



SPECIAL FEATURE:
EMPIRICAL PERSPECTIVES FROM MATHEMATICAL ECOLOGY

Slowing down wolves to protect boreal caribou populations: a spatial simulation model of linear feature restoration

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Citation: Spangenberg, M. C., R. Serrouya, M. Dickie, C. A. DeMars, T. Michelot, S. Boutin, and M. J. Wittmann. 2019. Slowing down wolves to protect boreal caribou populations: a spatial simulation model of linear feature restoration. *Ecosphere* 10(10):e02904. 10.1002/ecs2.2904

Abstract. In Canada, boreal caribou (*Rangifer tarandus caribou*) are declining in numbers, in part due to increased predation by wolves (*Canis lupus*). One management option to reduce wolf–caribou interactions and thus protect caribou is to remove man-made linear features (LFs), structures such as roads, trails, and cut lines, which are used by wolves as traveling paths. Linear features increase wolf traveling speed and could additionally facilitate wolf entry into caribou habitat. Our goal was to quantify the expected effect of LF removal on caribou mortality and investigate whether this LF restoration could be a sufficient measure to stop caribou declines. We simulated the effects of LF restoration on caribou adult and calf survival in spatially explicit wolf–caribou encounter models. The models were parameterized using Global Positioning System (GPS) data, hidden Markov models (HMMs), and information from the published literature. Complete LF restoration decreased wolf traveling speed and thus reduced caribou mortality. The proportional reduction in adult caribou mortality ranged from 10 to 25% of its original value, and the proportional reduction in calf mortality ranged from 8 to 23%, depending on caribou density, number of wolf packs, kill probability given an encounter, and detection distance of wolves for caribou. Building on the model output, we used empirical caribou data to calculate the effects of reduced mortalities on the finite rate of annual population change, λ . Assuming that 25% or less of calf mortality was wolf-related, λ stayed below one, that is, populations kept declining, even with complete LF restoration. With 50% of calf mortality due to wolves, caribou populations stopped declining ($\lambda \geq 1$) if adult and calf mortality were reduced by at least 19 to 24%. However, these values were not achieved in a majority of the parameter combinations in our study, not even with complete LF restoration. Given that LF restoration as a single measure is unlikely to stop boreal caribou populations from declining, we used a case example to illustrate how LF restoration could make a small contribution in a portfolio of short-term and long-term management options to reduce wolf predation on caribou.

Key words: Alberta; apparent competition; boreal woodland caribou (*Rangifer tarandus caribou*); caribou conservation; hidden Markov model; linear feature restoration; predator–prey interaction; recruitment–mortality equation; wolf (*Canis lupus*);

Received 15 May 2019; revised 8 August 2019; accepted 15 August 2019. Corresponding Editor: Laureano A. Gherardi.

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INTRODUCTION

Populations of boreal caribou, an ecotype of the woodland caribou (*Rangifer tarandus caribou*) subspecies, are declining in Canada (Environment Canada 2017). While other caribou subspecies and ecotypes can sometimes be food-limited (Ouellet et al. 1996), the widely accepted explanation for woodland caribou decline is “apparent competition” (Holt 1977) with moose (*Alces alces*) and deer (*Odocoileus* spp.), mediated by wolves (*Canis lupus*) as shared predator. That is, caribou numbers decline because high densities of moose and deer support high wolf densities in and around caribou habitat (Kinley and Apps 2001, Wittmer et al. 2007, Latham et al. 2011b). This process occurs in areas with intensive timber harvesting where the early seral forests (1–40 yr old) preferred by moose and deer are interspersed with caribou habitat (Bergerud 1974, Bergerud et al. 1984, Seip 1992, Vors et al. 2007, Wittmer et al. 2007). In Alberta, white-tailed deer densities increased between 1970 and 2000, driven mainly by climate change and partly by human land use (Dawe and Boutin 2016). Also, wolf densities increased near caribou habitats, resulting in more spatial overlap of wolves and caribou and a 10-fold increase in caribou in wolf diet (Latham et al. 2011b).

Another factor that enhances wolf predation on caribou is the use of human-made linear features (LFs) as wolf traveling paths (Apps et al. 2013). Linear features are corridors relatively free from woody vegetation and include roads, trails, cut lines, and seismic lines. In Alberta, industrial development such as the exploitation of oil, gas, and timber led to a mean LF density of 2.86 km/km² (Pattison et al. 2016), with densities up to 10 km/km² in some areas (Lee and Boutin 2006). From the early 1950s to 2000, vegetation was cleared using bulldozers, resulting in seismic lines of up to 8 m wide. In many instances, vegetation recovery on these lines is extremely slow (Schneider 2002), especially in wetter lowlands (van Rensen et al. 2015), which are important caribou habitats.

Linear features are hypothesized to increase wolf predation on caribou in several ways. First, wolves move farther and faster on LFs like roads and seismic lines (Dickie et al. 2017b). Increased traveling speed leads to an increased search area

per time unit, which results in higher encounter rates. Thus, encounter rates increase with increasing LF use of wolves (McKenzie et al. 2012). Second, LFs could enhance visual and olfactory encounters between wolves and caribou (Latham 2009). Finally, LFs could allow wolves to enter caribou refuge habitat more easily (DeMars and Boutin 2018, Mumma et al. 2018). In British Columbia, for example, estimated spatial overlap of caribou and wolves increased with increasing LF density (Mumma et al. 2018).

Consequently, one of the primary conservation measures currently explored for recovering caribou is to reduce the density of linear features that can be used by wolves. Concrete actions to achieve this include replanting trees on LFs, using fences, felled trees, or other debris to obstruct movement on LFs, and promoting natural succession (James and Stuart-Smith 2000, Pyper et al. 2014). We will generally refer to these measures as “LF restoration.” It has been shown that wolf traveling speed on LFs can be reduced with increased vegetation regrowth (Dickie et al. 2017a), and wolf use at specific sites can be reduced by placing woody debris on lines (Keim et al. 2019). Full LF restoration would imply returning all LFs to a state equivalent to the surrounding forest. However, van Rensen et al. (2015) estimated that one third of LFs in Alberta will not reach a vegetation height of 3 m in the next 50 yr. Furthermore, restoration costs of \$4,000 (CAD) or more per km (Schneider et al. 2010, Pyper et al. 2014) and continued economic pressure to extract petroleum resources could prevent full restoration.

The extent to which caribou populations will benefit from LF restoration is currently an active area of research. Recently, Johnson et al. (2019) estimated the costs and benefits of a large number of caribou recovery options and also included linear feature restoration. The relationship between linear feature density and caribou mortality in their model was based on a linear regression model taken from McCutchen (2007) where the data points represent different caribou ranges. As in all statistical models, the results might be confounded by other variables that differ between locations, for example, overall human impact. Since the study by McCutchen (2007), new GPS data have become available

(Dickie et al. 2017b) that allow to infer the actual use and movement patterns of wolves with respect to linear features.

