Wolverine (*Gulo gulo luscus*) movement, habitat selection, and foraging in a landscape with resource extraction

by

Matthew Allan Scrafford

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Department of Biological Sciences
University of Alberta

Abstract

Industrial infrastructure and activities can fragment boreal landscapes and alter the ecology of wildlife species. Wolverines (*Gulo gulo luscus*) are a species considered especially sensitive to resource extraction because wolverines are wide-ranging, low-density, and have low-reproductive rates. Wolverines *May be at Risk* in Alberta and are a *Species of Special Concern* in Canada. Both assessments relate a lack of information on the effects of industrial disturbance on wolverine ecology. The aim of my thesis was to better understand the movement, habitat selection, and foraging ecology of wolverines in the northern boreal forest of Alberta (Rainbow Lake) where resource extraction has been occurring since the 1950s. My first objective was to determine whether active logging and industrial infrastructure attracted or displaced wolverines. I used resource selection functions (mixed-effect logistic regression) to evaluate competing hypotheses regarding their effects on wolverine habitat selection. I found wolverines were not displaced but instead were attracted to areas of active logging. I also found that wolverines were attracted to seismic lines, borrow pits, and the edges of intermediate-aged cutblocks. I suggested that the attraction of wolverines to these features might be a result of foraging and movement opportunities. I also suggest attraction to the features might increase their mortality. My second objective was to evaluate the behavioral strategy wolverines use to reduce predation risk from roads and vehicle traffic, including, avoiding, increasing speed, or avoiding and increasing speed near roads. I collected traffic data on industrial roads using motion-sensor cameras and modeled variables explaining traffic volume using a mixed-effects linear regression model. I modeled wolverine space use relative to roads using an integrated step-selection analysis. Models that included variables for avoidance and increased speed nears roads better explained wolverine space use than all other models. Wolverines avoided roads and increase speed near roads, while increasing speed more near roads with greater volumes of traffic. I suggest that displacement of wolverines near roads, and especially high-traffic roads, could reduce suitable habitats in industrial landscapes. My third objective was to compare the habitat selection and movement of wolverines within their home range versus during dispersal. I classified wolverine movements into home range and dispersal categories based on plots of net-squared displacement. I found that males increased their selection strength for linear features (roads, streams) during dispersal, reduced their movement rate, and increased their foraging rate. These results align with optimal-dispersal strategies. Females habitat selection during dispersal appeared more flexible. In addition, females during dispersal did not change their movement or foraging rates when compared with their movements in the home range. These data show that wolverines might be limited during dispersal by food and predation risk. My final objective was to evaluate the foraging ecology of wolverines. I visited GPS radiotelemetry clusters in the field and documented the occurrence of wolverine scavenging, beaver-kill, and resting sites. I then predicted large-feeding sites (ungulate carcass, beaver-kill site) across all radiotelemetry data in winter and summer seasons. I used time-to-event models to investigate factors influencing the time to detection of large-feeding sites, the time spent at large-feeding sites, and return time to large-feeding sites after leaving. I found that the time to detection of a large-feeding site was lowest in summer when beavers were more available. I also found that the residency time during a visit to a large-feeding site decreased and return time increased with an increase in the cumulative time spent at a feeding site. Moreover, wolverines spent more time at large-feeding sites if there were other wolverines detected or if the visit was in the winter. Wolverines decreased their time at large-feeding sites if the wolverine also was visiting multiple other feeding sites. These data highlight the strategies wolverines use to reduce competition and opportunity costs while foraging. Overall, my work provides evidence that industrial disturbance can both attract and displace wolverines and that simply measuring the human footprint is a poor proxy for the suitability of wolverine habitats.

Preface

This thesis is an original work by Matthew Scrafford. Field methods were approved by the University of Alberta Animal Care and Use Committee (Protocol # AUP0000743 and AUP00000872).

A version of Chapter 2 is published in Forest Ecology and Management with Tal Avgar, Bill Abercrombie, Jesse Tigner, and Mark Boyce as co-authors. Matthew Scrafford collected and analyzed the data and wrote the manuscript. Tal Avgar and Mark Boyce provided recommendations on data analysis and writing. Jesse Tigner and Bill Abercrombie provided manuscript reviews. Mark Boyce and Bill Abercrombie provided help with fundraising for project expenses.

A version of Chapter 3 will be submitted to Journal of Animal Ecology and includes Tal Avgar, Rick Heeres, and Mark Boyce as co-authors. Matthew Scrafford collected and analyzed the data and wrote the manuscript. Tal Avgar and Mark Boyce provided recommendations on data analysis and writing. Rick Heeres helped with entering and analyzing vehicle-traffic data. All co-authors provided feedback on the manuscript.

A version of Chapter 4 will be submitted to Landscape Ecology and includes Mark Boyce as a co-author. Matthew Scrafford collected and analyzed the data and wrote the manuscript. Mark Boyce provided feedback on the manuscripts.

A version of Chapter 5 will be submitted to Oikos and includes Mark Boyce as a co-author. Matthew Scrafford collected and analyzed the data and wrote the manuscript. Mark Boyce provided feedback on the manuscripts.

In memory of my friends Will Hartman (1982-2016) and Jack Strange (1983-2016).

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1 General introduction

The growth of human populations and our reliance on natural resources has resulted in the fragmentation of natural areas throughout the world (Hansen et al. 2013). Roads, pipelines, seismic and transmission lines, processing plants, and cutblocks are created to map, extract, and transport natural resources to world markets. These industrial features quickly alter environments (Schnieder 2001; Pickell et al. 2014; Pickell et al. 2016) in which wildlife have evolved (Fahrig 2007). Some species can use anthropogenic developments and activities to their advantage (Berger 2007) while others are suppressed through increased mortality (Nielsen et al. 2004; McLintock et al. 2015; Niemi et al. 2017) or occlusion from preferred habitats (Frid and Dill 2002; Sawyer et al. 2006; Jacobson et al. 2016). An important aspect of managing wildlife populations in disturbed habitats is understanding how wildlife respond to anthropogenic developments so that methods can be devised to mitigate these effects.

Wolverines (*Gulo gulo luscus*) are mesocarnivores with a circumpolar distribution. Wolverines in Canada reside in tundra, mountain, and boreal-forest ecosystems. Wolverines in western Canada exist in habitats that are fragmented by resource extraction (Slough 2007; Pickell et al. 2013). Alberta wolverine populations are found in habitats with some of the highest-densities of linear features and other developments in Canada (Schneider 2002). Much like large-carnivores, wolverines have large territories (Magoun 1985; Persson et al. 2010; Inman et al. 2012) and exist at low population densities (Lofroth and Krebs 2007; Fisher et al. 2013; Heim 2015). Wolverines also have low-reproductive rates (Persson et al. 2006). These biological characteristics make wolverines especially sensitive to human activities and infrastructure (Rytwinski and Fahrig 2012). The intrusion of resource-extraction industries into the habitats of wolverines has promoted their listing as a *Species of Special Concern* in Canada because of concern that industry is reducing suitable habitats and increasing the mortality of wolverines (COSEWIC 2014). Wolverines are considered *Data Deficient* in the province of Alberta. Although research has occurred on wolverines in the Rocky Mountains of Alberta (Fisher et al. 2013; Heim 2015), little is known about northern boreal wolverine populations (although see Wright and Ernst 2004). My research looked to address data deficiencies both nationally and in the province of Alberta by focusing on the movement, habitat selection, and foraging of wolverines in the northern boreal forest.

My graduate work was a collaboration between trappers, conservation groups, industry, and First Nations. The Alberta Trappers Association (ATA) and the Alberta Conservation Association (ACA) began studying the distribution of wolverines throughout Alberta by placing run-poles in the registered fur management units of trappers. They then sought a graduate student to study wolverine ecology at a fine-grain. I was chosen to lead this study and I decided to study wolverines in the boreal forest of northwestern Alberta near the town of Rainbow Lake. I chose this site because trapper-harvest records indicated there were wolverines in the region and because there was extensive industrial development in the areas (forestry, oil, gas). I also established a study area in the Birch Mountains of northcentral Alberta but these data were not included in my thesis. Besides collaborating with the ACA and ATA in Rainbow Lake, I also enlisted the help of the Dene Tha First Nation and Husky Oil. These organizations provided knowledge and financial support to me throughout the entirety of my research. The land on which I worked is the traditional land of the Dene Tha and Husky Oil has assets throughout the Rainbow Lake area. Data collection began in the winter of 2013/2014 and continued through the winter of 2015/2016. My primary mode of data collection was attaching GPS radiocollars to wolverines that took fixes at two-hour intervals. I sampled wolverine home ranges across a range of industrial developments.

A paradigm in wolverine ecology is their sensitivity to anthropogenic disturbance (Hornocker and Hash 1981; May et al. 2006; Slough 2007; Krebs et al. 2007; Bowman et al. 2010; Dawson et al. 2010; Fisher et al. 2013; Heim 2015; Stewart et al. 2016). A shortcoming of our knowledge is how the magnitude of human use of infrastructure impacts avoidance (Ruggiero et al. 2007). For example, Krebs et al. (2007) proposed that wolverines do not necessarily avoid cutblocks but instead avoid human activity on roads near cutblocks. Human use of seismic lines also is suspected to negatively affect wolverines (Fisher et al. 2013; Heim 2015). However, these were speculations because there was no information available in these studies to evaluate how human activity influenced wolverine habitat selection. Human activity on roads and other infrastructure has proven to be an important determinant of animal distribution

(Jacobson et al. 2016), with animals generally avoiding infrastructure as the magnitude of human-use increases (Smith et al. 2000; Frid and Dill 2002; Houle et al. 2009; Northrup et al. 2012; Thurfjell et al. 2015; Ladle 2017). The second and third chapters of my thesis address some of these knowledge gaps for wolverines.

The second chapter of my thesis looks broadly at the effects of industrial disturbance and infrastructure on wolverine habitat selection. The first aim is to evaluate whether wolverines avoid areas that are being actively logged. Although we have evidence that wolverines often avoid regenerating cutblocks (Krebs et al. 2007; Bowman et. al 2010), we lack information on how active logging impacts wolverine distribution. I proposed that logging could attract wolverines because of foraging opportunities or alternatively displace them because of human activity. I used mixed-effects logistic regression in a used/available framework to quantify wolverine distribution before, during, and after logging activity in both summer and winter seasons. I also was interested in how wolverines responded to relic industrial features such as roads, borrow pits along roads, seismic lines, and intermediate-aged cutblocks (11-25 years old). Roads, seismic lines, and cutblocks are suggested to be poor wolverine habitats because of their use by humans and other predators (May et al. 2006; Krebs et al. 2007; Bowman et al. 2010; Fisher et al. 2013). However, some of these features also might provide foraging habitats, such as borrow pits occupied by beavers (*Castor canadensis*). I proposed competing hypotheses that these industrial features could attract wolverines because of foraging opportunities or repel them because of predation risk. Hypothesis evaluation was through weight of evidence using an information-theoretic approach (Burnham and Anderson 2002).

I investigated the effect of vehicle traffic on wolverine movements and habitat selection in Chapter 3. Roads are often the subject of habitat selection analyses because they are an interface between humans and wildlife (Foreman and Alexander 1988). Roads can increase the mortality of wildlife (McLintock et al. 2015; Niemi et al. 2017) and cause habitat loss (Abrahms et al. 2016; Jacobson et al. 2016). Wolverines will avoid roads when they occur within their home range (May et al. 2006; Copeland et al. 2007; Krebs et al. 2007; Inman et al. 2013). The cause of this aversion is generally considered to be predation risk associated with human activity on roads but there has been no quantitative evaluation of this hypothesis (Ruggiero et al. 2007). Wildlife often respond to roads based on their natural response to predation risk, with high-traffic volumes eliciting a greater response than low-traffic volumes (Frid and Dill 2002). These behavioral responses can include pausing, speeding, avoiding, or not responding to roads (Jacobson et al. 2016). I evaluated whether wolverines avoided, speeded, or avoided and speeded when near roads and how traffic volume further effected the behavioral response. I used a mixed-effects linear regression model to analyze traffic-count data collected with motion-sensor cameras on industrial roads. I then used an integrated step-selection analysis (Avgar et al. 2016) to examine wolverine habitat selection and movement relative to roads.

