Predicting the effects of restoring linear features on woodland caribou populations

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Executive Summary

Woodland caribou (*Rangifer tarandus*) are declining across much of Canada and multiple conservation levers are being used to halt their declines. Habitat restoration has been identified as a key management lever. The focus of restoration is on linear features such as roads and seismic lines, which have been implicated as a cause of caribou declines. While preliminary results of restoration trials have been successful at reducing wolf use of, and speed on lines – presumably decreasing wolf hunting efficiency – the capacity of habitat restoration to recover caribou populations is uncertain. The objective of our analysis was to predict changes to caribou density based on restoring linear features using predator-prey models that account for how changes to the wolf's foraging efficiency will simultaneously affect the abundance of caribou, wolves, and moose. These models represent wolves as the shared predator, moose as the primary prey, and caribou as the secondary or alternate prey. We explicitly address two possible mechanisms linking linear features to caribou declines: increased foraging efficiency via greater movement rates and increased overlap between wolves and caribou via access into peatlands. We used data from comparable systems to estimate foraging efficiency and evaluate resulting animal densities under current landscape conditions, when only seismic lines are restored (partial restoration) and when all linear features are restored (complete restoration).

The foraging efficiency of wolves on caribou was most affected by the spatial overlap between wolves and caribou, as opposed to wolf movement rate. When both movement rates and overlap between predators and prey were reduced, caribou density increased by 74.6 % if all linear features were restored. Comparatively, if only seismic lines were restored, caribou density increased by 20.9 %. The effect of only reducing wolf movement rate was also notable, because removing all linear features is expected to reduce daily movement from 10.9 to 8.4 km/day, resulting in an increase in caribou density of 32%. Moose populations were less affected by changes to wolf foraging efficiency, with the largest increase in moose density (3.3%) occurring when all linear features were restored and both mechanisms were considered. Restoration could have substantial benefits on caribou populations, but the clearest effects occur when all linear features are restored in conjunction. While predicting the effect of partial restoration is difficult, the benefit to caribou is likely bounded between the scenarios of partial and complete restoration of linear features. The reduction in spatial overlap between wolves and caribou had the largest potential for managing caribou declines via restoration efforts, suggesting limited conservation dollars could be focussed on restoring lines leading into peatlands, although the effect of both movement rate and overlap is synergistic and provides the greatest benefit when considered jointly.

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Introduction

Government and industry are embarking on a multi-million-dollar process to restore habitat for woodland caribou (*Rangifer tarandus caribou*; Hebblewhite 2017), a species that is declining or endangered in many portions of its range (Festa-Bianchet et al. 2011). In western Canada, the focus of restoration is directed at linear features created by humans, such as seismic lines that are used to locate petroleum deposits. In Northeast British Columbia, there are over 165,000 km of seismic lines (> 4 km/ km^2; Fig. 1) and at roughly $10,000 / km to restore, the cost to reclaim caribou habitat is expected to exceed a billion dollars.

Seismic lines increase the travel speed (Dickie et al. 2017) and foraging efficiency of wolves (McKenzie et al. 2012), and may lead wolves and other predators (e.g. black bears) into peatlands that were previously refuges for caribou (DeMars and Boutin, *in Review*). The ease of movement afforded by linear features may also attract caribou (Serrouya et al. 2017), creating the potential for an ecological trap. Caribou living in areas with higher densities of linear features and other human disturbances are known to have reduced recruitment (Environment Canada 2011), higher chance of predation-related mortality (Apps et al. 2013) and consequently lower population growth rates (Wittmer et al. 2007, Sorensen et al. 2008). For these reasons, the Canadian government has mandated that human disturbance within caribou ranges be reduced below a specific threshold (Environment Canada 2012).

Given that seismic lines are the most ubiquitous type of disturbance in many caribou ranges (Fig. 1), enormous effort is being directed at piloting restoration trials and prioritizing areas for restoration (Alberta Biodiversity Monitoring Institute 2017). However, evaluating the benefit of habitat restoration to recover caribou populations is in its infancy. Several trials have tested techniques intended to reduce wolf movement rates, such as depositing coarse woody debris (Neufeld 2006), bending trees across seismic lines, or mounding soil (which also accelerates the growth of conifers). These programs were designed to provide an immediate reduction of wolf use and travel speed as an interim step until vegetation recovery occurs. Preliminary results have been encouraging, with reduced wolf movements, in some cases to levels approaching an undisturbed forest (Sherman et al. *unpublished data*, Keim et al. 2014). However, habitat restoration trials have not demonstrated a population-level benefit to caribou primarily because the scale of implementation is much smaller than is needed to observe a numerical effect on caribou. Additionally, other ecosystem processes governed by climate change (Dawe et al. 2014) or complementary management actions (e.g. wolf control; Hervieux et al. 2014) will necessarily obscure results.

