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Original Article

# Roads elicit negative movement and habitat-selection responses by wolverines (*Gulo gulo luscus*)

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The fine-scale behavior of wildlife when crossing roads and interacting with traffic is likely to mirror natural responses to predation risk including not responding, pausing, avoiding, or increasing speed during crossing. We generated coarse-scale behavioral predictions based on these expectations that could be assessed with GPS radiotelemetry. We evaluated our predictions using an integrated step-selection analysis of wolverine (*Gulo gulo luscus*) space use in relation to spatially and temporally dynamic vehicle traffic on industrial roads in northern Alberta. We compared support for alternative models of road avoidance, increased speed near roads, and road avoidance and increased speed near roads. We predicted that wolverines would avoid roads and increase their speed near roads and that these behaviors would increase with traffic volume. We found that vehicle traffic was relatively low (0–30 vehicles/12 h) but important for explaining wolverine space use. Top winter and summer models indicated that wolverines avoided and increased speed near roads. Wolverine movement, but not avoidance, increased with traffic volume. We suggest that movement is a fine-scaled response that is more responsive to vehicle traffic than habitat selection. We show that roads, regardless of traffic volume, reduce the quality of wolverine habitats and that higher-traffic roads might be most deleterious. We suggest that wildlife behavior near roads should be viewed as a continuum and that accurate modeling of behavior when near roads requires quantification of both movement and habitat selection. Mitigating the effects of roads on wolverines would require clustering roads, road closures, or access management.

*Key words*: **boreal forest, *Gulo gulo*, habitat selection, movement, oil extraction, roads, step selection, traffic volume, wolverine.**

## INTRODUCTION

The growth of human populations and our demand for natural resources has caused the development of roads in wild areas throughout the world (Hansen et al. 2013). Road networks have expanded and densified for the extraction of oil, gas, mining, and timber resources resulting in forest fragmentation and reduction in core areas (Schnieder 2002; Pickell et al. 2014; Pickell et al. 2016). The change in the characteristics of forested landscapes has had cascading effects on the behavior and abundance of many wildlife species (Rytwinski and Fahrig 2012; Latham and Boutin 2015).

Roads are an interface between humans and wildlife. Roads can have positive effects on wildlife by providing protection from predators (Berger 2007), enhanced movement (Whittington et al. 2011), or foraging opportunities (Scrafford et al. 2017b). Roads also can have negative effects on wildlife (Forman and Alexander 1998; Rytwinski and Fahrig 2012) including vehicle-caused mortality (Da Rosa and Bager 2013; McClintock et al. 2015; Niemi et al. 2017) or displacement (Shannon et al. 2014; Abrahms et al. 2016). As per the risk-disturbance hypothesis, displacement of wildlife by roads is because wildlife perceives roads, and associated human activity, as a predation risk (Frid and Dill 2002). Road avoidance can result in a reduction of suitable habitats for wildlife (Beyer et al. 2016; D'Amico et al. 2016; Kite et al. 2016).

Road effects on wildlife are often discerned without data on traffic volume (e.g. Krebs et al. 2007; Roever et al. 2010; Beyer et al. 2016). However, this approach neglects the varied responses of wildlife to the magnitude of human use of roads. The risk-disturbance hypothesis predicts that wildlife perception of risk increases with human activity. A high frequency of vehicles should therefore be viewed by wildlife as a large-predator group that is a threat to their security (Frid and Dill 2002; Jacobson et al. 2016). For example, grizzly bears (*Ursus arctos*) avoided high-traffic roads by crossing roads at night when traffic volume was low (Northrup et al. 2012). Similarly, squirrels (*Tamiasciurus hudsonicus grahamensis* and *Sciurus aberti*) reduced their movement across roads as traffic

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volume increased (Chen and Koprowski 2016) and wild boar (*Sus scrofa*) avoided roads more when traffic volume was high (Thurfjell et al. 2015). Land and wildlife managers can use this information to mitigate the effects of roads on wildlife (Ruggiero et al. 2007).

Another important aspect of understanding road effects on wildlife is accurately modeling wildlife space use when near roads. Roads can affect both wildlife movement and habitat selection (Roever et al. 2010; Jacobson et al. 2016). Resource selection analyses (Johnson et al. 2006) can be used to evaluate the effects of road density or proximity on wildlife habitat selection but do not allow for evaluating the effects of these features on movement. Step-length analyses (Roever et al. 2010) can be used to quantify wildlife movement in relation to underlying habitats but do not control for habitat selection. The development of the integrated step-selection analyses (iSSA), which allows for evaluating habitat selection and movement simultaneously (Avgar et al. 2016), might be a particularly useful tool for investigating the unique and highly variable effects of roads on wildlife (Jacobson et al. 2016).

We evaluated the effects of roads and vehicle traffic on wolverine (*Gulo gulo luscus*) movement and habitat selection on an industrial road network in northern Alberta using an iSSA. These are roads used by industry to access natural resources and have relatively low volumes of vehicle traffic (0–30 vehicles/12 h). Wolverines have low reproductive rates (Persson et al. 2006) and are wide-ranging, inhabiting circumpolar alpine, forest, and tundra habitats (Hornocker and Hash 1981; Magoun 1985). The ability of wolverines to move long distances through the landscape to detect scavenging and foraging opportunities, as well as to patrol territories, is likely critical to their fitness. These biological traits make species such as wolverines especially sensitive to the effects of roads (Rytwinski and Fahrig 2012). As a result of this and other factors, wolverines in Canada are a “Species of Special Concern” (Committee on the Status of Endangered Wildlife in Canada 2014).

