

Managing animal movement conserves predator–prey dynamics

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Anthropogenic landscape change can lead to novel interactions among species with consequences for predator–prey dynamics. Population responses of predators and prey vary according to species abundance, movement, and distribution. Although conservation often involves managing species abundance, culling predators to benefit vulnerable prey is socially, ethically, and ecologically tenuous. We conducted a before–after control–impact experiment to test how well mitigations designed to disrupt animal movement reduce encounters between endangered caribou (*Rangifer tarandus*) and their predators in a human-modified landscape. Using camera traps, we quantified coincident habitat use by predators and prey. By deploying obstacles to disrupt ease of movement on human developments, we reduced the ratio of wolf (*Canis lupus*)–caribou encounters by 85% and reduced the ratio of black bear (*Ursus americanus*)–caribou encounters by 60%, without removing predators. By managing animal movements that regulate predator–prey encounters, risk to endangered species can be reduced without the disruptive trophic effects caused by intensive carnivore removals.

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Anthropogenic landscape change has wide-reaching implications for species persistence (Foley *et al.* 2005). Animal populations are limited by some combination of bottom-up (eg habitat) and top-down (eg predation) effects. Although often managed independently, landscape change can lead to novel interactions between predators and prey (Guiden *et al.* 2019). Predation is a consequence of predators and prey overlapping in time and space (ie encounters). Animals regulate the encounter process by deciding which resource patches to use, how long to use a patch, and how to travel among patches (Brown 1988; Van Moorter *et al.* 2016). However, anthropogenic landscape change can create novel conditions that increase predator use of prey habitats (Whittington *et al.* 2011), predator movement rates (McKenzie *et al.* 2012), and prey use of refuge habitats in both time and space (Visscher *et al.* 2017). These changes can alter animals' ability to access resources and avoid predation (Brown 1988), with consequences for predator–prey dynamics (Holling 1959; Holt 1984) that result in population declines of vulnerable species (Gause 1935; Serrouya *et al.* 2019).

Caribou and reindeer (*Rangifer tarandus*) populations have declined across their global range (Vors and Boyce 2009). Woodland caribou (*Rangifer tarandus caribou*) were recently extirpated from the contiguous US, and populations throughout much of Canada continue to decline (Serrouya *et al.* 2019). Caribou ranges overlap areas of timber, petroleum, and mineral resources that generate an estimated >US\$51 billion/year

(Anielski and Wilson 2006). Anthropogenic linear developments, such as seismic lines, pipelines, and roads, have increased the occurrence of predators in caribou habitat and are a contributor to caribou declines (DeMars and Boutin 2018). Because restoring habitat to mitigate this effect is too slow to save woodland caribou, governments are opting to remove 40–80% of wolf (*Canis lupus*) populations to reverse caribou declines (Hayes *et al.* 2003; Hervieux *et al.* 2014).

Research suggests that reducing predator abundance can benefit imperiled species (Serrouya *et al.* 2019), but doing so can have unintended consequences for ecosystems (Estes *et al.* 2011) and has been criticized for being invasive and ethically questionable (Vucetich and Nelson 2014). Rather than directly reducing the predator population, disrupting predators' ability to encounter prey may provide another option for protecting prey species. Animal movement is energetically costly (Crête and Larivière 2003), and therefore it stands to reason that impeding predator movement may reduce predator–prey encounters by lowering predator movement rates and limiting the spatiotemporal overlap between predators and their prey. Theoretically, the overlap between predators and prey can be altered with or without changes to animal movement rates (Brown 1988) or abundance (Keim *et al.* 2019).