Habitat restoration has intuitive appeal because it is considered an ultimate cause of population decline. However, a corollary of this reasoning is that restoration is an indirect approach to population recovery, because multiple trophic levels are implicated in caribou declines. The hypothetical pathways are that restoration can promote forest growth that will reduce forage for moose and deer, reduce predator foraging rates and predator abundance, and ultimately lead to more caribou. However, at each trophic level, uncertainty in population responses increases due to variation that accumulates across ecological scales. Therefore, establishing cause and effect will be challenging. In contrast, other approaches to caribou recovery can have much more direct and measurable effects on caribou numbers, such as predator control (Hayes et al. 2003, Hervieux et al. 2014) or *in-situ* predator exclosures (e.g. maternal penning; McNay et al. 2017), leading managers to question the efficacy of habitat restoration (Boutin and Serrouya 2015).

To reduce the uncertainty associated with habitat restoration to recover caribou, the objective of our analysis was to predict changes to caribou density based on restoring linear features. Previous research examining the effects of linear features on predator-prey relationships have focused on single prey systems (McKenzie et al. 2012, DeMars et al. 2017, *in prep*) and such analyses may have limited applicability to caribou population dynamics, which are highly influenced by population changes in both predators and other prey species (Serrouya et al. 2015, 2017). Moreover, these previous studies have separated the effects of the predators' foraging efficiency (e.g. the functional response) from the numerical response of predators and prey, without explicitly linking these two processes as a dynamic feedback (McCutchen 2007, McKenzie et al. 2012, DeMars et al. 2017, *in prep.*). Failing to account for these numerical responses may result in an underestimation of linear feature effects. Here, we used established predator-prey models that account for how changes to the wolf's foraging efficiency will simultaneously affect the abundance of caribou, wolves, and moose. Increased foraging efficiency is the hypothesized process linking linear features to increased predation of caribou. Specifically, linear features are thought to increase wolf movement rates and facilitate predator movement into caribou habitat, thereby increasing caribou-wolf spatial overlap. We explicitly addressed these two mechanisms when simulating the restoration of linear features. The management relevance of isolating these two mechanisms was to estimate the importance of restoring lines in areas that were once refuges for caribou (i.e. peatlands), or whether restoring lines uniformly across a wolf's territory will provide greater benefit to caribou.

Methods

We used Ordinary Differential Equations (ODEs) to represent the relationship between wolves, moose and caribou, whereby wolves were the shared predator, moose were the primary prey, and caribou were the secondary or alternate prey. We use equations similar to those used by Serrouya et al. (2015), which expanded Rosenzweig and Macarthur's (1963) predator-prey models to include a second prey species as well as density-dependent predator mortality (Equations 1 to 3). These models reflect a system where an increase in primary prey (moose) leads to increased predator populations, which incidentally increases caribou predation, a process termed apparent competition (Holt 1977). The model takes the form:

$$\frac{dP_1}{dt} = r_1 \cdot P_1 \cdot \left(1 - \frac{P_1}{K_1}\right) - \frac{a_1 \cdot P_1 \cdot C}{1 + T_{h1} \cdot (a_1 \cdot P_1 + a_2 \cdot P_2)} \quad \text{eqn 1}$$

$$\frac{dP_2}{dt} = r_2 \cdot P_2 \cdot \left(1 - \frac{P_2}{K_2}\right) - \frac{a_2 \cdot P_2 \cdot C}{1 + T_{h2} \cdot (a_1 P_1 + a_2 P_2)} \quad \text{eqn 2}$$

$$\frac{dC}{dt} = C \cdot \left(\frac{b \cdot (a_1 \cdot P_1 + a_2 \cdot P_2)}{1 + (a_1 \cdot T_{h1} \cdot P_1 + a_2 \cdot T_{h2} \cdot P_2)} - m \cdot C\right) \quad \text{eqn 3}$$

where P_i are the densities of the prey species (P_1 is the primary prey, moose and P_2 is the secondary prey, caribou), K_i and r_i are the corresponding carrying capacities and intrinsic growth rates, C is the predator density, a_i and T_{hi} are the predator foraging efficiencies and handling times on the respective prey species, b is the conversion factor of prey to predator density, and m is the natural mortality constant of the predator representing density-dependence. While Serrouya et al. (2015) used these models to represent a cougar-deer-caribou system, these models have broad applicability for various species and systems depending on how values are parameterized.

Parameter Values

For most parameters, we used data from boreal caribou habitat in British Columbia (BC) and Alberta (AB) or mountain caribou in BC, where caribou are alternate prey in a wolf-moose system. Where information did not exist within these areas, we used data from arctic caribou populations on Southampton Island, Belcher Islands (Heard 1990) and Alaska (Haber 1977).

Initial prey densities were based solely on boreal and mountain caribou data from BC and AB. McNay et al. (2013) estimated the density of moose within seven Caribou Core Areas in northeastern British Columbia as 0.095 moose/km^2 (95% CIs 0.076 – 0.12) using distance sampling. Hervieux (*unpublished data*) estimated the density of caribou within the Cold Lake and East Side Athabasca River caribou ranges in northeastern Alberta as 0.06 caribou/km^2. The initial wolf density was calculated by averaging 6 survey units within northwestern Canada (Serrouya et al. 2016).

