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Wolverine habitat selection in response to anthropogenic disturbance in the western Canadian boreal forest

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ABSTRACT

We evaluated alternative hypotheses that anthropogenic disturbance can attract versus displace wolverines (*Gulo gulo luscus*). Our research took place in boreal forests of northwestern Alberta where we employed radiotelemetry to track wolverine habitat use over three years. We used resource selection functions (used/available design) to analyze wolverine habitat selection patterns during summer and winter seasons. We focused our analyses on the effects of active logging, intermediate-aged cutblocks (11–25 years old), seismic lines, roads, and borrow pits on wolverine habitat selection. Our analysis of active logging used a before, during, interim, and after design. We found wolverines were attracted to logging areas. The strongest selection for logged areas occurred during logging and in the following summer. We suggest logged areas provide foraging opportunities and movement routes for wolverines. Male wolverines were attracted to the edges of intermediate-aged cutblocks (11–25 years old) during summer whereas females were attracted to cutblock edges in winter. However, females avoided intermediate-aged cutblock edges in summer. Moreover, both male and female wolverines avoided the interior of these cutblocks. We would suggest that cutblock edges can provide wolverines with foraging opportunities. We also found wolverines were attracted to seismic lines and borrow pits along roads. Regenerating seismic lines and borrow pits (inhabited by beavers) might offer wolverines foraging opportunities. Our research highlights the need for managers to appreciate the potential for anthropogenic disturbance to either attract or repel wolverines. We warn that attraction of wolverines to industrial features might lead to increased mortality. We also stress that the age of a disturbance can influence its effect on wolverines.

1. Introduction

The boreal forests of western North America are fragmented by resource extraction through the creation of infrastructure to access, harvest, and transport natural resource to markets (Schneider, 2002; Pickell et al., 2013, 2014). These developments continuously reshape the distribution of predation risks and foraging opportunities for wildlife. Therefore, it is imperative that we learn how animals perceive land-use changes so that boreal landscapes can be managed to conserve wildlife populations.

Wolverines (*Gulo gulo luscus*) are mesocarnivores that exist in remote circumboreal regions (Hornocker and Hash, 1981; Magoun, 1985; Banci, 1987). Wolverines in Canada are of conservation concern because of industrial development that is occurring throughout their range (COSEWIC, 2014). Our aim was to investigate the response of wolverines in the boreal forest to disturbances that are shown to have negative effects on populations in other regions of North America (e.g., Krebs et al., 2007; Fisher et al., 2013). More specifically, we used resource selection functions (RSFs, Manly et al., 2002; Lele et al., 2013) to evaluate competing hypotheses that individual wolverines were attracted versus displaced by logging, seismic lines, roads, and borrow pits. Aside from studies in northern Ontario (Bowman et al., 2010; Dawson et al., 2010), there has been limited research on wolverines in northern boreal forests.

Logging involves concentrated human activity to extract and transport timber from patches of forest to mills. Wolverines are considered sensitive to forestry activities (e.g., Krebs et al., 2007; Bowman et al., 2010; Fisher et al., 2013). Similarly, wolves (*Canis lupus*) and other wildlife avoid areas that are being actively logged (Smith et al., 2000; Houle et al., 2009; Lesmerisis et al., 2012). Therefore, it is probable that logging could displace wolverines

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from upland habitats they prefer (Wright and Ernst, 2004; Heim, 2015). However, wolverines could be attracted to areas with logging because of foraging opportunities on displaced small animals (Ferron et al., 1998; Potvin et al., 1999; Turcotte et al., 2000) or because logging roads provide travel routes (e.g., Copeland et al., 2007). Because wolves are displaced by logging activities (Houle et al., 2009; Lesmerisis et al., 2012), wolverines might be able to use these areas free of their predation risk.

After logging ends, timber-harvest companies typically replant cutblocks and leave them to regenerate so they can be logged again in the future. Early-seral cutblocks provide habitats for many wildlife species that wolverines either hunt or scavenge (Fisher and Wilkenson, 2005). For example, regenerating cutblocks can provide horizontal cover sought by snowshoe hares (*Lepus americanus*) and grouse (*Bonasa umbellus* & *Falcipennis canadensis*; Conroy et al., 1979; Parker, 1984; Potvin et al., 1999; Bellefeuille et al., 2001). These species might be more abundant at cutblock edges where habitat heterogeneity is high (Lidicker, 1999). Moreover, moose (*Alces alces*) abundance increases in early-seral cutblocks (Potvin et al., 2005). Wolverines are facultative scavengers (Magoun, 1987; van Dijk et al., 2008) and might feed on wolf-killed moose carcasses in or near regenerating cutblocks. While these factors suggest that wolverines could be attracted to cutblocks that offer foraging opportunities, some evidence indicates that wolverines avoid cutblocks and other regenerating areas (Hornocker and Hash, 1981; Lofroth et al., 2007; Bowman et al., 2010; Fisher et al., 2013). This avoidance is likely associated with hesitance to use open areas or because wolves often use regenerating cutblocks to hunt large prey (Courbin et al., 2009; Houle et al., 2009; Lesmerisis et al., 2012). Therefore, predation risk might deter wolverines from using these areas.

Seismic lines are another disturbance associated with resource extraction that could either displace or attract wolverines. Seismic lines are created during exploration for oil and gas resources. Prior to the late 1990s seismic lines were constructed to approximately 5–8 m wide by removing all vegetation (e.g., logging) and were distributed on the landscape in a grid-like pattern (Schneider, 2002; Pattison et al., 2016). Wolves are known to use seismic lines because they increase their movement and hunting efficiency (McKenzie et al., 2012; Dickie et al., 2016) so we might expect wolverines to avoid seismic lines because of predation risk from wolves (Fisher et al., 2013). However, industrial resource extraction and mapping has been occurring in some regions of the boreal forest since the mid-20th century, which has provided time for seismic lines to regenerate (Lee and Boutin, 2005; van Rensen et al., 2015). Once regenerated, these seismic lines can provide early-seral habitats for wildlife (Tigner et al., 2014, 2015) and poor movement routes for wolves (Dickie, 2015) which might provide wolverines foraging opportunities free of predation risk.