In Chapter 4, I investigated wolverine habitat selection, movement, and foraging when wolverines were within their home range versus during dispersal. Dispersal is important for the genetic health and range expansion of wildlife populations (Trakhtenbrot et al. 2005; Clobert et al. 2009). Wolverines have shown tremendous ability to move long distances during dispersals (Vangen 2001; Inman et al. 2009; Inman et al. 2012) and it has been proposed that dispersal from Canadian populations might be important to the expansion and sustainability of wolverine populations in the United States (McKelvey et al. 2014). Researchers have delineated habitat corridors for wolverines based on habitat selection within the home range (Schwartz et al. 2009; Inman et al. 2013; McLure et al. 2016). However, habitats used during dispersal often can be dissimilar to those used while in the home range (Abrahms et al. 2016; Blazquez-Cabrera et al. 2016; Jackson et al. 2016). Optimal-dispersal strategies suggest that wildlife will change behaviours during dispersal to lessen risk and energy expenditure in new habitats (Zollner et al. 2005). Therefore, I evaluated whether wolverines changed behaviour when within the home-range versus during dispersal. I was particularly interested in whether wolverines used linear features more during dispersal because of movement efficiency (e.g., Killeen et al. 2014) and whether wolverines take more risks during dispersal, such as using areas of human activity (e.g., Elliot et al. 2014; Gaston et al. 2016). I categorized movements of wolverines into dispersal and home-range categories using net-squared displacement (Turchin 1988) and a used an integrated step-selection analysis for analysis of wolverine space use within these categories. I also investigated differences in wolverine movement and foraging rates when in the home range versus during dispersal. These differences could include a reduction in movement rate to facilitate the detection of predators and an increase in foraging to take advantage of potentially limited foraging opportunities (Zollner et al. 2005). I compared the step lengths and the proportion of time a wolverine was resting/foraging during dispersal and home-range movements.

Chapter 5 focused on the foraging ecology of wolverines. I would visit GPS radiocollar clusters in the field to collect scat and document kill or scavenging sites. I accumulated a dataset of sites where wolverines rested or killed small prey and sites where wolverines killed or scavenged larger prey such as beavers or ungulate carcasses. The first aim of Chapter 5 was to quantify the rate at which wolverines encountered large-feeding sites (beaver kill sites, ungulate carcasses). These types of data are fundamental for understanding the effects of wolverines on prey populations and potentially how one might manage prey important to wolverine populations (Roemer et al. 2009, Merrill et al. 2010). Researchers have reported the kill rates of wolverines on reindeer in Scandinavia (*Rangifer tarandus*) (Mattison et al. 2016), but there is no information for comparison from North America. I used the spatial and temporal characteristics of observed feeding sites to train a model to identify large-feeding sites throughout the rest of the GPS data. Then, I used a Cox-proportional hazard model to determine the explanatory variables that influenced the time required for a wolverine to find a large feeding site (e.g., season, satiation). I also was interested in whether wolverines exhibited optimal-foraging strategies (Charnov 1976) at large-feeding sites, such as reducing their residency time and increasing their return time as the cumulative time spent feeding increased (e.g., law of diminishing returns). Moreover, wildlife are suspected to use a range of information to determine their foraging behaviours at large-feeding sites (Valone and Brown 1989). Therefore, I also investigated whether other variables influenced residency and return time at large-feeding sites, including, competition, opportunity costs, and seasonality.

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

2.1 Introduction

Animals face trade-offs when selecting habitats that ultimately influence their fitness. These trade-offs center on the relative risks versus rewards associated with use of a habitat patch. Ideally, an animal should seek to maximize time spent in habitats with high-energy gain and no predation risk. However, because few habitats are free of predation risk, animals must choose which habitats are worth the risk (Gilliam and Fraser 1987; Cowlishaw 1997).

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 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 et al. 2005). For example, regenerating cutblocks can provide horizontal cover sought by snowshoe hares (*Lepus americanus*) and grouse (*Bonasa umbellus* and *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. 2008; 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 2006; van Rensen et al. 2015). Once regenerated, these seismic lines can provide early-seral habitats for wildlife (Tigner et al. 2014; Tigner et al. 2015) and poor movement routes for wolves (Dickie 2016) 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 the wolverines were displaced avoiding human activity. We also surveyed borrow pits to report on the extent that pits were inhabited by beaver.

2.2 Methods

Study area

Our research took place the boreal forest surrounding the town of Rainbow Lake (population 870) (119°28'18.705"W, 58°32'22.361"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 well-sites, 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. 2.1). The average size of these cutblocks was 0.14 km^2 (SD = 0.21, Fig. 2.2) 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 2,380 km^2. Livetraps (Copeland et al. 1995) were placed across a range of road densities and separated by approximately 10 kms. 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.

Statistical analyses

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 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 hours a day. For selection of GPS relocations that coincided spatially and temporally with active logging, we first constructed a 100% MCP for each animal 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 animal's home range. We then selected GPS relocations for each animal that fell between the start and closing of logging activities (determined with selected cutblocks) within the animal's 100% MCP. The interim period included all GPS relocations from when logging finished within an animal'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 effect. 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. under review). 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.

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.

2.3 Results

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 animals, we were not able to monitor the same individuals throughout all six periods. There were six animals monitored for one period, five animals monitored for two periods, four animals for three periods, one animal for four periods, and two animals 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 animal 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 2.3).

We found support for the hypothesis that wolverines were attracted to areas of active harvest. We present model results (Table 2.4) and coefficient estimates (Table 2.5) in chronological order from the winter-before logging through the winter after. Coefficient estimates for base variables can be viewed in Table S2.1. 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 2.5). 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. 2.3). 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. 2.4). 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. 2.3). 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. 2.3). 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. 2.4).

Industrial infrastructure

The winter model was estimated from a sample of 21,540 GPS relocations from 31 wolverines (Table 2.3). 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 2.6). 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), with the potential mechanism for attraction being foraging opportunities or potentially movement (food habits data of wolverines in Table S2.2). There was only weak evidence that males avoided intermediate-aged cutblocks (coefficient estimate crossed zero) (Table 2.7). The most-supported model of female habitat selection in winter also was model eight (AIC_c weight = 1.00, Table 2.6). 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 2.7).

The summer model included 24,278 GPS relocations from 26 wolverines (Table 2.3). 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 2.6). 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 2.7). Female habitat selection in summer was best supported by model eight (AIC_c weight = 1.00, Table 2.6). 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 2.7).

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 1,445 borrow pits within the 2,380 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, 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 2.8).

2.4 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). In these circumstances, the costs of foraging (e.g., predation risk) were likely lower than the benefits wolverines acquired from foraging or mobility (Abrams 1993). 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), such that the costs were likely greater than the rewards (Abrams 1993). Here, we present on whether logging, intermediate-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 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 role of borrow pits in explaining summer habitat selection among our monitored males might have been reduced.

Wolverine avoidance of seismic lines also has been reported in the literature (Fisher et al. 2013; Heim 2015) yet we found wolverines were attracted to them. 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 1950's and extensive seismic exploration occurred from 1960-1990. As of 2016, these seismic lines were in intermediate-stages of regeneration (Lee and Boutin 2006; van Rensen et al. 2015; Tigner et al. 2014; Tigner et al. 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 1988; 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.

2.5 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. 2013) 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.

Finally, correlation studies in habitat selection suffer from an inability to accurately assess causation. We associated habitats with predation risk and foraging opportunities but we were unable to measure these attributes directly. Therefore, we would caution that the relationships we suggested between industrial infrastructure and activity is not causal and are instead associations that require additional research to establish causality.

Table 2.1. 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

Table 2.2. 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.

Table 2.3. 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	2,643	5	1,837	2	806
Logging program: summer before	3,876	2	1,465	2	2,411
Logging program: winter during	2,331	5	1,402	2	929
Logging program: winter interim	1,259	5	908	2	351
Logging program: summer after	6,671	4	3,878	3	2,793
Logging program: winter after	6,498	5	3,136	5	3,362
Industrial infrastructure: winter	21,540	16	9,813	15	11,727
Industrial infrastructure: summer	24,278	13	13,331	13	10,947

Table 2.4. 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 2.5. 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

Table 2.6. 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 2.7. 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)

Table 2.8. 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 = 1,445). 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

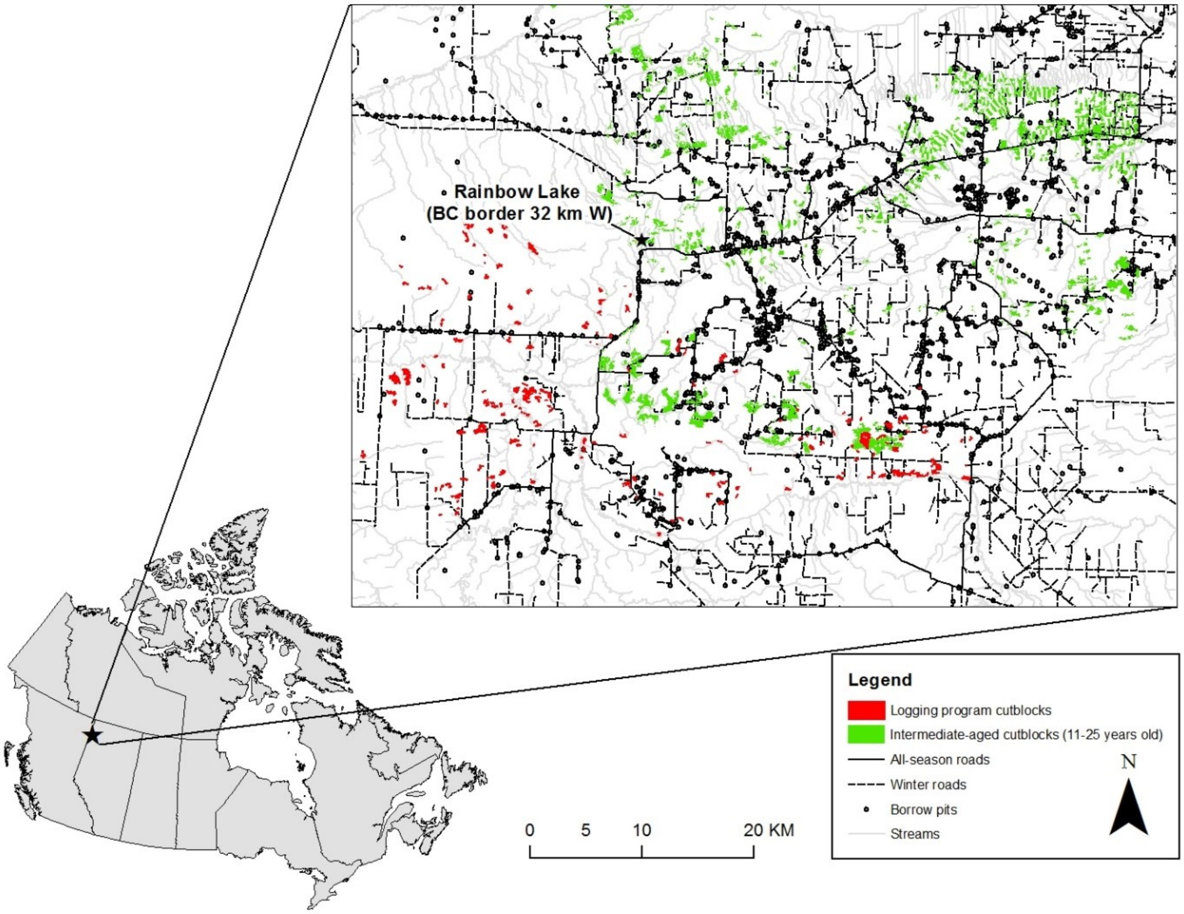

Fig. 2.1. Rainbow Lake study area in the NW corner of Alberta. The map shows cutblocks associated with the logging program during the second year of the study (winter 2014/2015) as well as cutblocks that are not of intermediate age (11-25 years old).

