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In search of evidence-based management targets: A synthesis of the effects of linear features on woodland caribou

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ABSTRACT

Effective species management relies on evidence-based goals that address the processes influencing population demography. These goals therefore require understanding how stressors affect the species of interest, and the food web within which the focal species is embedded. For woodland caribou, a conservation priority across much of its range, habitat loss and alteration is a primary cause of decline. Governments have identified maximum disturbance targets whereby a maximum of 35% total disturbance provides a 60% likelihood of self-sustaining caribou populations, but targets specific for linear features such as roads and seismic lines — which play a key role in altering ecological processes and are a primary focus for habitat restoration — have not been established. We created a framework to conceptually link stressors (linear features) to caribou declines via ecological mechanisms, and used this framework to guide a literature review to support the development of a linear feature-based management target for Southern Mountain Caribou. Despite the vast amount of research investigating the mechanisms leading to the negative relationship between caribou demography and linear features, our review of 54 peer-reviewed manuscripts and 99 grey-literature reports found little to no evidence of a threshold in these relationships in which to inform a linear feature-based management target for caribou population growth. Most studies evaluated how linear features modify space use of caribou, their predators, and the primary prey of those predators, whereas few mechanistically linked linear features to caribou demography. Our work provides a foundation in which other systems can conceptualize how stressors are linked to species declines, and to support the development of evidence-based management goals.

1. Introduction

Habitat loss is a primary mechanism causing, and accelerating, species extinctions across the globe (Powers and Jetz, 2019). When human land-use is a main cause of habitat loss and alteration (hereafter 'habitat alteration'), habitat restoration may be assumed as a means to reverse species declines – e.g., restore the vegetation community and the forest ecosystem will return to its former state (Ford, 2021; Suding, 2011). However, population dynamics are governed by a complex suite of ecological interactions, including predation, herbivory, and competition (DeCesare et al., 2010; Serrouya et al., 2021). Consequently, the total effects of habitat alteration on a given focal species arises through a myriad of pathways in the ecological community (Estes et al., 2011).

Clear targets, or indicators, to trigger changes in monitoring efforts and management interventions are essential components of effective adaptive management (Cook et al., 2016; Roberts et al., 2022). These targets should reflect meaningful changes in the response of a species or system to a particular stressor, and ideally the mechanistic pathways linking stressors to responses. When relationships between habitat and demography are clear, they provide managers with a tractable means to monitor progress towards habitat management targets (Morellet et al., 2007; Perry et al., 2023). In some cases, the relationship between habitat alteration and demography is gradual, such that managers must define arbitrary or socially-derived targets. In other cases, these relationships may have abrupt transitions in which the probability of population persistence declines suddenly or becomes highly uncertain (Huggett, 2005). Abrupt transitions could occur because of density-dependent

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population growth, for example via an Allee effect, and through demographic stochasticity. The identification of these abrupt transitions (i.e., thresholds or 'tipping points') provides an ecological-based approach to define management targets and reduce uncertainty.

Anthropogenic habitat alteration has been identified as a proximate cause of decline for many caribou (*Rangifer tarandus*) populations, including Threatened boreal and southern mountain woodland caribou populations (*R.t. caribou*; Banfield, 1974) in Canada (Environment Canada, 2014, 2012). To support the recovery of woodland caribou, managers adopted a habitat management target of a maximum of 35% total 'disturbed' habitat (Environment Canada, 2014, 2012). This management target is based on a continuum of risk, whereby populations have approximately 60% chance of being self-sustaining if the total disturbance within their range is <35% (Environment Canada, 2011), where disturbance accounts for natural disturbances such as wildfire, as well as anthropogenic habitat alteration from industrial activity like forestry and petroleum extraction. Though originally developed for boreal herds, the management target of a maximum of 35% disturbance has been adopted for both boreal and southern mountain caribou (hereafter SMC; Environment and Climate Change Canada, 2020; Environment Canada, 2014, 2012) despite differences in underlying ecology and uncertainty in the applicability of the underlying relationship between habitat alteration and demography among populations. Caribou habitat restoration efforts to date largely focus on linear features, such as roads and seismic lines, that are pervasive across the landscape but are no longer actively used for resource extraction. Many linear features, especially roads, do not naturally revegetate in a timely manner, making active decommissioning and access management a necessary, but costly, aspect of recovery planning (Lee and Boutin, 2006; Nagy-Reis et al., 2021).

Roads and other linear features are ubiquitous features across the globe used to facilitate human access, even in otherwise relatively intact landscapes (Ibisch et al., 2016). Linear features alter the movement behavior of animals, leading to disrupted migratory pathways, barriers to gene flow, the spread of invasive species, and altered predator–prey dynamics (Fahrig and Rytwinski, 2009; Forman and Alexander, 1998). Demographic responses to linear features have been used to develop management targets for some species. For example, road densities between 0.6 and 0.7 km/km^2 are correlated with grizzly bear population declines and lower densities of bears (Boulanger and Stenhouse, 2014; Lamb et al., 2018). Linear features are linked to caribou declines by providing efficient travel corridors for predators (Dickie et al., 2017; McKenzie et al., 2012), bringing predators into caribou habitat (DeMars and Boutin, 2017; Dickie et al., 2020), and thereby increasing predation. Despite the focus of research and habitat management on linear features, there remains uncertainty about the pathways through which linear features impact caribou, and what restoration targets are expected to have a meaningful, positive impact on caribou populations.