Finally, borrow pits are dug near well pads and along forest roads to provide materials for their construction. Over time, borrow pits fill with water and can provide habitats for beavers (*Castor canadensis*), a preferred prey of wolverines (Lofroth et al., 2007). Thus, wolverines could be attracted to borrow pits for preferred foraging opportunities. At the same time, borrow pits are found along roads that often are avoided by wolverines (May et al., 2006; Copeland et al., 2007; Krebs et al., 2007), potentially leaving this food source unexploited.

Here, we evaluated alternative responses by wolverines to five industrial developments: (1) wolverines were attracted to sites of active logging because of foraging opportunities and mobility or displaced because of predation risk from human activity; (2) wolverines were attracted to intermediate-aged cutblocks because of foraging opportunities at cutblock edges or displaced because of wolf activity; (3) wolverines were attracted to seismic lines because of foraging opportunities for small prey or displaced because of wolf activity; and (4) wolverines were attracted to borrow pits because beaver occupy these sites or displaced because of human activity on roads. We also surveyed borrow pits to report on the extent that pits were inhabited by beaver.

2. Materials and methods

2.1. Study area

Our research took place the boreal forest surrounding the town of Rainbow Lake (population 870) (119°28′18.705″W, 58°32′22.3 61″N) in the northwest corner of Alberta. Our study site was approximately 12,754 km^2 [100% minimum convex polygon (MCP) around GPS relocations] in area and bounded by the Hay River to the south, the Hay-Zama Lakes Complex to the north, and the Chinchaga River to the east. The British Columbia border was an approximate study area boundary to the west.

The town of Rainbow Lake is located in the central mixedwood subregion of the boreal forest. Broadleaf forests in the subregion consisted of trembling aspen (*Populous tremuloides*), balsam poplar (*P. balsamifera*), and white birch (*Betula papyrifera*). Coniferous forests included white (*Picea glauca*) and black spruce (*P. mariana*), balsam fir (*Abies balsamea*), and jack pine (*Pinus banksiana*). Wetlands were 30% of the landscape and were comprised of peatlands (bogs and fens) with black spruce forests. The climate of Rainbow Lake was characterized by long, cold winters and short, warm summers. Average annual temperature was −1.3 °C with 414 mm of precipitation (Strong and Leggat, 1981).

Industrial resource extraction had been occurring in Rainbow Lake since the 1950s and associated infrastructure included winter roads, all-season roads, pipeline rights-of-way's, oil and gas wellsites, processing plants, and industrial camps. Most seismic lines were created between the 1960s and early-1990s, with some seismic activity occurring through present albeit over a limited area.

A logging program took place in Rainbow Lake from November 26, 2014 to March 3, 2015. In total, 13.13 km^2 of harvest occurred among 165 cutblocks [average size = 0.08 km^2 (SD = 0.11)]. In addition, there were 848 cutblocks between the age of 11 and 25 years (as of 2015) (Fig. 1). The average size of these cutblocks was 0.14 km^2 (SD = 0.21, Fig. 2) and the average age was 17.97 years (SD = 3.81). Most cutblocks were harvested with a two-pass clearcut system (personal communication, Michael Morgan, Tolko Ltd., High Level, Alberta).

We established 22 livetraps that were used to capture and radiocollar wolverines. The MCP bounding livetrap locations was 2380 km^2. Livetraps (Copeland et al., 1995) were placed across a range of road densities and separated by approximately 10 km. We captured and collared at least one wolverine in every livetrap. We monitored wolverines with GPS radiocollars programmed to take fixes at two-hour intervals. All capture and handling procedures were approved by the University of Alberta Animal Care Committee Protocol No. 00000743 and Province of Alberta Collection and Research Permit No. 55714.

2.2. Statistical analyses

2.2.1. Logging program

We identified wolverine GPS relocations associated temporally and spatially with the logging program (referenced above) in four-winter periods (before, during, interim, and after logging) and two-summer periods (before and after logging) (Table 1). The winter season was from Nov. 1 to Apr. 1 and the summer season was from Apr. 2 to Oct. 31. We split GPS relocations by season to control for differences in habitat selection associated with snow-free periods. Moreover, wolverines will switch between scavenging