Researchers can predict the effects of roads on wildlife species based on their biological characteristics (Ford and Fahrig 2007; Cook and Blumstein 2013). For example, a framework built on ideas from the risk-disturbance hypothesis (Frid and Dill 2002) predicts wildlife road-crossing behavior in response to direct interactions with vehicles (Jacobson et al. 2016). Researchers organized wildlife species into 4 categories aligned with their natural methods of defense, including nonresponders, pausers, speeders, and avoiders. Wildlife that use speed to evade predation [e.g. pronghorn antelope (*Antilocapra americana*)] should increase their speed as direct encounters with vehicles on roads increase, allowing them to escape danger and cross roads through narrow gaps in traffic. Wildlife that pause when faced with danger to go undetected or stand their ground [e.g. porcupines (*Erethizon dorsatum*)] should pause more during road crossings with high-traffic volume. Species that can sense predation risk from afar [e.g. grizzly bears (*Ursus arctos*)] should avoid crossing roads and especially those with high-traffic volume. There is also the potential that wildlife can use more than 1 strategy, such as avoidance and speed (Jacobson et al. 2016).

We evaluated the ability of the framework developed by Jacobson et al. (2016) to predict wolverine behavior, with movement recorded by GPS radio-collars, relative to roads and traffic. The framework predicted wildlife road-crossing behavior in response to actual vehicles passing by on the road. Because of the coarse temporal and spatial scale of most GPS relocations, researchers are unaware of the number of times wildlife make road-crossing attempts or their behavior when interacting with vehicles. However, researchers can quantify how road proximity (e.g. distance to road) affects wildlife behavior. Therefore, we translated the fine-scaled responses of wildlife to roads predicted by Jacobson et al. (2016) to coarse-scale behaviors that could be recorded with GPS radiotelemetry. According to the framework, speeders increase speed when crossing high-traffic roads to use narrow gaps in traffic flow. At a coarse scale, we predict that speeders perceive roads as risky environments and therefore increase their speed near roads. Speed should increase more near high-traffic roads where speeders more often interact with passing vehicles. Pausers should reduce speed near roads and especially near high-traffic roads. Avoiders should avoid roadside habitats and increase their avoidance of high-traffic roads. The space use of nonresponders should not be altered by roads or vehicle traffic. Although not always the case, the change in wildlife movement when near roads could be accompanied by a change in habitat selection. Therefore, speeders and pausers could display more than a single behavior. For speeders, the increase in speed near roads could be accompanied by evidence of road avoidance because of displacement by vehicles from roadside habitats. Pausers could slow down near roads, which might increase their residency time and ultimately indicate selection of roadside habitats.

We predicted that roads were generally deleterious habitats for wolverines (Krebs et al. 2007; Scrafford et al. 2017b). We used the iSSA to evaluate the hypotheses that wolverines were primarily speeders, avoiders, or speeders and avoiders (combined category) when near roads. We predicted wolverines to be both avoiders and speeders based on their biological characteristics. The iSSA is uniquely capable of categorizing both habitat selection and movement singularly and simultaneously. This information could be used to better manage human developments and activities in landscapes occupied by wolverines.

## METHODS

### Study area

Our research took place in the boreal forest surrounding the town of Rainbow Lake, Alberta (population 870, elevation 500 m; 119°28’18.705”W, 58°32’22.361”N; Figure 1). Rainbow Lake is situated in the central mixed-wood subregion of the boreal forest. Upland forests in the subregion include aspen (*Populus tremuloides*), white spruce (*Picea glauca*), and jack pine (*Pinus banksiana*). Wetlands comprise 30% of the landscape and include peatlands (bogs and fens) with black spruce (*Picea mariana*) forests. Average annual temperature is −1.3 °C with 414 mm of precipitation (Strong and Leggat 1981). Industrial resource extraction has occurred in Rainbow Lake since the 1950s and includes oil, gas, mining, and forestry industries. Nonlinear industrial developments include cutblocks, well sites, processing plants, and industrial camps. Linear developments include roads (winter-ice roads and all-season roads), seismic lines, transmission lines, and pipeline rights-of-way.

