in this system. The stronger response to fire than cutblocks by moose and mule deer suggests that the vegetation composition after wildfire may be more attractive to ungulates, despite the minimal (7%) increase in productivity. Our finding that moose had increased relative abundance in and around burnt areas aligns with research from Alaska where moose were found to select burnt areas, depending on season, fire severity, time since fire, and sex (reviewed in Johnson and Rea 2024). Increased mule deer relative abundance in and around burnt areas is consistent with findings from northern Washington, where mule deer selected for burnt areas in summer to take advantage of increased forage availability (Ganz et al. 2022). Future research could investigate responses of primary prey to fire across a range of severities to better predict responses of moose and deer under different fire management regimes (Christianson et al. 2022), and across different levels of forest harvest and fire to investigate whether primary prey responses to disturbance change with availability of disturbed habitat (Holbrook et al. 2019). The role of mule deer in apparent competition dynamics with caribou has received little attention, with most studies focusing on areas where moose, white-tailed deer, or elk are the most abundant ungulates sympatric with caribou. Our results demonstrate that mule deer may similarly increase in disturbed forest patches near caribou.

Across their North American range, the documented responses of moose to cutblocks have been mixed, often dependent on season, successional stage, productivity, and availability of adjacent mature forest for cover (reviewed in Johnson and Rea 2024). The weak response of moose to forest harvest that we found aligns with the finding of Gagné et al. (2016) in northern Quebec, Canada, where moose decreased selection of cutblocks at higher latitudes where deciduous vegetation was less available. Mule deer selection of mature forest in winter ranges in British Columbia has been well documented (e.g., Armleder et al. 1994), as winter survival is considered a main limiting factor for mule deer (Mackie 1998). Summer habitat selection of mule deer has received less attention, but the weak response to cutblocks we found was consistent with research describing mixed responses to cutblocks in Utah, USA, where mule deer were found to preferentially forage in lodgepole pine cutblocks but stay near forest edges, and rest in undisturbed forest (Collins and Urness 1983). There may also be potential differences in selection of cutblocks of different ages and in different seasons by prey species (e.g., Mumma et al. 2021) that requires further investigation to fully understand the role of timber harvesting in DMAC in dry, cold ecosystems like the Chilcotin.

We were able to measure the relative abundance patterns of the species involved in DMAC but not their demographic trends over time. While increased relative abundance in or near disturbed areas would likely be a precursor to increased population sizes for these primary prey, this is not necessarily the case. In fact, there was a decline in the moose population in the Chilcotin from 2008 to 2014, following an outbreak of mountain pine beetle and subsequent increases in salvage logging (Kuzyk 2016). Population surveys for mule deer have not been conducted consistently in the Chilcotin, but licensed mule deer harvest data show that after accounting for hunter effort, the number of mule deer harvested in Wildlife Management Unit 5-12 in the study area has fluctuated year to year but remained roughly stable over the last 20 years (British Columbia Fish and Wildlife 2024). We suggest continued monitoring of population trends for moose, and monitoring of mule deer and predator species to test population-level predictions of DMAC in this region, such as by annual estimation density from camera trap sampling (Burgar et al. 2019, Palencia et al. 2021) or by aerial surveys (Peters et al. 2014).

Predator attraction

Overall, predator responses to the relative abundances of prey species aligned with our expectations based on DMAC, with wolves, bears, and coyotes having positive associations with ungulates (Figure 5). Wolves had the strongest association with snowshoe hare, followed by mule deer, and had no significant association with caribou, consistent with predation on caribou by wolves being incidental (Latham et al. 2013). The strong wolf response to hares relative to ungulate prey was unexpected. Curveira-Santos et al. (2024) found that higher availability of hares associated with habitat disturbances attracted coyotes, black bears, and lynx, but caribou did not avoid areas of increased hare use as they did with moose. The relationships between predators and hares could also change through time, as the hare population in this region undergoes population cycling (Krebs et al. 2001, 2013). Throughout the 3 years of our camera trapping study, we observed an increase in snowshoe hare detection events, from about 4 to 12 detections per 100 camera trap days in 2021 and 2023, respectively, indicating that the hare population may have been on the upswing of a population cycle, with hares providing a large source of food for a variety of predators. While snowshoe hares and caribou are 2 of the most studied species in northern forests, their dynamics have rarely been explicitly linked.

Positive associations of coyotes and lynx with snowshoe hares aligned with our expectations, as snowshoe hares and rodent species are dominant prey in their diets (O'Donoghue et al. 1998). Coyotes also had positive associations with moose and caribou, possibly reflecting predation on calves (Linnell et al. 1995), although coyotes have been shown to be capable of hunting adult ungulate prey, including moose, particularly in eastern North America when hunting in packs (Benson and Patterson 2013, Jensen et al. 2022). We had very few detections of coyotes in the caribou calving range during calving season, suggesting they may not be specializing on caribou neonates in this region but could be predating on calves later in the summer or fall at low elevation where they overlap spatially (Zager and Beecham 2006). While lynx have been reported as a predator of neonate caribou in Newfoundland (Bergerud 1983), they are generally considered lagomorph specialists (Linnell et al. 1995), which aligns with our results. We did not find that wolverines responded positively to either disturbance, caribou, or primary prey, indicating that they may not be contributing to DMAC in this region. This lack of association with focal prey species was unexpected because moose and caribou have been found to be major components of diet for wolverines in British Columbia (Lofroth et al. 2007), and wolverine are a major predator for caribou calves in northern British Columbia (Gustine et al. 2006). Because wolverines are facultative scavengers (Van Dijk et al. 2008), their detections may be more decoupled from the species they consume, resulting in the observed lack of prey associations.