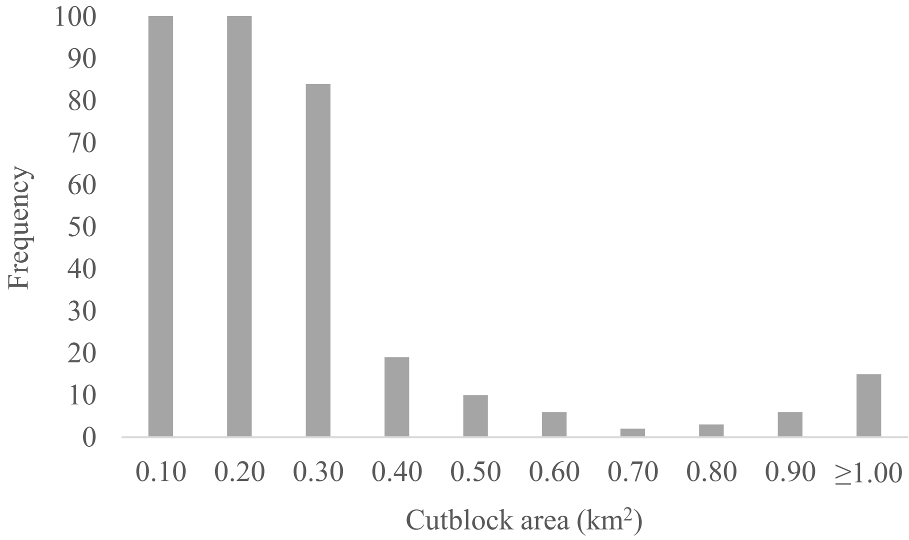

Fig. 2.2. Frequency of cutblock size (km^2) among intermediate-aged (11-25 years old as of 2015) cutblocks in Rainbow Lake. There were 445 cutblocks ≤ 0.10 km^2 and 258 that are ≥ 0.20 and ≤ 0.29 km^2. We cut these frequencies off at 100 for visualizing purposes.

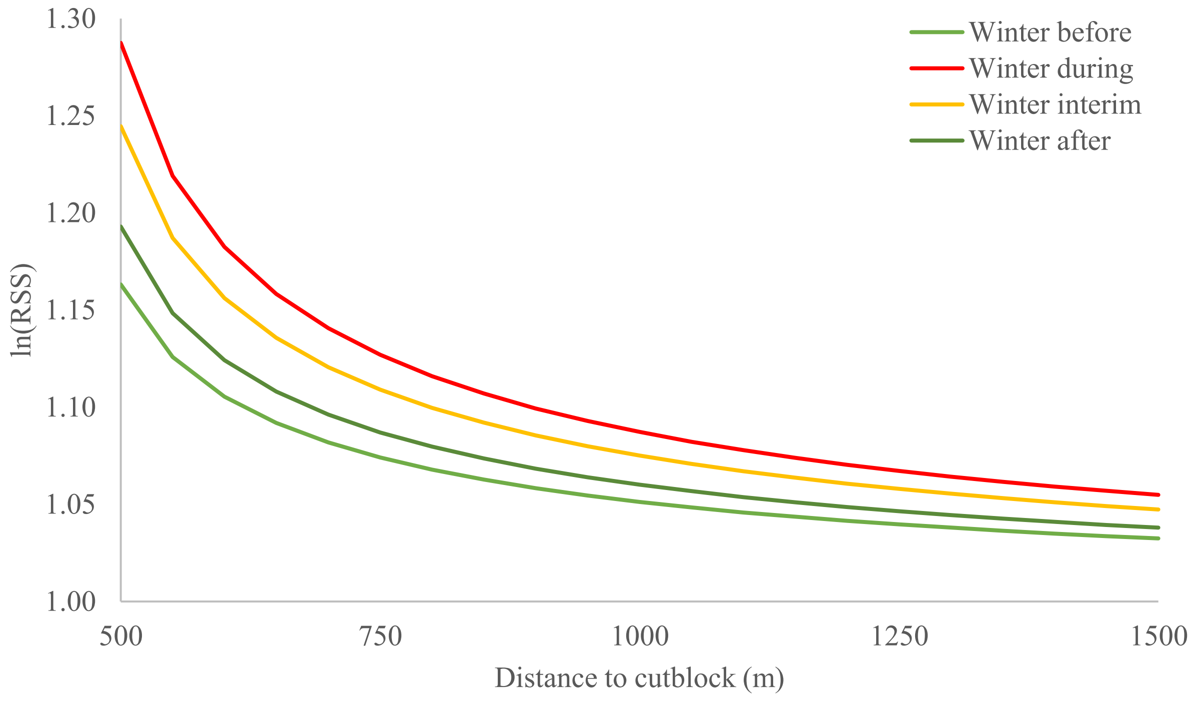

Fig. 2.3. Relative selection strength (RSS) for cutblocks the winter before, during, interim, and after logging activities. We used coefficient estimates from top-logging models for RSS calculation. For example, when a wolverine was 500 m from a cutblock the winter-before harvest, it was 1.16 times more likely to move towards it than away ($x = 500$, $\Delta_x = 450$, $\beta = -0.052$].

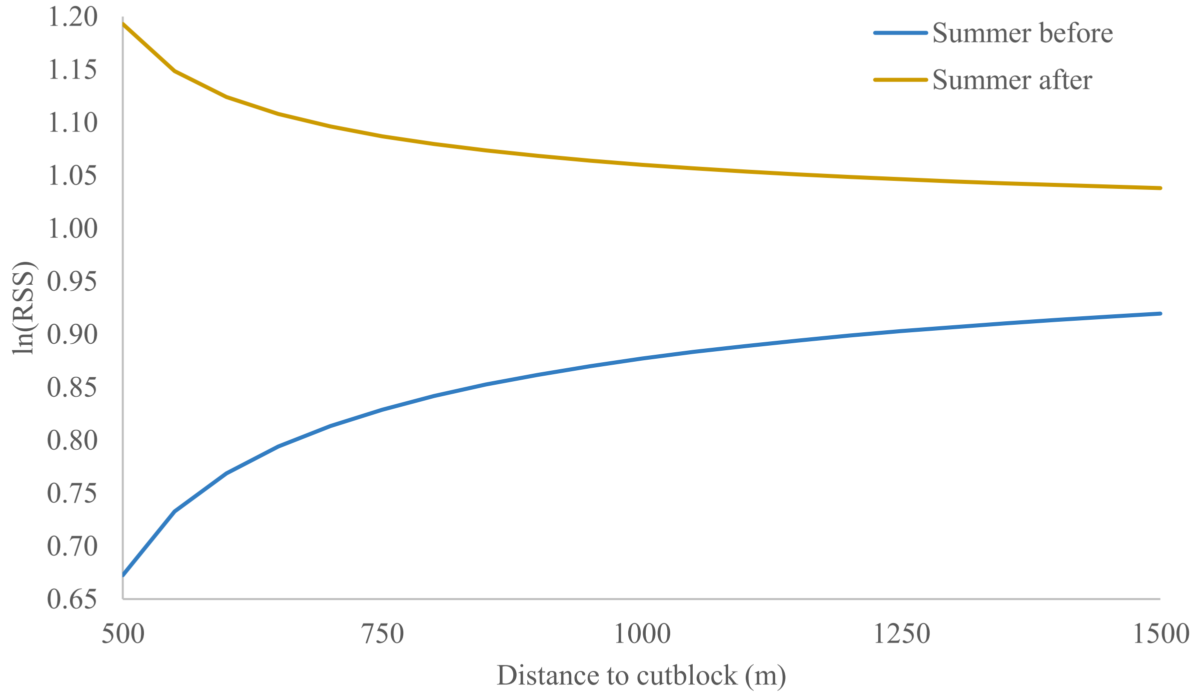

Fig. 2.4. Relative selection strength (RSS) for cutblocks the summer before and after logging activities. We used coefficient estimates from the top-logging models for RSS calculation. For example, when a wolverine was 500 m from a cutblock the summer-before harvest, it was 0.67 times more likely to move away from it than towards it ($x = 500$, $\Delta_x = 450$ m, $\beta = 0.136$).

3 The effects of roads and traffic on wildlife space use: an example with wolverines in Canada

3.1 Introduction

The growth of human populations and our demand for natural resources has caused the expansion of roads into wild areas throughout the world (Hansen et al. 2013). Roads have increased in density for the extraction of oil, gas, and forestry resources with resulting forest fragementation 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 behaviour and abundance of wildlife species (Rytwinski and Fahrig 2012; Latham and Boutin 2015).

Roads are of particular interest to ecologists because they are an interface between humans and wildlife. Roads can have positive effects on wildlife including protection from predators (Berger 2007) or enhanced movement (Whittington et al. 2011). Roads also can have many negative effects (Forman and Alexander 1998; Fahrigh and Rytwinski 2009; Rytwinski and Fahrig 2012), such mortality of wildlife hit by vehicles (de Rosa and Bager 2013; McLintock et al. 2015; Niemi et al. 2017) or displacement of wildlife from habitats adjacent to roads (Shannon et al. 2014; Abrahms et al. 2016). As per the risk-disturbance hypothesis, displacement of wildlife by roads is likely because wildlife percieve roads, and associated human activity, as a predation risk (Frid and Dill 2002). Road avoidance can result in a large reduction of suitable habitats for wildlife in heavily roaded areas (Beyer et al. 2016; D'Amico et al. 2016; Kite et al. 2016).

Road effects on wildlife are often discerned with spatial data of road networks without data on traffic volume (e.g., Krebs et al. 2007; Roever et al. 2010; Beyer et al. 2016; Prokopenko et al. 2017). However, information on the response of wildlife to variations in human use of roads is lost with this approach. The risk-distrbance hypothesis predicts that wildlife percieve high-levels of human activity as more risky than low-levels of human activity. This response is likely because a high frequency of traffic is viewed by wildlife as a large predator group that is a greater threat to their security (Frid and Dill 2002; Jacobson et al. 2016). Therefore, high-traffic roads should be most deliterious to wildlife space use. For example, grizzly bears (*Ursus arctos*) avoided high-traffic roads, crossing roads at night when traffic was low (Northrup et al. 2012). Similarly, squirrels (*Tamiasciurus hudsonicus grahamensis* & *Sciurus aberti*) reduced their movement across roads as traffic-volume increased (Chen and Koprowski et al. 2016) and wild boar (*Sus scrofa*) avoided roads more when traffic-volume was high (Thurfjell et al. 2015). Managers can use this informaiton to faciliate more precise management in dealing with the effects of roads on wildlife (Ruggiero et al. 2007).

Beyond modeling human use of roads, another important aspect of understanding road effects on wildlife is accurately modelling the behaviour of wildlife when near roads. There is evidence that roads can influence both widlife movement and habitat selection (Roever et al. 2010; Jacobson et al. 2016; Prokopenko et al. 2016). Resource selection analyses (Boyce et al. 2016) faciliate evaluating 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 simulatanously (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 traffic on wolverine (*Gulo gulo luscus*) movement and habitat selection on industrial roads in northern Alberta using an iSSA. Wolverines have low-reroductive rates and are wide-ranging, inhabiting circumpolar alpine, forest, and tundra habitats (Hornocker and Hash 1981; Magoun 1985; Persson et al. 2006). The ability of wolverines to move unfettered through the landscape to detect scavenging and foraging opportunties is likely critical to their fitness. These life-history and behavioural traits make species such as wolverines especially sensitive to the effects of roads (Rytwinski and Fahrig 2012). As a result, wolverines in Canada are a *Species of Special Conern* because of the potential threat of roads and other human developments on their habitat quality and survival (COSEWIC 2014).

There have been efforts by researchers to predict the effects of roads on wildlife species based on the species biological characteristics (Ford and Fahrig 2007; Cook and Blumstein 2013; Rytwinski and

Fahrig 2012; Jacobson et al. 2016). For example, large-bodied mammals with low-reproductive rates and large-home ranges are suspected to avoid roads. This behaviour reduces the amount of suitable habitat in roaded areas beyond the road itself but also decreases mortality risk (Rytwinski and Fahrig 2012). Researchers have further attempted to predict wildlife response to roads and traffic based on their predator-avoidance strategies. For example, animals that increase speed to evade predation [e.g., pronghorn antelope (*Antilocapra americana*)] should increase their speed near roads. Species that can sense predation risk from afar should avoid roads [e.g., grizzly bears (*Ursus arctos*)] and increase their avoidance of high-traffic roads. There is also the potential that wildlife can use more than one strategy near roads, such as avoiding roads while also increasing speed when near roads (Jacobson et al. 2016). This behaviour might be especially prevalent in mesocarnivores (Lovallo and Anderson 1996).