### Wolverine radiotelemetry

We established 22 live-traps (Copeland et al. 1995) that were used to capture wolverines over 3 winters (November 2013 to April 2016). Live-traps were placed across a range of road densities and separated by approximately 15 km. We captured and attached radio-collars to at least 1 wolverine in every live-trap. Wolverines were fitted with Telemetry Solutions Quantum 4000 or Tellus Ultra-Light radio-collars programmed to take GPS relocations every 2 h. All capture and handling procedures were approved by

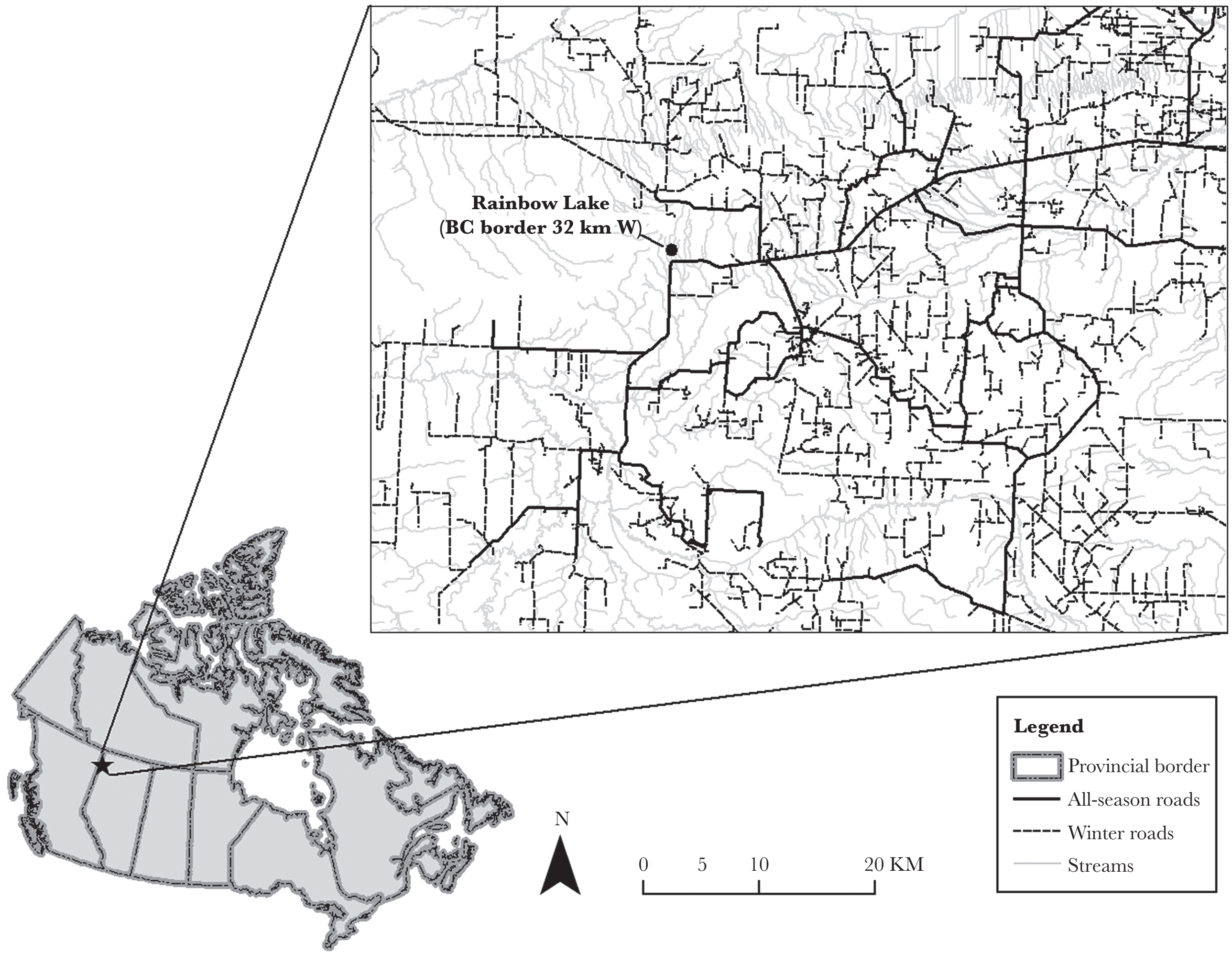

**Figure 1**
Map of the road network (all-season and winter roads) and streams surrounding the town of Rainbow Lake in the northwest corner of Alberta (119°28'18.705"W, 58°32'22.361"N). All-season roads are used by vehicles in both winter and summer seasons whereas winter roads are only used by vehicles in winter.

the University of Alberta Animal Care Committee Protocol No. 00000743 and Province of Alberta Collection and Research Permit No. 55714.

## Traffic modeling

We installed motion-activated cameras along industrial roads to quantify traffic volume in each of our 3 winter field seasons (1 November to 1 April) and 1 summer field season (2 April to 31 October) between 2013 and 2016. Cameras were placed where traffic could be recorded in both directions on both all-season and winter roads during the winter. Cameras in summer were only placed on all-season roads because winter roads are closed during the summer. Alberta Highway 58 ran through our study area but traffic speed was too great for using motion-activated cameras. Therefore, we estimated traffic volume on these roads with estimates from Alberta Transportation (station id# 997259 and station id# 997295).