It is important to consider how the ongoing removal of wolves from this system could be affecting responses of wolves and other focal species. In addition to annual changes in their abundance (Seip 2021), wolf behavior and habitat use patterns have also been shown to change following removal efforts—as pack dynamics are altered, remaining wolves are re-establishing territories, and responses to humans are changed. For example, wolves have been found to become more nocturnal (Frey et al. 2022) and avoid linear features following wolf reduction (Baillie-David et al. 2024). It is possible that the responses of wolves to habitat and prey that we found in this study are influenced by this disruptive management action. Additionally, the removal of wolves as the apex predator in this system could result in mesopredator release (Prugh et al. 2009), where non-dominant predators (coyote, bear, and lynx) could increase in abundance or change behavior, potentially increasing their predation pressure on caribou. There has not been evidence of mesopredator release following wolf control for caribou to date, and a study in western Alberta showed that habitat use by mesopredators and prey was more strongly associated with landscape disturbance than with wolves recolonizing following removal (Seip 2021). However, we did observe an increase in coyote detections throughout our sampling period, with 0.6 detections per 100 camera trap days in 2021 compared to 1.2 in 2023. In the future, we recommend implementing experimental designs to rigorously test the impacts of predator reduction efforts on not only caribou directly, but non-dominant predators and primary prey, including monitoring of the system prior to reduction efforts (Treves et al. 2016).

Notably, we found that coyotes, black bears, and grizzly bears were weakly positively associated with feral horses. There is evidence that wolves (Parr and McCrory 2023) and cougars (S. White, British Columbia Ministry of Water, Land and Resource Stewardship, unpublished data) are consuming feral horses in the Chilcotin, but to our knowledge relationships between feral horses and other predators have not been tested. It is possible that predation by large predators or other causes of horse mortality (e.g., starvation) are providing resource subsidies through scavenging opportunities for all predators, as suggested by White et al. (2020). Boyce and McLoughlin (2021) outlined the potential for feral horses to act as an apparent competitor with detrimental impacts on native ungulate populations, including caribou, due to artificially selected traits such as increased investment in reproduction allowing for rapid population growth. Feral horses in the study area have been found to select for wetland areas and avoid cutblocks (Tjaden-McClement 2024), so apparent competition with horses would likely be occurring independently of habitat disturbance. Investigation into the presence and prevalence of feral horses in predator diets in the Chilcotin could shed more light on this possibility, and whether management of feral horse populations should be considered for caribou conservation.

We found that coyotes and black bears had positive responses to both disturbance types, and lynx had increased relative abundance with increasing burnt area. Predation by wolves has been identified as the primary cause of adult mortality for the Itcha-Ilgachuz caribou (Shores 2019), so we had expected that wolves may be associating with cutblocks and roads for increased access and movement efficiency within caribou habitat, as found by Mumma et al. (2018). Our findings that wolves exhibited a neutral response to cutblocks and associated roads are consistent with those of Ehlers et al. (2016), where wolf responses to industrial features varied by pack and season, with no clear preference for linear features. However, we did see a strong positive response of wolves to cameras targeting roads, rather than game trails or other natural features, suggesting that they are using roads when available. Given the high density of roads within all 3 low-elevation grids, we suggest that wolves (and other predator species) may not need to select for areas of greater cutblock and road density at the scale of a 500-m buffer to use roads for efficient movement because of the sheer volume of road availability (Mysterud et al. 1998). Finer scale analysis of telemetry data has found that wolves increase their selection of linear features in areas with high availability (Muhly et al. 2019, Mumma et al. 2019), so use of roads by predators in this area requires further investigation. It is also possible that wolf responses to disturbance (and prey) vary seasonally (e.g., Lesmerises et al. 2012), which we were not able to test because of data limitation. Positive responses to cutblocks and burnt areas by black bears and coyotes may reflect increased vegetation forage resources in early seral patches (e.g., berry patches; Mosnier et al. 2008, Jensen et al. 2022), or increased ungulate prey availability. Grizzly bears have also been shown to have mixed responses to cutblocks, dependent upon the availability of preferred food (Colton et al. 2021), indicating that forage quality for grizzly bears in cutblocks may be low in our study area, given that we found no response to disturbance. Increased ease of travel on roads could also explain the positive responses of bears, coyotes, and lynx to cutblocks and roads.

While we only had 22 detections of cougars over the course of sampling, and thus insufficient sample size for these models, cougars have been confirmed to predate on caribou in the Chilcotin, so they may be playing a role in the decline of the Itcha-Ilgachuz caribou (White et al. 2020). Ultimately, our study supports the need for further research on the potential impacts of predation by a variety of predators on caribou, and the interactions among these predators and various prey (including smaller species like hares) rather than the typical focus of caribou management on only wolves, moose, and deer.