We parameterized the carrying capacities, intrinsic growth rates and handling time of both moose and caribou using various literature sources (Table 1). We used the same carrying capacities as presented in Serrouya et al. (2015) for moose (1.58 moose/km^2) and caribou (0.4 caribou/km^2). We also used the intrinsic growth rate for the primary prey reported in Serrouya et al (2015), 0.39/year, though this value was estimated for large deer, based on Hennemann (1983). We used an intrinsic growth rate of 0.30 caribou/year based on values presented by Heard (1990), where intrinsic growth rates of arctic caribou in Southampton islands and Belcher Islands ranged between 0.21 and 0.31 animals/year. We assumed the handling time, defined here as the proportion of the year spent consuming prey, of caribou was equal to that of moose. While moose may take longer to consume than caribou, which have less biomass, we can expect that larger ungulates are more prone to scavenging by other animals such as ravens or other carnivores, thereby reducing time spent at a kill (Sand et al. 2005). This assumption is consistent with findings that puma kill rates were better expressed as kilograms per day than ungulates per unit time, indicating that kill rates are not equivalent to consumption rates (Elbroch et al. 2014). We chose a default value of 50 for the predator mortality parameter, *m*, but given the uncertainty around this parameter we varied *m* from 40 to 60 to evaluate the results' sensitivity to this value (Appendix 1).

We calculated the conversion factor of prey to predator densities as the number of pups per adult per year divided by the average number of adult ungulates killed and consumed per adult (Serrouya et al. 2015). The number of pups per adult per year was calculated assuming 5.6 pups per pack (Webb et al. 2011), average pack size of 5.26 wolves (Serrouya et al. 2015, 2016), and one adult ungulate kill per 8.1 days (Ballard et al. 1987). Finally, we calculated the foraging efficiency of wolves, *a*, as the product of the buffer distance that wolves detect prey (m), the attack success (i.e. proportion of encounters resulting in a kill; Fryxell et al. 2007), the distance a wolf travels in one day (i.e. the movement rate; km/d), and an index of spatial overlap between the predator and prey species (Table 1; See below for details). The latter 2 parameters were the mechanisms we varied to test how foraging efficiency effects caribou numbers.

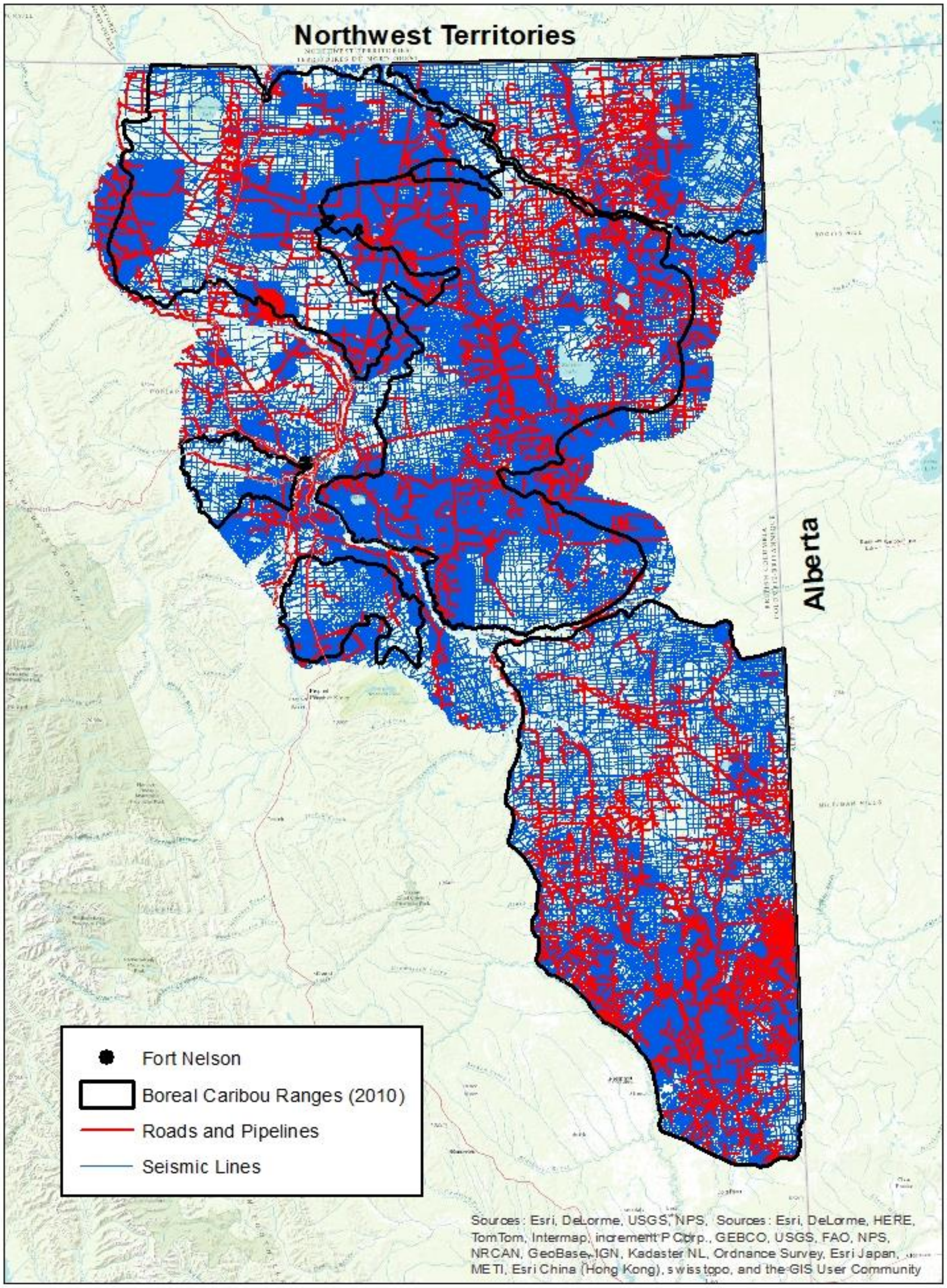
Social animals such as wolves hunt in packs, though pack structure breaks down in spring and summer (Metz et al. 2011). During these seasons, wolves hunting alone would increase encounter rates with prey but handling time would be longer and attack success lower. To deal with this complexity when estimating various components of wolf foraging efficiency, we assumed that wolves hunted in cohesive packs to maintain a simple system.