We identified explanatory variables that explained traffic volume on industrial roads using mixed-effects linear regression. The response variable was the log-transformed average count of traffic per camera during the day and night. We designated "day" from 07:00 to 18:59 because this is the period that oilfield workers are driving in the field, with "night" from 19:00 to 06:59. We used a random intercept to account for the pseudoreplication of cameras placed on the same road segment, defined as a section of road that was not intersected by another road. We modeled traffic volume for winter and summer seasons separately. Explanatory variables for the summer model included a Boolean variable for day ("1") or night ("0"), the road-network distance to Rainbow Lake town site (m), and the road-network distance to Alberta Highway 58 (m). We transformed continuous variables using the natural logarithm, thus allowing spatial effects to decay exponentially with distance. All variables from the summer model were included in the winter model, with the addition of a Boolean variable for all-season ("1") or winter road ("0"). We used Akaike Information Criterion corrected for small sample size ($\text{AIC}_\text{c}$) to determine the most supported winter and summer candidate model (Table 1). We report marginal (fixed-effects only) and conditional (with random intercept included) $R^2$ values to estimate goodness of fit of the top model (greatest $\text{AIC}_\text{c}$ weight). We then used the top winter and summer model to predict vehicle traffic on the road segment closest to each observed wolverine position at the time the fix was taken.

**Table 1**

**Candidate traffic-volume models in winter and summer, their relative support, and top model coefficient estimates**

| Season | Model | Explanatory variables | $\Delta\text{AIC}_c$ | $\text{AIC}_c$ weight | $R^{2(1)}$ | $R^{2(2)}$ |
|---|---|---|---|---|---|---|
| Winter[a] | Full | Road type[b] + day[c] + dist. to town[d] + dist. to highway | 0 | 1.00 | 0.51 | 0.71 |
| | Reduced | Road type + day | 18 | 0.00 | 0.44 | 0.71 |
| | Null | None | 377 | 0.00 | 0.00 | 0.30 |
| Summer | Reduced | Day | 0 | 0.92 | 0.64 | 0.78 |
| | Full | Day + dist. to town + dist. to highway | 5 | 0.08 | 0.66 | 0.79 |
| | Null | None | 51 | 0.00 | 0.00 | 0.00 |
| | Model | Explanatory variables | Estimate | SE | Lower | Upper |
| Winter | Full | Road type | 0.824 | 0.107 | 0.615 | 1.034 |
| | | Day | 1.422 | 0.060 | 1.304 | 1.539 |
| | | Dist. to town | −0.450 | 0.148 | −0.741 | −0.160 |
| | | Dist. to highway | −0.103 | 0.033 | −0.168 | −0.038 |
| Summer | Reduced | Day | 1.587 | 0.136 | 1.320 | 1.853 |

We modeled vehicle traffic (measured with motion-sensor cameras on industrial roads in Rainbow Lake, Alberta) using mixed-effects linear regression. We used the mean-traffic volume along a road section during day and night periods as the response variable. We designated a random intercept for all traffic-volume estimates along the same road section. For candidate models, we report change in Akaike's Information Criterion ($\text{AIC}_c$) between the current and top model ($\Delta\text{AIC}_c$), $\text{AIC}_c$ weight [exp(−0.5 * ΔAIC score for that model)], the marginal $r^{2(1)}$ (fixed effects), and the conditional $r^{2(2)}$ (fixed and random effects). For top models (greatest $\text{AIC}_c$ weight), we report coefficient estimates, their standard errors (SEs), and lower and upper 95% confidence intervals.

[a] Winter is from 1 November to 1 April and summer is from 2 April to 31 October.

[b] "1" = all-season road and "0" = winter road.

[c] The "day" period was from 07:00 to 18:59 and the "night" period was from 19:00 to 06:59.

[d] All distances are in meters and are ln-transformed.

## Habitat selection and movement modeling

We used an integrated step-selection analysis (iSSA; Avgar et al. 2016) to estimate parameters describing the relative probability of wolverine space use in relation to roads and vehicle traffic. We converted GPS radiotelemetry relocations into steps or lines between consecutive GPS relocations. We split steps into seasons (summer, 2 April to 31 October; winter, 1 November to 1 April) and by individual within seasons. Our winter data included 25 wolverines (11 females, 14 males). The median (range) number of steps per male in winter was 396 (153, 2006) and for females was 1052 (120, 1298). Our summer data included 20 wolverines (11 females, 9 males). The median (range) number of steps for males was 905 (179, 1579) and for females was 696 (158, 1614). We fit a gamma distribution to the observed step lengths of all male and female wolverines in winter and summer seasons (4 distributions in total) using the method of moments. We matched each observed step with 20 available steps whose turn angle and step length were randomly drawn from a uniform and the empirically parameterized gamma distributions, respectively. Attributes (e.g. habitats, step length) of observed steps were compared with available steps using conditional logistic regression, with models fitted to each individual in each season (Fieberg et al. 2010).

Our "base model" included the explanatory variables step length and natural log of step length (lnSL) which served to modify, for each wolverine, the initial population-level gamma scale and shape parameters (respectively) originally employed in sampling the available steps (Table 2). We further included an interaction between lnSL and time to civil dawn or dusk (script found at www.srrb.noaa.gov) at the step's start. This interaction allowed the shape of the selection-independent movement kernel ("the function governing movement in the absence of resource selection," Avgar et al. 2016) to vary with time to twilight. We expected the associated coefficient to be negative, supporting the prediction that wolverines increased movement at twilight (Mattison et al. 2010) when their prey [snowshoe hare (*Lepus americanus*) and beaver (*Castor canadensis*)] were most active (e.g. Dyck and Macarthur 1992; Buech 1995; Mech et al. 1966). We modeled wolverine movement relative to streams by including an interaction between distance to nearest stream at the step's start and lnSL. We expected a negative coefficient for the interaction of lnSL and distance to stream because wolverines are purported to use streams as movement corridors and hence move faster in their proximity (Copeland et al. 2007). We also included distance to the nearest stream at the step's endpoint to model wolverine habitat selection. We expected a negative coefficient for distance to stream (indicating stream attraction). All distances were in meters and were log-transformed to allow their effect to decay as distance to the feature increased (Table 2).