Caribou predation risk

We did not find evidence that caribou had lower relative abundance in or near cutblocks and associated roads (Figure 6). Increased caribou relative abundance in areas with more cutblocks at low elevation aligns with our expectation that caribou may not be able to effectively spatially segregate from predators and primary prey in this system, potentially resulting in increased rates of incidental predation (Kinley and Apps 2001, Ehlers et al. 2016). The positive response of caribou to cutblocks at low elevation is consistent with telemetry research for the Itcha-Ilgachuz population, which found they were selecting harvested areas for food in the summer and fall but avoiding them in the winter because of a lack of lichens, a preferred winter food source, and deep snow impeding movement and increasing energy expenditure when cratering for lichen (Apps and Dodd 2017). Caribou mortality in the Itcha-Ilgachuz population is associated with higher road density (Apps 2020). Caribou use of cutblock areas during non-calving periods could be an ecological trap (Hale and Swearer 2016), where caribou are attracted by forage resources but as a result have increased overlap with black bears and coyotes. We found that caribou had a weak positive association with wolves at low elevation, despite not sharing habitat preferences with them, but not during calving (Figure 6). During calving, caribou had increased relative abundance at sites with lower productivity, which could reduce overlap with other primary prey but require a trade-off in terms of reduced access to high-quality forage for caribou females undergoing energetic demands of lactation (Gustine et al. 2006). We found no association between caribou and wolf detections during calving but did find weak positive associations with wolverines and black bears, suggesting some overlap with potentially important predators of neonate caribou (Gustine et al. 2006, Latham et al. 2011*a*, Bonin et al. 2023).

Mechanism of caribou decline

Taken together, these results provide some support for the DMAC mechanism as a contributing cause of decline for the Itcha-Ilgachuz caribou, with an increase in primary prey and associated predators mediated through forest fire, and to a lesser extent forest harvest. We also found some support for a direct effect of linear features on predator movement efficiency and increased predation rates leading to caribou decline (Figure 1C), as described in Mumma et al. (2018). However, we were unable to decouple the responses of predators to cutblocks versus linear features because they are so tightly linked in the study area. We suggest that further work should be conducted to assess predator use of roads in this area, potentially through finer scale investigation of predator movement using telemetry data or experimental management trials of road restoration. Apparent competition independent of habitat disturbance (Figure 1B) with snowshoe hares or feral horses as the primary prey may also be contributing to the observed decline of the Itcha-Ilgachuz caribou and is also worth further investigation, as multiple predator species were positively associated with hares and horses, both of which may be unique to this caribou system.

The potential role of fire in the decline of the Itcha-Ilgachuz caribou underscores the need for improved fire management and landscape resiliency practices within caribou ranges, including the return of cultural burning by First Nations. Historical forest harvest and fire management practices in British Columbia focused on control and suppression of wildfires and have resulted in build-ups of fuels on the landscape (Copes-Gerbitz et al. 2022). Climate change is also creating new fire dynamics with more extreme heat events and dry conditions projected to increase the number, area, and severity of wildfires (Tymstra et al. 2020, Parisien et al. 2023). Together, this has led to an increasing number of large, high-intensity fires, such as those in the Chilcotin in 2017 (Copes-Gerbitz et al. 2022). This is not characteristic of natural and Indigenous-stewarded fire regimes with more frequent, lower-intensity fires that caribou had been coexisting with for millennia (Christianson et al. 2022). Shifting back to Indigenous-led fire management and cultural burning regimes may be key to habitat conservation for caribou as we move forward to a new era of fire-management in British Columbia, focused on coexisting with fire (Copes-Gerbitz et al. 2022).

MANAGEMENT IMPLICATIONS

The decline of the Itcha-Ilgachuz caribou population may be caused in part by forest fire in the area, which leads to increased use by moose and mule deer, prey species that are in turn associated with increased use by wolves, bears, and coyotes. Similar to areas of northern Saskatchewan (Johnson et al. 2020), we found a stronger role of forest fire contributing to the DMAC pathway. We also found some evidence that roads associated with forestry activities are facilitating predator movement and recommend further work to assess this contribution, including through monitoring the effects of road restoration. Cutblocks may be acting as an ecological trap for caribou in this region, exposing them to predators, which warrants further investigation and consideration about the rate and intensity of timber harvest within the range of this threatened caribou population. Overall, this study reinforces calls for context-specific research and adaptive management (Walters 1986, Walters and Holling 1990, Dickie et al. 2023) to determine what conservation actions will have the greatest benefit for different caribou populations, including those in low-productivity areas.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Ethics approval for camera trapping wildlife species for this study was granted under a University of British Columbia Animal Care Certificate (A22-0178).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

Alfaro, R. I., L. van Akker, and B. Hawkes. 2015. Characteristics of forest legacies following two mountain pine beetle outbreaks in British Columbia, Canada. Canadian Journal of Forest Research 45:1387-1396.

Apps, C. 2020. Exploring mechanisms by which landscape disturbances influence woodland caribou in west-central British Columbia. British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development, Williams Lake, Canada.

Apps, C., and N. Dodd. 2017. Caribou habitat modeling and evaluation of forest disturbance influences across landscape scales in west-central British Columbia – January, 2017. Ministry of Forests, Lands and Natural Resource Operations, Williams Lake, Canada.

Armleder, H. M., M. J. Waterhouse, D. G. Keisker, and R. J. Dawson. 1994. Winter habitat use by mule deer in the central interior of British Columbia. Canadian Journal of Zoology 72:1721-1725.

Baillie-David, K., J. P. Volpe, A. C. Burton, and J. T. Fisher. 2024. Grey wolves (*Canis lupus*) shift selection of anthropogenic landscape features following predator control in the Nearctic boreal forest. Biological Conservation 296:110677.

Baker, B. G. 1990. Winter habitat selection and use by moose in the West-Chilcotin Region of British Columbia. Thesis, University of British Columbia, Vancouver, Canada.

British Columbia Fish and Wildlife. 2024. Big Game Harvest Statistics 1976 to Current [Data set]. https://catalogue.data.gov.bc.ca/dataset/big-game-harvest-statistics-1976-to-current. Accessed 10 Mar 2024.