Aligned with these theories and the biological characteristics of wolverines, empircal studies have found that wolverines avoid roads (Carroll et al. 2001; Rowland et al. 2003; May et al. 2006; Copeland et al. 2007; Krebs et al. 2007; Bowman et al. 2010; Dawson et al. 2010; Scrafford et al. 2017). However, none of the above studies quantified traffic effects on wolverines or the effect of roads or traffic on wolverine movement. Theory would predict that wolverines avoid roads even with low-traffic volumes and that avoidance increases as traffic-volume increases, ultimately leading to barrier effects of roads (Frid and Dill 2002; Jacobson et al. 2016). However, as a mesocarnivore known for its movement capability, wolverines might also increase their speed near roads and especially near those roads with greater-traffic volume (Jacobson et al. 2016). Therefore, wolverines' road response could potentially encompass behavioral traits of wildlife that both avoid and increase speed when there is predation risk from human activity. The iSSA is uniquely capable of categorizing both behavioral traits simultaneously. We evaluated whether wolverine space use is best represented through road avoidance, increased speed near roads, or a combination or road avoidance and speed.

3.2 Methods

Study area

Our research took place in the boreal forest surrounding the town of Rainbow Lake, Alberta (Fig. 3.1) (population 870, elevation 500m) (119°28'18.705"W, 58°32'22.361"N). Rainbow Lake is the central mixed-wood subregion of the boreal forest. Upland forests in the subregion are comprised of aspen (*Populous 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 1950's, and includes oil, gas, mining, and forestry industries. Non-linear industrial developments include cutblocks, well sites, processing plants, and industrial camps. Linear developments include roads, seismic lines, transmissions lines, and pipeline rights-of-way.

Wolverine radiotelemetry

We established 22 live-traps (Copeland et al. 1995) that were used to capture and radiocollar wolverines over three-winters (Nov. 2013 to Apr. 2016). Livetraps were placed across a range of road densities and separated by approximately 10 km. We captured and collared at least one wolverine in every live-trap. Wolverines were fitted with radiocollars programmed to take GPS fixes every two hours. 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.

Traffic modeling

We installed motion-activated cameras along industrial roads to take pictures of vehicles in each of our three winter field seasons (Nov. 1 to Apr. 1) and one summer field season (Apr. 2 to Oct. 31). Cameras were placed where traffic could be recorded in both directions on both all-season roads and winter roads during the winter. Winter roads are closed to vehicle traffic in summer, so cameras were only placed on all-season roads during 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 Alberta Transportation (station id# 997259 and station id# 997295) traffic-count data.

We identified explanatory variables that explained traffic volume using a mixed-effects linear regression model. 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 as this is the period that oilfield workers are in the field, with "night" from 19:00 to 06:59. We used a random intercept to account for 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 distances. All variables from the summer model were included in the winter model, with the addition of a boolean variable for an all-season ("1") or winter road ("0"). We used AIC_c to determine the best candidate model for winter and summer (Table 3.1). We report marginal (fixed-effects only) and conditional (with random intercept included) r^2 values to estimate goodness of fit. We then used the top winter and summer model to predict vehicle traffic on study area roads.

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 relative to roads and vehicle traffic. We converted GPS radiotelemetry relocations into steps, or lines connecting the start and end points of GPS relocations. We split steps by individual and summer (Apr. 2 to Oct. 31) and winter (Nov. 1 to Apr. 1) seasons. Our winter models 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 1,052 (120, 1298). Our summer models 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 steps of all male and female wolverines in winter and summer seasons using the method of moments, with these four distribtuions defining the distributions of available steps within each sex-season category. We matched each observed step with twenty available steps whose turn angle and step length were randomly drawn from a uniform and gamma distributions, respectively. Attributes (e.g., habitats, step length) of observed steps were compared with available steps using a conditional logistic regression model, fitted to each individual in each season (Fieberg et al. 2010).

Our 'base model' included the explantory 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 (for details see Avgar et al. 2016). 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 to vary with time to twilight. We expected the associetd coefficient to be negative, supporting the hypothesis thatwolverines increased movement at twilight (Mattison et al. 2010) when their prey [snowshoe hare (*Lepus americanus*), beaver (*Castor canadensis*)] were most active (e.g., Mech et al. 1966; Dyck and Macarthur 1992; Buech 1995). We modelled 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 (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. All distances were in meters and were log-transformed to allow their effect to decay as distance of available or used points to the feature increased (Table 3.2).

The 'avoid model' represented the hypothesis that the primary response of wolverines to road proximity is avoidance (Table 3.2). 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 (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. 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 three-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 there. This model included all the variables in the base, avoid, and speed models (Table 3.2).

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 a minimum of 10% of available steps within 2 km of road. We calculated AIC_c weights for each model set for each wolverine-season. We used a non-parametric bootstrap of these values (10,000 iterations) to calculate an 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 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 non-parametric bootstrap (10,000 iterations) of coefficient estimates (Fieberg et al. 2010). To account uncertainty in parameter estimateswe weighted the coefficient estimate by the inverse-variance. We calculated an average for males and females seperately. We also calculated a population level bootstrapped average and stratified the sample by male and female.

We calculated mean movement rates for each wolverine in each season by multiplying the shape and parameters from the gamma distribution. We varied the value of an explanatory variable of interest, while holding all other variables with step length included at the median value of observed steps. We used a sample-size weighted non-parametric bootstrap (10,000 iterations) of movement rates from each wolverine to calculate the mean movement rate (metres/2 hours) for male and female wolverines.

3.3 Results

Traffic modeling

The top model of traffic volume in winter was the full model (AIC_c weight = 1.00, Table 3.1). All other models had minimal support from the data. Traffic volume was greater on all-season roads versus winter roads, greater during the day than at night, and increased further from the town of Rainbow Lake (Fig. 3.2) and Highway 58. The best winter model explaind 51% (marginal; fixed effect only) and 71% (conditional; fixed and randome effects) of the observed variability. The traffic model in summer only included all-season roads because winter roads are closed during the summer. The top traffic model in summer was the reduced model (AIC_c weight = 0.92, Table 3.1), with all other models garnering minimal support from the data. The best summer model explaind 64% (marginal; fixed effect only) and 78% (conditional; fixed and randome effects) of the observed variability. Traffic volume increased during the day on all-season roads (Table 3.1).

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 (SD = 0.24 km/km^2) and 0.58 (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 the behavioural strategy that wolverines use near roads in winter is avoidance and speed [AIC_c weight = 0.47 (0.36-0.58)] (Table 3.3). However, based on overlapping confidence intervals, there also was support for the speed model alone [AIC_c weight = 0.36 (0.26-0.46)]. We report coefficient estimates from the avoid and speed model because of the overall greater AIC_c weight (Table 3.2). We calculated a population (male and female combined) coefficient average becuase male and female wolverines showed similar space-use patterns (Table 3.3). 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), however, wolverines increased their movement near roads and increased their movement even more as traffic volume increased (Fig. 3.3, Table 3.3).

Summer

The average density of roads within male (*n* = 11) and female (*n* = 9) summer 95% minimum convex poygons (MCPs) was 0.66 (SD = 0.19 km/km^2) and 0.55 (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 behaioural strategy wolverine use near roads is to avoid and speed near roads. The avoid and speed model [AIC$_c$ weight = 0.53 (0.42-0.65)] had 2.52 times the support as the speed model [AIC$_c$ weight = 0.21 (0.11-0.30)] (Table 3.3). At the population level, wolverines increased their speed near to civil twilight and streams. Wolverines also avoided roads, increased speed near roads, and increased speed more near roads with greater traffic volumes. Females showed results identical to that at the population level except they avoided streams in summer. Males increased speed near civil twilight and near streams while also selecting for streams. The only road variable that influenced males (confidence interval of coefficient estimate not crossing zero) was an increase in speed when near high-traffic roads (Table 3.3).

3.4 Discussion

Roads are risky habitats for wildlife, therefore, wildlife are theorized to display a variety of behaviours when near roads that mirror their natural methods of reducing predation risk (Frid and Dill 2002). These behaviours including avoiding, speeding, pausing, or not responding to roads (Jacobson et al. 2016). We evaluated the behavioural strategies that wolverines used when faced with predation risk from roads and vehicle traffic. We found support for the hypothesis that wolverines both avoid and increase speed when near roads. As traffic-volume increased, wolverines increased their speed even more. Another mesocarnivore, the bobcat (*Felis rufus*), is also suggested to avoid and increase speed near roads (Lovallo and Anderson 1996). Elk (*Cervus elaphus*) display both behaviours as well (Prokopenko et al. 2017). Therefore, our results provide additional evidence that some wildlife species use a blend of behavioural strategies to reduce predation risk from roads. We would suggest that wildlife behaviour when near roads should be viewed as a continuum between distinct categories (e.g., avoiders, speeders) proposed by Jacobson et al. (2016). The iSSA is uniquely capable of testing for both movement and habitat selection

(Avgar et al. 2016) and is therefore a useful tool for elucidating the diversity of wildlife behaviours when near roads.

Of the two behavioural strategies displayed by wolverines, the strength of evidence indicates speed is their key method of reducing predation risk. Although coefficient estimates for distance to road consistently indicated road avoidance, and the avoidance and speed model had the greatest AIC_c weight in both seasons, coefficient estimates overlapped zero for males in both seasons and females in summer. The more consistent signal from the data, both in winter and summer, was that wolverines increased their speed near roads. Wolverines might have evolved this predator avoidance technique in response to sharing landscapes with apex predators such as wolves (*Canis lupus*), mountain lions (*Puma concolor*), black bears (*Ursus americanus*), and grizzly bears that attempt to chase wolverines from scavenging carcasses they also are feeding upon. Mortality from apex predators has been documented throughout North America (Krebs et al. 2004) and in our study where we found three male wolverines killed by wolves near roads.

Our results provide support for the predictions the risk-disturbance hypothesis makes regarding the effects of traffic volume on wildlife. The hypothesis states that wildlife should perceive high-levels of human activity as greater risk than low-levels of human activity, either because of increased noise or because they perceive more traffic as a larger group of predators (Frid and Dill 2002). Moreover, wildlife that approach high-traffic roads are more likely to be at the road when a vehicle is there, prompting more readily a fleeing or avoidance response. Our results support these predictions, as wolverine displacement increased as traffic-volume increased. Therefore, we would suggest that high-traffic roads are more likely to displace wolverines than low-traffic roads. This result would not have been evident had we only investigated the space use of wolverines relative to roads without traffic-volume attributes. Our study therefore joins the body of literature that finds road effects on wildlife vary based on the magnitude of human activity (e.g., Northrup et al. 2012; Thurfjell et al. 2015; Chen and Koprowski et al. 2016). This information could be used to more precisely manage the effects of human activity on wildlife space use.

We found that even low-traffic roads were deleterious to wolverine space use. This result is to be expected for species such as wolverines whose biological characteristics make them sensitive to even low levels of human activity (Jacobson et al. 2016). Our traffic model indicated that low-traffic roads are winter roads as well as remote all-season roads. Winter roads are single-lane roads used by industry between December and March to access pipelines, well sites, or other industrial assets off all-season roads and are generally created with a layer of ice. Industry workers are not allowed to drive on winter roads during the summer because of potential for damage to soils and vegetation, leaving them free of traffic in summer months. Besides avoiding low-traffic roads because of their association with current or past human activity, wolverines might also be avoiding low-traffic roads because of predation risk from wolves that use these roads to hunt ungulates (Whittington et al. 2011; Lesmerises et al. 2012; Dickie et al. 2016). This suggestion is purely speculative as we did not measure predator activity on roads, although we would suggest that wolverine response to predator activity on roads or other features (e.g., streams and seismic lines) would 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, such as low-density and wide-ranging mammals with low-reproductive rates, are at low-risk of mortality from roads. We recorded a single mortality from vehicles in our study area, although nine wolverines were reportedly struck by vehicles immediately north in Zama City, Alberta between September 2013 and April 2015 (data provided by the Government of Alberta). Therefore, there is mixed results for this prediction. The larger hypothesized effect of roads on 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). There could be a considerable loss of habitats for wolverines in landscapes with extensive road networks. Although there is the potential that displacement has negatively affected wolverines at the population level in some regions (Bowman et al. 2010; Fisher et al. 2013; Heim 2015), wolverine populations in Rainbow Lake appear robust based on our capture history of individuals. This likely means that the threshold of road density, or the magnitude of human use of roads, necessary to illicit negative effects at the population level has not yet occurred in our study area. This suggestion is speculative and should be the subject of further research.