The "avoid model" represented the hypothesis that the primary response of wolverines to road proximity is avoidance (Table 2). This model included, in addition to all variables in the base model, distance to road at the step's end (to evaluate habitat selection relative to roads) and an interaction between distance to the nearest road at the step's end and traffic volume on the nearest road (to evaluate habitat selection relative to traffic volume). We predicted wolverines would avoid roads (positive coefficient) and that avoidance would increase with greater traffic volume (positive coefficient). Conversely, the "speed model" represented the hypothesis that the primary response of wolverines to road proximity is to increase their speed and that wolverine speed would increase with traffic volume. This model included, in addition to all variables in the base model, an interaction between lnSL and distance to road at the step's start to evaluate movement relative to roads. The "speed model" also evaluated wolverine movement relative to traffic with a 3-way interaction between lnSL, distance to the nearest road at the step's start, and traffic on the nearest road from step's start. We predicted that wolverines would increase speed near roads (negative coefficient) and increase speed more near roads as traffic-volume increased (positive coefficient). The "avoid and speed model" represented the hypothesis that wolverines both avoid road proximity and move faster when near roads. This model included all the variables in the base, avoid, and speed models (Table 2).

We estimated individual models for each wolverine in each season to account for inter-individual variability in space-use behavior and to avoid pseudoreplication. We only included wolverines with

**Table 2**

**Candidate models used to evaluate the relative influence of roads, traffic volume, and other habitats on wolverine movement and habitat selection in winter (1 November to 1 April) and summer (2 April to 31 October) seasons in Rainbow Lake, Alberta**

| Model | Explanatory variables |
|---|---|
| Null | None |
| Base | SL[a] + lnSL[b] + [lnSL x time to civil twilight (start[c])] + d2.[d] stream (end) + [lnSL × d2. stream (start)] |
| Avoid | Base + d2. rd (end) + [d2. rd (end) × traffic[e] (end)] |
| Speed | Base + [lnSL × d2. Rd (start)] + [lnSL × d2. rd (start) × traffic (start)] |
| Avoid and speed | Base + d2. rd (end) + [d2. rd (end) × traffic (end)] + [lnSL × d2. rd (start)] + [lnSL × d2. rd (start) × traffic (start)] |

[a] SL = step length (m).
[b] lnSL = $\log_e$ of step length (m).
[c] "start" and "end" designate that the point value comes from the start and end of the step, respectively.
[d] d2. = distance to a feature (m, ln-transformed).
[e] traffic = traffic volume (vehicles/12 h) is ln-transformed.

a minimum of 10% of available steps within 2 km of road. We calculated $\text{AIC}_c$ weights for each model set for each wolverine-season. We used a nonparametric bootstrap of these values (10 000 iterations) to calculate an $\text{AIC}_c$ average weight and confidence interval (2.5 and 97.5 percentile values) across all individuals within each season. We weighted the bootstrap by the sample size and stratified by sex to ensure that male and females were counted evenly. The model with the highest average $\text{AIC}_c$ weight was chosen as the top model for each season. We calculated an average-coefficient value and confidence interval for explanatory variables in the top model with a nonparametric bootstrap (10 000 iterations) of coefficient estimates (Fieberg et al. 2010). To account for uncertainty in parameter estimates, we weighted the coefficient estimate by its inverse-variance. We calculated an average coefficient for males and females separately. We also calculated a population-level estimate by stratifying the sample by sex.

We calculated mean movement rates for each wolverine in each season by multiplying the adjusted shape and scale parameters from the gamma distribution. We varied the value of an explanatory variable of interest, while holding all other variables interacting with lnSL at their median value (across all observed steps). We used a sample-size weighted nonparametric bootstrap (10 000 iterations) of movement rates from each wolverine to calculate the mean movement rate (meters/2 h) for male and female wolverines.

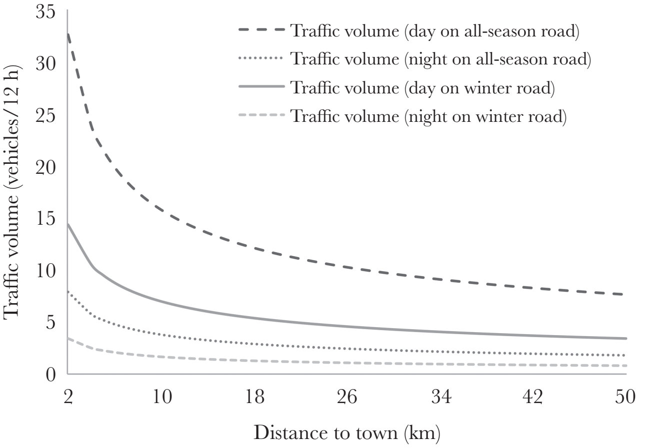

**Figure 2**

Mean-traffic volume on all-season and winter roads during day and night periods relative to distance to Rainbow Lake (m). We modeled the response mean-traffic volume, measured with motion-sensor cameras along roads, during summer and winter seasons using mixed-effect linear regression. The "day" period was from 07:00 to 18:59 and the "night" period was from 19:00 to 06:59. We held distance to Highway 58 at its median for model predictions.