British Columbia Ministry of Forests - Forest Analysis and Inventory Branch. 2022. Harvested Areas of BC (Consolidated Cutblocks) [Data set]. https://catalogue.data.gov.bc.ca/dataset/harvested-areas-of-bc-consolidated-cutblocks-. Accessed 23 Feb 2022.

British Columbia Ministry of Land, Water and Resource Stewardship. 2022. Predator Reduction to Support Caribou Recovery: 2021-2022 Summary. https://www2.gov.bc.ca/assets/gov/environment/plants-animals-and-ecosystems/wildlife-wildlife-habitat/caribou/predator_reduction_to_support_caribou_recovery_2021-2022.pdf. British Columbia Ministry of Land, Water and Resource Stewardship, Victoria, Canada.

British Columbia Ministry of Water, Land and Resource Stewardship. 2023. Predator Reduction to Support Caribou Recovery: 2022-2023 Summary. British Columbia Ministry of Land, Water and Resource Stewardship, Victoria, Canada. https://www2.gov.bc.ca/assets/gov/environment/plants-animals-and-ecosystems/wildlife-wildlife-habitat/caribou/predator_reduction_to_support_caribou_recovery_2022-2023.pdf

British Columbia Wildfire Service. 2022. Fire Perimeters – Historical [Data set]. https://catalogue.data.gov.bc.ca/dataset/fire-perimeters-historical. Accessed 23 Feb 2022.

Beery, S., D. Morris, and S. Yang. 2019. Efficient pipeline for camera trap image review. ArXiv:1907.06772.

Benson, J. F., and B. R. Patterson. 2013. Moose (*Alces alces*) predation by eastern coyotes (*Canis latrans*) and eastern coyote × eastern wolf (*Canis latrans* × *Canis lycaon*) hybrids. Canadian Journal of Zoology 91:837–841.

Berger-Tal, O., T. Polak, A. Oron, Y. Lubin, B. P. Kotler, and D. Saltz. 2011. Integrating animal behavior and conservation biology: a conceptual framework. Behavioral Ecology 22:236–239.

Bergerud, A. T. 1983. Prey switching in a simple ecosystem. Scientific American 249:130-141.

Bergerud, A. T. 1988. Caribou, wolves and man. Trends in Ecology & Evolution 3:68–72.

Bergerud, A. T., H. E. Butler, and D. R. Miller. 1984. Antipredator tactics of calving caribou: dispersion in mountains. Canadian Journal of Zoology 62:1566–1575.

Blanchet, F. G., K. Cazelles, and D. Gravel. 2020. Co-occurrence is not evidence of ecological interactions. Ecology Letters 23:1050–1063.

Bonin, M., C. Dussault, J. Taillon, J. Pisapio, N. Lecomte, and S. D. Côté. 2023. Diet flexibility of wolves and black bears in the range of migratory caribou. Journal of Mammalogy 104:252–264.

Boyce, P. N., and P. D. McLoughlin. 2021. Ecological interactions involving feral horses and predators: review with implications for biodiversity conservation. Journal of Wildlife Management 85:1091–1103.

British Columbia Ministry of Water Land and Air Protection Environmental Stewardship Division. 2002. Itcha Ilgachuz Provincial Park and Ilgachuz Range Ecological Reserve Management Plan. British Columbia Ministry of Water Land and Air Protection Environmental Stewardship Division, Victoria, Canada.

Burgar, J. M., A. C. Burton, and J. T. Fisher. 2019. The importance of considering multiple interacting species for conservation of species at risk. Conservation Biology 33:709–715.

Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, E. Bayne, and S. Boutin. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology 52:675–685.

Christianson, A. C., C. R. Sutherland, F. Moola, N. Gonzalez Bautista, D. Young, and H. MacDonald. 2022. Centering Indigenous voices: the role of fire in the boreal forest of North America. Current Forestry Reports 8:257–276.

Collins, W. B., and P. J. Urness. 1983. Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. Journal of Wildlife Management 47:646–663.

Colton, C. P., N. C. Coops, and A. C. Burton. 2021. Grizzly bear (*Ursus arctos*) responses to forest harvesting: a review of underlying mechanisms and management recommendations. Forest Ecology and Management 497:119471.

Committee on the Status of Endangered Wildlife in Canada [COSEWIC]. 2014. COSEWIC assessment and status report on the Caribou *Rangifer tarandus*, Northern Mountain population, Central Mountain population and Southern Mountain population in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario, Canada.

Cooke, S. J., C. L. Madliger, R. J. Lennox, J. D. Olden, E. J. Eliason, R. L. Cramp, A. Fuller, C. E. Franklin, and F. Seebacher. 2023. Biological mechanisms matter in contemporary wildlife conservation. iScience 26:106192.

Copes-Gerbitz, K., S. M. Hagerman, and L. D. Daniels. 2022. Transforming fire governance in British Columbia, Canada: an emerging vision for coexisting with fire. Regional Environmental Change 22:48.

Côté, I. M., E. S. Darling, and C. J. Brown. 2016. Interactions among ecosystem stressors and their importance in conservation. Proceedings of the Royal Society B: Biological Sciences 283:20152592.

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.

DeMars, C. A., C. J. Johnson, M. Dickie, T. J. Habib, M. Cody, A. Saxena, S. Boutin, and R. Serrouya. 2023. Incorporating mechanism into conservation actions in an age of multiple and emerging threats: the case of boreal caribou. Ecosphere 14:e4627.