Mechanisms and Scenarios

We tested two mechanisms in which linear features increase kill rates: increased movement rates and increased spatial overlap between predators and prey. We calculated foraging efficiency for three variations of these mechanisms under current landscape conditions and when all linear features are restored: i) restoration reduces wolf movement rates, ii) restoration reduces overlap between predators and prey and iii) restoration reduces both predator movement rates and overlap (Table 2). We also considered a scenario where only seismic lines were restored, as opposed to all anthropogenic linear features (Figure 1). Any specific selection or avoidance of linear features by caribou was not considered in our analyses.

Linear features increase wolf traveling speed while on lines, and therefore increase daily movement rates (i.e. distance moved per day). Therefore, we simulated reductions in movement rates due to restoration by decreasing the amount of time wolves spent on linear features, thereby reducing daily movement rates. The distance wolves travel in a day was calculated using data from AB where wolves spent approximately 15 % of their time traveling on linear features, and linear features increased speed by factor of 3, resulting in an average speed of 0.35 km/hr off lines and 1.05 km/hr on lines (Dickie et al. 2017). This resulted in an average of 10.92 km moved per day in the current landscape scenario, and an average of 8.40 km moved per day in a landscape where restored lines reduce movement rates. For the scenario where only seismic lines were restored, distance moved per day was estimated as 10.80 km by reducing wolf use of lines from 15 % to 10%, because approximately 5 % of wolf GPS locations were on seismic lines (Dickie et al. 2017).

We estimated the current overlap between wolves and their prey using wolf GPS locations and landcover summarized into moose-preferred habitat (deciduous and mixed wood forest) and caribou habitat (peatlands; defined as bogs and nutrient-poor fens). Based on GPS locations in northeastern British Columbia, wolves spent on average 0.30 and 0.15 of their time in moose and caribou habitat, respectively (*DeMars, unpublished data*). We then calculated the expected overlap between wolves and their prey when all linear features are restored by examining the selection differences between moose and caribou habitat with and without lines (Appendix I). The presence of linear features increased wolf selection of caribou habitat by 1.48 times and by 1.04 times for moose habitat (*DeMars, unpublished data*). Therefore, we multiplied the proportion of GPS locations in each habitat class by the back-transformed selection coefficients to calculate the expected proportion of GPS locations in each of the habitat categories of interest with no lines, resulting in 0.28 and 0.10 overlap with moose and caribou, respectively. For the scenario where only seismic lines were restored, we reduced overlap between predators and prey



Sources: Esri, DeLorme, USGS, NPS, Sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, and the GIS User Community

Figure 1: Map displaying the abundance of seismic lines compared to other linear features across the landscape within caribou range in northeast British Columbia. Two scenarios were simulated, one where all seismic lines were restored, and the second where all linear features were restored.

because we did not have data to estimate proportion of time spent in moose and caribou habitat when there are no seismic lines but other linear features are still present, we reduced overlap by a third to 0.29 and 0.13 for moose and caribou, respectively.

We calculated the daily foraging efficiency of wolves for caribou and moose, and converted it to an annual value by multiplying by the average number of days in a year (364.25). We assumed linear features do not influence attack success or the detection buffer in which predators can detect prey. Therefore, wolf attack success was kept constant across scenarios at 0.064 for moose and 0.43 for caribou (Haber 1977) and a 200-m detection buffer was used (Serrouya et al. 2015). While Serrouya et al.'s detection buffer of 200 m was for cougars, to our knowledge this value has not been quantified for wolves in the wild, and we had no *a priori* reason to assume there would be differences for wolves.