Our results provide ideas for how to mitigate the negative effects of roads and other linear developments (traveled by people) on wolverine populations. Although wolverines would benefit from a reduction in road density, removing or reclaiming roads currently used by industry to access assets is probably infeasible. However, reclaiming roads once they lose utility to industry would likely benefit wolverine populations. During the planning phase of projects, managers could cluster industrial developments (housing near to industrial plants) on the landscape so that barriers to wolverine movement and sources of mortality are concentrated. Vehicle speeds should also be adjusted to reduce risk to wolverine populations. This is not the case on winter roads, as vehicle speeds are generally low. However, traffic speed on high-traffic roads (two-lane paved and dirt roads) should be reduced to lessen the risk of vehicles striking wolverines. We did show that wolverines increased their movement at civil twilight and often were attracted to streams [likely to hunt beaver (Lofroth et al. 2007)] and used them as movement corridors. Therefore, we would suggest that wolverines might cross roads at streams near civil twilight. Thus, speeds on high-traffic roads should be lowered at twilight/evening and at stream crossings (bridges) to reduce the potential for wolverine mortality as well as the mortality of other wildlife species.

The growing popularity of off-highway vehicle (OHVs) use in wild areas is of conservation concern for land and wildlife managers (Boyle et al. 1985). The extraction and mapping of natural resources leaves an abundance of linear features, such as seismic lines (Schneider 2002), that are often used by recreationalists in nearby population centers. Use of linear features by OHVs can have significant deleterious effects on wildlife populations (Wasser et al. 2011; Pigeon et al. 2016; Ladle 2017). Researchers suspect that linear feature use by OHVs negatively affects wolverines (Krebs et al. 2007; Fisher et al. 2013) although this has never been tested. We observed limited use of seismic lines by OHVs, which is likely related to the remoteness of our study area from population centers. We suggest this study area characteristic might explain some of the reasons why wolverines were not displaced by seismic lines (Scrafford et al. 2017) as they have been in other landscapes (Fisher et al. 2013). Although our study area had limited recreational activity, our finding that increased vehicle traffic negatively effects wolverine space use could provide insight into how high levels of OHV use might impact wolverines. Reclaiming seismic lines so they are not available for motorized recreation, or blocking access during sensitive times of the year (denning), might benefit wolverines in areas close to population centers.

Table 3.1. Candidate models, model results, and coefficient estimates for the modeling of vehicle traffic in Rainbow Lake, Alberta. We used a mixed-effects linear model to model traffic volume in winter and summer seasons. For candidate models, we report Akaike's Information Criterion (AIC_c), change in AICc between the current and top model (ΔAIC_c), the marginal $r^{2(1)}$ (fixed effects) and the conditional $r^{2(2)}$ (fixed and random effects).

Season	Model	Explanatory variables	ΔAIC_c	AIC_c weight	$R^{2(1)}$	$R^{2(2)}$
Winter	Full	Road type + day + dist. to town + 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

Table 3.2. Candidate iSSA models used to evaluate the relative influence of roads and traffic on wolverine movement and habitat selection.

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

[a] lnSL = $\log_e$ of step length (m)

[b] "start" and "end" designate that the point value comes from the start and end of the step, respectively

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

[d] traffic = traffic volume (vehicles/12 hours) is ln-transformed

Table 3.3. AIC_c model weights from iSSA models in winter and summer. For each wolverine, we calculated the AIC_c weight of each model within the full model set (*n* = 4). When then bootstrapped the model weights (10,000 iterations, weighted by sample size and stratified by sex) for a mean and 95th percentile confidence bound.

Model	Winter mean AIC_c weight	Lower bound	Upper bound	Summer mean AIC_c weight	Lower bound	Upper bound
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

Table 4. Coefficient averages and confidence intervals from the top wolverine iSSA model in winter and summer. Coefficient averages and confidence intervals are from a bootstrapped sample that is weighted by the inverse-variance. Bold font indicates that the 2.5 and 97.5 percentile values do not cross zero. The average of population coefficients is measured with a bootstrap sample that is stratified by sex, such that both males and females contribute equally to the sample.

Winter model – avoid and speed	Population average β ($n = 25$)	Female average β ($n = 11$)	Male average β ($n = 14$)
ln(SL) x time to civil twilight	**-0.621**	**-0.598**	**-0.642**
D2. stream	**-0.076**	**-0.048**	**-0.098**
ln(SL) x d2. stream	**-0.025**	**-0.023**	**-0.026**
D2. rd	0.011	0.015	0.008
D2. rd x traffic	0.011	0.018	0.005
ln(SL) x d2. rd	**-0.041**	**-0.048**	**-0.035**
ln(SL) x 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) x time to civil twilight	**-1.064**	**-1.084**	**-1.044**
D2. stream	-0.015	**0.063**	**-0.094**
ln(SL) x d2. stream	**-0.025**	**-0.025**	**-0.024**
D2. rd	**0.046**	**0.065**	0.027
D2. rd x traffic	0.000	0.003	-0.003
ln(SL) x d2. rd	**-0.023**	**-0.036**	-0.009
ln(SL) x d2. rd x traffic	**0.005**	**0.004**	**0.006**

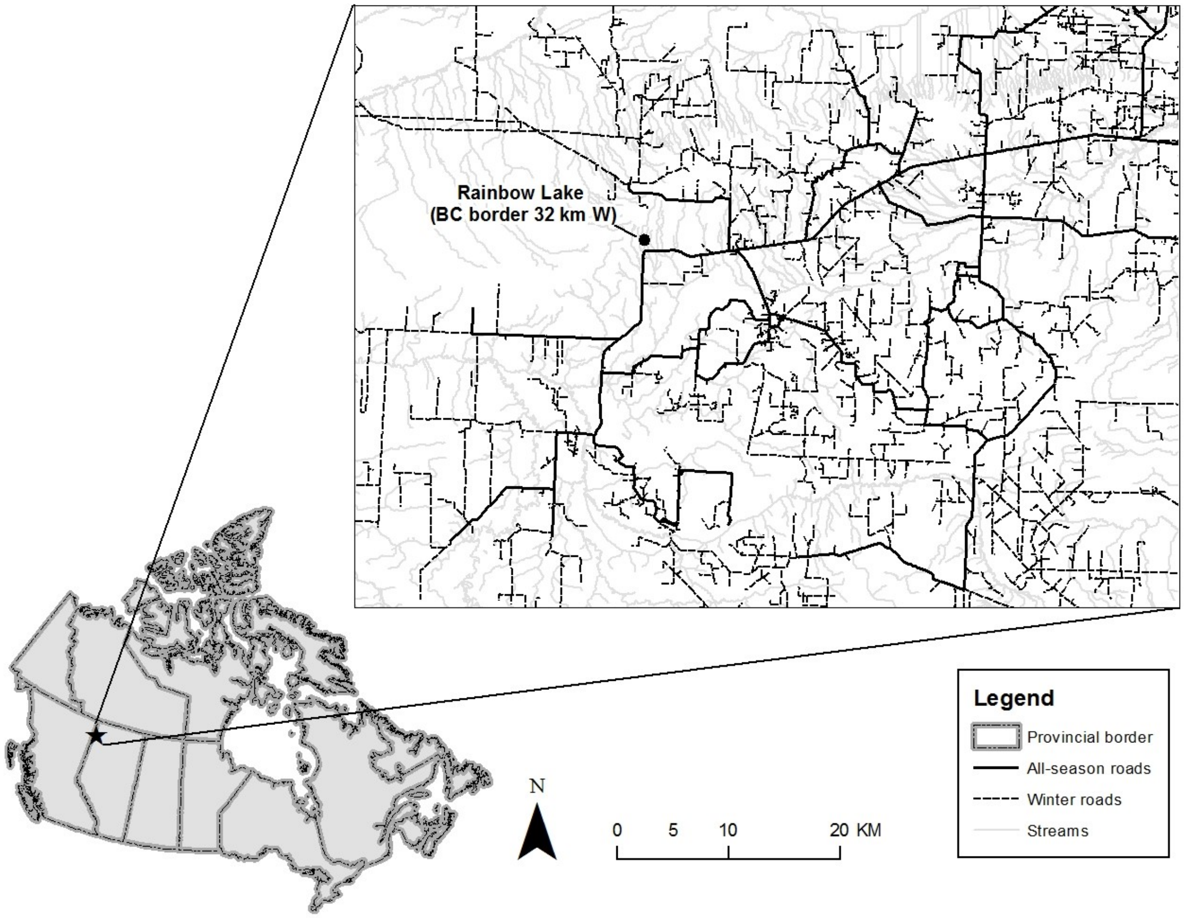

Fig. 3.1. Map of the road network and streams surrounding the study area near the town of Rainbow Lake, Alberta (119°28'18.705"W, 58°32'22.361"N).

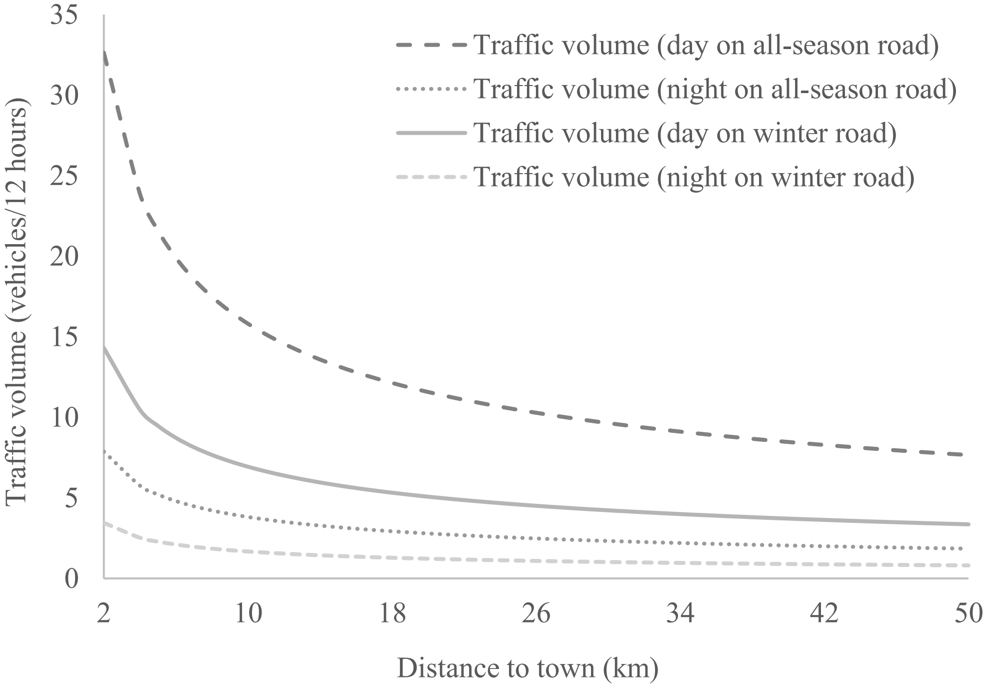

Fig. 3.2. Predicted traffic volume on all-season and winter roads in winter during day and night periods relative to distance to the town of Rainbow Lake. We held distance to highway 58 at its mean for predictions.