In this study, we used these new GPS data to develop a more mechanistic approach to estimating the effects of LF restoration on caribou survival and population recovery. We first estimated wolf movement parameters from GPS data using a hidden Markov model (HMM), taking into consideration wolf use of LFs. Building on this, we developed spatially explicit wolf–prey encounter models to simulate effects of LF restoration on caribou mortalities. To study the population dynamic consequences, we then used a recruitment–mortality (R/M) equation approach (Hatter and Bergerud 1991, DeCesare et al. 2012) to compute the effects of full LF restoration on the finite rate of annual change, λ . Furthermore, we quantified the extent of other conservation measures, such as wolf reduction or habitat restoration, necessary to stop caribou declines.

USING AN HMM TO PARAMETERIZE WOLF MOVEMENT FROM GPS DATA

In this section, we describe an HMM to estimate movement characteristics of wolves in relation to linear features from GPS data. All analyses and simulations were done in R 3.4.3 (R Core Team 2017). Global Positioning System data were inspected visually in QGIS 2.8.6 (QGIS Development Team 2016).

Linear feature (LF) data

Linear feature data were collected between 2012 and 2015 in Alberta and Saskatchewan (Canada) and provided by the Alberta Biodiversity Monitoring Institute (Dickie et al. 2017b). The data set includes the positions of all conventional seismic lines, cut lines (7 to 10 m wide), roads, trails, driveways, railways, and electrical transmission lines (>20 m wide) within the study area. Low impact (3D) seismic lines were not included because wolves do not move faster on them (Dickie et al. 2017b). Linear feature data are provided in Data S1. Linear feature densities are illustrated in Appendix S1: Fig. S1.

Wolf GPS data

Global Positioning System data of 23 wolves from five packs were collected between 2013 and

2015 in Alberta and Saskatchewan (Canada) and provided by the Regional Industry Caribou Collaboration (Dickie et al. 2017b). On all GPS wolf days that were used in this study, positions were recorded in 5-min intervals. We only used wolf days with >280 GPS positions/d. Wolf capture and collaring are described in Dickie et al. (2017b). Table 1 displays the area (100% minimum convex polygon), LF length, and LF density (LF length/area) for each wolf. The wolves W026D, W027D, and W029 had the lowest LF densities within their areas. Since we aimed to parameterize our model with data reflecting LF use of wolves given substantial availability of LFs, these three individuals were removed from further analyses. Linear feature densities within the 100% minimum convex polygons of the 20 wolves used in our analyses ranged from 0.98 to 3.06 km/km².

We refer to the movement of a wolf over the 5-min interval between successive GPS positions as

Table 1. Wolf Global Positioning System (GPS) data overview.

ID	Area	LF length	LF density	Days
W003D	438.15	858.33	1.96	97
W004D	424.94	461.19	1.09	6
W005D	214.09	245.59	1.15	5
W006D	390.30	798.73	2.05	11
W007D	66.42	155.68	2.34	8
W008D	330.62	674.11	2.04	7
W012D	312.99	901.18	2.88	7
W012F	997.63	1209.28	1.21	59
W013D	439.92	437.63	0.99	18
W015D	293.36	629.14	2.14	43
W021D	484.94	1263.65	2.61	17
W022D	1626.68	4139.74	2.54	76
W023D	274.19	593.77	2.17	51
W024D	331.65	519.18	1.57	28
W025D	435.86	761.16	1.75	23
W026D	602.19	475.11	0.79	26
W027D	1084.21	625.24	0.58	32
W028D	448.56	869.96	1.94	24
W029D	5572.76	1843.54	0.33	28
W030D	313.13	883.97	2.82	25
W031D	311.15	876.20	2.82	17
W032D	417.51	1277.89	3.06	34
W033D	2482.44	3745.75	1.51	13

Notes: Area = 100% minimum convex polygon (km²), linear feature (LF) length (km) and LF density (km/km²), and number of days with >280 GPS positions for each wolf. Data were collected between March 2013 and July 2015 in Alberta, Canada.

a movement step. For each movement step, we computed the step length as the Euclidean distance between start and end position and the turning angle as the change in the moving direction compared to the previous step. We classified a step as being on an LF if the starting point was within a 20 m buffer of a linear feature. Such a buffer is necessary to account for GPS errors and LF width. To check the sensitivity of our results to LF buffer size, we also used LF buffer sizes of 10 and 30 m.

Fitting a 4-state HMM to the wolf GPS data

Hidden Markov models can reveal underlying behavioral patterns in animal movement data (Langrock et al. 2012). They assume that animals can switch between several behavioral states, which are not directly observable but have characteristic distributions of step lengths and turning angles. The behavioral states are modeled as a Markov chain, and the probabilities of switching from one behavioral state to another, or to stay within the current state, are characterized by a state transition-probability matrix.

Step lengths were modeled using a mixture of a gamma distribution and a point mass at zero. Thus, the distribution of step lengths is characterized by three parameters: mean μ and standard deviation σ of the gamma distribution, and the proportion of steps with length zero, z (zero mass). Turning angles were modeled using the von Mises distribution (Michelot et al. 2016) which has two parameters: mean turning angle (θ) and turning angle concentration (κ). As κ goes to zero, the von Mises distribution converges to the uniform distribution and there is no preference in the direction of the next moving step. On the other hand, if κ goes to infinity, the von Mises distribution converges to a point mass at the mean direction (Fisher 1993).

A 4-state HMM was fitted to the wolf GPS data. We constrained two of the states to capture the wolves' movement off linear features (states S1 and S2), and two of the states to capture the movement along linear features (states S3 and S4). Defining such constraints is straightforward in HMMs, and we explain the method in Appendix S2. A version of the R package `moveHMM` (Michelot et al. 2016), which we modified to allow for constraints in the state process, is provided in the supplementary material together with the code of the analyses. The starting parameter values are given in Appendix S3: Table S1.

Estimates of the wolf movement parameters are summarized in Table 2. States S1 and S3 correspond to slow undirected movement off or on LFs, with short step lengths and variable turning angles. We refer to these states as "resting" states. The movement in states S2 and S4 is faster and more persistent, captured by longer step lengths and small turning angles. Wolf movement in state S4 (on LFs) is approximately 1.6 times faster than in state S2 (off LFs). Distributions of estimated step lengths and turning angles, and wolf GPS movement paths are provided in Appendix S3. The estimated transition-probability matrix is shown in Table 3. For example, wolves in the state S4 (moving on LF) stayed within this state with a probability of 0.56 and had a probability of 0.40 to be in state S2 in the next step. From the transition-probability matrix, we computed the stationary distribution of the Markov chain, that is, its equilibrium, which gives the proportion of time a wolf spends in each state in the long run (Table 2).