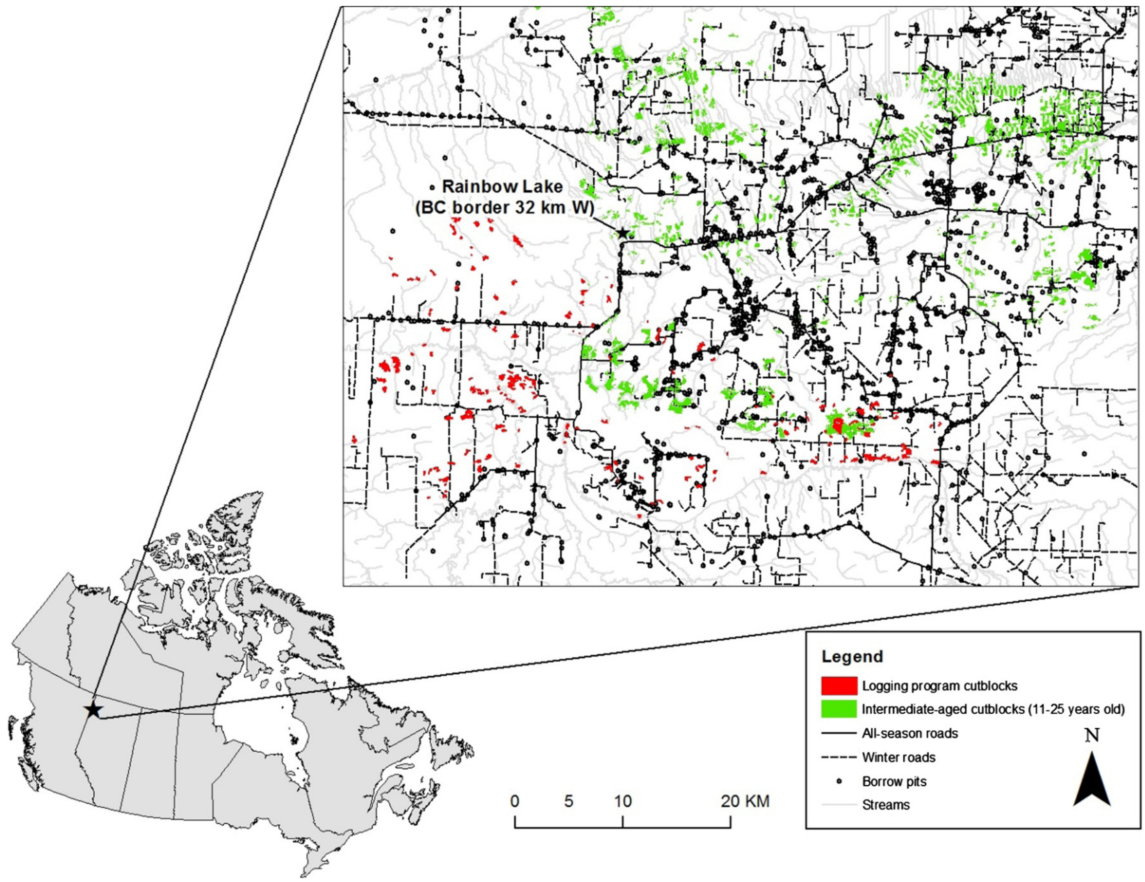

Fig. 1. Rainbow Lake study area in the NW corner of Alberta. The map shows cutblocks associated with the logging program during the second year of the study (winter 2014/2015) as well as cutblocks that are of intermediate age (11–25 years old). Also included are borrow pits along industrial roads.

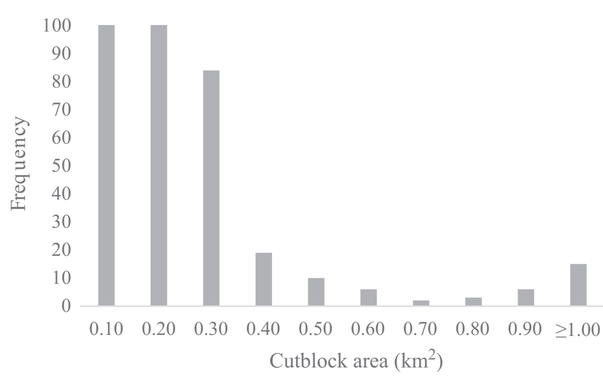

Fig. 2. Frequency of cutblock size (km^2) among intermediate-aged (11–25 years old as of 2015) cutblocks in Rainbow Lake. There were 445 cutblocks $\leq$ 0.10 km^2 and 258 that are $\geq$0.20 and $\leq$0.29 km^2. We cut frequencies off at 100 for visualizing purposes.

Table 1
Timeline used to select GPS relocations for the analysis of wolverine habitat selection relative to the logging program. Wolverine GPS relocations were included in periods if they aligned temporally and if the 100% minimum-convex polygon of GPS relocations (from that period) overlapped areas that were logged in the winter of 2014/2015.

Period	Dates
Winter before	Nov. 1, 2013 – Apr. 1, 2014 & Nov. 1, 2014 – harvest start
Summer before	Apr. 2, 2014 – Oct. 31, 2014
Winter during	Harvest start – harvest end
Winter interim	Harvest end – Apr. 1, 2015
Summer after	Apr. 2, 2015 – Oct. 31, 2015
Winter after	Nov. 1, 2015 – Apr. 1, 2016

in winter and hunting small prey in summer (Magoun, 1987; Lofroth et al., 2007) and so seasons account for changes in behaviour that might accompany changes in foraging. A wolverine's GPS relocations were included in each period if they aligned temporally with the period and a portion of the 100% MCP (based on GPS relocations) included areas that were logged in the winter of 2014/2015. We analyzed wolverine selection for cutblocks before logging occurred to determine the pre-disturbance importance of these areas to wolverines. We predicted that wolverines selected for cutblocks before logging because these areas are upland forested habitats that wolverines prefer (Wright and Ernst, 2004; Heim, 2015). The during period included all GPS relocations during logging operations. Each cutblock had a start date that indicated when logging began within the cutblock. We added two weeks to the start date to indicate when logging in that cutblock was likely to have finished (personal communication, Michael Morgan, Tolko Ltd., High Level, Alberta). During this active period, logging was occurring 24 h a day. For selection of GPS relocations that coincided spatially and temporally with active logging, we first constructed a 100% MCP for each wolverine that included all relocations from the winter of 2014/2015 (Nov. 1, 2014 to Apr. 1, 2015). This MCP was then used to select all cutblocks that occurred within the wolverine's home range. We then selected GPS relocations for each wolverine that fell between the start and closing of logging activities (determined with selected cutblocks) within the wolverine's 100% MCP. The interim period included all GPS relocations from when logging finished within a wolverine's 100% MCP through Apr. 1, 2015. This period was created to represent a time when the roads and cutblocks were still present (e.g., snow-packed roads) but there was minimal human use of that infrastructure. Cutblock spatial data were obtained from Tolko Ltd (High Level, Alberta).