Directly measuring encounter rates between predators and prey is difficult; however, measuring coincident habitat use provides an indirect measure of species' encounters. We used camera traps to study the intensity of habitat use in space and time by caribou, wolves, black bears (*Ursus americanus*), and moose (*Alces alces*) across the Parker Caribou Range in British Columbia, Canada. We used a before–after control–impact (BACI) design (Green 1979) to test how well mitigations designed to impede predator movement on anthropogenic linear developments would reduce encounters between caribou

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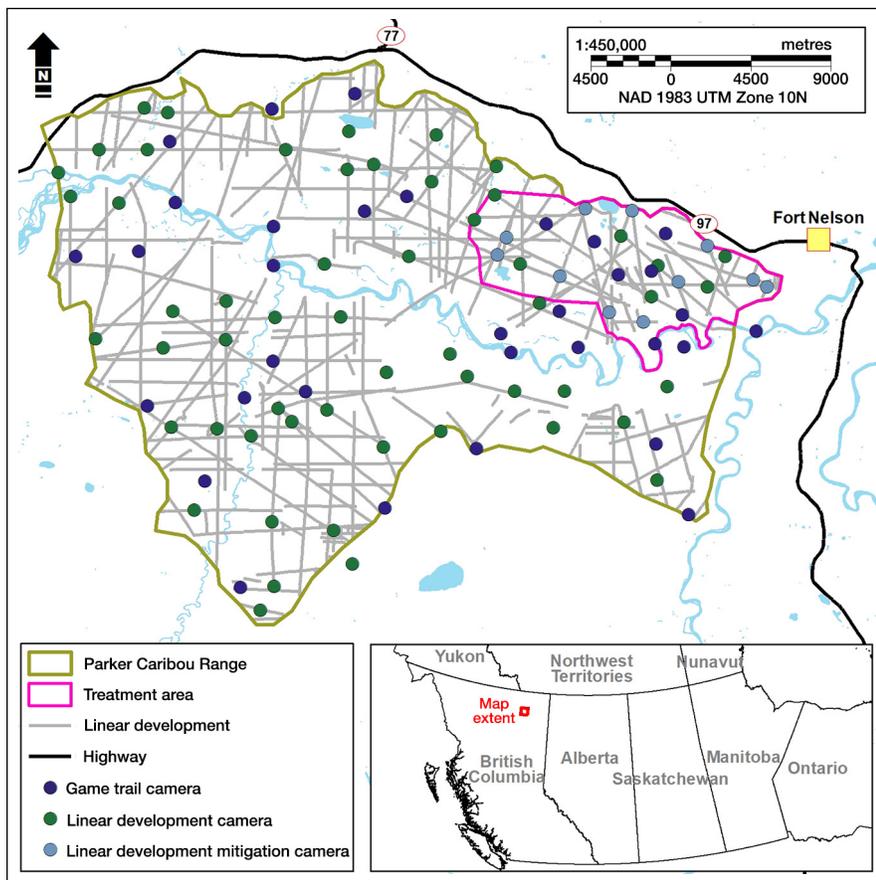


Figure 1. Map of the Parker Caribou Range in British Columbia, Canada, displaying the locations of linear developments, camera monitoring locations, and the treatment area.

and their predators. We assessed this concept in two complementary stages. First, we hypothesized that predator use would be associated with ease of movement and prey availability (Keim *et al.* 2011; Newton *et al.* 2017). We evaluated evidence for this behavioral mechanism by comparing a series of intensity of use models that included covariates related to travel speed, snow depth, presence of a movement mitigation, prey, and vegetation conditions. Second, we used a BACI analysis to test our hypothesis that movement mitigations would also reduce encounters at the caribou range scale. We show that managing coincident habitat use by predators and prey provides an immediate benefit to vulnerable prey and an alternative to predator removals or awaiting habitat restoration.

Methods

Study design

We studied intensity of use by predators and ungulate prey in the designated Parker Caribou Range (Environment and Climate Change Canada 2020) in northeastern British Columbia, Canada (58.8°N, 123.1°W), over 2.5 years of sampling (82,289 camera days). We deployed 100 cameras throughout the range on natural (game) trails and anthropogenic linear developments, such as oil and gas seismic lines and

roads. Camera monitoring sites were randomly generated and we confirmed that monitoring sites were unbiased with respect to ecosystem characteristics that could influence the habitat use patterns of study species.