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.

Denryter, K. A., R. C. Cook, J. G. Cook, and K. L. Parker. 2017. Straight from the caribou's (*Rangifer tarandus*) mouth: detailed observations of tame caribou reveal new insights into summer–autumn diets. Canadian Journal of Zoology 95:81–94.

Devarajan, K., T. L. Morelli, and S. Tenan. 2020. Multi-species occupancy models: review, roadmap, and recommendations. Ecography 43:1612–1624.

Díaz, S., J. Settele, E. S. Brondízio, H. T. Ngo, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, et al. 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. Science 366:eaax3100.

Dickie, M., A. T. Ford, R. Steenweg, and R. Serrouya. 2023. Intervention-forward adaptive management in the face of extinction. Trends in Ecology & Evolution 38:505–506.

Dickie, M., R. Serrouya, R. S. McNay, and S. Boutin. 2017. Faster and farther: wolf movement on linear features and implications for hunting behaviour. Journal of Applied Ecology 54:253–263.

Didan, K. 2021. MOD13Q1 MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SIN Grid V061 [Data set]. NASA EOSDIS Land Processes Distributed Active Archive Center, Sioux Falls, South Dakota, USA.

Doddington, B. J., J. Bosch, J. A. Oliver, N. C. Grassly, G. Garcia, B. R. Schmidt, T. W. J. Garner, and M. C. Fisher. 2013. Context-dependent amphibian host population response to an invading pathogen. Ecology 94: 1795–1804.

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

Dulude-de Broin, F., S. Hamel, G. F. Mastromonaco, and S. D. Côté. 2020. Predation risk and mountain goat reproduction: evidence for stress-induced breeding suppression in a wild ungulate. Functional Ecology 34:1003–1014.

Ehlers, L. P. W., C. J. Johnson, and D. R. Seip. 2016. Evaluating the influence of anthropogenic landscape change on wolf distribution: implications for woodland caribou. Ecosphere 7:e01600.

Environment Canada. 2014. Recovery Strategy for the Woodland Caribou, Southern Mountain Population (*Rangifer Tarandus Caribou*) in Canada. Species at Risk Act Recovery Strategy Series. Environment Canada, Ottawa, Ontario, Canada.

Environment Canada. 2020. Amended Recovery Strategy for the Woodland Caribou (Rangifer tarandus caribou), Boreal Population, in Canada 2020. Species at Risk Act Recovery Strategy Series. Environment Canada, Ottawa, Ontario, Canada.

Festa-Bianchet, M., J. C. Ray, S. Boutin, S. D. Côté, and A. Gunn. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. Canadian Journal of Zoology 89:419–434.

Franzmann, A. W., and C. C. Schwartz, editors. 2007. Ecology and management of the North American moose. Second edition. University Press of Colorado, Boulder, USA.

Frenette, J., F. Pelletier, and M.-H. St-Laurent. 2020. Linking habitat, predators and alternative prey to explain recruitment variations of an endangered caribou population. Global Ecology and Conservation 22:e00920.

Frey, S., D. Tejero, K. Baillie-David, A. C. Burton, and J. T. Fisher. 2022. Predator control alters wolf interactions with prey and competitor species over the diel cycle. Oikos 2022:e08821.

Gabry, J., and M. Modrák. 2024. Visual MCMC diagnostics using the bayesplot package. https://cran.r-project.org/web/packages/bayesplot/vignettes/visual-mcmc-diagnostics.html

Gagné, C., J. Mainguy, and D. Fortin. 2016. The impact of forest harvesting on caribou–moose–wolf interactions decreases along a latitudinal gradient. Biological Conservation 197:215-222.

Gannon, K. 2023. Itcha-Ilgachuz June population survey. British Columbia Ministry of Environment and Parks, Victoria, Canada. http://a100.gov.bc.ca/pub/siwe/details.do?projectId=5955

Ganz, T. R., M. T. DeVivo, B. N. Kertson, T. Roussin, L. Satterfield, A. J. Wirsing, and L. R. Prugh. 2022. Interactive effects of wildfires, season and predator activity shape mule deer movements. Journal of Animal Ecology 91: 2273–2288.

Gelman, A., Carlin, J. B., Stern, H. S., and Rubin, D. B. 1995. Bayesian data analysis. Chapman and Hall, New York, New York, USA.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457-472.

GeoBC. 2022. Freshwater Atlas Wetlands [Data set]. https://catalogue.data.gov.bc.ca/dataset/freshwater-atlas-wetlands. Accessed 21 Apr 2022.

Gillingham, M. P., and K. L. Parker. 2008. Differential habitat selection by moose and elk in the besa-prophet area of northern British Columbia. Alces 44:41–63.

Gomes, D. G. 2022. Should I use fixed effects or random effects when I have fewer than five levels of a grouping factor in a mixed-effects model? PeerJ 10:e12794.

Goodrich, B., J. Gabry, I. Ali, and S. Brilleman. 2020. rstanarm: Bayesian applied regression modeling via Stan. R package version 2.21.1. https://mc-stan.org/rstanarm

Government of Canada. 2022. Lakes and rivers in Canada - CanVec – Hydro Features [Data set]. https://maps.canada.ca/czs/index-en.html. Accessed 20 Apr 2022.

Government of Canada. 2024. Monthly Climate Summaries for Puntzi Mountain (AUT). [Data set]. https://climate-change.canada.ca/climate-data/#/monthly-climate-summaries. Accessed 20 Nov 2024.