# RESULTS

## Traffic modeling

We monitored vehicle traffic on an average of 163 road sections per winter during 3 winters. During winter, all-season roads averaged 4.58 vehicles/12 h (SD = 5.29 vehicles/12 h) at night and 21.55 vehicles/12 h (SD = 36.50 vehicles/12 h) during the day. Winter roads averaged 0.45 vehicles/12 h (SD = 1.50 vehicles/12 h) at night and 3.50 vehicles/12 h (SD = 7.18 vehicles/12 h) during the day. We monitored vehicle traffic on 54 all-season road sections during a single summer. In summer, all-season roads had an average of 3.31 vehicles/12 h (SD = 2.88 vehicles/12 h) at night and 19.83 vehicles/12 h (SD = 12.78 vehicles/12 h) during the day.

The top model of traffic volume in winter was the full model ($\text{AIC}_c$ weight = 1.00, Table 1). All other models had minimal support from the data. Traffic volume was greater on all-season roads than winter roads, greater during the day than at night, and decreased further from the town of Rainbow Lake (Figure 2) and Highway 58. The best winter model explained 51% (marginal; fixed effect only) and 71% (conditional; fixed and random effects) of the observed variability. The traffic model in summer only included all-season roads. The top traffic model in summer was the reduced model ($\text{AIC}_c$ weight = 0.92, Table 1), with all other models garnering minimal support from the data. The best summer model explained 64% (marginal; fixed effect only) and 78% (conditional; fixed and random effects) of the observed variability. Traffic volume increased during the day on all-season roads (Table 1).

## Habitat selection and movement modeling

### *Winter*

The average density of roads within male ($n = 14$) and female ($n = 11$) 95% minimum convex polygons (MCPs) in winter was 0.62 km/km$^2$ (SD = 0.24 km/km$^2$) and 0.58 km/km$^2$ (SD = 0.21 km/km$^2$), respectively. The maximum road density within a wolverine's winter home range was 0.96 km/km$^2$ (female wolverine). We found support for the hypothesis that wolverines are both avoiders and speeders in winter ($\text{AIC}_c$ weight = 0.47 [95th percentile = 0.36–0.58]; Table 3). However, based on overlapping confidence intervals, there also was some support for the speed model alone

**Table 3**

**The strength of candidate models in explaining wolverine space use relative to roads, traffic, and other habitats in winter (1 November to 1 April) and summer (2 April to 31 October) seasons in Rainbow Lake, Alberta**

| Model | Winter mean AIC$_c$ weight | Lower | Upper | Summer mean AIC$_c$ weight | Lower | Upper |
|---|---|---|---|---|---|---|
| Null | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Base | 0.03 | 0.00 | 0.07 | 0.02 | 0.00 | 0.04 |
| Avoid | 0.15 | 0.08 | 0.21 | 0.24 | 0.13 | 0.36 |
| Speed | 0.36 | 0.26 | 0.46 | 0.21 | 0.11 | 0.30 |
| Avoid and speed | 0.47 | 0.36 | 0.58 | 0.53 | 0.42 | 0.65 |

Mean model weights were based on Akaike's Information Criterion (AIC$_c$), with AIC$_c$ weight [exp(−0.5 * ΔAIC$_c$ score for that model)] calculated for each model (*n* = 4) for each wolverine (winter = 11 females and 14 males, summer = 11 females and 9 males). When then bootstrapped the model weights (10 000 iterations weighted by sample size and stratified by sex) to calculate a mean AIC$_c$ weight and 95th percentile confidence bound.

(AIC$_c$ weight = 0.36 [95th percentile = 0.26–0.46]). We report coefficient estimates from the avoid and speed model because of the overall greater AIC$_c$ weight (Table 3). We calculated a population (male and female combined) coefficient average because male and female wolverines showed similar space-use patterns (Table 4). Among base variables, the top model indicated that wolverines increased their movement near to civil twilight and when near streams. Wolverines also selected for distances closer to streams. Roads and traffic did not have a strong effect on wolverine habitat selection (confidence interval of the coefficient estimate crossed zero) although coefficient averages indicated road avoidance. Wolverines increased their movement near roads and increased their movement even more as traffic-volume increased (Figure 3, Table 4).