We developed a framework to link linear features (i.e., a stressor) to caribou declines, directly and via community-level interactions, and compiled evidence for each of these pathways to support the development of habitat management targets for SMC populations, and woodland caribou more generally. We summarized the current state of knowledge on the effects that linear features have on caribou, the dominant predator species of mountain caribou (e.g., wolves *Canis lupus*, cougars *Puma concolor*, black bears *Ursus americanus,* and grizzly bears *Ursus arctos*; Wittmer et al., 2005) as well as moose (*Alces alces*), a primary prey species of those predators. We then used this literature review to identify linear feature density thresholds in these behavioral and demographic pathways, and gauge if these thresholds would effectively support evidence-based caribou habitat management. To further support linear feature management and restoration planning, specifically for SMC populations as a case study, we translated the current maximum total disturbance target of 35% (Environment Canada, 2014) to a linear feature-based target, and compared this value to those identified in the literature. Finally, we discuss the appropriateness of area-based versus linear feature-based targets based on their sensitivity to data imperfections and ecological relevance.

2. Methods

2.1. Mechanisms linking linear features to caribou declines

We developed a process model to identify the mechanisms linking anthropogenic linear features to caribou declines (Box 1). We used this process model to guide our literature review, to choose key-words, and summarize reported effects. We also used this model to assess the relative support for each pathway linking linear features to caribou, and identify any knowledge gaps that are needed to effectively manage linear features within caribou range. We reviewed literature from all caribou populations, including Scandinavian reindeer. Given our focus on linear features, we note that this review is not an exhaustive review of the mechanisms leading to caribou declines, human-caused or otherwise, nor is it an exhaustive review of each of the pathways not mediated by linear features (for example, the impacts of prey space use on predator space use more generally).

We searched peer-reviewed literature using Web of Science. Web of Sciences is an effective principal search system for scientific literature review because it provides access to multiple databases simultaneously, but we nonetheless recognize that our results may be impacted by search engine choice (Gusenbauer and Haddaway, 2020). We prioritized groupings of search terms that we predicted would link linear features to caribou demography, populations, and predation using the process model (Box 1; Table A1.1).

We recorded information about the study design (data type, independent metrics, and dependent metrics), observed effects, any reported thresholds in responses, and management recommendations (Table A1.2). To facilitate comparison across studies, we consolidated varying descriptions of study design, methods, and results into broad terms (Appendix 2). We also scored the relevance of each paper to the objectives of our research, and our subjective confidence in the study's methods (high, medium, low). Manuscripts that scored low in "Relevance" or "Confidence" were filtered out of subsequent analysis or summary (Appendix 1). Manuscripts that used more than one method, study design, species, or statistical analysis were partitioned by analysis to capture each effect studied. When analyses were multi-species (i.e., co-occurrence of caribou and wolves), we recorded the effect for each species. We assigned each analysis to the corresponding pathway(s) in which linear features are predicted to influence caribou (Box 1). At least two co-authors reviewed each paper, and where discrepancies occurred in any of the variables recorded, the paper was co-reviewed to reach consensus. We focus on results of dependent metrics, linear feature types, species studied, impacts and thresholds identified, but see Appendix 3 for additional results. Many studies did not report sufficient detail to facilitate a formal *meta*-analysis, and as such we used a simple ordinal approach to summarize the direction of responses (see Fahrig and Rytwinski, 2009).

2.2. Literature review to inform linear feature-based management targets

For the targeted goal of identifying a threshold in the response to linear features to support a linear feature-based management target, we included both peer-reviewed and grey literature. Any thresholds identified within the peer-reviewed literature were recorded (see Section 2.1). Because highly applied and specific results may be underrepresented in peer-reviewed literature, we also compiled grey literature by combining target websites and database records in conjunction with a more broad search using Google Scholar (Godin et al., 2015; Haddaway et al., 2015). We reviewed all reports from four funding and research agencies known to host research on woodland caribou in Western Canada: British Columbia Oil and Gas Research and Innovation Society (BCOGRIS), Canada's Oil Sands Innovation Alliance (COSIA),

Box 1

Process model depicting the mechanistic pathways evaluated to describe the effects of linear features (LFs; stressor) on caribou. LFs exert impacts on agents (colored boxes, "2–5"), which influence caribou populations ("1") via proximate stressors (hollow boxes), connected by mechanistic pathways. Peer-reviewed literature was assigned to pathway(s), as follows:

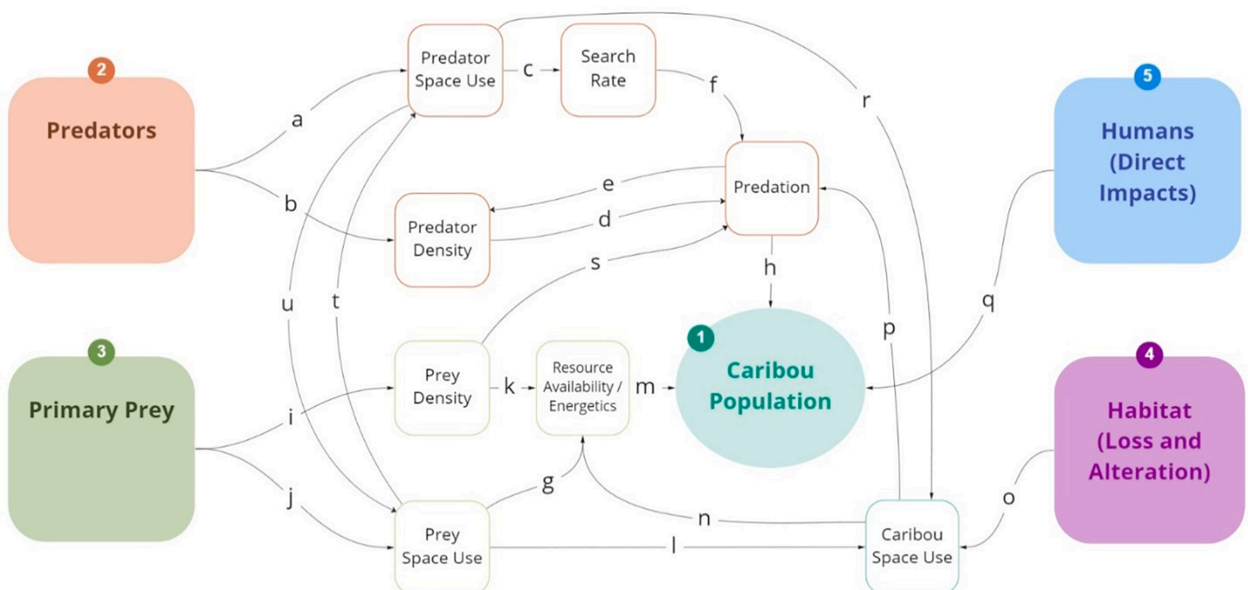
1. Effects of LFs on caribou populations, without an explicit mechanism.