Gustine, D. D., K. L. Parker, R. J. Lay, M. P. Gillingham, and D. C. Heard. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. Wildlife Monographs 165:1–32.

Hale, R., and S. E. Swearer. 2016. Ecological traps: current evidence and future directions. Proceedings of the Royal Society B: Biological Sciences 283:20152647.

Hebblewhite, M. 2017. Billion dollar boreal woodland caribou and the biodiversity impacts of the global oil and gas industry. Biological Conservation 206:102-111.

Hebblewhite, M., J. Whittington, M. Bradley, G. Skinner, A. Dibb, and C. A. White. 2007. Conditions for caribou persistence in the wolf-elk-caribou systems of the Canadian Rockies. Rangifer 27:79.

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.

Hijmans, R. J. 2023. terra: spatial data analysis. R package version 1.6-53. https://CRAN.R-project.org/package=terra

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.

Hufkens, K. 2022. The MODISTools package: an interface to the MODIS Land Products Subsets Web Services. https://github.com/bluegreen-labs/MODISTools

Hughes, J., S. D. Albon, R. J. Irvine, and S. Woodin. 2009. Is there a cost of parasites to caribou? Parasitology 136: 253–265.

Jensen, A. J., C. J. Marneweck, J. C. Kilgo, and D. S. Jachowski. 2022. Coyote diet in North America: geographic and ecological patterns during range expansion. Mammal Review 52:480–496.

Johnson, C. A., G. D. Sutherland, E. Neave, M. Leblond, P. Kirby, C. Superbie, and P. D. McLoughlin. 2020. Science to inform policy: linking population dynamics to habitat for a threatened species in Canada. Journal of Applied Ecology 57:1314–1327.

Johnson, C. J., and R. V. Rea. 2024. 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.

Kinley, T. A., and C. D. Apps. 2001. Mortality patterns in a subpopulation of endangered mountain caribou. Wildlife Society Bulletin 29:158–164.

Konkolics, S., M. Dickie, R. Serrouya, D. Hervieux, and S. Boutin. 2021. A burning question: what are the implications of forest fires for woodland caribou? Journal of Wildlife Management 85:1685–1698.

Krebs, C. J., R. Boonstra, S. Boutin, and A. R. E. Sinclair. 2001. What drives the 10-year cycle of snowshoe hares? BioScience 51:25.

Krebs, C. J., K. Kielland, J. Bryant, M. O'Donoghue, F. Doyle, C. McIntyre, D. DiFolco, N. Berg, S. Carriere, R. Boonstra, et al. 2013. Synchrony in the snowshoe hare (*Lepus americanus*) cycle in northwestern North America, 1970–2012. Canadian Journal of Zoology 91:562–572.

Kuzyk, G. W. 2016. Provincial population and harvest estimates of moose in British Columbia. Alces 52:1-11.

Lamb, C. T., S. Williams, S. Boutin, M. Bridger, D. Cichowski, K. Cornhill, C. DeMars, M. Dickie, B. Ernst, A. Ford, et al. 2024. Effectiveness of population-based recovery actions for threatened southern mountain caribou. Ecological Applications 34:e2965.

Latham, A. D. M., M. C. Latham, and M. S. Boyce. 2011*a*. Habitat selection and spatial relationships of black bears (*Ursus americanus*) with woodland caribou (*Rangifer tarandus caribou*) in northeastern Alberta. Canadian Journal of Zoology 89:267-277.

Latham, A. D. M., M. C. Latham, K. H. Knopff, M. Hebblewhite, and S. Boutin. 2013. Wolves, white-tailed deer, and beaver: implications of seasonal prey switching for woodland caribou declines. Ecography 36:1276–1290.

Latham, A. D. M., M. C. Latham, N. A. Mccutchen, and S. Boutin. 2011*b*. Invading white-tailed deer change wolf–caribou dynamics in northeastern Alberta. Journal of Wildlife Management 75:204–212.

Laurent, M., M. Dickie, M. Becker, R. Serrouya, and S. Boutin. 2021. Evaluating the mechanisms of landscape change on white-tailed deer populations. Journal of Wildlife Management 85:340–353.

Leblond, M., C. Dussault, and J. Ouellet. 2010. What drives fine-scale movements of large herbivores? A case study using moose. Ecography 33:1102–1112.

Lemoine, N. P. 2019. Moving beyond noninformative priors: why and how to choose weakly informative priors in Bayesian analyses. Oikos 128:912-928.

Lesmerises, F., C. Dussault, and M.-H. St-Laurent. 2012. Wolf habitat selection is shaped by human activities in a highly managed boreal forest. Forest Ecology and Management 276:125–131.

Linnell, J. D. C., R. Aanes, and R. Andersen. 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. Wildlife Biology 1:209–223.

Lofroth, E. C., J. A. Krebs, W. L. Harrower, and D. Lewis. 2007. Food habits of wolverine *Gulo gulo* in montane ecosystems of British Columbia, Canada. Wildlife Biology 13:31–37.

Mackie, R. J. 1998. Ecology and management of mule deer and white-tailed deer in Montana. Montana Fish, Wildlife, and Parks, Wildlife Division, Helena, USA.

Mallory, C. D., and M. S. Boyce. 2018. Observed and predicted effects of climate change on Arctic caribou and reindeer. Environmental Reviews 26:13–25.

Maltman, J. C., N. C. Coops, G. J. M. Rickbeil, T. Hermosilla, and A. C. Burton. 2024. Quantifying forest disturbance regimes within caribou (*Rangifer tarandus*) range in British Columbia. Scientific Reports 14:6520.