We evaluated competing hypotheses regarding the effects of logging on wolverine habitat selection with a third-order (use versus available within the home range) habitat selection analysis (Johnson, 1980; Manly et al., 2002). To estimate the parameters of an exponential RSF, we used a generalized linear mixed-effects model (binomial family, logit link) with individual wolverine as a random intercept. We included a random effect term to account for pseudoreplication and an unbalanced sampling design (Gillies et al., 2006). Statistical analyses were completed in the R software program using the lme4 package [R version 3.2.5 (2016-04-14)]. We modeled wolverine habitat selection separately for each logging period (e.g., before, during). Available points were drawn from the wolverine's 100% MCP created for each specific period and sampled uniformly every 200 m. We created three candidate models for each period (Table 2). Our null model included only an intercept term. The base model included distance (metres) to stream, bog or fen, coniferous forest, mixed forest, broadleaf forest, seismic lines, and all-season and winter roads and represented the hypothesis that logging had no effect on wolverine habitat selection. We log-transformed all distances (m) in our models to allow for a decay in the effect as distance increased. We added distance to cutblock (m) to the base model to create the full model and to test whether inclusion of cutblocks improved the fit of the model. If the full model was selected as the top model, the sign of the coefficient value of distance to cutblock indicated whether wolverines were attracted or displaced by harvest activities. We ranked the strength of candidate models to predict the data using Akaike Information Criterion adjusted for small sample size (AIC_c). We report the top model as the one with the greatest weight (Burnham and Anderson, 2002). We report evidence that cutblocks have a strong effect on wolverine habitat selection when the 95% confidence interval of the coefficient does not overlap zero. We report the relative selection strength (RSS) for one landscape location relative to another, given the difference in a particular habitat attribute between the two locations, while holding all other habitat attributes at a constant level (Avgar et al., 2017). Spatial data from the Alberta Biological Monitoring Institute (ABMI Wall-to-wall Land Cover Map 2010 Version 1.0) and the British Columbia Vegetation Resources Inventory were used to identify forest-cover type. Wetland spatial data were identified using the Duck Unlimited Enhanced Wetland Classification (Ducks Unlimited Canada 2013). Roads, seismic lines, and stream spatial data were obtained from IHS.

Table 2
A priori candidate models for the analysis of wolverine habitat selection relative to the logging program and industrial infrastructure. Separate models were built for wolverine GPS relocations in each logging period. Both models were organized by winter (Nov 1. to Apr. 1) and summer (Apr. 2 to Oct. 31) seasons.

Model	Explanatory variables
Logging program	
Null	Intercept only
Base	Stream[a] + bog/fen + coniferous forest + mixed forest + broadleaf forest + seismic line + all-season road + winter road
Full	Base + cutblock (period specific[b])
Industrial infrastructure	
Null	Intercept only
Base	Stream + bog/fen + coniferous forest + mixed forest + broadleaf forest
Three	Base + winter rd + all-season rd
Four	Base + active well + borrow pit
Five	Base + active well + borrow pit + winter rd
Six	Three + seismic line + intermediate-aged cutblock
Seven	Four + seismic line + intermediate-aged cutblock
Eight	Five + seismic line + intermediate-aged cutblock

[a] All variables are calculated as the distance to the feature or landcover (m, log-transformed).
[b] The periods include the winter before, winter during, winter interim, and winter-after logging as well as the summer before and after logging.

2.2.2. Industrial infrastructure

We evaluated competing hypotheses of wolverine distribution relative to industrial infrastructure with third-order RSFs (Johnson, 1980). This analysis included a larger subset of GPS relocations from the study area than the logging analysis described above. We modeled summer and winter seasons separately for males and females and used the same statistical model and availability design as for the logging analysis. Our base model was identical to that used in the logging model except it did not include seismic lines or roads (Table 2). The base model represented the hypothesis that industrial infrastructure had no effect on wolverine habitat selection. We then added complexity to the base model with additional explanatory variables. Because roads, well sites, and borrow pits are all spatially correlated, we created three candidate models that minimized this spatial collinearity (model 3, 4, and 5). We then created additional complexity by adding seismic lines and cutblocks (model 6, 7, and 8) to see if they improved model fit. The cutblock explanatory variable is measured as distance to the edge of the cutblock. We only used cutblocks that were 11–25 years old (intermediate-aged cutblocks). If a model besides the base model was chosen as the top model, the sign of the coefficient values were used to indicate whether wolverines were attracted to or displaced by the industrial feature. We compare models with AIC_c and report top model coefficients and confidence intervals (Table 2). Cutblock spatial data were obtained from logging companies and Alberta Environment and Parks. ABMI Human Footprint Inventory (Version 3) for 2012 conditions and the BC Oil and Gas Commission were the sources of spatial data for borrow pits.

We also were interested in whether wolverines were found within the interior of cutblocks. To quantify this, we conducted a bivariate analysis to indicate whether wolverines were more often found within the interior of cutblocks versus outside (1 = inside cutblock polygon, 0 = outside polygon). We used the same mixed-effects logistic regression model structure described above. We simply report the coefficient estimate and confidence interval from this bivariate analysis.

To accompany our use of borrow pits as an explanatory variable, we randomly sampled 90 borrow pits from the ABMI spatial data for a survey of use by beavers. Only borrow pits within the study area were part of the random sample. When a borrow pit was visited, we recorded whether the pit had an active colony (visible cache), an inactive lodge without a cache, had beaver cutting evident (any age), was unoccupied, or was not a borrow pit (misclassification). We also opportunistically sampled borrow pits as we drove along industry roads with these same methods. Surveys were conducted during winter-field work.

3. Results

3.1. Logging program

A total of 19 wolverines were followed in at least a single period. Because of mortality, radiocollar failure, and the inability to recapture wolverines, we were not able to monitor the same individuals throughout all six periods. There were six wolverines monitored for one period, five wolverines monitored for two periods, four wolverines for three periods, one wolverine for four periods, and two wolverines for five periods. The average (range) number of GPS relocations per wolverine for the before and after summer periods were 969 (349, 1216) and 953 (571, 1254), respectively. The number of GPS relocations per wolverine for the winter before, during, interim, and after periods were 377 (136, 644), 333 (51, 794), 179 (86, 336), and 650 (96, 1158), respectively (Table 3).