Final output from the models included the estimated moose, caribou and wolf density (animals/km^2), and the annual predation rate of moose and caribou, expressed as the proportion of the population killed by wolves. Below we present results from simulations using an m = 50 and equilibria at 800 years. Initial densities used in simulations were 0.06, 0.095 and 0.008 animals/km^2 for caribou, moose and wolves, respectively.

Table 1: The values and sources used for starting densities and to parameterize Ordinary Differential Equations to simulate predator-prey dynamics using the functional and numerical response of wolves to their primary (moose) and secondary (caribou) prey.

	Parameters	**Value**	**Unit**	**Reference**
Primary Prey (Moose)	P	0.095	moose/km^2	McNay et al. 2013
	r	0.39	moose/year	Serrouya et al. 2015
	K	1.58	moose/km^2	Serrouya et al. 2015
	a min	10.5	km^2/year	See predator below for components
	a max	15	km2/year	See predator below for components
	C	0.008	wolves/1000 km2	Serrouya et al. 2016
	Th	0.112	proportion of year	Serrouya 2013
	P	0.06	caribou/km2	Wilson et al. *unpublished data*

Parameters			Value	Unit	Reference
Secondary Prey (Caribou)	r		0.3	caribou/year	Heard 1990
	K		0.4	caribou/km2	Serrouya et al. 2015
	a min		25	km2/year	See predator below for components
	a max		50	km2/year	See predator below for components
	C		0.008	wolves/1000 km2	Serrouya et al. 2016
	Th		0.112	proportion of year	Serrouya 2013
Predator (Wolf)	C		0.008	wolves/km2	Serrouya et al 2016
	b		0.114	(#offspring/adult/year) /# of prey eaten	Ballard et al. 1987; Serrouya et al. 2016 ; Webb and Merrill 2011
	Foraging Efficiency, Primary Prey	Distance/day (min)	8.4	km/day	Dickie et al. 2017
		Distance/day (max)	10.92	km/day	Dickie et al. 2017
		Detection Buffer	0.2	km	Serrouya et al. 2015
		Attack success	0.064	probability	Haber 1977
		Overlap (min)	0.28	proportion	DeMars *unpublished data*
		Overlap (max)	0.3	proportion	DeMars *unpublished data*
		Cohesion	1	proportion	Assumed
	Foraging Efficiency, Secondary Prey	Distance/day (min)	8.4	km/day	Dickie et al. 2017
		Distance/day (max)	10.92	km/day	Dickie et al. 2017
		Detection Buffer	0.2	km	Serrouya et al. 2015
		Attack success	0.43	probability	Haber 1977
		Overlap (min)	0.1	proportion	DeMars *unpublished data*
		Overlap (max)	0.15	proportion	DeMars *unpublished data*

Parameters	Value	Unit	Reference
Cohesion	1	proportion	Assumed
Th Primary	0.112	proportion of year	Serrouya 2013
Th Secondary	0.112	proportion of year	Serrouya 2013
m	40-60	*No Units*	Assumed

Table 2: Values used to calculate the foraging efficiency '*a*' of wolves in a wolf-moose-caribou system for simulations representing partial habitat restoration (i.e. only seismic lines restored) and full habitat restoration (i.e. all linear features restored). The three scenarios represent mechanisms in which habitat restoration are hypothesized to influence '*a*' i) restoration reduces wolf movement rate only, ii) restoration reduces spatial only, and iii) restoration reduces both movement rates and overlap.

Scenario	**Components of Foraging Efficiency, *a***	**Caribou**			**Moose**		
		Current	**Partial Restoration**	**Full Restoration**	**Current**	**Partial Restoration**	**Full Restoration**
Movement Rate Only	Distance (km/day)	10.92	10.80	8.40	10.92	10.08	8.40
	Detection Buffer (km)	0.20	0.20	0.20	0.20	0.20	0.20
	Attack Success (Proportion)	0.43	0.43	0.43	0.06	0.06	0.06
	Overlap (%)	0.15	0.15	0.15	0.30	0.30	0.30
	a	51.31	50.75	39.47	15.27	14.10	11.75
Overlap Only	Distance (km/day)	10.92	10.92	10.92	10.92	10.92	10.92
	Detection Buffer (km)	0.20	0.20	0.20	0.20	0.20	0.20
	Attack Success (Proportion)	0.43	0.43	0.43	0.06	0.06	0.06
	Overlap (%)	0.15	0.13	0.10	0.30	0.29	0.28
	a	51.31	45.61	34.21	15.27	14.93	14.26
Movement Rate and Overlap	Distance (km/day)	10.92	10.80	8.40	10.92	10.80	8.40
	Detection Buffer (km)	0.20	0.20	0.20	0.20	0.20	0.20
	Attack Success (Proportion)	0.43	0.43	0.43	0.06	0.06	0.06
	Overlap (%)	0.15	0.13	0.10	0.30	0.29	0.28
	a	51.31	45.11	26.31	15.27	14.77	10.97