Matasci, G., T. Hermosilla, M. A. Wulder, J. C. White, N. C. Coops, G. W. Hobart, D. K. Bolton, P. Tompalski, and C. W. Bater. 2018. Three decades of forest structural dynamics over Canada's forested ecosystems using Landsat time-series and lidar plots. Remote Sensing of Environment 216:697–714.

McLoughlin, P. D., E. Dzus, B. Wynes, and S. Boutin. 2003. Declines in populations of woodland caribou. Journal of Wildlife Management 67:755.

Microsoft. 2022. AI for Earth camera trap image processing API. (4.1) [Computer software]. Microsoft. https://github.com/microsoft/CameraTraps/blob/master/megadetector.md

Ministry of Forests, Lands, Natural Resource Operations and Rural Development [MFLNRORD]. 2011. Amended Order – General Wildlife Measures: Wildlife Habitat Areas #5-086, 5-087, 5-118, 5-872 and 5-873. MFLNRORD, Victoria, Canada. https://www.env.gov.bc.ca/wld/documents/wha/RATA_5-086-873_ord.pdf

Ministry of Forests, Lands, Natural Resource Operations and Rural Development [MFLNRORD]. 2018. Biogeoclimatic Ecosystem Classification Subzone/Variant Map for the Chilcotin Subunit. MFLNRORD, Victoria, Canada.

Ministry of Forests, Lands, Natural Resource Operations and Rural Development [MFLNRORD]. 2021. Predator Management to Support Caribou Recovery: 2020-2021 Summary. MFLNRORD, Victoria, Canada. https://www2.gov.bc.ca/assets/gov/environment/plants-animals-and-ecosystems/wildlife-wildlife-habitat/caribou/predator_management_to_support_caribou_recovery.pdf

Mosnier, A., J.-P. Ouellet, and R. Courtois. 2008. Black bear adaptation to low productivity in the boreal forest. Ecoscience 15:485–497.

Muhly, T. B., C. A. Johnson, M. Hebblewhite, E. W. Neilson, D. Fortin, J. M. Fryxell, A. D. M. Latham, M. C. Latham, P. D. McLoughlin, E. Merrill, et al. 2019. Functional response of wolves to human development across boreal North America. Ecology and Evolution 9:10801–10815.

Mumma, M. A., M. P. Gillingham, C. J. Johnson, and K. L. Parker. 2019. Functional responses to anthropogenic linear features in a complex predator-multi-prey system. Landscape Ecology 34:2575–2597.

Mumma, M. A., M. P. Gillingham, S. Marshall, C. Procter, A. R. Bevington, and M. Scheideman. 2021. Regional moose (*Alces alces*) responses to forestry cutblocks are driven by landscape-scale patterns of vegetation composition and regrowth. Forest Ecology and Management 481:118763.

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.

Mysterud, A., and E. Østbye. 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. Wildlife Society Bulletin 27:385-394.

Nagy-Reis, M., M. Dickie, A. M. Calvert, M. Hebblewhite, D. Hervieux, D. R. Seip, S. L. Gilbert, O. Venter, C. DeMars, S. Boutin, and R. Serrouya. 2021. Habitat loss accelerates for the endangered woodland caribou in western Canada. Conservation Science and Practice 3:e437.

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.

Neumann, W., S. Martinuzzi, A. B. Estes, A. M. Pidgeon, H. Dettki, G. Ericsson, and V. C. Radeloff. 2015. Opportunities for the application of advanced remotely-sensed data in ecological studies of terrestrial animal movement. Movement Ecology 3:1-13.

O'Donoghue, M., S. Boutin, C. J. Krebs, G. Zuleta, D. L. Murray, and E. J. Hofer. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. Ecology 79:1193.

Palencia, P., J. M. Rowcliffe, J. Vicente, and P. Acevedo. 2021. Assessing the camera trap methodologies used to estimate density of unmarked populations. Journal of Applied Ecology 58:1583–1592.

Parisien, M.-A., Q. E. Barber, M. L. Bourbonnais, L. D. Daniels, M. D. Flannigan, R. W. Gray, K. M. Hoffman, P. Jain, S. L. Stephens, S. W. Taylor, and E. Whitman. 2023. Abrupt, climate-induced increase in wildfires in British Columbia since the mid-2000s. Communications Earth & Environment 4:1–11.

Parr, S., and W. P. McCrory. 2023. Gray wolves (*Canis lupus*) consume free-ranging horses (*Equus ferus caballus*) on the Chilcotin plateau, British Columbia. Canadian Field-Naturalist 136:237–246.

Parsons, A. W., C. T. Rota, T. Forrester, M. C. Baker-Whatton, W. J. McShea, S. G. Schuttler, J. J. Millspaugh, and R. Kays. 2019. Urbanization focuses carnivore activity in remaining natural habitats, increasing species interactions. Journal of Applied Ecology 56:1894–1904.

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.

Peters, W., M. Hebblewhite, K. G. Smith, S. M. Webb, N. Webb, M. Russell, C. Stambaugh, and R. B. Anderson. 2014. Contrasting aerial moose population estimation methods and evaluating sightability in west-central Alberta, Canada. Wildlife Society Bulletin 38:639–649.

Prugh, L. R., and S. M. Arthur. 2015. Optimal predator management for mountain sheep conservation depends on the strength of mesopredator release. Oikos 124:1241–1250.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The rise of the mesopredator. BioScience 59:779–791.