2. Effect of LFs on predators (e.g., wolves, black bears, etc.), which flows through changes to space use (a) or changes to predator density (b), for example through vehicle collisions. LFs alter predator space use (a) via habitat use, selection, and movement, which is hypothesized to modify their search rate (c). The predator's search rate, predator density, and prey density combine to influence the predation rate (f, d, and s, respectively), which then directly influences caribou populations (h), and can in turn feed back into predator density (e) through changes in reproductive rates.

3. Effect of LFs on primary prey species of caribou predators (e.g., moose, deer, etc.), which flows through changes to space use (j) or direct changes to density (i). LFs alter the density of the primary prey species, for example via vehicle collisions, habitat loss in the case of creation of hard surfaces such as roads, or the creation of early seral habitat in the case of forest cutting for soft surfaces such as seismic lines (i). Changing prey density influences predator densities (s), as well as the availability of resources on the landscape and energetics (k), having implications to caribou survival and reproduction (m). LFs also alter primary prey space use (j), which can influence resource availability on the landscape and energetics (g), or influence caribou space use (l) for example via competitive exclusion. In addition, as prey avoid encounters and predators seek encounters, predator space use can influence space use of primary prey (u), and vice-versa (t).

4. Effect of LFs on caribou habitat. LFs directly reduce caribou habitat, and can have a zone of influence, further reducing access to otherwise viable habitat. Habitat loss and change results in changes to caribou space use (o), which in turn influences resource availability and energetics (n), thereby reducing caribou survival or reproduction (m). Changes to caribou space use can also result in increased predation (p) via increased encounter rates, and is in turn influenced by predator space use (r) via caribou avoidance of predators.

5. Effect of LFs on humans. LFs can facilitate access into caribou habitat, resulting in human-caused mortality (q) from vehicle collisions, hunting, and poaching.



Alberta Biodiversity Monitoring Institute (ABMI), and Foothills Research Institute (fRI). We included all reports from the BCOGRIS "Boreal Caribou" program (https://www.bcogris.ca), the fRI Caribou program (https://friresearch.ca) and all reports from COSIA and ABMI with the search term "caribou". We then systematically searched for unpublished research theses using Google Scholar and the search terms "Mountain caribou" AND "linear features", or "Mountain caribou" AND "roads". While the literature review was generalized beyond mountain caribou, we targeted the grey literature search, with its more applied goal, to be most applicable to SMC populations.

We searched the Abstract, Executive Summary, Figures, Tables, and Management Recommendations sections of each report or thesis for identified thresholds or management recommendations. We also searched for the terms "threshold", "breakpoint", "management", "recommendation". We recorded the geographic area, ecoregion, data type, linear feature type, if the report evaluated a mammal response to linear features, species, as well identified management recommendations and thresholds using the same definitions as the peer-reviewed literature. We again scored the relevance of each report and our confidence in the methods, and filtered out reports that scored low in "Relevance" or "Confidence" for subsequent analysis (Appendix 1).

2.3. Translating the area-based target to linear feature density

To translate the area-based maximum disturbance target of 35% disturbed to a linear feature-based target, we assessed the relationship between estimated road density and total disturbance across 6 SMC central group ranges (Burnt Pine, Kennedy Siding, Klinse-za, Narraway, Scott West, and Quintette). The predominant linear feature type within SMC ranges are roads associated with forestry activities and recreation, though some more northeastern ranges are also disturbed via seismic exploration (Canadian Wildlife Service, 2012). While other linear features undoubtedly contribute to linear feature density within central SMC ranges, road density represents a more consistent metric across all ranges.

We used data compiled by ECCC to calculate total disturbance by buffering all anthropogenic disturbances by 500 m, converted to the percent area for each range, and road density as the total length of roads divided by the area of each range. We used the range boundaries as delineated by ECCC for each herd. The ECCC data were primarily created using 30-m resolution Landsat 5 satellite imagery, emulating the methods used to identify the 35% maximum disturbance identified in boreal populations (Canadian Wildlife Service, 2012; Environment Canada, 2011). Landsat imagery underestimates smaller features, particularly narrow roads and other linear features (Dickie et al., 2023; Pasher et al., 2013). We therefore assessed the sensitivity of our conclusions to the data source used to classify roads and other disturbances by comparing ECCC data to higher-resolution data compiled by Mann and Wright (2018). Mann and Wright (2018) used the Government of British Columbia's Digital Road Atlas, circa 2018, to identify roads including primary, secondary, and tertiary roads. To understand the differences and similarities between the two data sources, we evaluated the Pearson's correlation between each dataset for both total disturbance and road density, with herd was the sampling unit. We then tested the correlation between each metric (road density and total disturbance) within each of the two datasets with herd was the sampling unit, and used a linear model to regress road density against total disturbance to estimate the road density that corresponded to 35% total disturbance.