We found support for the hypothesis that wolverines were attracted to areas of active harvest. We present model results (Table 4) and coefficient estimates (Table 5) in chronological order from the winter-before logging through the winter after. Coefficient estimates for base variables can be viewed in Table S1. The full model was the top model in all periods (largest AIC_c weight). Wolverines selected for distances closer to cutblocks in all periods except the summer-before harvest (Table 5). We calculated the RSS for cutblocks in each period using the following equation:

$$\left[\frac{x - \Delta x + 1}{x + \Delta x + 1}\right]^{\beta_i}.$$

When a wolverine was 500 m from a cutblock the winter-before harvest, the wolverine was 1.16 times more likely to move towards than away from the cutblock (x = 500, Δ_x = 450, β = −0.052]. We then calculated the RSS at increasing distances of 50 m from the cutblock (Fig. 3). When a wolverine was 500 m from a cutblock the summer-before harvest, the wolverine was 0.67 times more likely to move away than towards the cutblock (x = 500, Δ_x = 450 m, β = 0.136) (Fig. 4). When a wolverine was 500 m from a cutblock during harvest, the wolverine was 1.29 times more likely to move towards than away from the cutblock (x = 500, Δ_x = 450 m, β = −0.086) (Fig. 3). Relative to all other periods, the strongest selection for cutblocks occurred during active harvest. When a wolverine was 500 m from a cutblock in the interim period, the wolverine was 1.24 times more likely to move towards than away from the cutblock (x = 500, Δ_x = 450 m, β = −0.075) (Fig. 3). Wolverines switched from avoidance of cutblocks the summer-before harvest to selection for them the summer after. When a wolverine was 500 m from a cutblock the summer after harvest, the wolverine was 1.19 times more likely to move towards than away from the cutblock (x = 500, Δ_x = 450 m, β = −0.060). And finally, when a wolverine was 500 m from a cutblock the winter after harvest, the wolverine was 1.19 times more likely to move towards than away from the cutblock (x = 500, Δ_x = 450 m, β = −0.060) (Fig. 4).

3.2. Industrial infrastructure

The winter model was estimated from a sample of 21,540 GPS relocations from 31 wolverines (Table 3). Both male and female data in winter supported the hypothesis that the base model is inadequate in explaining wolverine habitat selection relative to models that included industrial infrastructure. The most-supported winter model of male habitat selection included the base model in addition to active wells, borrow pits, winter roads, seismic lines, and cutblocks (model "eight", AIC_c weight = 1.00, Table 6). Among base variables, wolverines selected streams, broadleaf forests, coniferous forests, mixed forests, and bogs/fens. Males avoided active-well sites and winter roads. Male results supported the hypothesis that they were attracted to borrow pits and seismic lines (negative coefficients) for foraging opportunities. There was only weak evidence that males avoided intermediate-aged cutblocks (coefficient estimate crossed zero) (Table 7). The most-supported model of female habitat selection in winter also was model eight (AIC_c weight = 1.00, Table 6). Females selected streams, broadleaf forests, coniferous forests, mixed forests, and bogs/fens. Females avoided winter roads and active-well sites, however, the active well coefficient estimate crossed zero. Female results supported the hypothesis that they were attracted to borrow pits, seismic lines, and intermediate-aged cutblocks (negative coefficients) (Table 7).

The summer model included 24,278 GPS relocations from 26 wolverines (Table 3). Again, both male and female data in summer supported the hypothesis that the base model is inadequate in explaining wolverine habitat selection relative to models that included industrial infrastructure. Male habitat selection in summer was most supported by a model that included the base model in addition to winter roads, all-season roads, seismic lines, and cutblocks (model "six", AIC_c weight = 1.00, Table 6). Males selected streams, coniferous forests, mixed forests, and bogs/fens. Males avoided broadleaf forests, all-season, and winter roads (winter road confidence interval crossed zero). Male results supported the hypothesis that they were attracted to cutblocks and seismic lines, however, the confidence bound of seismic lines crossed zero (Table 7). Female habitat selection in summer was best supported by model eight (AIC_c weight = 1.00, Table 6). Female wolverines selected coniferous forests, mixed forests, and bogs/fens. Females avoided streams, broadleaf forests, active-well sites, and winter roads. Female results supported the hypothesis that seismic lines and borrow pits were attractive industrial features (negative coefficient) while intermediate-aged cutblocks were avoided (positive coefficient) (Table 7).

There were 335 GPS relocations located within the interior of intermediate-aged cutblocks in winter and 362 GPS relocations located within cutblocks in summer. Our bivariate analysis indicated that wolverines avoided the interior of intermediate-aged cutblocks. In winter, males (β = −0.815, lower CI = −0.981, upper CI = −0.650) and females (β = −0.201, lower CI = −0.327, upper CI = −0.074) selected against the interior of cutblocks. In summer, males (β = −0.486, lower CI = −0.630, upper CI = −0.342) and females (β = −0.156, lower CI = −0.288, upper CI = −0.025) also avoided cutblock interiors.

There were 1445 borrow pits within the 2380 km^2 100% MCP around wolverine livetrap locations. We surveyed 87 borrow pits that were randomly sampled and 97 that were opportunistically sampled. Of the 87 borrow pits that were randomly sampled,

Table 3
Wolverine GPS relocations used for the analysis of wolverine habitat selection relative to the logging program and industrial infrastructure. GPS relocations were collected at two-hour intervals in summer and winter seasons.

Period/model	Total relocations	Males	Male relocations	Females	Female relocations
Logging program: winter before	2643	5	1837	2	806
Logging program: summer before	3876	2	1465	2	2411
Logging program: winter during	2331	5	1402	2	929
Logging program: winter interim	1259	5	908	2	351
Logging program: summer after	6671	4	3878	3	2793
Logging program: winter after	6498	5	3136	5	3362
Industrial infrastructure: winter	21,540	16	9813	15	11,727
Industrial infrastructure: summer	24,278	13	13,331	13	10,947

Table 4
Top ranked models of wolverine habitat selection relative to the logging program. Modeling results are presented in chronological order from the winter before logging through the winter after. We modeled wolverine habitat selection within each period with a mixed-effects generalized linear model (binomial family, logit link) with the individual as a random intercept. We report the top model as having the greatest AIC_c weight [exp(−0.5 * ΔAIC score for that model)]. K indicates the number of model parameters and ΔAIC_c is the difference in AIC_c between each model and the top model within that period.