Halfway through the study, soil mounding, tree planting, and tree felling mitigations were deployed on 61 km of 166 km of linear developments in a treatment area comprising 9,215 ha (or 12%) of the caribou range. Of the 100 cameras, 85 were deployed at the beginning of the study, and an additional 15 were installed within the treatment area after the mitigations had been established. Within the treatment area, we monitored animal use on ten linear developments without mitigation, 11 linear developments with mitigation, and seven game trails. Two of the camera monitoring sites in the treatment area changed condition from a linear development without mitigation in the pre-treatment sampling session to a linear development with mitigation in the post-treatment session. Overall, we monitored animal use on 58 linear developments without mitigation, 11 linear developments with mitigation, and 33 game trails (Figure 1).

Animal use data

Animal monitoring followed the methods described in Keim *et al.* (2019). We deployed one PC900 HyperFire Professional Covert camera (Reconyx; Holmen, WI) at each monitoring site. Cameras were programmed to record five images and immediately rearm when triggered by animal movements. In addition, we programmed cameras to take one image each day at a fixed time to confirm camera operation and provide information on snow depth and snow condition. Each camera was installed 1 m above ground level and positioned to capture use across each anthropogenic linear development or game trail. We placed cameras where vegetation, topography, and feature alignments narrowed feature widths and improved visibility. The width of the linear developments at the monitoring sites ranged between 3 m and 12 m (mean 6.0 m).

We visually inspected each image to identify caribou, wolves, black bears, and moose. Following Keim *et al.* (2019), we considered multiple images of a single animal as one discrete count event and considered multiple individuals of the same species as a multiple-count event. If an individual animal recognizable by coloration, scars, or other physical features left the monitoring site but returned <10 minutes after the original trigger, we considered it to be a single event. Over the course of the study 795 wolf, 2,032 caribou, 1,489 moose, and 1,720 black bear events were recorded. For each individual event, we recorded species, sex, age class, time, and date.

We evaluated the rate of missed detections by the presence of animal tracks in images when snow was present (48,240 or 59% of the camera monitoring days). Comparing daily fixed-time images to movement-triggered images revealed 24 missed detections (0.60%). Although the actual rate might have been higher because we may not have detected every track (eg tracks buried by overnight snowfall), we believe that our detection error of large mammal species was <1%. Detailed data collection methods are provided in WebPanel 1.

Ease of movement

To estimate the impedance of animal movement on anthropogenic linear developments (both treated and untreated) and game trails, we collected seasonal ease of movement metrics at each camera monitoring location. We used travel speed (kilometers per hour) to measure ease of movement on each feature in summer. Speed of travel was measured by conducting a 70-m, timed-walk survey on each monitoring feature. For comparison, we also walked a paired, parallel transect located in the adjacent forest. In winter, we collected snow depth and condition data by visually interpreting daily images at each monitoring site. For every day a camera was operational, we visually estimated snow depth (centimeters) and condition (ie snow packed by vehicles or unpacked). Deep snow increases the energetic cost of movement (Crête and Larivière 2003), so we considered daily snow depth and snow condition to be surrogates of ease of movement in winter.

Hypothesis 1: testing the behavioral response

To evaluate the behavioral response of each predator and prey species, we estimated the intensity of habitat use (Keim *et al.* 2019) as the count of animals (by species) observed at each camera location per day. As we were interested in studying movement mechanisms and predator–prey overlap with and without mitigations across time and space, we considered covariates related to travel speed, snow depth and condition, intensity of use by prey, ecological conditions, Julian date, and the presence of a mitigation at each camera monitoring site (WebTable 1).

Briefly, animal-use events were modeled using a zero-inflated, non-homogeneous Poisson process, in which the rate of occurrence of an event varies over time and space. Under the non-homogeneous Poisson process model, we modeled the mean function as an additive log-linear regression model where multiple covariates were included to modify time- and space-varying occurrence rates (Keim *et al.* 2019). Under the model, the counts from different time intervals were independent of one another and counts from different cameras were potentially spatially dependent. Although estimates of the regression coefficients are known to be consistent even when the spatial dependence is ignored in the estimation procedure (eg Liang and Zeger 1986), their standard errors could potentially be affected by large spatial association. We reduced the

effect of this spatial dependency on statistical inference by keeping the camera locations sufficiently distant (>2.0 km) from one another. The effect of spatial association on statistical inference was further controlled by incorporating location-specific, time-varying covariates in the model.