Parameter estimates and transition-probability matrices obtained from using alternative LF buffer sizes of 10 and 30 m and the starting parameters used for all 4-state HMMs are shown in

Table 2. Estimates of the wolf movement parameters for the 4-state hidden Markov model.

State	Behavior	Stationary (%)	μ (km/h)	σ (km/h)	z	θ (radian)	κ
S1	Resting (off LF)	65.9	0.08	0.07	0.004	3.14	0.68
S2	Moving (off LF)	22.9	2.35	1.93	5.0×10^{-8}	0.01	1.33
S3	Resting (on LF)	5.2	0.11	0.09	0.003	-3.12	0.60
S4	Moving (on LF)	6.0	3.85	2.75	5.6×10^{-7}	0.01	1.86

Notes: The stationary distribution gives the percentage of time spent in each state in the long run. Step length mean (μ) and step length standard deviation (σ), both converted to km/h, step length point mass on zero (z), turning angle mean (θ), and turning angle concentration (κ). Linear feature (LF) buffer size was 20 m.

Table 3. Transition-probability matrix of estimated wolf movement for the 4-state hidden Markov model.

State	Behavior	S1	S2	S3	S4
S1	Resting (off LF)	0.958	0.035	0.007	9.5×10^{-8}
S2	Moving (off LF)	0.093	0.793	0.010	0.104
S3	Resting (on LF)	0.093	0.013	0.845	0.049
S4	Moving (on LF)	0.024	0.400	0.019	0.560

Notes: Left column: behavioral state at time t , upper row: behavioral state at time $t + 1$. Here, linear feature (LF) buffer size was 20 m.

Appendix S3. The parameter estimates were generally robust to the choice of LF buffer size. Some quality-control simulations will be presented below.

WOLF–CARIBOU ENCOUNTER MODELS

The goal of this section is to investigate the effects of LF restoration on caribou survival. Therefore, we built two spatially explicit wolf–prey encounter models: an adult caribou scenario and a caribou calf scenario. In these models, wolf movement was simulated using parameter estimates derived from the 4-state HMM.

Area

Simulated wolf–caribou encounters took place in a 60×50 km area ($x \in [0, 60]$, $y \in [0, 50]$). The area of 3000 km^2 was sufficiently large to encompass typical caribou home ranges of $229 \pm 259 \text{ km}^2$ (Beauchesne et al. 2014) and typical wolf home ranges. For example, winter home ranges of wolves in Minnesota range from 51 to 223 km^2 (Fuller 1989), and annual wolf home ranges in Scandinavia range from 259 to 1676 km^2 (Mattisson et al. 2013).

Wolf densities

For Alberta, wolf densities ranging from 0.0016 to 0.0156 km^{-2} were reported (Serrouya et al. 2016). These wolf densities result in 5 to 46 wolves per 3000 km^2 in our spatial model. However, wolves often move and hunt as packs or hunting units consisting of 6.4 wolves on average (Fuller et al. 2003). In our simulation, we therefore modeled the movement of packs, with each pack having a single movement path. Each simulated parameter combination was run using 1–8 wolf

packs, corresponding to wolf densities ranging from 0.002 to 0.017 km^{-2} . If more than one pack was simulated, they were simulated simultaneously in the same landscape and not one after another.

Wolf movement and prey encounters

To simulate wolf movement in the presence of LFs, that is, before restoration, we used the parameter estimates for the 4-state HMM. The starting state for each wolf pack was drawn from the stationary distribution (Table 2), which was obtained from the transition-probability matrix (Table 3). Then, the transition-probability matrix was used to randomly draw further behavioral states. At each step, step lengths and turning angles were drawn according to the current wolf state (see Table 2).

As a quality check, we summed up step lengths to daily wolf moving distances. Daily moving distances, both for all the 569 available GPS wolf days and for 569 simulated wolf days, are presented in Fig. 1. Although simulated movement was missing extreme values observed in GPS data, daily movement distance was comparable to empirical wolf data.

To simulate wolf movement in the absence of LFs, that is, after full restoration (for partial restoration, see Appendix S5), we again used the estimated transition probabilities from Table 3, but in states S3 and S4 we used the distributions of step lengths and turning angles of states S1 and S2, respectively. As a result, the wolves did not move faster in states S3 and S4, because they did not benefit from increased speed on LFs. It was suggested that LFs could potentially also enhance visual and olfactory encounters (Latham 2009) or facilitate wolf hunting forays into caribou habitat (DeMars and Boutin 2018). We did not include these effects in our simulations, but we will discuss below how they might affect our findings.

Packs that crossed the boundaries of the simulated area were reflected back into the area. For example, a pack attempting to reach the position $x = 3$, $y = -2$ was placed at the position $x = 3$, $y = 2$. Wolf locations were simulated in 5-min intervals, resulting in 288 daily locations.

Only packs in the fast-moving states S2 and S4 could encounter and kill prey. When the distance between a moving pack and a prey item was below the detection distance, the prey was

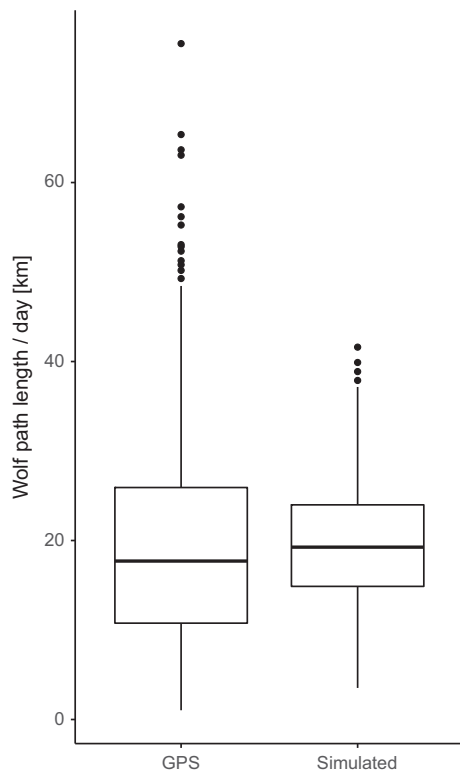


Fig. 1. Comparison of empirical Global Positioning System (GPS data, $n = 20$ wolves, 569 d, left) and simulated (569 d) daily path length of wolves. Each data point represents movement within one day. Median wolf movement was 17.7/19.3 km/d (GPS/simulated), and mean wolf movement was 19.7/19.6 km/d (GPS/simulated).

encountered and killed with a certain kill success probability. DeMars et al. (2016) used a wolf detection distance for calves of 1 km; we used detection distances of 0.5 or 1 km. Note that it is possible that encounters between wolves and prey are missed because we only simulate wolf positions every five minutes. However, typical 5-min step lengths are small enough compared to the detection distance such that these cases should be rare, especially with a detection distance of 1 km. An example plot of simulated encounters of one pack and prey is presented in Appendix S4: Fig. S1.