Finally, we placed the current disturbance conditions in context with the calculated management target by calculating the difference between the road density within each SMC range and the estimated road density target, for each data source.

Peer-reviewed and grey literature were searched as of August 2020. All analyses were conducted in R (R Core Team, 2022).

3. Results

We identified 105 manuscripts in the systematic peer-reviewed literature search (Appendix 1, Table A1.1), 60% of which studied boreal woodland caribou. After filtering for relevance and confidence, and removing analyses that did not report on the effect of linear features (for example, measured disturbance in general), we used the results of 620 unique analyses from 54 manuscripts from the peer-reviewed literature, as well as 72 reports and 27 theses from the grey literature. The majority (85%) of manuscripts had multiple analyses that included additional species and/or interacting effects like season, habitat type, and species co-occurrence. See Appendix 4 for a full list of manuscripts and reports evaluated.

Linear features were categorized into 5 main classes; general linear features (which typically occurred when multiple linear feature classes were evaluated simultaneously, but also included infrequently studied linear feature types such as railways), natural linear features (such as rivers and creeks), pipelines and powerlines, roads, and seismic lines (Table A2.3). While we recorded information on the degree of human activity on these linear features (such as traffic levels), there were insufficient analyses to further analyze how the response to linear features depended on human use of these linear features (Appendix 2).

3.1. Mechanisms linking linear features to caribou declines

The majority (65%) of manuscripts we reviewed focused solely on caribou response to linear features, and 28% of manuscripts used a multi-species approach. The most commonly-used dependent metrics for all species studied were grouped into five broad categories: space use (67%), movement (12%), demographics (12%), caribou-predator co-occurrence (6%), and caribou-primary prey co-occurrence (3%). Metrics of space use were used over five-times more than any other dependent metric in the evaluated peer-reviewed manuscripts (Appendix 2; Table A2.1).

There were 60 analyses that specifically evaluated caribou demography, 42% of which directly related linear features to demographics without specifying a pathway. Only 1% of analyses evaluated the effect of linear features on caribou predation rates ("h"), none evaluated how linear features affect the direct impact of humans on caribou populations ("q"), and none evaluated how the influence of linear features on resource availability or energetics in turn influenced caribou populations ("m"; Fig. 1).

The majority of analyses reviewed were relevant to 3 pathways in our process model: the pathway between linear features and caribou space use ("o"; 40% of analyses), predator space use ("a"; 32% of analyses), and prey space use ("j"; 8% of analyses; Fig. 1). Together, 82% of all analyses examined metrics of space use (i.e., habitat use and selection). Approximately 3% of analyses evaluated how changes in predator space use from linear features in turn influenced predator search rate

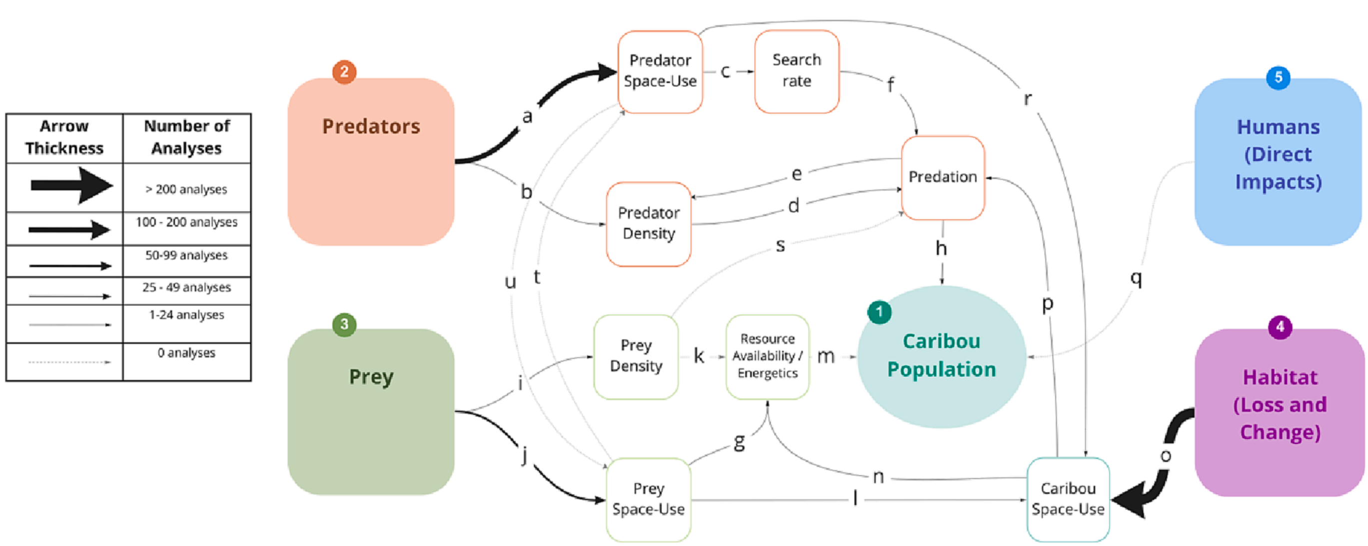


Fig. 1. Process model (see Box 1) showing pathway widths that are weighted by quantity of research focus. The number of analyses in each pathway are provided in Appendix 5.