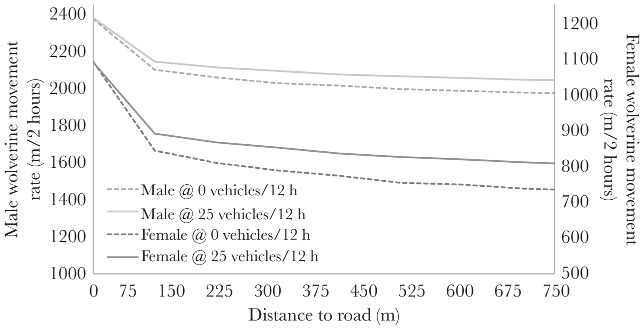

**Figure 3**

Wolverine movement rate relative to distance to road and traffic volume in winter. We calculated the movement rate for each wolverine at 100 m intervals, starting at 0 m from a road and ending at 750 m from a road, while holding all other modeled variables with step length at the median of available steps. We then bootstrapped these estimates (10 000 times and weighted by sample size of observed steps) to produce a mean.

### *Summer*

The average density of roads within male (*n* = 11) and female (*n* = 9) summer 95% MCPs was 0.66 km/km$^2$ (SD = 0.19 km/km$^2$) and 0.55 km/km$^2$ (SD = 0.18 km/km$^2$), respectively. The maximum road density within a wolverine's summer home range was 0.98 km/km$^2$ (female wolverine). We found support for the hypothesis that wolverines are both speeders and avoiders in summer. The avoid and speed model (AIC$_c$ weight = 0.53 [95th percentile = 0.42–0.65]) had 2.52 times the support as the speed model (AIC$_c$ weight = 0.21 [95th percentile = 0.11–0.30]; Table 3). At the population level, wolverines increased their speed near to civil twilight and near to streams. Wolverines also avoided roads, increased speed near roads, and increased speed more near roads with greater traffic volumes. Females displayed results identical to that at the population level except they avoided streams in summer. Males selected strongly for streams and increased their speed when near high-traffic roads (Table 4).

## DISCUSSION

We used an integrated step-selection analysis to evaluate the behavioral response of wolverines to industrial roads with spatially and temporally dynamic traffic-volume estimates. Although Jacobson et al. (2016) had created a framework to predict road-crossing behavior when wildlife directly encounters vehicles, we used their fine-scaled framework to predict coarse-scale responses of wolverines to roads and traffic measured with GPS relocations. We evaluated whether wolverines were speeders, avoiders, or a combination of speeders and avoiders. We found that the combined category of speed and avoidance best explained wolverine space use near roads. Wolverines increased speed near roads and this displacement led to evidence of selection against roadside habitats. Wolverine speed but not avoidance increased with traffic volume. We suggest that displacement of wildlife near roads has implications for fitness, including the potential for a reduction in available habitats and barrier effects.

Wildlife movement and habitat selection are often coupled. For example, an increase in speed near roads should reduce an animal's residency time and lead to evidence of road avoidance (Prokopenko et al. 2017). However, some animals could use one behavior more than another. For example, wildlife that can perceive risk from afar might simply avoid roads but not alter their speed. This might be true for species with smaller home ranges that do not need to expose themselves to risk through road crossings to complete life-history goals. Wildlife that are unable to perceive risk from afar could increase movement when near roads to avoid risks but never be displaced far enough from the road corridor to indicate selection against roads. We found that wolverines were between these extremes and that movement was more important in space-use models than habitat selection. This result suggests that wolverines are always forced to be near roads because of the abundance of roads on the landscape and their need to move across roads to find foraging and breeding opportunities as well as patrol their home range. However, wolverines attempt to stay away from the immediate road corridor, where the risk of predation is likely greatest, with increased movement. We hypothesize that wolverines disproportionally rely on speed when there is risk from roads because strong avoidance would prohibitively increase the time needed to patrol their expansive home ranges in environments with abundant roads.

**Table 4**

**Coefficient averages from the top model of wolverine space use in winter (1 November to 1 April) and summer (2 April to 31 October) seasons in Rainbow Lake, Alberta**

| *Winter model—avoid and speed* | Population average β ($n$ = 25) | Female average β ($n$ = 11) | Male average β ($n$ = 14) |
|---|---|---|---|
| ln(SL)[a] × time to civil twilight | **−0.621** | **−0.598** | **−0.642** |
| D2.[b] stream | **−0.076** | **−0.048** | **−0.098** |
| ln(SL) × d2. stream | **−0.025** | **−0.023** | **−0.026** |
| D2. rd | 0.011 | 0.015 | 0.008 |
| D2. rd × traffic[c] | 0.011 | 0.018 | 0.005 |
| ln(SL) × d2. rd | **−0.041** | **−0.048** | **−0.035** |
| ln(SL) × d2. rd x traffic | **0.007** | **0.009** | **0.005** |
| *Summer model—avoid and speed* | Population average β ($n$ = 20) | Female average β ($n$ = 11) | Male average β ($n$ = 9) |
| ln(SL) × time to civil twilight | **−1.064** | **−1.084** | **−1.044** |
| D2. stream | −0.015 | **0.063** | **−0.094** |
| ln(SL) × d2. stream | **−0.025** | **−0.025** | **−0.024** |
| D2. rd | **0.046** | **0.065** | 0.027 |
| D2. rd × traffic | 0.0001 | 0.003 | −0.003 |
| ln(SL) × d2. rd | **−0.023** | **−0.036** | −0.009 |
| ln(SL) × d2. rd × traffic | **0.005** | **0.004** | **0.006** |

We calculated average-coefficient values for male and female wolverines from a bootstrapped sample of individual coefficients weighted by their inverse-variance. The population average was stratified by sex. Bold font indicates that the 2.5 and 97.5 percentile values do not cross zero.