Results

The foraging efficiency of wolves (‘*a*’) for caribou was most affected by the spatial overlap between wolves and caribou, as opposed to movement rate. Reducing spatial overlap reduced *a* from 51.3 to 34.2 (Table 2), whereas reducing movement rate changed *a* to 39.5. The reduction in wolf movement was from 10.92 km/day (current landscape) to 8.40 km/day under complete restoration (Table 2), and resulted in caribou density changing from 0.145 to 0.191/km^2 (Table 3), an increase of 32 %. If both the overlap and movement rate mechanisms are considered, then *a* is further reduced, to 26.3 (Table 2). Assuming that both mechanisms are at play and all linear features are restored, the reduction to *a* resulted in an increase to caribou density of 74.6 %, from 0.14 to 0.25 animals/km^2 (Table 3). If only seismic lines are restored, the increase in caribou density would be 20.9 %. The proportion of caribou killed per year by wolves declined from 0.19 to 0.11 if all linear features were restored and both mechanisms were affected by restoration (Table 3).

Wolf foraging efficiency for moose was relatively unaffected by changes in wolf movement rate or the spatial overlap between wolves and moose related to restoration (Table 3). When both mechanism are considered and all linear features are restored, the proportion of moose killed by wolves was reduced by only 1 %, resulting in an increase moose density of 3.3 %, from 1.35 to 1.39 animals/km^2. If only seismic lines are restored, moose density increased by 0.5 %, to 1.36 animals/km^2.

Wolf density was minimally affected by restoration simulations, and only decreased by 6.3 % from 0.154 to 0.145 animals/km^2 when all linear features were restored, but by less than 1 % when only seismic lines were restored, and when both mechanism were considered in conjunction.

Table 3: Simulations of wolf-moose-caribou population dynamics assuming current landscape conditions, partial habitat restoration (i.e. only seismic lines restored) and full habitat restoration (i.e. all linear features restored) reducing wolf movement rate, overlap with prey and both movement rate and overlap. The density of animals (/km^2) and the proportion of prey killed are presented. Results presented assumed the predator mortality parameter values (*m*) of 50.

Scenario		**Foraging Efficiency ‘*a*’**		**Density (no. /km^2) ***			**Proportion Killed**	
		Caribou	**Moose**	**Caribou**	**Moose**	**Wolf**	**Caribou**	**Moose**
Movement Rate Only	Current	51.3	15.3	0.145	1.352	0.015	0.19	0.06
	Partial Restoration	50.7	14.1	0.139	1.360	0.015	0.20	0.05
	Full Restoration	39.5	11.7	0.191	1.385	0.015	0.16	0.05
Overlap Only	Current	51.3	15.3	0.145	1.352	0.015	0.19	0.06
	Partial Restoration	45.6	14.9	0.174	1.355	0.015	0.17	0.06

Scenario		Foraging Efficiency ‘*a*’		Density (no. /km^2) *			Proportion Killed	
		Caribou	Moose	Caribou	Moose	Wolf	Caribou	Moose
	Full Restoration	34.2	14.3	0.227	1.364	0.015	0.13	0.05
Movement Rate and Overlap	Current	51.3	15.3	0.145	1.352	0.015	0.19	0.06
	Partial Restoration	45.1	14.8	0.176	1.356	0.015	0.17	0.06
	Full Restoration	26.3	11	0.255	1.394	0.014	0.11	0.05

*To calculate the abundance (number of animals / 1000 km^2), multiply densities by 1000

Discussion

We simulated two mechanisms to predict the effectiveness of restoring caribou habitat at increasing caribou populations: reducing the movement rates of wolves, and reducing the spatial overlap between wolves and their prey. We also combined the effects of the two mechanisms, and examined the scenarios of restoring all linear features, or only seismic lines. Clearly, restoring all linear features is an optimistic scenario, but was intended to predict the maximum effect of how human-created linear features would affect caribou populations. This optimistic restoration scenario, combined with reducing movement rates and spatial overlap, appears to have a substantial effect on caribou by increasing their equilibrium density by 75 %. Most of this effect is caused by the reduction in spatial overlap between wolves and caribou, although the effect of both movement rate and overlap is synergistic and provides the greatest benefit. In reality, restoration will likely affect both mechanisms, with a reduction in movement contributing to less overlap with caribou, suggesting that maximum benefits can be realized.

Predicting the effect of partial restoration is more difficult because of two contrasting assumptions. The first assumption conservatively estimated that restoring seismic lines will reduce the spatial overlap at the same proportion as the estimated reduction in movement rates from the decreased use of lines. Because seismic lines cover a much greater area than other linear features, and extend into areas where there are no other disturbances, it is conceivable that removing seismic lines will create much more predator-free space (i.e. reduced overlap) than removing other linear features (Fig. 1). For example, a study in northeast Alberta showed that the zone of influence of seismic lines was 15 to 30 times greater than other linear features (Alberta Biodiversity Monitoring Institute 2017), simply because seismic lines are much more abundant and widely distributed than other linear features (Fig. 1). The second assumption is that restoring seismic lines will not cause compensatory use of other linear features; i.e., wolves would not increase their use of other linear features due to the removal of seismic lines. Compensatory behaviour is likely to occur, but we argue that the predator-free space created by clearing vast areas of human disturbance that is dominated by seismic lines would be greater than the effect of compensatory behaviour by wolves. Although we can only speculate as to the relative magnitude of these two assumptions, we can state with greater certainty that the benefit to caribou is likely bounded between the scenarios of partial and complete restoration of linear features.