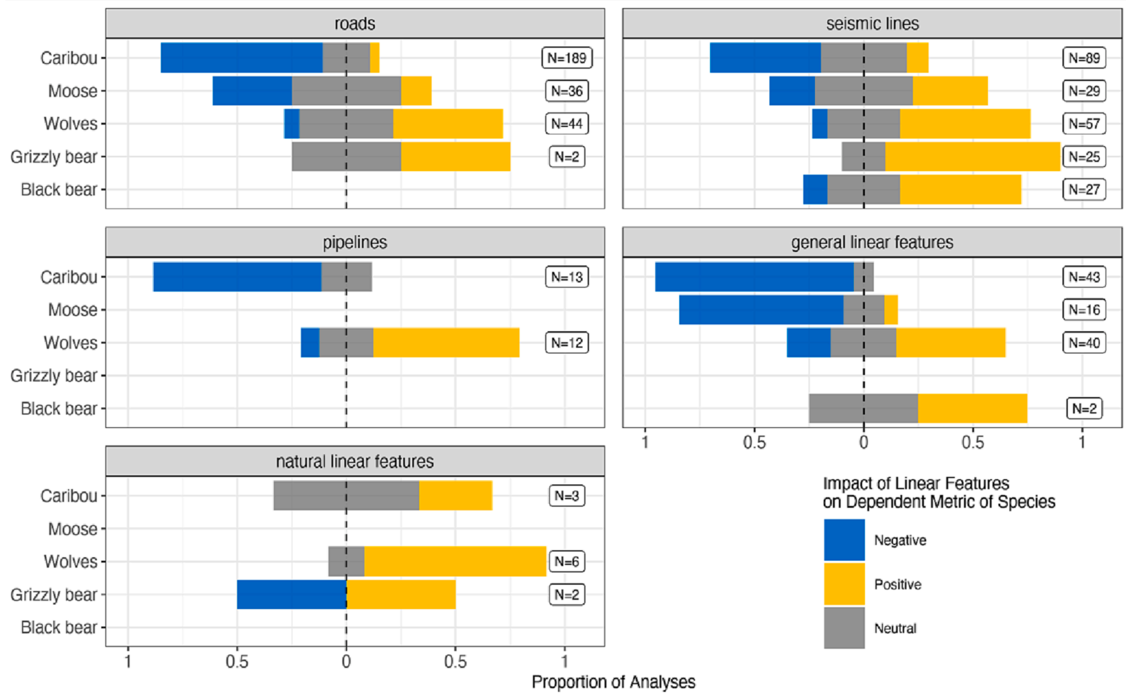


Fig. 2. The impact of linear features on caribou and the large-mammal community implicated in caribou declines (see Box 1). The proportion of analyses from peer-reviewed manuscript reviewed reporting positive, negative, or null effects of linear features are presented for the five most-studied species, partitioned by five linear feature types. Positive or negative effects indicate increased or decreased use, selection, movement, or density, whereas neutral indicate no response to linear features. The total number of analyses for each species and linear feature category are presented.