Prey movement

We modeled prey as stationary because daily prey movement compared to daily wolf

movement is low: Wolf mean daily path length (GPS data, $n = 20$ wolves) was 19.7 km (Fig. 1). Mean movement of female caribou (given >8 h GPS intervals) was below 1.2 km/d (Metsaranta and Mallory 2007, Rettie and Messier 2011). Also for caribou calves, we can assume small movement rates compared to wolf movement. Caribou calves rarely moved further than 1 km away from their calving site within the neonatal period (Gustine et al. 2006). Therefore, the predator's contribution to predator-prey encounters is at least ten times greater.

Caribou scenario

Caribou were modeled as groups, using one position for each group. Typical group size for woodland caribou outside calving time in Saskatchewan was between 3.9 and 8.2 individuals (Rettie and Messier 1998). We used a group size of 7 ± 0.8 (normal distribution, mean \pm SD, rounded to the nearest natural number). Given an encounter with a wolf pack, default kill success probability was 0.45 per caribou group, but we also ran simulations with kill success probabilities of 0.25 and 0.65. These values were in the range of those reported for barren ground caribou *R. tarandus granti* (Haber 1977). If successful, the wolf pack killed one caribou of the group and then entered a 1.3-d handling time (Hayes and Harestad 2000) during which it kept moving but did not make other kill attempts. After a kill, the remaining caribou, if any, were assumed to flee (Haber 1977) and (as a group) replaced to another random position exactly 4 km away from their former position. They did not avoid areas of previous attacks. Lacking literature data, we chose a flight distance of 4 km to prevent that the caribou group was encountered again by the same wolf pack immediately after the end of their handling time. After an unsuccessful encounter, we eliminated further encounters between the same wolf pack and caribou group for 24 h, although both could encounter other groups. Because the wolf's positions in the next movement steps will often still be within detection distance, this served to prevent follow-up attacks that would lead to an unrealistically high kill success rate.

In Alberta, caribou densities in all 12 boreal caribou ranges were between 0.0079 and 0.0669 km^{-2} (COSEWIC 2014). We simulated six

evenly spaced caribou densities between 0.01 and 0.06 km⁻². Given an area of 3000 km², this resulted in 30, 60, 90, 120, 150, or 180 caribou in our simulations. We simulated wolf–caribou encounters for 365 d and refer to it as one “season.”

Calving scenario

During calving time, caribou cows separate from each other to reduce predation risk (Stuart-Smith et al. 1997, Rettie and Messier 1998, DeMars et al. 2016). We assumed that when a wolf encountered a caribou cow with her calf, only the calf was killed. Thus, we simplified our model by modeling only calves as individuals. Given an encounter with a wolf pack, simulated kill success probabilities were either 0.7 or 1. If successful, the wolf pack entered a 2-h handling time. If unsuccessful, further encounters between the same wolf pack and calf were eliminated for 24 h, as above. Assuming a calf:adult caribou ratio of roughly 1:2, we simulated calf numbers of 30, 65, or 100 calves in our simulations. Caribou calf mortality was highest within the first month or two of life (Fuller and Keith 1981, Stuart-Smith et al. 1997, Rettie and Messier 1998). For calves, we therefore simulated calf–wolf encounters for 31 d and refer to it as one “calving season.” Note that since we will be mostly interested in relative changes in mortality, the results should be robust to the exact duration of a season.

Simulation experiments and proportional reduction in caribou mortality (P) due to LF restoration

For each of the scenarios and parameter combinations summarized in Table 4, we ran 1000 replicate simulations with linear features and 1000 replicates with all linear features fully

Table 4. Parameter combinations used in the spatially explicit wolf–caribou encounter models.

Scenario	Days	Packs	Detection (km)	<i>n</i> Prey	KS
Caribou	365	1–8	0.5/1	30–180	0.25/0.45/0.65
Calving	31	1–8	0.5/1	30–100	0.70/1.00

Notes: Packs = wolf packs; detection = distance at which wolves detect caribou; KS = kill success probability for wolves to kill one individual prey, given an encounter either with an adult caribou group or with calves modeled as solitary individuals in the calving scenario.

restored. Our main quantity of interest was the effect size of LF restoration on prey mortality, which is the difference in mean prey mortality after full LF restoration compared to the scenario before any LF restoration. For each parameter combination, we calculated the proportional reduction in mean prey mortality (*P*):

$$P = \frac{B - A}{B}, \quad (1)$$

where *A* is mean caribou mortality after full LF restoration and *B* is mean caribou mortality before LF restoration. For example, with a caribou mortality of 28% after full restoration (*A*) and 34% before restoration (*B*), the proportional reduction in mortality would be $P = (34 - 28)/34 = 0.18$, or 18%. The uncertainties in each mean mortality (Δ = standard error of the mean) were accounted for by an error propagation formula (Papula 2016):

$$\frac{\Delta P}{P} = \sqrt{\left(\frac{\Delta A}{A}\right)^2 + \left(\frac{\Delta B}{B}\right)^2}. \quad (2)$$

WOLF–PREY ENCOUNTER MODEL RESULTS

Linear feature restoration reduced the mortalities of adult caribou and calves for all simulated parameter combinations (Fig. 2, see also Appendix S4: Fig. S2 for results with other LF buffer sizes). Across parameter combinations, the proportional reduction in mean adult caribou mortality due to full LF restoration ranged from 10% to 25% of its original value. Proportional reduction in mean caribou calf mortality due to full LF restoration ranged from 8% to 23%.

In the adult caribou scenario, both detection distances of wolves for caribou (0.5 and 1 km) led to comparable maximum proportional reductions in mortality (Fig. 2a). However, with a detection distance of 1 km, proportional reduction in caribou mortality varied more across scenarios and the minimum proportional reduction was smaller. With increasing prey density, variability in proportional reduction in prey mortality decreased. Proportional reduction in calf mortality was more variable when the detection distance of wolves for caribou was 1 km, compared with a detection distance of 0.5 km (Fig. 2b). The effects of prey density and kill