Our findings add to the limited amount of work on this topic, yet highlight that consistent conclusions among studies are lacking. McKenzie et al. (2012) explicitly examined how the functional response of predators could be enhanced by linear features. They simulated a range of seismic line densities and prey densities to determine how these factors affect encounter rates between predators and prey. Encounter rates were most affected by seismic lines at low prey density. In other words, seismic lines were expected to alter the functional response enough to affect encounter and presumably predation rates of prey. Two studies based on spatially explicit simulations found that a very modest increase in wolf numbers dwarfed any effect of line density or configuration on the predator's kill rate of caribou (DeMars et al. *In Prep*., McCutchen 2007) suggesting that manipulating the foraging efficiency through restoration would have a limited effect on caribou numbers. The increase in wolf numbers was assumed to occur from mechanisms other than foraging efficiency, such as a numerical response directly linked to increased ungulates caused by climate warming or forestry cutting units (Serrouya et al. 2011, Dawe et al. 2014). However, in the latter 3 studies, there was no dynamic linkage between the functional and numerical response of predators, whereas in reality, these two components are difficult to disentangle. A dynamic approach using ODEs accounts for the fact that an increased foraging efficiency will simultaneously affect the ratio of prey to predators, which ultimately affects predation rates (Vucetich et al. 2011). We suggest that our use of dynamic feedback accounts for the different results from these studies, particularly the latter two where functional aspects were examined independently from numerical components.

The above studies used approaches based on predator movement and foraging, but Boutin et al. (*In Prep*) used a habitat-based equation to predict recovery options for caribou, including the restoration of seismic lines. Landscape attributes, including levels of human disturbance, were correlated with caribou population growth rates (Boutin and Arienti 2008), then the removal of seismic lines was simulated (Boutin et al. in Prep). Their results suggested limited potential to affect caribou growth rates based on the restoration of seismic lines. We suggest that the different outcomes from our study are because the habitat-based equation includes early seral forest caused by wildfire and human disturbance such as forestry cutting units. Boutin et al. (in prep) suggest that the early seral vegetation is likely enough to sustain deer and moose numbers regardless of seismic line abundance.

Our simulations indicated that wolf numbers did not change in response to restoration. Our predator equation (Eq. 3) was a type II numerical response, meaning that wolves were subjected to density dependent mortality (m). In other words, as prey numbers increase, wolf numbers increase but at a declining rate because of social constraints among packs. Recent research has shown that wolves undergo significant increases to inter-pack mortality as the number of packs increases (Cariappa et al. 2011; Cubaynes et al. 2014), suggesting that a linear increase of wolf numbers to prey biomass is not correct. Nonetheless, the predation rate on caribou declined with restoration because the ratio of prey to wolves increased (i.e., a similar number of wolves but fewer ungulates; Vucetich et al. 2011, Serrouya et al. 2015), which ultimately led to a higher density of caribou.

Assumptions and how they should be challenged

The strength of this analysis is predicated on the dynamic and simultaneous feedback between the functional and numerical responses of wolves and consequent impacts to their prey. However, all models make simplifying assumptions that require evaluation and we address the most important ones here.

First, our analysis is a-spatial, and therefore we assume no compensatory behaviour of wolves to restoration. Some degree of compensatory behaviour is likely, but nonetheless restored areas would increase refugia for caribou. Because any function that would capture compensatory behaviour would be speculative, the best advice we have is to examine the range of caribou densities between partial and complete restoration. Challenging this assumption with empirical data (either radio collars or camera traps on linear features that include roads and pipelines) is needed to address this uncertainty.

Tied to this assumption is that wolf use of linear features and the resulting changes in movement rates in NE Alberta is similar to that of NW BC. The time wolves spend on seismic lines may be influenced by their availability, as well as the availability of other linear features. The density of linear features in the study by Dickie et al (2017) varied between 1 to 3 km/km^2, which is similar to that of NW BC where linear feature density varies between 1 and 4 km/km^2. Wolves in AB did not select lines dependent on their availability, and instead use of lines increased as availability increased (Dickie 2015). Wolves in northeastern British Columbia only weakly decreased their selection for linear features as a function of availability (DeMars and Boutin 2017). Given the density of lines in BC is slightly higher than in AB, we may have under-estimated the initial movement rates on lines. Under-estimating wolf movement on linear features would make our predictions conservative, in that the effect of restoration on caribou populations in NE BC would potentially be greater than what we state.