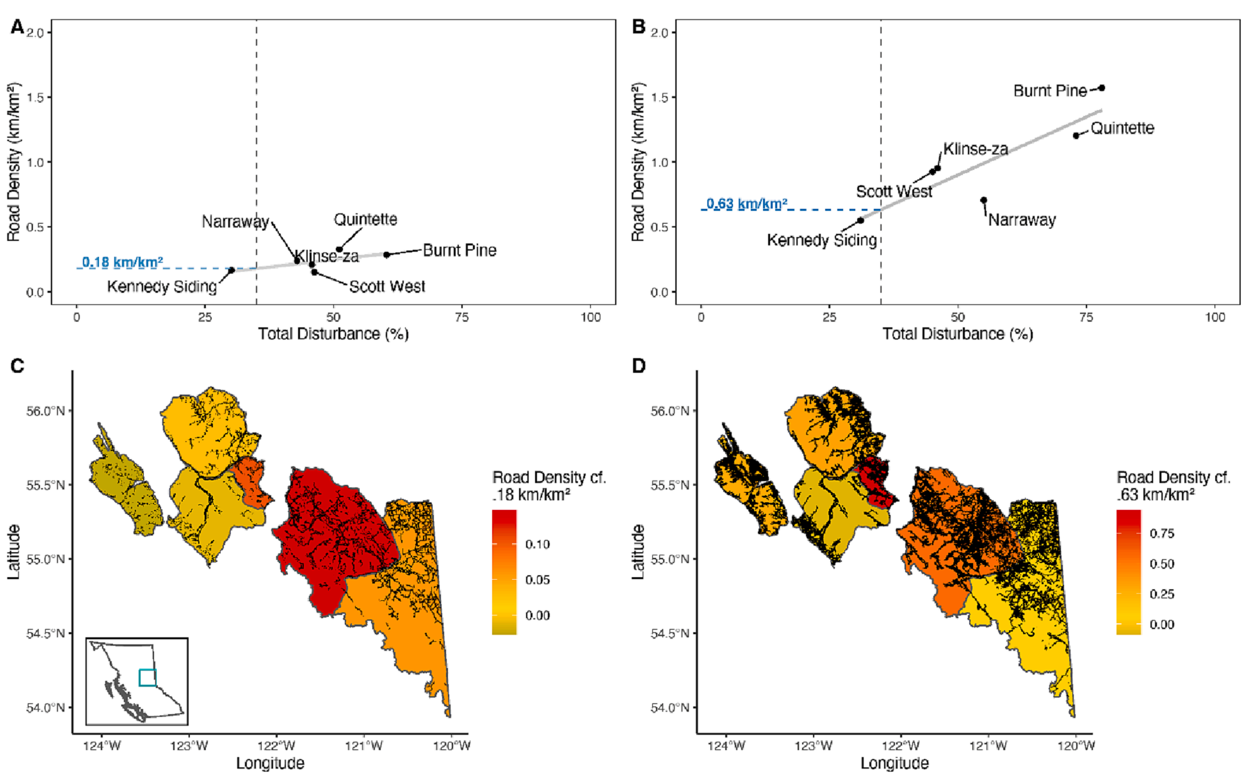


Fig. 3. The relationship between road density (km/km^2) and total disturbance (percent area; including 500-m buffers on anthropogenic disturbances) used to estimate a road density target (Panel A and B), and visual representation of the state of each herd relative to calculated road density target for the 6 Southern Mountain Caribou - central group herds in British Columbia (Panels C and D). Panels A and C were derived from ECCC data. Panel B and D were derived from Mann and Wright (2018) data. The blue dashed line represents the point at which the 35% maximum total disturbance target (Environment Canada, 2014) intersects the modelled relationship between total disturbance and road density. Grey shading in C and D represent roads for the respective data sources, and range boundaries match those used in ECCC.

("c"), and 1% evaluated how this in turn influenced predation rates ("f"), though none evaluated how changes in predator space use from linear features in turn influenced caribou space use ("r"). Approximately 2% of analyses evaluated how changes in caribou space use in turn influenced predation rates ("p"), while few (<1%) evaluated how changes in caribou space use influenced resource availability and energetics ("n"). Few (<1%) analyses evaluated how changes in primary prey space in turn influences resource availability and energetics (g), and none evaluated how changes in primary prey space use influenced caribou space use ("l"). No analyses evaluated how linear features impacted how predator space use influenced primary prey space use ("u") or vice-versa ("t").

Few of the analyses reviewed (<1%) evaluated how linear features influenced the density of predators ("b"), how changes in predator density influenced predation rates were mediated by linear features ("d"), or how the influence of linear features on predation rates in turn influences predator density ("e"). Few analyses (<1%) evaluated how linear features influences the density of primary prey ("i"), and none evaluated how this in turn influenced predation rates ("s") or resource availability and energetics ("k").

There were 36 analyses that could not be attributed to a single pathway. Approximately 3% of analyses evaluated how linear features influenced the co-occurrence of moose and caribou ("o", "j", and "l"), and few (<1%) tested how these changes in co-occurrence affected caribou mortality risk ("g", "n", and "m"). Few analyses (<1%) evaluated how linear features influenced the co-occurrence of caribou and predators ("o", "a", and "r"), and how these changes effected caribou mortality risk ("p" and "h"). Few analyses (<1%) evaluated how linear features interacted with moose space use ("o" and "l") or predator space use ("o" and "r") to influence caribou space use, and how caribou survival depended on moose density, without testing the causal pathway between ("k" and "m").

Caribou were predominantly negatively impacted by linear features (Fig. 2). Negative impacts of linear features on caribou were reported 2.3 times more than both null and positive effects combined. Positive effects were typically reported in cases where linear features were associated with decreased overlap between caribou and predators or their primary prey, which following the process model predicts a positive outcome for caribou populations. The two most-studied categories of linear features were roads and seismic lines (combined, 77% of analyses; Appendix 2; Table A2.3). Of the 189 analyses that evaluated the relationship between roads and caribou, negative impacts were reported 2.9 times more than null and positive effects combined (Fig. 2). Negative impacts of seismic lines on caribou were reported at approximately the same frequency as null impacts, but 5 times more than positive impacts. All other linear feature types combined had an 83% negative, 2% positive, and 15% null impact on caribou. Of the analyses that evaluated the impact of linear features on caribou demographics, 70% found negative impacts.

The response of moose to linear features was highly variable across linear feature types, seasons, and sex (Fig. 2). The number of analyses that reported a null effect (42%) of linear features on moose was similar to the number that reported a negative impact (38%), whereas 19.8% reported a positive effect. The majority (80%) of the analyses on the impact of linear features on moose focused on roads and seismic lines. Of the 81 analyses that examined the impact of linear features on moose, 63% included interacting metrics like season or habitat type, and all were multi-species.

The majority of analyses that evaluated predator responses to linear features in the context of caribou predation found a positive effect, such that linear features were inferred to facilitate predation. This effect was largely driven by seismic lines; positive effects were reported 1.9 times more than null and negative effects combined (Fig. 2). The majority of wolf-specific analyses that we reviewed used metrics of space use (90 of 159 analyses) or movement (46 of 159 analyses). The majority of analyses on wolves were spread between roads, seismic lines, and general linear features. Within these linear feature types, 54% of analyses reported positive impacts on wolves and 36% reported null impacts (Fig. 2). Metrics of space use were also common for black bears (all 29 analyses) and grizzly bears (23 of 29 analyses; Appendix 3; Fig. A3.1B). Of the 58 analyses on bears, the majority (90%) focused on seismic lines and 67% reported positive impacts of these features on bears (Fig. 2). Comparatively, only 3% of analyses evaluated the impact of roads on bears, in which positive and null effects were reported equally. Metrics of caribou-predator co-occurrence and density were only reported for wolves, and constituted <15% of the 159 wolf analyses (Appendix 3; Fig. A3.1B).