R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Russell, K. L. M., and C. J. Johnson. 2019. Post-fire dynamics of terrestrial lichens: implications for the recovery of woodland caribou winter range. Forest Ecology and Management 434:1–17.

Seip, C. R. 2021. Effects of anthropogenic disturbance and wolf population reduction on caribou predators and competitors in west-central Alberta. Thesis, University of British Columbia, Vancouver, Canada.

Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Canadian Journal of Zoology 70:1494–1503.

Serrouya, R., M. Dickie, C. Lamb, H. Van Oort, A. P. Kelly, C. DeMars, P. D. McLoughlin, N. C. Larter, D. Hervieux, A. T. Ford, and S. Boutin. 2021. Trophic consequences of terrestrial eutrophication for a threatened ungulate. Proceedings of the Royal Society B: Biological Sciences 288:20202811.

Serrouya, R., M. J. Wittmann, B. N. McLellan, H. U. Wittmer, and S. Boutin. 2015. Using predator-prey theory to predict outcomes of broadscale experiments to reduce apparent competition. American Naturalist 185:665–679.

Shores, C. R. 2019. 2019 Itcha-Ilgachuz caribou subpopulation post-calving population survey. Prepared for Ministry of Forests, Lands and Natural Resource Operations, Cariboo Region, British Columbia, Canada.

Sih, A., M. C. O. Ferrari, and D. J. Harris. 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evolutionary Applications 4:367–387.

Smith, V., A. Patterson, S. Elwell, and C. Mackay. 2019. 2019 Chilcotin Free Range Horse Survey. Prepared For Ministry of Forests, Lands, Natural Resource Operations and Rural Development, British Columbia, Canada.

Stewart, F. E. C., J. J. Nowak, T. Micheletti, E. J. B. McIntire, F. K. A. Schmiegelow, and S. G. Cumming. 2020. Boreal caribou can coexist with natural but not industrial disturbances. Journal of Wildlife Management 84:1435–1444.

Superbie, C., K. M. Stewart, C. E. Regan, J. F. Johnstone, and P. D. McLoughlin. 2022. Northern boreal caribou conservation should focus on anthropogenic disturbance, not disturbance-mediated apparent competition. Biological Conservation 265:109426.

Tape, K. D., D. D. Gustine, R. W. Ruess, L. G. Adams, and J. A. Clark. 2016. Range expansion of moose in Arctic Alaska linked to warming and increased shrub habitat. PloS one 11:e0152636.

Tattersall, E. R., J. M. Burgar, J. T. Fisher, and A. C. Burton. 2020. Boreal predator co-occurrences reveal shared use of seismic lines in a working landscape. Ecology and Evolution 10:1678–1691.

Tjaden-McClement, K. 2024. Understanding drivers of caribou decline and feral horse dynamics in the Chilcotin Plateau of British Columbia. Thesis, University of British Columbia, Vancouver, Canada.

Treves, A., M. Krofel, and J. McManus. 2016. Predator control should not be a shot in the dark. Frontiers in Ecology and the Environment 14:380–388.

Tymstra, C., B. J. Stocks, X. Cai, and M. D. Flannigan. 2020. Wildfire management in Canada: review, challenges and opportunities. Progress in Disaster Science 5:100045.

Van Dijk, J., L. Gustavsen, A. Mysterud, R. May, Ø. Flagstad, H. Brøseth, R. Andersen, R. Andersen, H. Steen, and A. Landa. 2008. Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. Journal of Animal Ecology 77:1183–1190.

Walters, C. J. 1986. Adaptive management of renewable resources. Macmillan, New York, New York, USA.

Walters, C. J., and C. S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology 71:2060–2068.

White, J. C., T. Hermosilla, M. A. Wulder, and N. C. Coops. 2022. Mapping, validating, and interpreting spatio-temporal trends in post-disturbance forest recovery. Remote Sensing of Environment 271:112904.

White, S. C., C. R. Shores, and L. DeGroot. 2020. Cougar (*Puma concolor*) predation on Northern Mountain Caribou (*Rangifer tarandus caribou*) in central British Columbia. Canadian Field-Naturalist 134:265–269.

Whittington, J., M. Hebblewhite, N. J. DeCesare, L. Neufeld, M. Bradley, J. Wilmshurst, and M. Musiani. 2011. Caribou encounters with wolves increase near roads and trails: a time-to-event approach. Journal of Applied Ecology 48: 1535–1542.

Wittmer, H. U., B. N. Mclellan, R. Serrouya, and C. D. Apps. 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. Journal of Animal Ecology 76:568–579.

Wittmer, H. U., A. R. E. Sinclair, and B. N. McLellan. 2005. The role of predation in the decline and extirpation of woodland caribou. Oecologia 144:257–267.

Young, H. S., D. J. McCauley, R. Dirzo, J. R. Goheen, B. Agwanda, C. Brook, E. Otárola-Castillo, A. W. Ferguson, S. N. Kinyua, M. M. McDonough, T. M. Palmer, R. M. Pringle, T. P. Young, and K. M. Helgen. 2015. Context-dependent effects of large-wildlife declines on small-mammal communities in central Kenya. Ecological Applications 25:348–360.

Young, H. S., D. J. McCauley, M. Galetti, and R. Dirzo. 2016. Patterns, causes, and consequences of anthropocene defaunation. Annual Review of Ecology, Evolution, and Systematics 47:333–358.

Zager, P., and J. Beecham. 2006. The role of American black bears and brown bears as predators on ungulates in North America. Ursus 17:95–108.

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