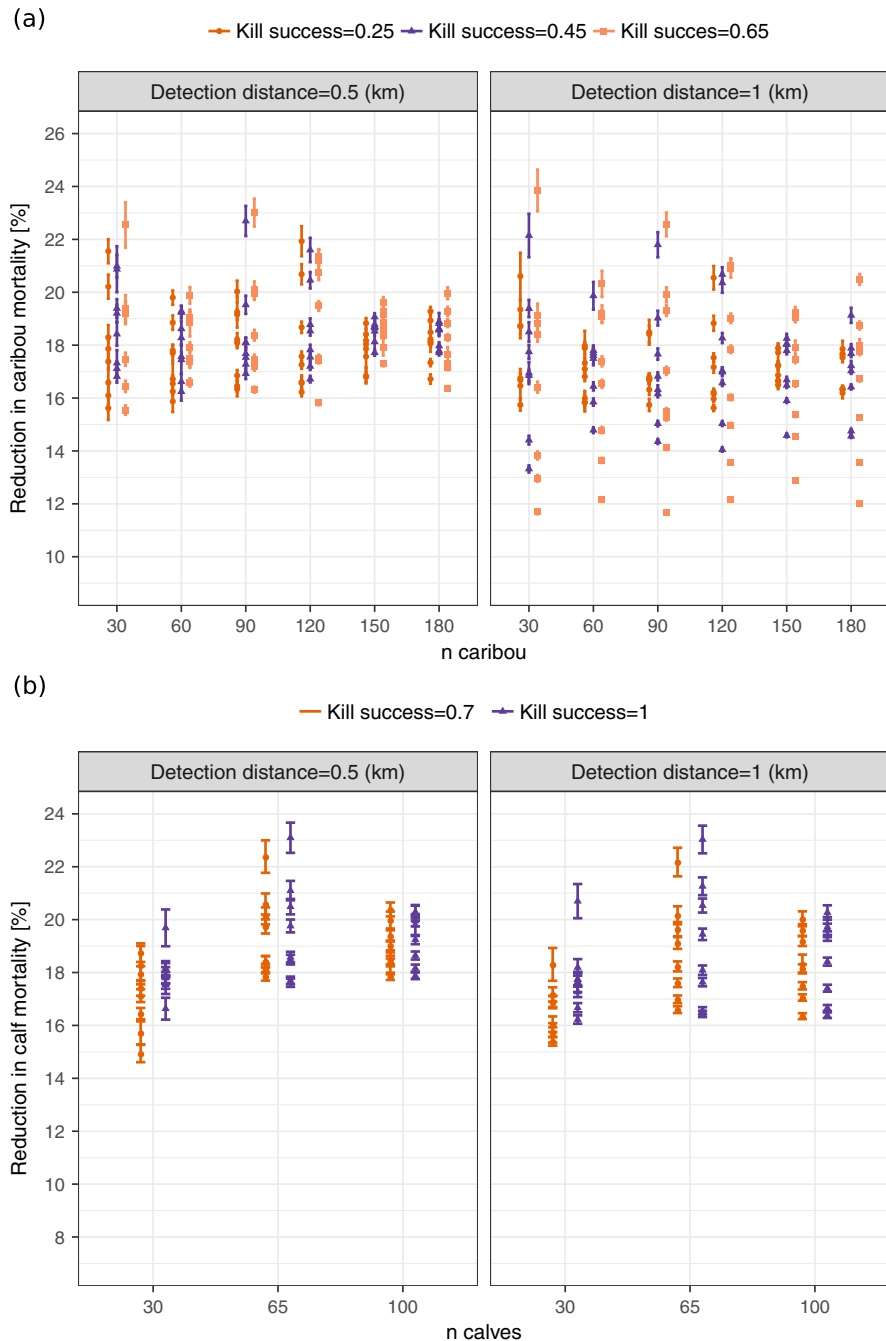


Fig. 2. Proportional reduction in mean caribou mortality due to full linear feature (LF) restoration in the spatially explicit caribou-wolf encounter model. Encounters between caribou and 1–8 wolf packs were simulated, and a LF buffer size of 20 m was used. (a) Proportional reduction in adult mortality; (b) proportional reduction in calf mortality. Each point represents results from one number of packs. Number of packs and proportional reduction in mortality are not necessarily correlated. Detection distance is the distance at which wolves detected their prey; kill success probability is the probability to kill one caribou given an encounter of a caribou group and a wolf pack. Proportional reduction in prey mortality was calculated using Eq. 1. Bars represent standard errors of the mean, estimated using Eq. 2.

success probability were less clear than for the adult caribou scenario.

Table 5 shows the underlying absolute mortalities for a subset of the parameter combinations (see Data S1 for complete tables). With increasing numbers of wolf packs, absolute prey mortalities increased, while restoration-related proportional reductions in caribou and caribou calf mortalities decreased in many but not all cases. Absolute mortalities also increased with increasing values of the kill-success probability parameter. However, as can be seen in Fig. 2a, these patterns had only minor effects on the restoration-related proportional reduction in mortality.

ESTIMATING EFFECTS OF LF RESTORATION ON CARIBOU POPULATION GROWTH RATES

We used an adjusted version of the recruitment–mortality method or R/M equation (Hatter

and Bergerud 1991) to calculate the effects of a proportional reduction in caribou and calf mortalities on caribou annual population growth rates, λ . If N_t is the population size in year t , $N_{t+1} = \lambda \times N_t$. Thus, $\lambda < 1$ means that the population is declining and $\lambda > 1$ means that the population is growing. We followed the female-only model of DeCesare et al. (2012) and estimated the annual rate of change as

$$\lambda = \frac{1 - M}{1 - R_{RM}}, \quad (3)$$

where M is the annual adult mortality and R_{RM} is the annual recruitment, that is, the proportion of new recruits in the female population at the end of a year. Assuming a 50:50 sex ratio, the annual recruitment can be computed as

$$R_{RM} = \frac{X/2}{1 + X/2}, \quad (4)$$

Table 5. Example results from spatial wolf–caribou encounter simulations in a 3000-km² area.

Scenario	<i>n</i> Prey	Packs	KS	Detection (km)	Mortality (%)		<i>P</i> (%)
					Before	After	
Caribou	60	1	0.25	1.0	6.48	5.24	19.2
	60	2	0.25	1.0	13.37	10.89	18.6
	60	3	0.25	1.0	19.73	16.23	17.7
	60	4	0.25	1.0	25.86	21.60	16.5
	60	5	0.25	1.0	31.88	26.94	15.5
	60	6	0.25	1.0	38.13	31.93	16.2
	60	7	0.25	1.0	44.35	37.13	16.3
	60	8	0.25	1.0	49.68	41.20	17.1
Caribou	60	1	0.45	1.0	10.88	8.58	21.1
	60	2	0.45	1.0	22.12	17.68	20.1
	60	3	0.45	1.0	32.26	26.48	17.9
	60	4	0.45	1.0	41.72	34.76	16.7
	60	5	0.45	1.0	50.33	42.01	16.5
	60	6	0.45	1.0	59.01	49.15	16.7
	60	7	0.45	1.0	66.22	56.10	15.3
	60	8	0.45	1.0	72.53	61.90	14.7
Calves	65	1	1.0	0.5	6.16	4.74	23.1
	65	2	1.0	0.5	11.86	9.36	21.1
	65	3	1.0	0.5	17.07	13.57	20.5
	65	4	1.0	0.5	22.11	17.74	19.8
	65	5	1.0	0.5	26.70	21.74	18.6
	65	6	1.0	0.5	31.13	25.38	18.5
	65	7	1.0	0.5	35.21	29.00	17.6
	65	8	1.0	0.5	39.19	32.25	17.7