3.2. Literature review to inform linear feature density targets

Within the peer-reviewed literature, we found no instances of explicitly identified thresholds in the impact of linear features on the behavior or demography of caribou, their competitors, or predators. In the grey literature, we found multiple reported thresholds of linear feature densities. The probability of caribou occurrence was reduced significantly when primary roads exceeded 0.01 km/km^2 and when secondary roads exceeded 0.1 km/km^2 across all ecoregions in Western Canada (Neveux, 2017). McCutchen (2007) identified a number of thresholds in which roads and seismic lines influenced the behavior of wolves in boreal Alberta using simulations, and noted that thresholds typically occurred at low linear feature densities. Most relevantly, McCutchen (2007) identified that in more than 65% of the cases in which simulated wolf kill rates and caribou survival rates reached asymptotes as a function of linear feature density, these asymptotes occurred prior to 1 km/km^2.

3.3. Translating the area-based target to a linear feature density

Total disturbance was strongly correlated between the two datasets (Pearson's R = 0.90), whereas road density was less so (Pearson's R = 0.68). On average, total disturbance using the Mann and Wright (2018) data was 1.2 times higher than the ECCC data, whereas road density was 4.2 times higher than the ECCC data. Total disturbance and road density were highly correlated for the Mann and Wright (2018) data (Pearson's R = 0.88), and less so for the ECCC data (Pearson's R = 0.67). Total disturbance significantly predicted road density for both datasets ($\beta_{ECCC} = 0.005$; $F_{ECCC} = 3.198$; $\beta_{Mann\ and\ Wright} = 0.018$; $F_{Mann\ and\ Wright} = 13.760$). The 35% maximum total disturbance target corresponded to a road density of 0.18 km/km^2 using the ECCC data, and 0.63 km/km^2 using the Mann and Wright (2018) data (Fig. 3).

Of the 6 SMC central group herds assessed, only Kennedy Siding had total disturbance below the boreal 35% maximum total disturbance target (Fig. 3). The density of roads within Kennedy Siding was also below the translated road density target regardless of the dataset used. While total disturbance in the Scott West herd was above the total disturbance target for both ECCC and Mann and Wright (2018) data, Scott West was below the translated road density target for ECCC. No other herd was below the total disturbance or road density target using either dataset.

4. Discussion

Decades of applied research have contributed to a vast body of literature on the effects of habitat alteration on woodland caribou. In particular, many studies have evaluated the impact of linear features, ubiquitous features across western Canada's boreal and montane forests that are at the forefront of habitat management discussions. Yet, we found little empirical evidence that specifically and mechanistically linked linear features to caribou demography, nor evidence for a threshold in behavioral or demographic responses to linear features that could be used to support a management target for land-use and restoration planning, beyond the 35% maximum total habitat disturbance management target.

Many studies emphasized an impact of linear features on caribou without explicitly evaluating the links between the ultimate stressor (linear features) and the mechanistic links and proximate stressor(s) in which those impacts flow to caribou demography. For example, studies tested how linear features impact space use of caribou, and inferred resulting impacts on caribou populations without demonstrating demographic effects, nor testing if changes in space use influenced resource availability, competition, and/or predation. The most studied mechanisms were how linear features modify space use of caribou, their predators, and the primary prey of those predators. Although numerous studies show that the main predators of caribou use linear features and travel more efficiently on them (Dickie et al., 2017; Latham et al., 2011; McKenzie et al., 2012), it is unclear if these changes result in increased encounter rates with prey, and ultimately increased kill rates of caribou and other ungulates (but see Whittington et al., 2011), or how these effects compare to how disturbance influences prey abundance, and therefore predator abundance.

For mechanisms that did receive ample research, limited generalities could be made because of variable outcomes reflecting context-dependencies. For example, Mumma and colleagues (2018) found that female moose generally avoided roads, whereas male moose selected for areas with high density of roads during calving, but avoided roads during early and late winter. The strength and direction of behavioral responses often depend on the animal's sex, age, or reproductive status, landscape context, and even the scale in which they are measured (Avgar et al., 2020; Boyce et al., 2003; Prokopenko et al., 2017). Indeed, functional responses in habitat selection, i.e., how behavior changes based on the availability and quality of resources in different habitats (Muhly et al., 2019; Mumma et al., 2019; Mysterud and Ims, 1998), can impact our ability to make generalizations about the impacts of habitat alteration on species. The variability and lack of support for each pathway indicate important areas of research to discern the contribution of these mechanisms to caribou declines and subsequent recovery.

While behavioral studies are beneficial for identifying species-habitat associations that may have important implications for populations, they may not alone inform population recovery targets. For example, behavioral analyses showed that boreal woodland caribou avoid burned areas, yet use of these habitats does not appear to affect adult female survival (Konkolics et al., 2021). If wildlife managers based management decisions only on the behavioral analyses from Konkolics et al. (2021) they may erroneously shift their focus on wildfire mitigation, which would unlikely increase caribou survival. We caution against the tendency to interpret behavioral studies as having implications on demography, and in turn population recovery, without these linkages being tested empirically. To recover caribou populations, we recommend that habitat management targets link to demographic rates – population growth and its components, survival and recruitment – to ensure that habitat contributes positively to demography.