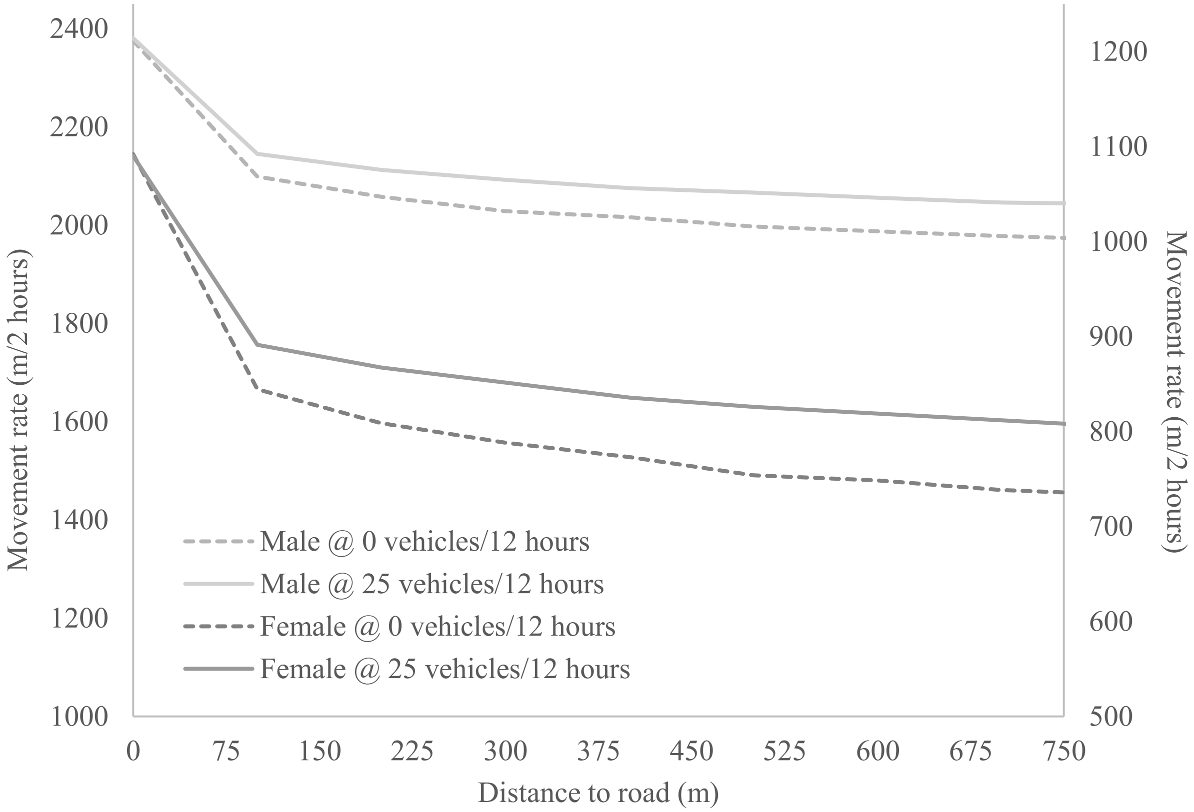

Figure 3.3. Wolverine movement rate relative to distance to road and traffic volume in winter. We calculated the movement rate for each wolverine at 100 m intervals, starting at 0 m from a road and ending at 750 m from a road, while holding all other modeled variables with step length at the median of available steps. We then bootstrapped these estimates (10000 times, weighted by sample size of observed steps) to produce a mean.

4 A comparison of the space use of wolverines during dispersal and home-range movements

4.1 Introduction

The dispersal of wildlife between metapopulations has significant implications for population dynamics and health (Trakhtenbrot et al. 2005; Clobert et al. 2009). Although there are many benefits to dispersal, including disassociation with kin and overcrowding, animals also face risks including starvation, predation, and aggression from conspecifics (Sweanor et al. 2000; Waser et al. 2013). Knowledge of the space use of wildlife during dispersal movements, especially for low-density large carnivores, can aid the understanding of behavioral strategies and habitats important for connectivity (Squires et al. 2013; Morrison et al. 2014; Jackson et al. 2016). Connectivity of animal populations is important considering the rapid expansion of human footprint in wild areas (Pickell et al. 2013; Pickell et al. 2016) and climate change mediated shifts in species distributions (Hilty et al. 2012; Travis et al. 2013).

Dispersal movements are outside the confines of the home range and into novel environments (Burt 1943; Dall and Johnstone 2002). These movements serve to identify potential territories for establishment and reproduction and often occur at sexual maturity (Bowler and Benton 2005; Clobert et al. 2009). Whereas an animal in its home range likely has stored information in its memory of foraging locations (Van Moorter et al. 2016) and predation risk, an animal in a novel environment is unaware of these opportunities and risks (Dall and Johnstone 2002). Therefore, it is suggested that animals behave differently during dispersal to increase survival (Schtickzelle et al. 2006; Soulsbury et al. 2011), including, reduced movement to facilitate predator detection and resource acquisition (Zollner et al. 2005).

Besides changes in movement and foraging, animals also might alter their selection of habitats during dispersal. Dispersing animals may select habitats that increase the likelihood of foraging opportunities (Elliot et al. 2014) or select habitats that make movement more energetically efficient (Killeen et al. 2014) or safe from predation risk (Elliot et al. 2014; Morrison et al. 2015). There also has been an indication that dispersing animals have greater tolerance for human disturbance than those that are within the home range (Elliot et al. 2014; Abrahms et al. 2016; Gaston et al. 2016). This type of behavior could increase the mortality of dispersing animals and therefore reduce connectivity.

The importance of dispersal and habitat connectivity to metapopulation dynamics, in combination with limited conservation funds to preserve lands, have placed the priority on scientist to accurately define habitats important for corridors (Chetkiewicz et al. 2006). Corridor habitats for a given species are often designated using habitat suitability analyses of GPS relocations within the home range (Johnson 1980; Chetkiewicz and Boyce 2009). Because of the uniqueness of habitat selection during dispersal, and especially during long-distance movements, there has been an effort for landscape connectivity models to be based on habitat requirements during dispersal movements (Abrahms et al. 2016; Benz et al. 2016; Blazquez-Cabrera et al. 2016; Jackson et al. 2016). Habitat selection models derived through step-selection analyses (Fortin et al. 2005; Avgar et al. 2016) incorporate movement into defining the availability domain and therefore might provide a more realistic representation of habitats important for connectivity (Squires et al. 2013; Killeen et al. 2014; Keeley et al. 2017).

Our aim was to compare the space use of wolverines (*Gulo gulo luscus*) during dispersal and home-range movements in the northern boreal forest of Alberta. Wolverines are a low-density mesocarnivore that resides in mountain, boreal, and tundra habitats (Slough 2007). Mountain wolverines exist as island populations reliant on dispersal for population fitness and sustainability (Schwartz et al. 2009; Inman et al. 2013). Much like metapopulation dynamics with lynx (*Lynx canadensis*) (Murray et al. 2008), dispersal from wolverine populations in Canada might be important to the sustainability of southern wolverine populations (McKelvey et al. 2014). Therefore, it is critical to understand the space use of wolverines during dispersal events so that efforts can be made to increase connectivity. There has been research on the timing and dispersal distances of wolverines in Scandinavia but there was no fine-grain analysis of habitat selection or movement during these events (Vangen et al. 2001). Habitat corridors have been discerned for wolverines in the northern United States (Copeland et al. 2010; Inman et al. 2013; McClure et al. 2016), however, this research based corridors on habitat selection within the home range.

We tested several hypotheses related to the space use of wolverines during home range and dispersal movements. Aligned with Zollner et al. (2005), we hypothesized that movement rates of wolverines are greater when the wolverine is in the home range and that foraging rates are greater when the wolverine is dispersing. We also hypothesized that during dispersal wolverines are more attracted to habitats that increase movement efficiency and that wolverines use riskier habitats during dispersal. We included roads, streams, and forest cover into our habitat models. Aligned with predictions from other studies (May et al. 2006; Copeland et al. 2007; Inman et al. 2013), we suggest roads will be avoided by wolverines within the home range. This is because wolverines associate roads with the predation risk because of their use by predators (Whittington et al. 2011; Dickie et al. 2016) and humans. We also predicted that wolverines in the home range would select for streams for foraging and movement (Copeland et al. 2007) and select forests for cover and foraging opportunities (Heim 2015). During dispersal, we would predict that wolverines select for roads and increase their use of streams to increase their movement efficiency. We also predicted that forests would be more strongly selected during dispersal because of the cover from predation that forests provide.

4.2 Methods

Study area

Our research took place in the boreal forest surrounding the town of Rainbow Lake, Alberta (population 870, elevation 500m) (119°28'18.705"W, 58°32'22.361"N). Rainbow Lake is the central mixedwood subregion of the boreal forest. Upland forests in the subregion are comprised of aspen (Populous tremuloides). white spruce (Picea glauca), and jackpine (Pinus banksiana). Wetlands comprise 30% of the landscape and include peatlands (bogs and fens) with black spruce (Picea mariana) forests. Topography in the Rainbow Lake area is relatively flat except for narrow river valleys and an escarpment on the northern border of the study area. 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 1950's, and includes oil, gas, mining, and forestry industries. Non-linear industrial developments include cutblocks, well sites, processing plants, and industrial camps. Linear developments include roads, seismic lines, transmissions lines, and pipeline rights-of-way.

Wolverine radiotelemetry

We established 22 live-traps (Copeland et al. 1995) that were used to capture and radiocollar wolverines over three-winters (Nov. 2013 to Apr. 2016). Livetraps were placed across a range of road densities and separated by approximately 10 km's. We captured and collared at least one wolverine in every one of our live-traps. Wolverines were fitted with Telemetry Solutions store-on-board (Quantum 4000) or Tellus Ultralight satellite-Global Positioning System (GPS) radiocollars programmed to take GPS fixes every two hours. 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.

Categorizing movements of wolverines

Dispersal has been documented for wolverines between November and July, with most cases occurring from February (denning) through April (Inman et al. 2012). Exploratory movements are more random and occur near dispersal and all the way through the fall (Vangen et al. 2001). Therefore, we decided to restrict our analysis of radiotelemetry data from February through September to align with the start of the denning period and end when GPS radiocollars often failed (battery). We refer to both exploratory and dispersal movements as "dispersal".

Our first step was to distinguish movement types of wolverines. We plotted graphs of net-squared displacement (NSD), which is the squared distance from each GPS relocation for that wolverine to its first GPS relocation in the data set (Turchin 1998). We used the NSD patterns to identify movement types that could be considered as home range, exploratory, or nomadic (Bunnefeld et al. 2011). Movements were within the home range if there was a flat NSD through time and exploratory if the NSD spiked or indicated they left the home range. Movements were considered nomadic if NSD continuously changed through time. We categorized all GPS relocations from wolverines that showed consistent nomadic movements during the entirety of their monitoring as dispersal. For wolverines with exploratory movements, we only categorized GPS relocations as dispersal if they occurred outside of its 80% MCP. If the NSD graph showed the animal consistently stayed within a home range, we categorized all its GPS relocations as belonging within the home range. If a wolverine showed dispersal movements, its movements within the home range were not used in further analyses. We applied the clustering algorithm created by (Knopff et al. 2009) to all wolverine GPS relocation in dispersal and home-range categories to identify the locations of feeding or resting events. The algorithm returns a cluster centroid and radius that we used to create a polygon for each cluster. We then selected all GPS relocations that were outside these polygons as being associated with movement. Both home range and dispersal movements outside of these polygons were then used for wolverine-space use modeling.

Movement and foraging rates

We estimated an average movement rate for steps in the home range and during dispersal using a non-parametric bootstrap, with the 95th percentile of values as the confidence bound. If movement rate was greater in the home range rather than during dispersal, we would expect the confidence bound between the two estimates would not overlap. We evaluated the time a wolverine spent foraging/resting during dispersal and home-range movements by dividing the number of GPS relocations inside cluster polygons by the total number of GPS relocations. If wolverines spend more time foraging during dispersal than they do while in the home range, we would expect to see an increase in the percent of time spent within clusters during dispersal. We calculated the average time spent in a cluster for each wolverine using a non-parametric bootstrap and weighted this average by the total number of GPS relocations collected for the wolverine. We would suggest support for the hypothesis that wolverines spend more time foraging during dispersal if the average time spent at a cluster during dispersal is greater than during home-range movements and the 95th percentile confidence bound does not overlap zero.

Integrated step-selection analysis

We used an integrated step selection analysis (iSSA) to derive parameters for describing the relative probability of wolverine-space use (Avgar et al. 2016). We first converted GPS radiotelemetry relocations associated with movement outside of clusters into steps or lines connecting the start and end points of GPS relocations. Within the home range, there were 4,058 steps among 9 males and 3,607 steps among 9 females. For dispersal, there were 1,064 steps among 4 females and 1,434 steps among 6 males. We fit a gamma distribution to the observed steps of male and female wolverines using the method of moments, with these four distributions defining the distributions of available steps for each sex-category combination. We matched each observed step with twenty available steps that were randomly sampled [random step headings were uniformly distributed (0-2π)]. These steps shared the same starting point as the observed step but differed in the location of end points. Attributes of observed steps were then compared with available steps using conditional-logistic regression.