Notes: Packs = wolf packs; KS = kill success probability for wolves to kill one individual prey, given an encounter either with an adult caribou group or with calves modeled as solitary individuals in the calving scenario; detection = distance at which wolves detect caribou; mortality = killed percentage of available prey in simulations before and after linear feature (LF) restoration; *P* = mean proportional reduction in prey mortality due to full LF restoration, calculated using Eq. 1. Simulations were replicated 1000 times.

where X is the number of surviving calves per female per year. Here, all females born before the current year are counted, independently of whether they are of breeding age or not (DeCesare et al. 2012). Since most females have either one calf or none, we can write

$$X = 1 - M_W - M_A, \quad (5)$$

where M_W is calf mortality due to wolves and M_A is the probability that a female does not produce a surviving calf for an alternative reason, for example, because the female is too young or because the calf dies of a non-wolf-related cause. Non-wolf-related causes, for example, are diseases, malnutrition, and predation by bears, wolverine, and lynx. Similarly, adult mortality M can be written as

$$M = M_{W,ad} + M_{A,ad}, \quad (6)$$

that is, as the sum of wolf-related and non-wolf-related mortality. We assumed LF restoration to have an impact on wolf-related mortality for calves and adults, but not on non-wolf-related mortality.

Using the Little Smoky caribou population in Alberta as a case study, we combined empirical data and the results derived from the wolf-caribou encounter simulations to predict the effects of LF restoration on λ . In the Little Smoky caribou range, mean adult caribou cow mortality was 0.11 and mean calf recruitment X was 0.12 without wolf reduction (Hervieux et al. 2014). These parameters defined our baseline scenario before LF restoration. Using Eqs. 3 and 4, this resulted in a λ of 0.95. Since we lacked good estimates for the fraction of total mortality that is due to wolves, we varied these parameters and compared the results. We assumed that spatial overlap between caribou and wolves was 100%.

In case of full LF restoration, our simulations predict a proportional reduction in caribou and caribou calf mortality by up to 25% and 23%, respectively. Thus, to estimate the population dynamic consequences of LF restoration, we reduced both adult mortality, M_W , and calf mortality due to wolves, M_W , simultaneously by 0–25% and calculated the resulting λ using Eq. 3.

With increasing proportional reduction in prey mortality due to LF restoration, λ increased, but in many cases not sufficiently to stabilize caribou

populations (Fig. 3). Especially, if the proportion of calf mortality due to wolves was relatively low, for example, less than 25%, even a 25% proportional reduction in adult and caribou calf mortality due to LF restoration still resulted in $\lambda < 1$. When wolves had a relatively large share in adult and calf mortality, reduction in wolf mortality due to LF restoration was sufficient in some cases to stabilize populations. For example, with 50% of calf mortality and 75% of adult

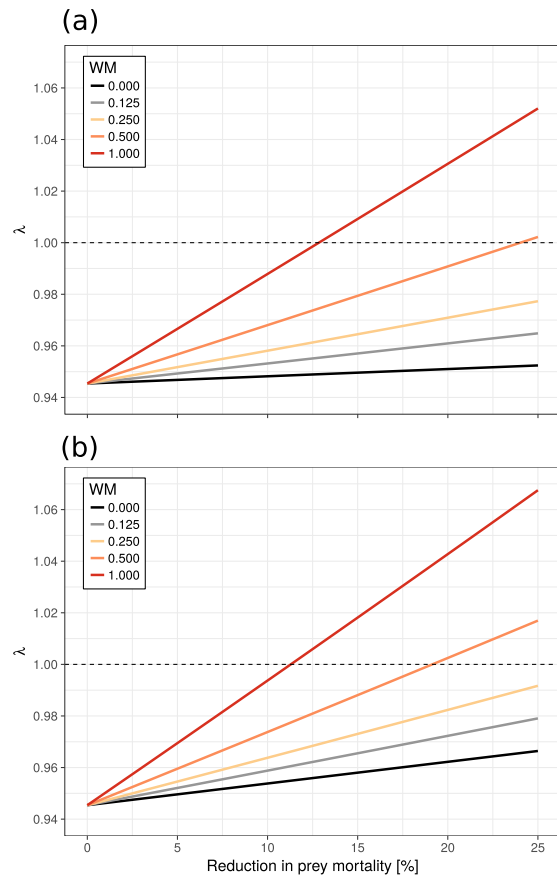


Fig. 3. Annual rate of change (λ) in a caribou population after a given proportional reduction in wolf-related mortality. In the spatial models, full linear feature restoration reduced both adult caribou and calf mortality by up to 25% and 23%, respectively. Here, adult caribou and caribou calf mortality due to wolves were reduced simultaneously by 0–25% and λ_{RM} was calculated using Eq. 3. We assumed that either 25% (a) or 75% (b) of adult caribou mortality was caused by wolf predation. The different colors in each panel represent different proportions of calf mortality caused by wolf predation $WM = M_W/(M_W + M_A)$.

mortality caused by wolves, population recovery ($\lambda > 1$) was achievable with a restoration-related proportional reduction of at least 19% in adult and calf mortality (Fig. 3a). For even higher proportions of calf mortality due to wolves, smaller proportional reductions in mortality were sufficient for $\lambda > 1$. The results were qualitatively similar to 25% or 75% of adult mortality due to wolves (compare Fig. 3a, b), with slightly larger benefits of LF restoration in the case of 75%.

LINEAR FEATURE RESTORATION AND OTHER CONSERVATION MEASURES

In this section, we put LF restoration in perspective by exploring how it may be combined with other conservation measures to reduce wolf predation on caribou and stabilize caribou populations. Since full LF restoration will take time, we here consider also partial LF restoration, that is, restoration of only a fraction of LFs. We assumed that partial LF restoration reduced prey mortality in a linear way (as indicated by the results in Appendix S5). Since partial restoration allows wolves to use the remaining LFs, we will discuss below how this compensatory behavior might affect our findings. Other conservation measures include direct and indirect wolf reduction, caribou penning, and long-term habitat restoration leading to lower densities of primary prey and thus fewer wolves. We focus on measures that reduce wolf predation on caribou, although, as discussed below, other measures to reduce, for example, predation by bears or other predators could also be useful.