Testing relationships between habitat alteration and demography is becoming increasingly possible through cross-population analyses. For example, Johnson et al. (2020) combined 58 study areas, finding that the effect of total anthropogenic habitat alteration had much larger effects on adult female caribou survival and recruitment than fire disturbance. To inform uncertainty around the demographic impacts of linear features on caribou, cross-population analyses evaluating the effect of linear feature density on population growth rate (see Environment Canada, 2011 for a similar analysis), ideally calculating thresholds in which populations are stable, would be ideal. Additionally, contrasting cause-specific mortality rates of caribou, caribou recruitment, or wolf kill rates of caribou in areas with low and high linear feature densities would inform these linkages, particularly if the contextual dependency of additional habitat disturbance (e.g., forestry) was additionally explored. However, demographic data across such large scales is not always feasible for large mammals, particularly for species that are not as intensely monitored and widely distributed as caribou. In these cases, research can focus on understanding how habitat alteration influences the survival and reproduction of telemetered individuals, as long as individual animals experience differing levels of habitat quality and human pressures. These studies also provide the opportunity to explicitly link behavior to vital rates. Additionally, monitoring vital rates as habitat restoration expands will provide a pseudo-experiment to test the effect of linear features on population demography. While it is challenging to collect the data needed to rigorously test these linkages, understanding the contribution of linear features relative to other features and cumulative effects on caribou vital rates is necessary to predict the effectiveness of linear feature restoration.

Despite a substantial body of literature associating linear features with caribou declines, we found no peer-reviewed evidence of a linear feature density threshold. In the grey literature, we identified four potential thresholds from two studies, at which a change in the effect of linear features on caribou or their predators was observed: 0.1, 0.17, 0.63 and <1 km/km^2 (McCutchen, 2007; Neveux, 2017). None of these thresholds, however, are explicitly supported in peer-reviewed literature. To support land-use and restoration planning, we transformed the current total disturbed habitat target of 35% (Environment Canada, 2014) to a road density target. The resulting road density target depended on the underlying data source used to quantify total percent disturbance and road density; 0.18 km/km^2 from ECCC and 0.63 km/km^2 from Mann and Wright (2018). The potential thresholds and targets identified through these two exercises ranged across an order of magnitude, suggesting substantial uncertainty for management targets as well as likely context-dependencies limiting the ability to extrapolate specific targets across sub-populations. However, all are below 1 km/km^2, which may serve as an upper limit for any potential maximum road density target, though mostly points to a maximum road density target that is substantially lower.

Linear feature density differed more between data sources than did total area altered. The observed increase in both road density and total disturbance (i.e. area altered) from the ECCC to the Mann and Wright (2018) data partially reflects an increase in habitat alteration over time (Nagy-Reis et al., 2021), given these data represent the landscape approximately 6 years apart. However, the average 13% increase in total disturbance from ECCC to Mann and Wright (2018) was much less than the 350% average increase in road density. Landsat imagery has been found to underestimate habitat alteration in other regions, particularly narrow features such as roads and other linear features (Dickie et al., 2023; Pasher et al., 2013). Differences may also reflect the configuration of disturbances; as road density increases these features likely fall within the buffers of existing disturbance, resulting in a non-linear relationship. In other words, in relatively intact landscapes road density and total disturbance are highly correlated because roads are required infrastructure for access, but, when disturbance is high, additional roads disproportionately impact road density over total disturbance. Together, this suggests that management targets derived from road densities are more sensitive to differences in data compilation methodology than area-based targets, particularly when buffering is used. However, if compiled well, linear feature-based targets may be more sensitive to increased habitat alteration in areas where human land-use is already pervasive; area-based targets saturate in highly-disturbed areas as new disturbances fall within existing disturbed areas, particularly when buffers are used. When conflict between conservation and economic impacts is high (Hebblewhite, 2017), there may be additional scrutiny placed on the data underlying scientific analyses and evidence-based recommendations. As such, developing publicly-available datasets on key variables like linear features and disturbance will remain a critical need for operators, decision makers, and scientists.

Identifying management targets for linear features is important for supporting land-use and restoration planning, but may not reflect additional or alternative mechanisms of decline, such as increased wolf abundance as a result of forestry activities providing increased resources for primary prey species (Serrouya et al., 2021, Serrouya et al., 2011) and cumulative effects (Sorensen et al., 2008; Theobald et al., 1997). As such, there may be a need for multiple management targets that address separate mechanisms of decline. The issue of density- versus area-based targets has been considered for other species, such as grizzly bears (Proctor et al., 2019), and area-based metrics are often preferred or used in conjunction with density-based metrics to guide species recovery (Fish and Wildlife Service, 2013).

While well-defined demographic-disturbance relationships are a laudable goal, meaningful action should not cease in the face of uncertainty. Indeed, rigorous monitoring of the effectiveness of management actions can also inform causal mechanisms and any tipping points within these pathways. Despite a well-defined total disturbance target for woodland caribou, there has been little progress towards reducing disturbance to below this target, and many herds continue to lose habitat at an accelerating rate (Nagy-Reis et al., 2021). Once a target has been adequately identified, implementation of management towards this target is needed to achieve the desired outcomes. We hope that our work provides a foundation in which other systems can emulate or improve on to empirically investigate mechanisms linking habitat alteration to population declines with the ultimate goal of supporting evidence-based and effective habitat management.

CRediT authorship contribution statement

Melanie Dickie: Conceptualization, Methodology, Data curation, Writing – original draft. **Nicola Love:** Conceptualization, Methodology, Data curation, Writing – original draft, Visualization, Investigation. **Robin Steenweg:** Conceptualization, Writing – review & editing. **Clayton T. Lamb:** Conceptualization, Methodology, Data curation, Writing – review & editing. **Jean Polfus:** Conceptualization, Writing – review & editing. **Adam T. Ford:** Conceptualization, Methodology, Writing – review & editing, Supervision.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Efforts by Melanie Dickie, Nicola Love, and Clayton Lamb while working on this manuscript were partially funded by Environment and Climate Change Canada. Dr. Steenweg and Dr. Polfus are employees of Environment and Climate Change Canada. All authors agree that these financial interests or personal relationships did not influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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