We fit the regression models via a stepwise model selection approach using Akaike's information criteria (AIC; Akaike 1973). We first employed a forward selection process where a covariate was added to the count and zero-inflation components of the model based on its statistical significance and its biological meaningfulness in affecting animal movement. A pure forward selection process can lead to a choice of spurious covariates that are highly colinear with important causal covariates; to avoid this possibility, after adding a covariate, we used backward selection to reevaluate the model and to remove possibly spurious covariates. We continued this process until the AIC scores did not change substantially, yielding a final model. At the end of the process, model adequacy was evaluated by comparing the aggregated observed counts to the aggregated predicted counts, as described in Keim *et al.* (2019). Model adequacy evaluations indicated that the fitted models were well calibrated with slopes near one, multiple *R*-squared values >0.85, and homogenous residuals.

Hypothesis 2: testing for a population-level response

A potential consequence of deploying movement mitigations is that predators could move to an area where mitigations had not been deployed. To model the before–after and treatment–control area effects, we analyzed data only from cameras that were active across the entire study duration ($n = 85$ cameras). In contrast with the previous analysis, here we classified all monitoring sites within the treatment area as “treated” to infer the effect of mitigations in relation to the entire caribou range. We used the same statistical model described above to parallel the counting process in the behavioral analysis but limited our models to four covariates: (1) a binary covariate defining the year before or after the deployment of mitigations; (2) a binary covariate defining whether cameras were located inside or outside the treatment area; (3) an interaction term between the two binary covariates; and (4) the fitted values from the behavioral analysis to account for known variation arising from habitat types, seasonality, and local mitigation effects. Including the fitted values was important because failing to account for such variation could have led to overestimating the before–after and treatment area effects across the caribou range.

■ Results

Hypothesis 1: the behavioral response

Travel speed and snow conditions were significant effects in the intensity-of-use models for all four species after accounting for habitat types and time-based conditions