We again use the Little Smoky caribou population as a case example. In its range, ~45% of the wolf population were removed every winter between 2005 and 2012 (Hervieux et al. 2014). Mean adult caribou cow survival increased from 89.4% to 90.7%, and mean calf recruitment X increased from 0.115 to 0.186. We used this information and Eq. 5 to estimate calf mortality due to wolves, M_W , with or without wolf removal and calf mortality due to other causes, M_A (Appendix S6). With the estimated values, 17.8% of calf mortality was due to wolves. Then, we determined the proportional reduction in wolf-related mortality necessary to stabilize the population, that is, achieve $\lambda = 1$ (see Appendix S7 for derivation and formulas).

Consistently with the results in Fig. 3, LF restoration on its own was not sufficient to stabilize population dynamics. The necessary reduction in wolf-related mortality could be achieved by a combination of LF restoration and other measures to reduce wolf predation on caribou (Fig. 4). Based on our earlier results, we assumed that the proportional reduction in caribou mortality with full LF restoration was between 10% (solid lines) and 25% (dashed lines). The larger the proportion of LF restoration, the lower the necessary additional reduction in wolf-related mortality. With full LF restoration, depending on the parameters, it was still necessary to reduce wolf-related mortality by 13% to 50%. LF restoration combined with 45% wolf reduction as in Hervieux et al. (2014) was in many cases

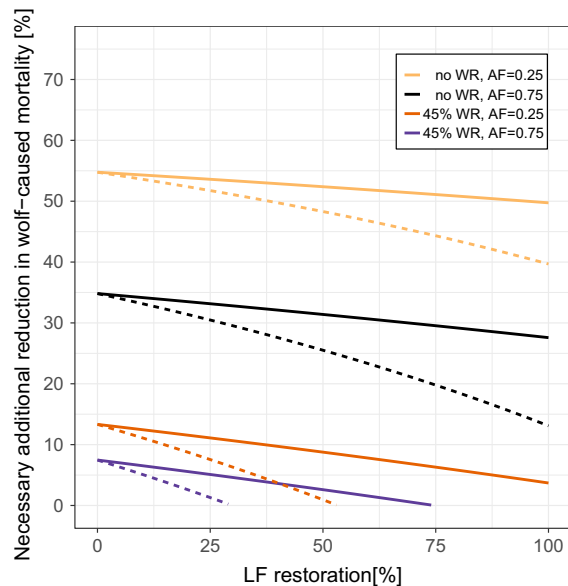


Fig. 4. Proportional reduction in wolf-related mortality due to factors other than linear feature (LF) restoration that is necessary to achieve $\lambda = 1$, that is, a stable population (see Appendix S7 for derivation). We compare scenarios without wolf reduction (no WR) to scenarios where wolves are reduced by 45% as in Hervieux et al. (2014). The baseline parameters (i.e., those at 0% LF restoration) are $M_A = 0.727$ and $M_W = 0.158$ without wolf reduction and $M_W = 0.087$ with wolf reduction. Total adult mortality M in scenarios without wolf reduction is 0.106 and 0.093 in scenarios with 45% wolf reduction. AF is the fraction of adult mortality due to wolves.

expected to be sufficient to stabilize the caribou population, with wolf reduction making the greater contribution.

Based on the results in Fig. 4 (and focusing here on the case with 25% of adult mortality due to wolves), we now outline an example management plan that uses different management measures at different times to keep the caribou population stable. We assume, optimistically, that about 2% of LFs are restored every year and that long-term habitat restoration to reduce apparent competition is possible, even in the face of climate change, and also happens on a scale of decades. If we want to stabilize the caribou population right away (time 0 from now), there is thus no LF restoration and apparent competition is still strong. Wolf-related mortality would then need to be reduced by about 55% by short-term measures such as penning or by culling roughly the same percentage of wolves. As time passes and LFs and habitat are restored, the short-term measures like culling and penning could then gradually be reduced. After 25 yr or so, 50% of LFs might be restored, but since the effect of LF restoration is relatively weak, we would still need to reduce wolf-related mortality by around 50%. If habitat restoration has substantially reduced apparent competition at this point, then much less culling or penning might be necessary at this point to stabilize the caribou population. After 50 yr, if LFs are completely restored and the effect is on the optimistic side (dashed line in Fig. 4), wolf-related mortality would still need to be reduced by 40%. If habitat restoration has not reduced wolf densities sufficiently by this time to achieve this, then further culling or penning might be necessary. Overall, it is clear that LF restoration is expected to make a relatively small contribution in such a management portfolio.

DISCUSSION

We modeled the effects of LF restoration on predation risk for caribou by wolves. Full LF restoration reduced wolf predation on adult caribou by 10–25% and on caribou calves by 8–23% across all simulated parameter combinations (Fig. 2). Possible other LF effects like facilitating wolf movement into caribou habitats and changes in wolf detection distances for prey (Latham 2009) were not included in our model.

Thus, reduced wolf moving speed was responsible for reduced prey mortalities in our model. Only for a limited range of parameter combinations and only when a large proportion of calf mortality was assumed to be caused by wolves, LF restoration led to stable or positive population growth rates ($\lambda \geq 1$). In conjunction with other measures to reduce wolf predation on caribou, LF restoration could contribute to stabilizing caribou populations, but its contribution may be small compared to other measures.

For some parameter combinations, absolute prey mortalities predicted by our model deviated from empirical values. Given the maximum number of 8 wolf packs, maximum mortalities per year were 73% for caribou and 39% for calves in our default simulations (Table 5). Reported mortalities for adult caribou (7–22%, Fuller and Keith 1981, McLoughlin et al. 2003, Serrouya et al. 2017b) were up to an order of magnitude lower. The calf mortalities in our findings were comparable to reported ranges (58% within the first two months after calving, Fuller and Keith 1981). In our simulations, absolute prey mortality ultimately was a product of encounter probability and wolf kill success given an encounter. In contrast to real wolves, simulated wolves detected all stationary prey that were within their detection distance, while, for example, elk (*Cervus elaphus*) have been shown to reduce predation risk by selecting forest cover when wolves are present (Muhly et al. 2010). In addition, we did not include wolf home ranges or territories that were revisited by the wolves frequently. Thus, wolves in our simulations probably explored a larger area and encountered more caribou than they naturally would have. However, the overestimation of encounter probabilities should affect the results in both LF scenarios (no LF/full LF restoration) to the same degree, and hence, there should be no major effect on the proportional reduction in prey mortality (i.e., as estimated from Eq. 1). Since we varied wolf densities (1–8 packs), detection distances of wolves for caribou (1 and 0.5 km), kill success probabilities (low to high), and prey densities (low to high), our model should provide a robust estimate for proportional reduction in caribou mortality in the full LF restoration scenario.