We fit a single model to animals in each category and then compared the direction of coefficient estimates to gauge support for our hypotheses. We included the log of step length (m) (lnSL) to modify the population level shape parameter originally employed in sampling the available steps. We included the logged distance (m) from the step's end point to the nearest road, stream, and upland forest to test wolverine habitat selection relative to these features. We log-transformed distances to allow their effect to decay as distance of available or used points to the feature increased. We predicted that wolverines in the home range would select streams and forests (negative coefficient) but avoid roads because of predation risk (positive coefficient). We also included an interaction between lnSL and distance to road and stream at the step's start to test whether wolverines increase or decrease movement when near these features. We predicted that wolverines in the home range would increase movement near roads because of predation risk and increase movement near streams because they are used as movement corridors. We would suggest support for the hypothesis that home-range and dispersal space use is similar if coefficient values do not change between the models. We would suggest support for the hypothesis that streams and roads are important for wolverines during dispersal if they select more strongly for these features during dispersal than when they are in the home range. We ran individual models for each wolverine to account for inter-individual variability in space-use behavior and pseudoreplication. We used a two-stage modeling approach for population level coefficient estimates, where fixed-effects models were estimated for individuals and then averaged with restricted maximum likelihood estimation (TwoStepCLogit in R version 3.2.5, Craiu et al. 2011). An explanatory variable is suggested as being important for all wolverines in the population if the 95% confidence estimate of the population coefficient does not cross zero. For an estimate of effect size, we report the relative selection strength (RSS) for one landscape location relative to another, given the difference in a habitat attribute between the two locations, while holding all other habitat attributes at a constant level (Avgar et al., under review). We used landcover type 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. Wetland spatial data were identified using the Duck Unlimited Enhanced Wetland Classification (Ducks Unlimited Canada 2013). Roads and stream spatial data were obtained from IHS.

3.3 Results

A map of some dispersal movements can be seen in Fig. 4.1. There were four males and two females that showed NSD patterns indicative of exploratory movements. There were two males and two females that showed nomadic NSD patterns. Most dispersal movements occurred between March and April (SF4.1-4.10). The 100% MCP around GPS relocations for wolverines with evidence of dispersal movements was approximately five-times larger than the 100% MCP of animals that only displayed home-range movements (Table 4.1). The straight-line distance from the center of a wolverine's home range to the furthest exploratory movement ranged from 22.70 to 204.66 km. The straight-line distance between the further apart GPS relocations for nomadic wolverines ranged from 36.54 to 114.89 km (Fig. 4.2).

We found support for the hypothesis that male movement rates are greater in the home range than during dispersal. Females movement rates were similar during dispersal and in the home range. Female and male dispersal-movement rates were similar in magnitude (Table 4.2). We found support for the hypothesis that males stopped to forage/rest more often during dispersal. Males were at feeding/resting sites 46% (95th percentile = 36-53) of the time when in the home range and 58% (95th percentile = 55-60) of the time when dispersing. We did not find evidence that females stopped to forage/rest more often during dispersal. Females were at feeding/resting sites 53% (95th percentile = 49-58) of the in the home range and 57% (95th percentile = 49-64).

We found support for the hypothesis that male wolverines are attracted to habitat features during dispersal that make movement more efficient and are risky (Table 4.3). Males in the home range selected streams and forests and increased their movement when near both streams and roads. Males showed some indication of selecting for roads in the home range, but the confidence bound of the estimate crossed zero, indicating variation in male response. During dispersal, males selected for roads and streams while also increasing their speed near these features. Forests were less important to males during dispersal than in the home range (Table 4.3). When 500 m from a road during home-range movements, a male was 1.04 times more likely to move towards the road than away. During dispersal movements, a male was 1.20 times more likely to move towards the road. When 500 m from a stream during home-range movements, a male was 1.52 times more likely to move towards the stream than away. During dispersal, a male was 1.60 times more likely to move towards the stream. We did not find that forests were more strongly selected during dispersal movements versus home-range movements (Fig. 4.3). Overall, our results indicated that males selected more strongly for roads and streams during dispersal and that forests were not important during dispersal.

We found some support for the hypothesis that female wolverines are attracted to habitat features that make movement more efficient and are risky (Table 4.3). However, the RSS was weak for many explanatory variables (Fig. 4.4). Females in the home range selected forests and increased their speed near roads and streams. Females weakly selected for streams and roads, however, the confidence bound of distance to roads and streams for females crossed zero, however, the positive coefficient value indicate that females avoided roads and streams (especially when combined with an increase in movement near these features). Females continued to select for forests during dispersal, but roads and streams had a muted effect regarding both habitat selection and movement (confidence bound crossed zero) (Table 4.3). When 500 m from a road during home-range movements, a female was 0.91 times more likely to move away from the road than towards the road. During dispersal movements, a female was 1.00 times more likely to move towards the road than away. When 500 m from a stream during home-range movements, a female was 0.38 times more likely to move away from the streams than towards streams. During dispersal movements, a female was 1.08 times more likely to move towards the stream than away. When 500 m from a forest during home-range movements, a female was 1.15 times more likely to move away from the forest than towards the road. During dispersal movements, a female was 1.17 times more likely to move towards the forest than away (Fig. 4.4). Overall, our resulted indicated that females selected more strongly for roads, streams, and forests during dispersal, however, roads and streams had confidence intervals that crossed zero.

3.4 Discussion

We found differences in the space use of wolverines when in the home range versus during dispersal. These differences were more obvious for males than for females. Compared to when within the home range, male wolverines during dispersal decreased movement rate, stopped to rest and forage more often, and selected strongly for landscape features we suspect are important to movement efficiency. To our knowledge, this is the first quantitative study investigating fine-scale movement and habitat selection patterns of dispersing wolverines. These data can be used to assess the connectivity of wolverine populations.

The timing of dispersal in our study area aligned with the approximate date of female parturition (February and March, Inman et al. 2012). We found that dispersals could be short excursions, or exploratory movements, outside of natal areas. Dispersals also could be long-distance movements. We observed one male that dispersed 70 km and then returned to settle approximately 20 km from his natal range. Another male wolverine traveled 205 km to the Northwest Territories and then settled in British Columbia (where he was killed by a trapper). We also observed a female with nomadic movements travel 115 km (straight-line distance). This movement capacity is likely why North America wolverine populations are panmictic (Kyle and Strobeck 2002). We found male dispersals were two times as far as females and more males showed dispersal movements than females. Male biased dispersal and philopatry by females has resulted in genetic structure among female wolverine populations (Wilson et al. 2000).

The movements of dispersing wolverines enlarged their home-range estimates. The average home-range size of resident wolverines (those without evidence of dispersal movements) in our study area

(306 km^2 for females and 951 km^2 for males) were near estimates of adult wolverines in the Greater Yellowstone Ecosystem (Inman et al. 2012). The idea that one resident male territory overlaps three female territories has been proposed in other studies (Perrson et al. 2010) and that ratio also holds based for our data. Slightly smaller home-ranges in Sweden might be because of abundant semi-domestic reindeer (Perrson et al. 2010). Dispersing wolverines, conversely, used areas that were nearly five-times larger than residents (1,153 km^2 for females and 4,999 km^2 for males).

A comparison of wolverine behaviours when within the home range versus during dispersal indicated that males during dispersal moved slower and stopped more often to forage or rest. Long-distance movements by males in the home range could be directionally oriented toward foraging patches or caches stored in their memory (Van Moorter et al. 2016). These enhanced movements might also be necessary to defend the boundaries of large-home ranges (Persson et al. 2010; Inman et al. 2012). Males might not move as quickly during dispersal to facilitate the detection of predators in new landscapes. Males might stop to forage more often during dispersal to fully use available resources because of the uncertainty associated with foraging opportunities in new landscapes. These behaviours by males align with optimal strategies for dispersal that have been hypothesized through simulations (Zollner et al. 2005) and suggest that energy availability and predation risk might be limiting factors during dispersal.

Unlike males, female wolverines did not show differences in movement and foraging rates when compared between dispersal and home-range movements. The movement results might indicate that females move slowly and cautiously both within and outside the home range, as females are generally thought to be more risk-averse than males (Krebs et al. 2007; Scrafford et al. 2017). Females also have smaller home-ranges, which might not require increased speed to defend, and therefore reduces the disparity between home range and dispersal movement rates. The similar rate of movement between males and females during dispersal might highlight that this rate is optimal for maximizing detection of predation risk and efficient energy use.

Although males were attracted to roads and streams when within the home range, their attraction to these features increased during dispersal. Starvation is a major source of wolverine mortality (Krebs et al. 2004) and the risk of starvation might be high for dispersing wolverines in novel landscapes. Therefore, wolverines should select for landscape features that improve their chances of survival. We would suggest males select more strongly for streams and roads during dispersal because these features improve the movement efficiency of wolverines and increase their foraging opportunities. Streams likely provide wolverines with foraging [e.g., beavers (*Castor canadensis*)] and scavenging opportunities [e.g., wolf (*Canis lupus*)-killed moose (*Alces alces*)]. Logging setbacks have protected uplands adjacent to riparian areas in Alberta (AFPS 2006) which might provide efficient movement because of a limited understory. Roads also might provide efficient movement corridors for wolverines, as has been found for other wildlife species (Roever et al. 2010; Dickie et al. 2016), and road edges could provide foraging opportunities for snowshoe hare (*Lepus americanus*) and grouse (e.g., *Falcipennis canadensis*).

Female habitat selection during dispersal was more flexible than during home-range movements. Whereas females showed avoidance of roads and streams during home-range movements, these features appeared to be either innocuous or attractive to females during dispersal. As was found for males, this result provides some support for the idea that linear features are important during dispersal for movement. However, females selected for forests during home-range movements and continued this selection during dispersal movements. We suspect this result is because cover is important in reducing predation risk (Morrison et al. 2014).

We would suggest that dispersal corridors for wolverines should be comprised of habitats important to males because they disperse long-distances and are therefore more likely to reach isolated metapopulations. It has been suggested that habitats important for wolverines during home-range movements also are important for dispersal (McClure et al. 2016). Our data suggest that this is true for males but that linear features might be especially important during dispersal. Females showed some flexibility in their habitat selection during dispersal which means corridor placement could be more flexible (Jackson et al. 2016). However, we would warn that our small sample of females (n = 4) and wide confidence bounds for coefficient estimates limits our ability to be conclusive about dispersal habitat selection.

The attraction of wolverines to roads during dispersal is a conservation concern. Dispersing wolverines in our study and others had high-levels of mortality (Vangen et al. 2001; Krebs et al. 2004). The attraction of wolverines to roads during dispersal, combined with the potential that they are food limited, might attract wolverines to high-risk areas, such as traplines (trap bates) or industrial camps (Johnson et al. 2005), where their mortality could be increased. This could ultimately reduce the survival of dispersing animals and therefore reduce metapopulation connectivity. We also would caution that the predominant roads in our study area were winter roads (0-5 vehicles/12 hours) and that high-traffic industrial roads are likely a hindrance to movement and dispersal (Scrafford et al., in preparation). We would suspect that paved highways also are a hindrance to dispersal.

Table 4.1. The home-range size (100% MCP, km^2) of wolverines that showed evidence of dispersal movements versus those wolverines that only stayed within the confines of a home range. Averages were calculated with a non-parametric bootstrap.

Sex	Status	Home-range size (km^2)	Lower 95th percentile	Upper 95th percentile
Male (n = 6)	Dispersal	4,999	2,669	8,170
Male (n = 8)	Home range	951	834	1,077
Female (n = 4)	Dispersal	1,153	451	2,429
Female (n = 11)	Home range	306	285	325

Table 4.2. Wolverine movement rates within the home range versus during dispersal. We calculated the average based only on movements outside of foraging clusters. The average was calculated with a nonparametric bootstrap.