Period	Model	K	AICc	ΔAIC_c	AIC_c weight	Likelihood
Winter before	Full	11	23379.44	0.00	0.99	−11678.72
	Base	10	23389.35	9.91	0.01	−11684.67
	Null	2	24026.51	647.07	0.00	−12011.26
Summer before	Full	11	28084.85	0.00	1.00	−14031.42
	Base	10	28191.67	106.83	0.00	−14085.84
	Null	2	28709.69	624.84	0.00	−14352.84
Winter during	Full	11	20760.14	0.00	1.00	−10369.07
	Base	10	20789.86	29.72	0.00	−10384.93
	Null	2	21307.43	547.29	0.00	−10651.72
Winter interim	Full	11	12213.72	0.00	0.98	−6095.86
	Base	10	12221.15	7.43	0.02	−6100.57
	Null	2	12320.98	107.26	0.00	−6158.49
Summer after	Full	11	48536.27	0.00	1.00	−24257.13
	Base	10	48655.63	119.36	0.00	−24317.81
	Null	2	49078.17	541.90	0.00	−24537.08
Winter after	Full	11	45909.58	0.00	1.00	−22943.79
	Base	10	45943.40	33.82	0.00	−22961.70
	Null	2	46290.51	380.93	0.00	−23143.25

Table 5
Wolverine coefficient estimates (β), standard errors (SE), and confidence intervals for distance to cutblock from top logging-program models for each period. We modeled wolverine habitat selection within each period with a mixed-effects generalized linear model (binomial family, logit link) with the individual as a random intercept.

Season/model	β (distance to cutblock)	SE	Lower 95% confidence interval	Upper 95% confidence interval
Winter before	−0.052	0.015	−0.080	−0.023
Summer before	0.136	0.014	0.109	0.162
Winter during	−0.086	0.015	−0.116	−0.057
Winter interim	−0.075	0.024	−0.121	−0.028
Summer after	−0.091	0.008	−0.107	−0.076
Winter after	−0.060	0.010	−0.080	−0.041

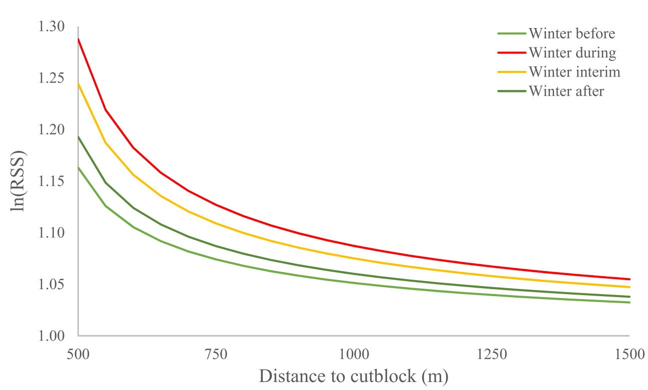

Fig. 3. Relative selection strength (RSS) for cutblocks the winter before, during, interim, and after logging activities. We used coefficient estimates from top-logging models for RSS calculation. For example, when a wolverine was 500 m from a cutblock the winter-before harvest, the wolverine was 1.16 times more likely to move towards than away from the cutblock (x = 500, Δ_x = 450, β = −0.052].

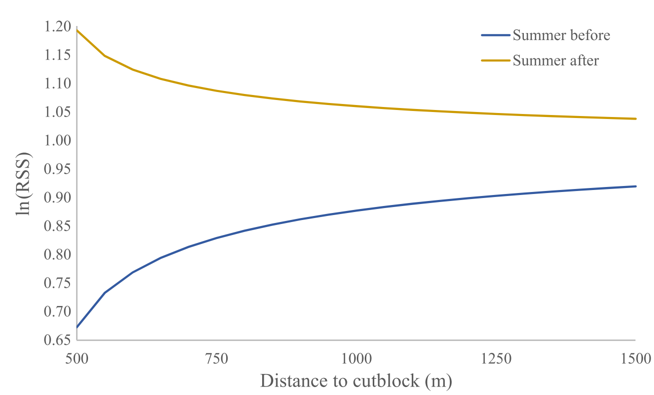

Fig. 4. Relative selection strength (RSS) for cutblocks the summer before and after logging activities. We used coefficient estimates from the top-logging models for RSS calculation. For example, when a wolverine was 500 m from a cutblock the summer-before harvest, the wolverine was 0.67 times more likely to move away than towards the cutblock (x = 500, Δ_x = 450 m, β = 0.136).

67% showed some sign of recent beaver use. Of the 97 opportunist samples, 80% showed evidence of recent beaver use. Approximately 20% of random and opportunistically sampled borrow pits had active-beaver colonies at the time of sampling (Table 8).

4. Discussion

Wolverine habitat selection patterns in relation to industrial activity and infrastructure reflect a balance between exposure to predation risk and foraging opportunities. We found evidence that wolverines were attracted to some industrial infrastructure and disturbances, which we suggest can be related to foraging opportunities (e.g., cutblocks in Nielsen et al., 2004; seismic lines and roads in Dickie et al., 2016). We also found instances where disturbances displaced wolverines, which we attribute to perceived predation risk (e.g., human developments in Knopff et al., 2014; Latham et al., 2013). Here, we present on whether logging, intermediate-

Table 6
Top ranked models of wolverine habitat selection relative to industrial infrastructure. We modeled male and female wolverine habitat selection in summer and winter seasons with a mixed-effects generalized linear model (binomial family, logit link) with the individual as a random intercept. We report the top model as having the greatest AIC_c weight [exp(−0.5 * ΔAIC score for that model)]. K indicates the number of model parameters and ΔAIC_c is the difference in AIC_c between each model and the top model within that period.