We compared scenarios with all LFs present to scenarios with full LF restoration, but high LF

restoration costs (Schneider et al. 2010, Pyper et al. 2014) could prevent full LF restoration. For example, the Little Smokey caribou range had an area of 2927 km² and an LF density of 3.36 km/km² (Schneider et al. 2010), and therefore, full linear feature restoration would cost roughly \$39 million. In the best case, partial LF restoration could lead to a proportionally lower proportional reduction in mortality (see Appendix S5). However, wolves might show compensatory behavior and intensify the use of the remaining LFs. This could make full LF restoration within caribou habitats necessary to assure the expected proportional reduction in caribou and caribou calf mortalities.

Linear features are hypothesized to increase prey detection for wolves (Latham 2009). First, prey using or crossing LFs could leave olfactory cues. We expect this additional effect of LFs to be weak, as long as wolves crossing prey paths off LFs do have the same probability to detect olfactory cues of prey there. Second, compared to the forest, LFs provide a larger line of sight. This will play a role when wolves and caribou appear on or near LFs at the same time. Since caribou avoid LFs (James and Stuart-Smith 2000, Dyer et al. 2001, but see Serrouya et al. 2017a) and appear in low densities (COSEWIC 2014), we expect this effect to be weak, as long as caribou have access to enough habitat without LFs. In any case, if the wolf detection distance is increased by LF use of wolves, our findings would underestimate the effects of LF restoration on wolf predation.

Additionally, LFs are hypothesized to increase spatial overlap between wolves and caribou (Seip 1991, Dyer et al. 2001, DeMars and Boutin 2018, Mumma et al. 2018). Wolves avoided wetlands and selected for LFs in wetlands (DeMars and Boutin 2018), and Mumma et al. (2018) estimated higher wolf–caribou co-occurrence due to LFs. Both studies are thus indicating a loss of caribou refuge due to LFs. The additional effects of LFs on refuge loss were not included in our simulations, since we varied wolf movement rates only. For some of the cases where we predict continued decline of caribou populations ($\lambda < 1$) after LF restoration, adding the effects of LF restoration on habitat overlap might change the prediction to population growth ($\lambda > 1$). For this, however, the additional effects would need to be quite large in many cases, especially if the caribou annual rate of change λ is low before restoration or if the

contribution of wolves to calf mortality is low (Fig. 3). However, a better understanding of the various effects of LF restoration on caribou survival and population dynamics is needed, including also potential indirect effects of predator exposure. For this, field experiments comparing areas before and after full LF restoration would be very valuable.

In all our spatial simulations, removal of one wolf pack increased prey survival at least roughly to the same extent as full LF restoration (Table 5). Our results for a case example based on data from Hervieux et al. (2014) suggest that wolf reduction might contribute more to increasing caribou λ than full LF restoration. Thus, our findings suggest that compared to LF restoration, wolf management could be a more effective measure to reduce predation pressure on caribou. However, in addition to ethical issues there are also many uncertainties associated with wolf management. In southern British Columbia, moose (primary prey) proportional reduction by 70% resulted in lower wolf density and an increase in adult caribou survival from 0.78 to 0.88, but there was no significant effect on calf recruitment (Serrouya et al. 2017b). In Alberta, British Columbia, and Idaho (USA), annual rate of change (λ) increased for five out of six caribou populations after wolf removal (Serrouya et al. 2019). Direct wolf management in northeastern British Columbia increased prey recruitment by a factor 2–5, but wolves recolonized removal zones quickly (Bergerud and Elliott 1998). If only wolves were reduced, primary prey could also increase in numbers and apparent competition pressure on caribou would be amplified in the long term. Conversely, proportional reduction of only primary prey could trigger prey switching of wolves toward caribou (Serrouya et al. 2015). In the short term, joint proportional reduction of primary prey and wolves could reduce wolf predation on caribou (Serrouya et al. 2015), but, as long as the habitat remains suitable, primary prey and wolves would invade after programs are stopped.

In this study, we focused on conservation measures that reduce caribou mortality due to wolves, but mortality due to other causes (M_A and $M_{A,ad}$ in our model) may often be substantial and might be a good target for additional conservation measures. Since bears (*Ursus* spp.) prey on both adult caribou and calves (Latham

et al. 2011a, Burgar et al. 2018), and in Quebec black bears (*Ursus americanus*) were the main predator for caribou calves (57.2% of 64 monitored calf deaths) (Pinard et al. 2012), reducing bear predation on caribou could contribute to stopping caribou decline. Whether LF restoration would reduce bear predation on caribou is still under research. Bears use LFs as traveling paths (Tigner et al. 2014, DeMars and Boutin 2018), and recovering vegetation on LFs provides more key bear food than the interior forest (Finnegan et al. 2018). Thus, incidental bear predation on caribou could be reduced to some degree by LF restoration, unless vegetation on former LFs still provides more bear food. In our models, LF restoration only affected M_W , but not M_A . Consequently, if LF restoration reduced non-wolf-related caribou mortality, we would underestimate the effects of LF restoration. We argue that both the proportion of caribou mortality which is caused by other predators and the effects of LF restoration on the non-wolf-related predation should be evaluated further.

Compared to direct management of primary prey and predators, the advantage of habitat restoration measures like linear feature restoration is that they are more sustainable. Primary prey and predators will recover quickly if the habitat is still suitable, whereas restored LFs will need no ongoing effort. Linear feature restoration and the subsequent reduced wolf predation success could even lead eventually to a proportional reduction in wolf abundance, but not necessarily so given that also more prey will be available with reduced mortalities. To make better predictions for the effects of the various management options, alone or in combination, further modeling studies taking into account ecological feedbacks between multiple species and more detailed empirical information on population dynamic parameters are necessary.

In conclusion, caribou populations increased only if large proportions of calf mortality were caused by wolves and only for some parameter combinations. Thus, our findings indicate that caribou populations would clearly benefit from full LF restoration, but under our model assumptions LF restoration as a single measure is unlikely to stop boreal caribou populations from declining in numbers. This is broadly in agreement with

Johnson et al. (2019) who estimated the costs and benefits of a large number of caribou recovery options and also included linear feature restoration (based on a statistical model by McCutchen 2007). They found that, in extreme cases, LF restoration could lead to recovery, but was also more expensive than some of the other management options. Thus, if caribou populations are to be recovered, direct population management, such as predator and prey reductions or fenced refuges from predators, should be used in combination with habitat restoration to maximize the opportunity for self-sustaining caribou populations (Serrouya et al. 2019).

ACKNOWLEDGMENTS

We would like to thank Roland Langrock and members of the Theoretical Biology Group at Bielefeld for discussion, the Regional Industry Caribou Collaboration for providing GPS data, the Alberta Biodiversity Monitoring Institute for providing the LF data, and two anonymous reviewers for their constructive and detailed comments.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2904/full>

Data S1: We provide the LF layer, one single wolf movement track, the modified moveHMM R package and the code used for our simulations in Data S1.