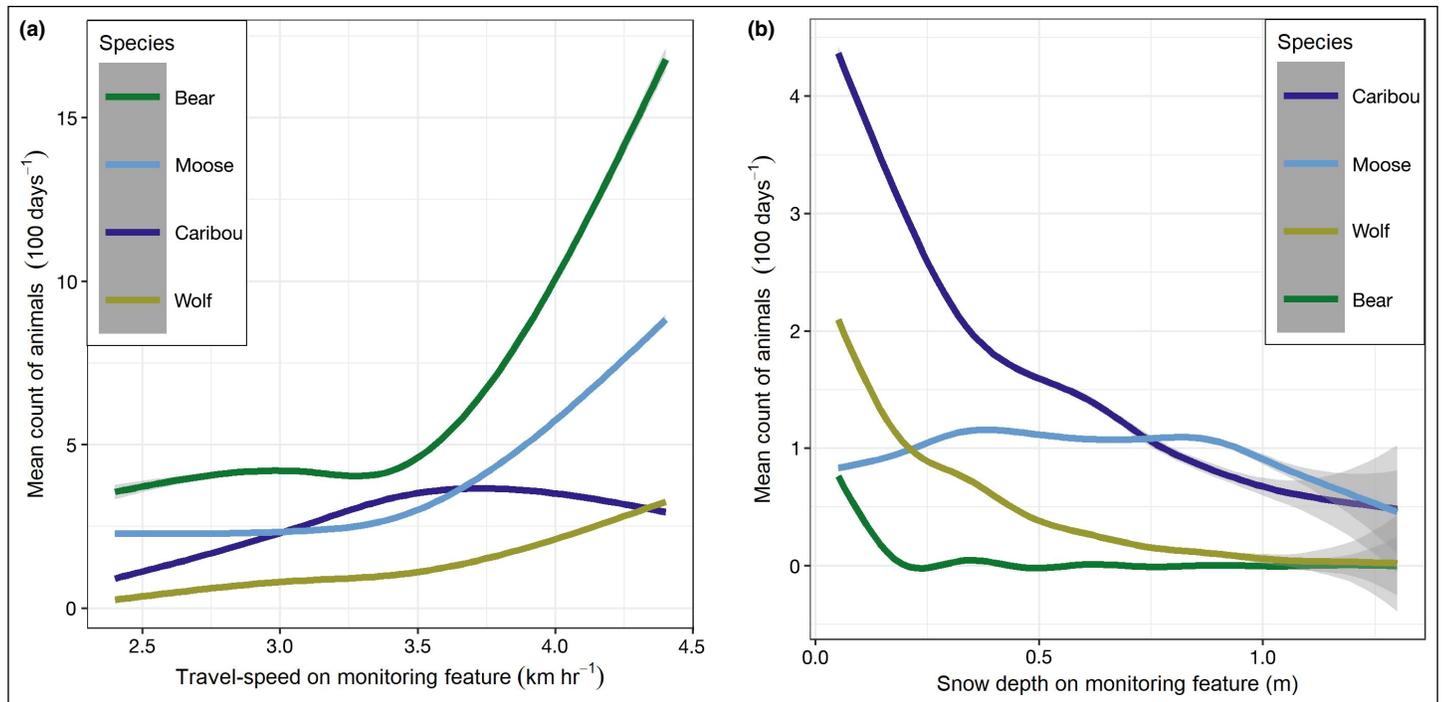


Figure 2. Mean marginal effect of (a) travel speed and (b) snow depth in the intensity of use model for each species. The plotted lines show the mean change in the multivariate intensity of use models (y-axis) as the ease of travel covariates vary along the x-axis.

(WebPanels 2–5). The marginal effect between intensity of use and travel speed varied in magnitude and shape by species (Figure 2a). Intensity of use increased monotonically for moose, wolves, and black bears, with mean intensities increasing substantially in areas where travel speed was >3.5 km per hour. The mean intensity of use by caribou also increased with travel speed but stabilized at approximately 3.5 km per hour. This was in part because maximum observed travel speeds were lower in boreal peatland (peat soil wetlands) habitat types where caribou spend much of their time (WebPanel 3). Within peatland ecosystems, the linear development mitigations reduced the intensity of habitat use by all four species relative to unmitigated anthropogenic developments; this effect was most evident for caribou and wolves (WebFigure 1; WebPanels 2–5).

Similarly, mean intensity of habitat use by caribou, wolves, and black bears decreased over the range of observed snow depths (Figure 2b). While moose were relatively insensitive to snow depth, their mean intensity of habitat use declined at depths >80 cm. Packed snow conditions mitigated some of the constraints imposed by deep snow. The intensity of habitat use by wolves and caribou was higher on linear developments where snow had been packed by recreational snowmobiling (WebFigure 2); in effect, snow-packed surfaces created by snowmobiling increased coincident habitat use by wolves and caribou.

Caribou were the only species to exhibit a significantly higher intensity of use in peatland ecosystems compared to upland ecosystems (WebFigure 3; WebPanels 2–5). This is consistent with an anti-predator strategy wherein caribou avoid

upland habitat types preferred by predators and alternative prey species, such as moose. However, when using peatland ecosystems, moose, wolves, and black bears used anthropogenic linear developments more frequently than game trails (WebPanels 2–5). This effect was most evident for wolf, suggesting that linear developments provide a mechanism for increasing encounters between wolves and caribou.

Hypothesis 2: the population-level response

Within the treatment area, animal use was reduced on anthropogenic linear developments directly through the mitigations (WebPanel 6), and indirectly by discouraging snowmobile use. In the post-treatment year, the number of winter days with packed snow conditions on linear developments was reduced by 66% (229 days) compared to the pre-treatment year. The before–after effect of movement mitigations reduced the mean intensity of use by wolves by 65% and black bears by 63% within the treatment area ($P < 0.0001$). The before–after treatment effect was not significant ($P > 0.05$) for caribou or moose and the marginal intensity of habitat use for these two species changed by $<25\%$ pre- and post-treatment. We calculated the ratio of the estimated intensity of use between each predator and caribou across each camera monitoring day in both the control and treatment areas, and found that the mean ratio of wolf-to-caribou use declined by 85% and the mean ratio of black bear-to-caribou use declined by 60% within the treatment area, pre- and post-treatment (Figure 3). Notably, the intensity of habitat use by wolves increased in the control area post-treatment; yet

this increase was not compensatory with the reduction measured in the treatment area, suggesting that movement mitigations may have displaced wolves to both the control area and locations outside of the caribou range.