	Male				Female			
	Model	K	ΔAIC_c	AIC_c weight	Model	K	ΔAIC_c	AIC_c weight
Winter	Eight	12	0.00	1.00	Eight	12	0.00	1.00
	Six	11	50.12	0.00	Seven	11	21.06	0.00
	Five	10	84.32	0.00	Five	10	33.54	0.00
	Seven	11	86.66	0.00	Four	9	51.29	0.00
	Three	9	132.76	0.00	Six	11	129.25	0.00
	Four	9	168.90	0.00	Three	9	164.51	0.00
	Base	7	239.37	0.00	Base	7	179.83	0.00
	Null	2	950.00	0.00	Null	2	913.42	0.00
Summer	Six	11	0.00	1.00	Eight	12	0.00	1.00
	Three	9	147.43	0.00	Seven	11	10.79	0.00
	Seven	11	173.02	0.00	Six	11	62.63	0.00
	Eight	12	175.02	0.00	Five	10	86.84	0.00
	Four	9	252.29	0.00	Four	9	97.00	0.00
	Five	10	254.22	0.00	Three	9	151.01	0.00
	Base	7	268.75	0.00	Base	7	164.05	0.00
	Null	2	1438.11	0.00	Null	2	1519.36	0.00

Table 7
Wolverine coefficient estimates (β), standard errors (SE), and confidence intervals (LCL = lower 95% confidence interval, UCL is upper 95% confidence interval) for models of wolverine habitat selection relative to industrial infrastructure. We modeled wolverine habitat selection with a mixed-effects generalized linear model (binomial family, logit link) with the individual as a random intercept.

	Winter male				Winter female			
Explanatory variable	β	SE	LCL	UCL	β	SE	LCL	UCL
Stream	−0.101	0.006	−0.113	−0.088	−0.056	0.007	−0.069	−0.043
Broadleaf forest	−0.095	0.005	−0.105	−0.085	−0.075	0.005	−0.084	−0.065
Coniferous forest	−0.082	0.006	−0.093	−0.071	−0.090	0.005	−0.100	−0.080
Mixed forest	−0.059	0.006	−0.070	−0.048	−0.094	0.005	−0.104	−0.084
Bog/fen	−0.054	0.004	−0.062	−0.045	−0.030	0.004	−0.039	−0.021
Active well	0.083	0.013	0.058	0.108	0.022	0.012	−0.003	0.046
Borrow pit	−0.074	0.014	−0.101	−0.047	−0.159	0.013	−0.185	−0.134
Seismic line	−0.049	0.005	−0.059	−0.039	−0.014	0.005	−0.024	−0.004
Cutblock[a]	0.011	0.007	−0.004	0.025	−0.034	0.006	−0.046	−0.022
All-season rd	–	–	–	–	–	–	–	–
Winter rd	0.087	0.010	0.069	0.106	0.043	0.009	0.025	0.061
	Summer male				Summer female			
Stream	−0.135	0.005	−0.145	−0.124	0.065	0.008	0.050	0.081
Broadleaf forest	0.019	0.004	0.010	0.027	0.047	0.006	0.035	0.058
Coniferous forest	−0.041	0.004	−0.050	−0.032	−0.108	0.005	−0.119	−0.097
Mixed forest	−0.019	0.005	−0.028	−0.010	−0.005	0.006	−0.016	0.007
Bog/fen	−0.072	0.004	−0.080	−0.065	−0.025	0.005	−0.034	−0.016
Active well	–	–	–	–	0.076	0.014	0.050	0.103
Borrow pit	–	–	–	–	−0.095	0.014	−0.121	−0.068
Seismic line	−0.008	0.005	−0.017	0.002	−0.031	0.005	−0.041	−0.021
Cutblock	−0.072	0.006	−0.083	−0.060	0.052	0.007	0.038	0.066
All-season rd	0.127	0.009	0.109	0.145	–	–	–	–
Winter rd	0.010	0.007	−0.004	0.023	0.034	0.010	0.015	0.053

[a] cutblock = intermediate-aged cutblock (11–25 years old).

aged cutblocks, seismic lines, and borrow pits were perceived as a predation risk versus a foraging opportunity for wolverines.

Our finding that active logging did not displace wolverines is a unique contribution to wolverine ecology. There is abundant evidence that wolverines are displaced by human developments that have been on the landscape and used by humans for long periods of time (e.g., May et al., 2006; Krebs et al., 2007; Fisher et al., 2013). Our analysis of active logging was unique in that we investigated wolverine habitat selection relative to a novel disturbance within a wolverine's home range. The paradigm that wolverines avoid human developments could be rooted in a learned avoidance of long-established human developments where wolverines have repeatedly experienced threats. New disturbances, however, might be viewed naively by wolverines that have not encountered these disturbances before.

Wolverines selected logging areas throughout all winter periods but selected most strongly for them during and immediately after logging. We suspect wolverines were using logging areas before harvest because upland forests provide enhanced foraging opportunities or movement routes because of shallow snow (Wright and Ernst, 2004; Heim, 2015). The strong selection strength for cutblocks during active harvest was unexpected. Potentially, wolverines are simply curious and are attracted to logging activity because it is a novel disturbance. However, the potential exists for these areas to provide foraging opportunities from displaced prey (Ferron et al., 1998; Potvin et al., 1999; Turcotte et al., 2000), for the human activity to act as a predator shield (Berger, 2007), or

Table 8
Occupancy of borrow pits by beavers based on random and opportunistic surveys in the winter of 2015/2016. The random sample of borrow pits ($n = 87$) were from borrow pits within the study area (total = 1445). Opportunistic surveys were conducted when field crews had free time and saw borrow pits near roads.

Category	n	% of sample
Random sample ($n = 87$)		
Active beaver colony (lodge and cache present)	16	18
Beaver cutting evident (but no beaver structure)	30	34
Unoccupied (no sign of beaver occupation)	17	20
Inactive beaver lodge (no cache present)	13	15
Not a borrow pit	11	13
Opportunistic sample ($n = 97$)		
Active beaver colony	23	24
Beaver cutting evident	28	29
Unoccupied	20	21
Inactive beaver lodge	26	27

for wolverines to use roads near cutblocks as movement corridors. Sites that were to become cutblocks were avoided by wolverines the summer before logging. The importance of upland forests to wolverines in the summer appears reduced in our industrial infrastructure models as well. Wolverines then switched to selection for cutblocks the summer after harvest occurred. This switch in habitat selection lends support to the idea that harvest areas provide either enhanced foraging or movement capabilities to wolverines and are therefore sought after.