[a] lnSL = log$_e$ of step length (m).

[b] d2. = distance to a feature (m, ln-transformed).

[c] traffic = traffic volume (vehicles/12 h) is ln-transformed.

Our results highlight the need to investigate both movement and habitat selection when using radiotelemetry data and make sound predictions based on the species' biology. For example, pausers might slow their speed near roads to avoid danger. If the researcher only investigated habitat selection and was unaware of a pauser's risk-avoidance strategy (e.g. Jacobson et al. 2016), then this behavior could indicate selection of habitats near roads. However, this is a false signal and could lead to poor management decisions. Likewise, an increase in speed by wildlife near features does not necessarily explain the feature's suitability to wildlife. For example, increased speed by wolverines near roads could suggest that they are using roads for movement. The combination of speed and selection, however, broadens our understanding of habitat suitability. Wolverines increase speed near roads and select against distances closer to roads. These 2 metrics indicate that wolverines spend a disproportionately lower amount of time in roadside habitats and often flee quickly from these areas, suggesting that roads are poor habitats for wolverines. In contrast, we found that male wolverines selected streams and increased movement when near streams, indicating that they were likely hunting near streams and using them as movement corridors.

Traffic volume was an important predictor of wolverine speed but not avoidance. Wolverines increased speed most when near roads with greater relative traffic volume. This result suggests that wolverines are more likely to be flushed by vehicles from habitats along roads with higher-traffic volume. Unlike speed, wolverine avoidance of roads was constant regardless of traffic volume. Numerous explanations could be made for this result, including: traffic volume was not high enough to evoke increased avoidance, the strength of avoidance of roads was the same regardless of traffic volume, or that speed and avoidance measure behavior at different scales. The first 2 explanations are suspect based on our finding that the speed of wolverines increased when near roads and especially when near higher-traffic roads. More likely our results indicate that avoidance behavior occurs at a coarse scale relative to speed and does not necessarily adjust to passing vehicles but instead to the general risk of roads. Therefore, quantifying both movement and habitat selection enables a multiscale approach, which might elucidate a response of wildlife to habitats that would not be evident when only investigating these metrics in isolation (e.g. Roever et al. 2010).

Although we found that wolverines were displaced by higher-traffic roads, our models also indicated that roads scarcely used by vehicles were deleterious to wolverine habitat suitability. This finding aligns with the prediction that wildlife species with low density and fecundity, such as wolverines, would be sensitive to roads even with low traffic volumes (Jacobson et al. 2016). Grizzly bears also showed avoidance of roads with low traffic volume (20 vehicles per day) (Northrup et al. 2012). However, many of the roads in our study area are winter roads with infrequent vehicle traffic (0–5 vehicles/12 h). Wolverines might be avoiding or increasing speed near these roads because of past or present human activity. Wolverines also could be avoiding winter roads because of risk from wolves that use these roads to move throughout the landscape and hunt ungulates (Whittington et al. 2011; Lesmerises et al. 2012; Dickie et al. 2016). We found 3 male wolverines killed by wolves near winter roads during our field work. This suggestion is speculative because we did not measure predator activity on roads; we suggest that wolverine response to predator use of roads or other features (e.g. streams and seismic lines) could be an important line of research.

How our findings manifest at the population level is important information to help manage wolverine populations. Researchers suggest that wildlife species capable of sensing and avoiding risk from afar are at low risk of mortality from roads because they are rarely near roads (Rytwinski and Fahrig 2012; Jacobson et al. 2016). We found wolverines used both speed and avoidance to reduce their residency time in roadside habitats, which should ultimately reduce their mortality from roads. The larger hypothesized effect of roads on species such as wolverines is the barrier effect through either avoidance or displacement, which often extends beyond the road corridor itself (Rytwinski and Fahrig 2012) and results in a reduction of available habitats (e.g. Beyer et al. 2016; D'Amico et al. 2016). Although there is the potential that displacement has negatively affected wolverines at the population level in some regions (Bowman et al. 2010), wolverine populations in our study appear robust based on the capture history of individuals. This probably means that the threshold of road density, or the magnitude of human use of roads necessary to elicit negative effects at the population level, has not yet occurred in our study area.

Our results suggest ideas for how to mitigate the negative effects of roads on wolverine populations. We found that roads generally reduce the suitability of wolverine habitats, so road building should be limited in habitats that wolverines occupy. Removing roads currently used by industry to access natural resources is probably infeasible. However, reclaiming roads once they lose utility to industry would likely benefit wolverine populations by increasing habitat connectivity. Roads with higher relative traffic volumes in our study area appeared most deleterious to wolverine space use. Managers should limit the footprint of high-traffic roads during the planning phase of projects by clustering their distribution on the landscape. Limiting traffic or temporarily closing roads during the wolverine's denning period in landscapes with declining wolverine populations also might aid populations (e.g. access management; Northrup et al. 2012).

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