Discussion

In this study, we show how animal movement behaviors can be leveraged as a mechanism to reduce the coincident habitat use by caribou and their predators (ie encounters) in a caribou range. For wide-ranging species occupying compromised landscapes, applying mitigations that reduce predator movements can immediately and cost-effectively disrupt predator–prey interactions, and serve as an alternative to predator control while long-term actions are implemented to restore and protect critical habitat. To bring about a population-level response among vulnerable prey, such as caribou, we need to mitigate a sufficient proportion (but not all) of the species' habitat. In our study, treating <40% of anthropogenic linear developments was enough to reduce wolf–caribou encounters in the treated area by 85%. We speculate that generating a similar effect by killing wolves alone would require removing most of the population. Applying movement mitigations may ultimately lower predator populations if management reduces access to all prey resources; however, strategic application may redistribute predators from areas dominated by vulnerable prey to areas dominated by more abundant prey. For example, in the boreal forest, we would expect mitigations deployed within lowland caribou habitat to redistribute wolves to upland ecosystems preferred by moose and deer (*Odocoileus* spp) (Wasser *et al.* 2011). By leaving a top predator intact in the ecosystem, our study reduced risk to an endangered species without the disruptive trophic effects that can result from intense carnivore control (Estes *et al.* 2011).

Human-modified landscapes alter the costs and benefits associated with movement, foraging, and predation, with consequences for ecological function (Foley *et al.* 2005; Tucker *et al.* 2018). That making movement more difficult can reduce encounter rates independent of population density (McKenzie *et al.* 2012) supports our conclusion that managing energetic costs can improve ecological function. We show that increasing predator travel costs in habitats of vulnerable prey can reduce predator–prey encounters. However, the opposite should also be true: reducing travel costs outside of these habitats could draw predators away from vulnerable prey. For example, encouraging snowmobiling outside of a caribou range may reduce lethal encounters by promoting predator movement on packed features away from caribou and toward more abundant and less-threatened prey.

Our sampling design was focused on anthropogenic linear developments and game trails, where we could more readily observe large mammals. In boreal ecosystems, both wolves and black bears select for natural and anthropogenic linear developments that promote movement (eg Tigner *et al.* 2014;