Second, our analysis assumes that the carrying capacity of moose (K_1) was unaffected by the abundance of seismic lines or by climate change. Seismic lines cover many linear kilometers, but their surface area is minimal relative to other sources of young forest (e.g. wildfire and forestry). Therefore, we do not think that seismic lines have a substantial impact on K_1 and in this context, our assumption is unlikely to affect results. On the other hand, climate change can increase moose and deer through increased wildfire (Schwartz & Franzmann 1991) and reduced winter severity (Dawe et al. 2014). Our analysis did not explicitly contrast the effect of changing ungulate carrying capacity against predator foraging efficiency, but this is an obvious avenue for future work. Such an analysis could contrast the relative importance of climate with human-induced changes to foraging efficiency. However, estimating the magnitude of change in moose carrying capacity will be similarly burdened with assumptions and could make comparisons challenging.

A final assumption is that restoration treatments achieve the intent of reducing wolf movement to levels that approximate an undisturbed forest. As with the first assumption, the periodic radio collaring of wolves in areas of restored habitat will be the best approach to validate this assumption. This information could be obtained in a relatively short time frame, because it is not necessary to wait for large areas to be restored. Large areas of restored lines are needed to observe a population-level effect on wolves and caribou, but are not needed to evaluate the behavioural responses of wolves to restoration treatments.

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Appendix 1

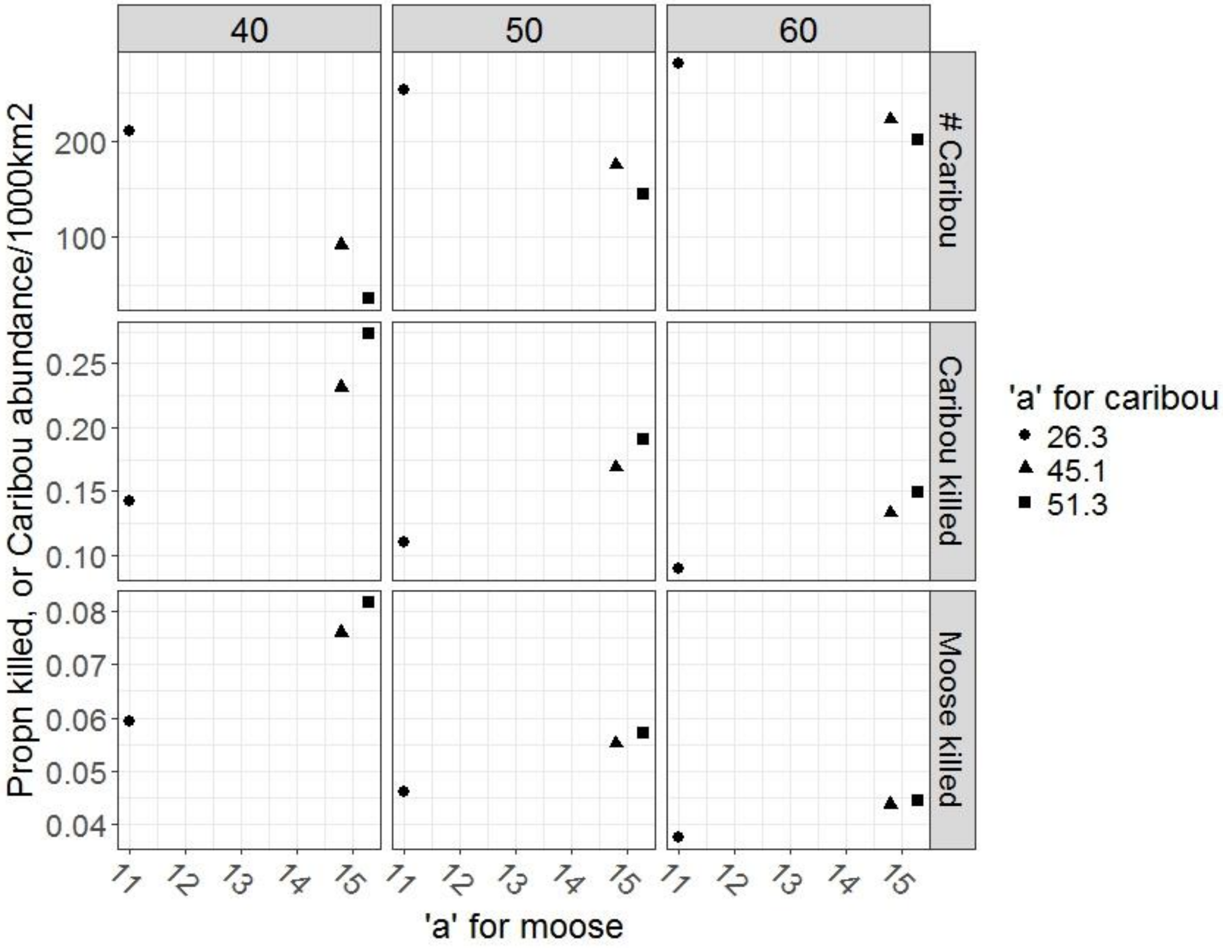

Figure A1: Simulations of wolf-moose-caribou population dynamics across various predator mortality parameter values (*m*) assuming current landscape conditions (squares), partial habitat restoration (i.e. only seismic lines restored; triangles) and full habitat restoration (i.e. all linear features restored; circles) reducing wolf movement rate and overlap with prey. The density of animals (/km^2) and the proportion of prey killed are presented.