The aversion of wolverines to roads is well reported by researchers (Rowland et al., 2003; May et al., 2006; Copeland et al., 2007; Lofroth et al., 2007). While we found evidence of road avoidance, we also found that roads can be attractive to wolverines. Wolverines avoided low-traffic winter roads in summer and winter seasons. We attribute this avoidance to predation risk from wolves that use these roads for movement (Whittington et al., 2005; Dickie et al., 2016). Wolves killed three male wolverines near winter roads during our field-work which provides evidence of a mechanism behind this avoidance pattern. Wolverine mortality from apex predators has been found in other study areas as well (Krebs et al., 2004). Contrarily, we found that wolverines were attracted to all-season road sections with borrow pits. We would suggest the reward of foraging opportunities at borrow pits outweighs the risk of encountering humans along all-season roads that generally have greater traffic volume. Because wolves avoid all-season roads (Latham et al., 2013), wolverines might be able to use these areas with less predation risk.

Borrow pits did not explain male habitat selection during the summer. One possible explanation is that males are focused on patrolling home ranges and mating during the summer (Inman et al., 2012), such that the importance of borrow pits for hunting is reduced. In addition, we captured and placed radiocollars on numerous juvenile male wolverines in spring that were not residents. We suggest that these animals appeared in our study area during exploratory or dispersal movements (Vangen et al., 2001). Many of these animals used habitats in Rainbow Lake for a few weeks or months and then returned, presumably back to their natal range in northeastern British Columbia, where there are fewer borrow pits. Thus, the ability of borrow pits to explain summer habitat selection among our monitored males might have been reduced.

Wolverine avoidance of seismic lines has been reported in the literature (Fisher et al., 2013; Heim, 2015) yet we found wolverines were attracted to seismic lines. We suggest there is variation in the characteristics of seismic lines that might explain the different responses by wolverines. Oil and gas resources in our study area were developed in the 1950s and extensive seismic exploration occurred from 1960 to 1990. As of 2016, these seismic lines were in intermediate-stages of regeneration (Lee and Boutin, 2005; van Rensen et al., 2015; Tigner et al., 2014, 2015) which might make them attractive foraging areas for wolverines hunting small prey. Moreover, it is likely seismic lines in our study area are not used as readily for recreation as they are in southern Alberta (e.g., Fisher et al., 2013; Heim, 2015) which, because they lack packed down snow and cleared brush, might make them less attractive to apex predators for movement (e.g., Dickie et al., 2016). Therefore, wolverines might be hunting for small prey along the edges of regenerating seismic lines with minimal risk of encountering humans or wolves.

Finally, we did not find clear evidence to support either the predation risk or foraging hypothesis for intermediate-aged cutblocks. Wolverines avoided the interior of cutblocks in winter and summer. The edges of cutblocks were avoided by females in summer whereas they were selected by males in summer and females in winter. The avoidance of cutblock interiors could be because thick pole-sized trees present within intermediate-aged cutblocks are unsuitable for wolverine movement and house less prey relative to the edges of cutblocks (e.g., Niemuth and Boyce, 1997; Lidicker, 1999; Knopff et al., 2014). Female avoidance of cutblock edges in summer could be because of predation risk from wolves that also use cutblock habitats (Houle et al., 2009; Lesmerisis et al., 2012) or because of human activity on roads near cutblocks (Krebs et al., 2007). Female selection for cutblocks edges in winter might be because they are less risk-averse in winter when they must meet the energetic demands of preparing for parturition (Magoun and Copeland, 1998; Persson et al., 2006; Inman et al., 2012). We would suggest that overall intermediate-aged cutblocks are not deleterious habitats and might offer some foraging opportunities in remote locations with limited human activity.

5. Conclusions

When assessing the suitability of a landscape for wolverines, managers should consider the potential for industrial infrastructure and activity to both degrade and create habitats. In particular, we show that the temporal characteristics of disturbances need to be considered. For example, freshly cut seismic lines will not be as beneficial to wolverine populations as regenerating lines.

Our results provide evidence that wolverines take risks for foraging opportunities, such as using areas of active harvest, cutblocks, or road-side habitats such as borrow pits. Road-side habitats could prove to be a population sink (e.g., Battin, 2004) for wolverines in landscapes with high levels of traffic. For example, nine wolverines were reported to be struck and killed by vehicles in the Hay-Zama region (north of Rainbow Lake) of Alberta between September 2013 and April 2015 (data provided by Government of Alberta, High Level). Moreover, we know of one radiocollared wolverine that was struck and killed by a vehicle in Rainbow Lake. Such mortality events could contribute to a long-term reduction in wolverine populations if reproduction or immigration could not keep pace with mortality.

The use of industrial developments by wolverines could be the proximate cause of wolverine population decline in other industrialized areas such as southern Ontario (Bowman et al., 2010) and Alberta (Fisher et al., 2013; Heim, 2015). However, the effect of predator populations in these areas is also likely significant. Industrial development can increase the abundance of large prey and predators (Latham et al., 2011) and has therefore been suggested to increase wolverine mortality (Bowman et al., 2010; Fisher et al., 2013; Heim, 2015; Stewart et al., 2016). We have documented both predator and human mortality in Rainbow Lake but we do not believe that either is currently at a level to cause population decline. This might be because ungulate populations in the northern boreal are limited by severe winters (Dawe et al., 2014), which in-turn reduces the potential for wolverine mortality through abundant predators preying on a large ungulate population. In ecosystems with milder winters, such as southern Ontario and southern Alberta, the potential for increased wolverine mortality from large predator populations responding to industrial development might be a risk to wolverine populations.

The wolverines' attraction to upland forested habitats is of conservation concern because these areas are the target of logging activities. However, there are several practices that forestry companies could use to lessen their effects on wolverine populations. We found a wolverine natal den within a slash pile and another natal den within a log deck. Both natal dens were within cutblocks with thick regenerating pole-sized aspen trees that provided substantial cover around the debris pile. Therefore, slash piles should be left within cutblocks when possible to provide habitat for wolverines, their prey such as snowshoe hare (Cox et al., 1997), and for other mammals such as lynx (*Lynx canadensis*) and black bears (*Ursus americanus*; Powell et al., 1997; White et al., 2001). Moreover, managers could leave transitional edges between cutblocks and adjacent forests to provide foraging habitats for wolverines.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.03.029.

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