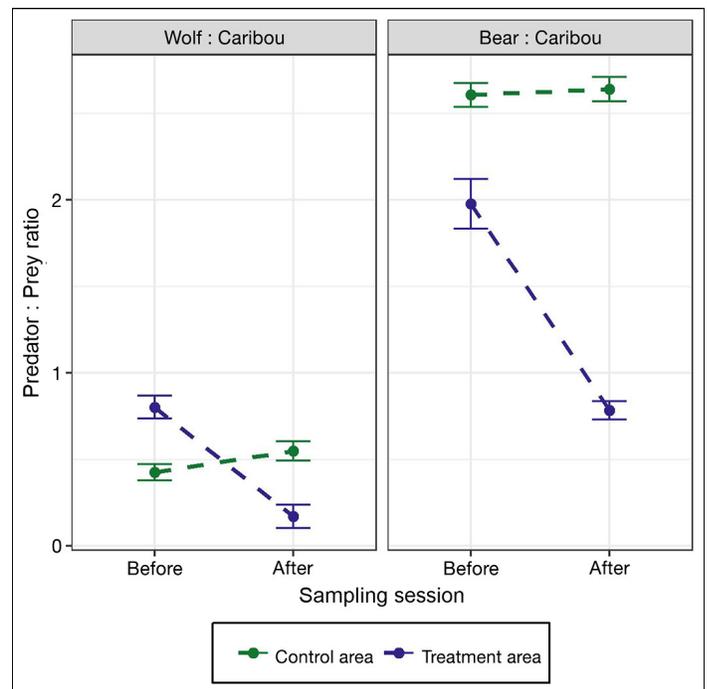


Figure 3. The mean intensity of use ratios by predators and woodland caribou (*Rangifer tarandus caribou*) in the treatment and control areas 1-year before and 1-year after the mitigation treatments were deployed. The y-axis depicts the ratio of the fitted values from the intensity-of-use models for a predator species divided by the fitted values from the intensity-of-use model for caribou (eg [wolves/camera/day]/[caribou/camera/day]). Confidence intervals (95%) were estimated by bootstrapping the ratio of the fitted values by each category 5,000 times.

Newton *et al.* 2017; Dickie *et al.* 2020), particularly where they increase access to prey (Wasser *et al.* 2011; DeMars and Boutin 2018). The fact that we observed a >60% reduction in encounters between caribou and their predators after mitigating <40% of the anthropogenic linear developments in the treatment area indicates that predators did not fully compensate by increasing their use of unmitigated linear developments or game trails within the treatment area (Figure 3). Thus, although we did not monitor animal use off of game trails, our results are consistent with the mechanistic and empirical expectation that predator–prey encounters decline across landscapes when habitat features, such as linear developments, no longer facilitate movement or promote coincident use by interacting predators and prey (Whittington *et al.* 2011; McKenzie *et al.* 2012).

Predator–prey dynamics vary based on landscape characteristics and animal behaviors (Kareiva 1987). There is immense pressure for animals to optimize costs and benefits because of the immediate payoff (Sih 1980) and long-lasting consequences related to reproduction and fitness (DeWitt *et al.* 2019). Managing costs and benefits of movement has wide-reaching effects for terrestrial species, and may be required to maintain vulnerable species and ecosystem function in both human-dominated and natural landscapes (Whittington *et al.* 2011; Tucker *et al.* 2018). Managing animal movement may not benefit all species equally, as vulnerability

to habitat loss, predation, and novel ecological interactions varies based on life-history strategies (Foley *et al.* 2005; Whittington *et al.* 2011; Tucker *et al.* 2018). Many mammalian predator–prey communities exhibit a Type II functional response, wherein encounter rates limit predation at low prey densities and handling times limit predation at high prey densities. As a result, encounter-based management may benefit woodland caribou more than more gregarious animals, such as barren ground caribou (*Rangifer tarandus groenlandicus*) or saiga antelope (*Saiga tatarica*).

The effect of encounter-based management on predator populations is complex and will depend on the availability of alternate prey. In a system with one prey species, we would expect lower encounter rates to reduce predator densities (Holling 1959) through decreased reproduction or survival. In systems with multiple prey species, predators may compensate by switching to more economical prey. The ecological effects of prey switching depend on the abundance and distribution of alternate prey. Depending on the energetic economy, predator densities could decline, remain constant, or possibly increase (eg if prey switching triggered a trophic interaction with novel prey). In boreal ecosystems such as those in our study, caribou primarily use peatland ecosystems, whereas moose and white-tailed deer (*Odocoileus virginianus*) primarily use more productive upland forests (Wasser *et al.* 2011). Because wolf densities usually respond to moose and white-tailed deer populations (Serrouya *et al.* 2019), encounter-based management is likely to redistribute wolves with little or no impact on wolf populations.

Anthropogenic landscape change is creating novel interactions that have consequences for trophic relationships and species coexistence (Holt 1984; Guiden *et al.* 2019). There is increasing evidence that animal movement integrates behavioral and evolutionary processes by which species use geographic and environmental space (Van Moorter *et al.* 2016). Given the behavioral and evolutionary consequences of species interactions, we expect that managing animal movement will be most critical where population processes are primarily encounter-driven, such as with predation, exploitation, reproduction, and disease transmission.

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■ Data availability statement

Animal use, movement, and associated vegetation data (Keim 2021) used in the analyses are available at <https://doi.org/10.5061/dryad.xsj3tx9f6>.

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■ Supporting Information

Additional, web-only material may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/fee.2358/supinfo>