Sex	Model	Average step length (m)	Lower 95th percentile	Upper 95th percentile
Male (n = 8)	Home range (n = 4,058)	2733	2652	2813
Female (n = 11)	Home range (n = 3,607)	1769	1708	1828
Male (n = 6)	Dispersal (n = 1,434)	1581	1476	1688
Female (n = 4)	Dispersal (n = 1,064)	1778	1676	1885

Table 4.3. Wolverine movement and habitat selection within the home range and during dispersal. We used an integrated step-selection function to derive parameter estimates. All explanatory variables are the log-transformed distance (m) to a feature. An asterisk represents whether the coefficient estimates (β) crosses zero. The standard error (SE) of the coefficient estimate also is reported.

Male	Home-range movement β	SE	Dispersal movement β	SE
ln[a](SL[b])	0.501*	0.110	0.584	0.172
ln[road(end[c])]	-0.012	0.016	-0.061*	0.024
ln[stream(end)]	-0.142*	0.028	-0.161*	0.027
ln[forest(end)]	-0.021*	0.010	-0.006	0.025
ln(SL) x ln[road(start[d])]	-0.063*	0.011	-0.035*	0.014
ln(SL) x ln[stream(start)]	-0.061*	0.012	-0.057*	0.018
Female	Home-range movement β	SE	Dispersal movement β	SE
ln(SL)	0.086	0.174	0.389*	0.171
ln[road(end)]	0.032	0.028	-0.002	0.029
ln[stream(end)]	0.033	0.038	-0.025	0.065
ln[forest(end)]	-0.048*	0.017	-0.054*	0.025
ln(SL) x ln[road(start)]	-0.043*	0.018	-0.026	0.022
ln(SL) x ln[stream(start)]	-0.035*	0.010	-0.063	0.034

[a] log-transformed

[b] step length (m)

[c] measured from the end of a used or available step (m)

[d] measured from the start of a used or available step (m)

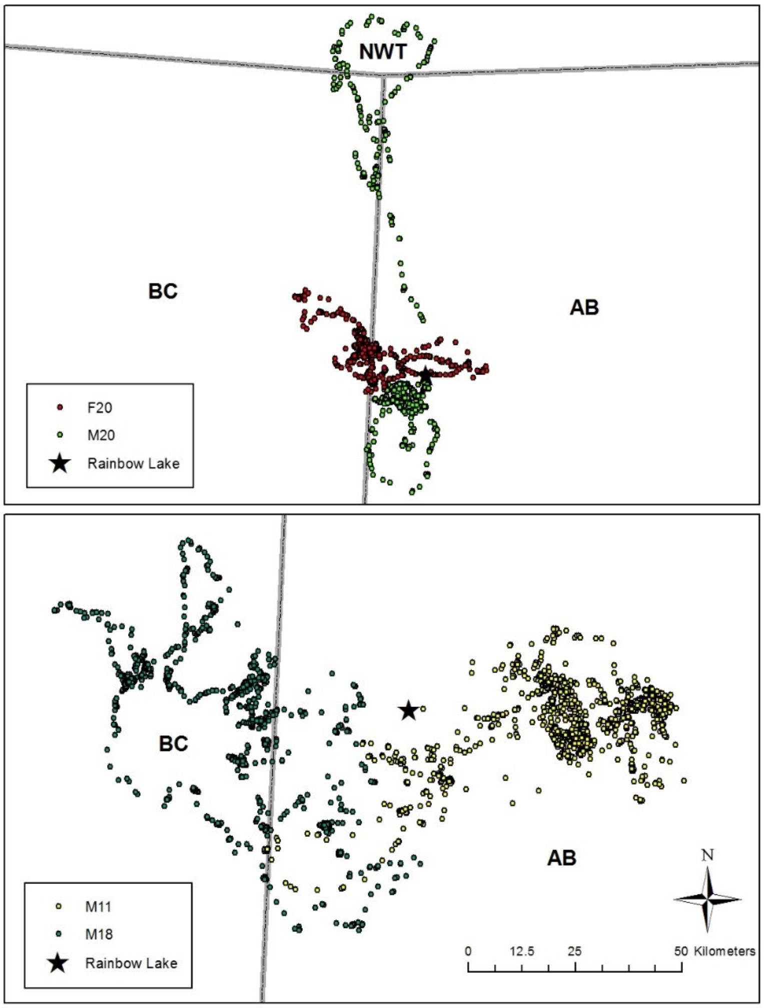

Fig. 4.1. Sample of dispersal movements in Rainbow Lake, Alberta. Wolverine F20 and M18 displayed nomadic movements while wolverine M11 and M20 displayed exploratory movements. Data were collected between February and August and GPS relocations were collected at two-hour intervals.

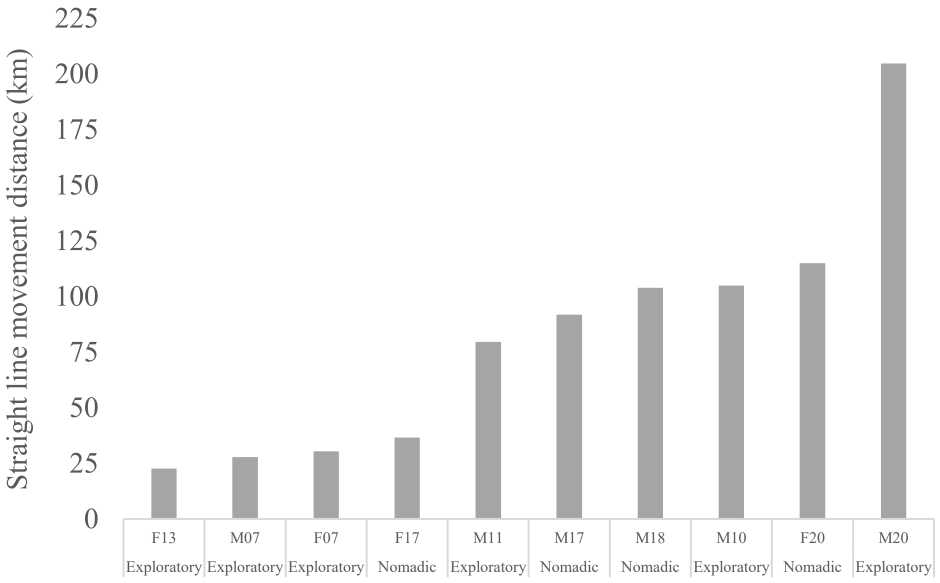

Fig. 4.2. Dispersal distances by wolverines. The exploratory distance is from the home-range center to the GPS relocations furthest from the home-range center. The nomadic distance is the distance between the furthest separated GPS relocations.

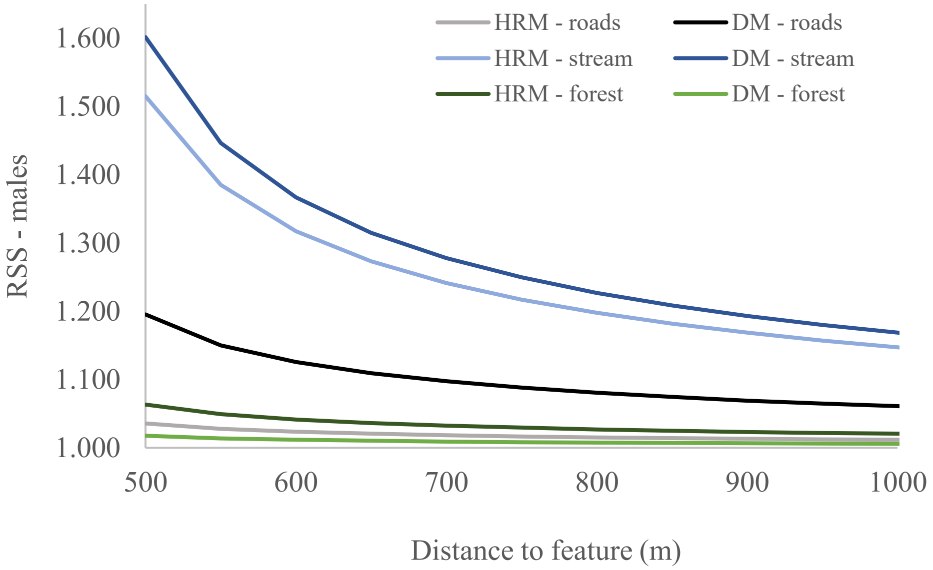

Fig. 4.3. Relative selection strength (RSS) for roads, streams, and forests during male home-range (HRM) and dispersal movements (DM). For example, when a male was 500 m from a stream during dispersal movements, it was 1.60 times more likely to move towards it than away.

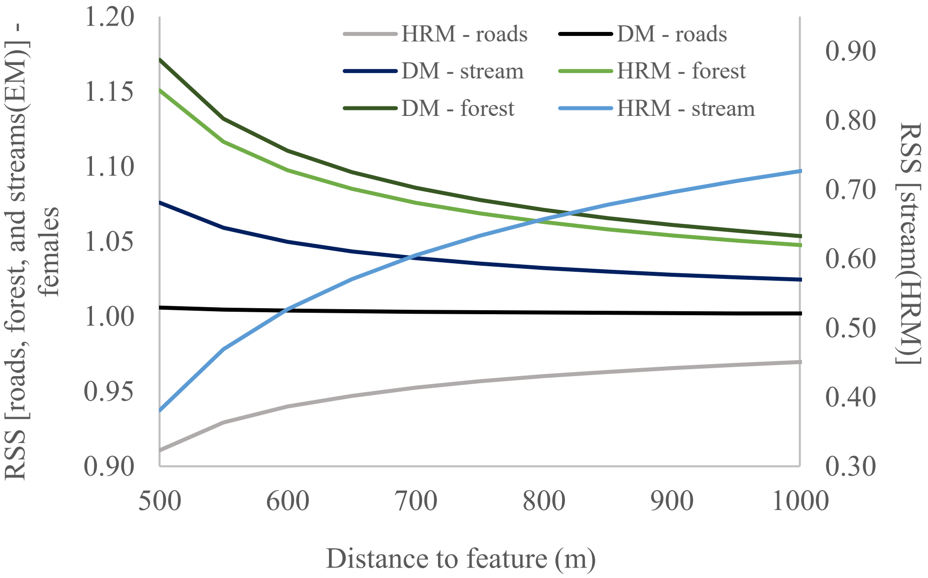

Fig. 4.4. Relative selection strength (RSS) for roads, streams, and forests during female home-range (HRM) and dispersal movements (DM). For example, when a female was 500 m from a forest during dispersal movements, the wolverine was 1.02 times more likely to move towards than away from the forest.

5 Wolverine (*Gulo gulo luscus*) foraging in the northern boreal forest

5.1 Introduction

The acquisition of prey is energetically costly and risky for carnivores (Carbone et al. 2007). The infrequent discovery of large-feeding events by many facultative scavengers (e.g., Mattison et al. 2016), coupled with their likely importance to energy budgets, makes the development of effective foraging at these events critical to their fitness. Optimal foraging theory provides a basis from which to test the effectiveness of feeding strategies (Charnov 1976). Our aim is to investigate factors influencing the wolverine's encounter rate, residency time, and return time to feeding sites in lowland boreal forests of northern Alberta. This information will enable a better understanding of the energetic constraints on wolverine populations.

Quantifying the rate at which carnivore's encounter prey is fundamental to our knowledge of their effects on prey populations and to predator management (Roemer et al. 2009; Merrill et al. 2010). A null hypothesis of encounter rates assumes that foods are discovered randomly or at regular times and locations (Pyke 1984). Therefore, spatial and temporal variables would be ineffective at differentiating encounter rates. An alternative hypothesis would assume that encounter rates change based on environmental factors (Pereira et al. 2014). For example, predators increase their interactions with prey as the density of prey increases (Holling 1959). Such a functional response is evidenced from an increase in kill rates of ungulates by large carnivores in spring when ungulate neonates are at a high-density (Scheel 1992; Adams et al. 1995; Knopff et al. 2010; Metz et al. 2012).

Once prey is acquired, an animal must make choices on how to allocate time to feeding. The marginal value theorem (MVT) can be used to predict an optimal amount of time to spend feeding based on the return rate. Per the law of diminishing returns, the energetic return from a feeding site should decrease with time spent at the site because of biomass depletion. An animal should decide to leave when the costs of foraging equal the average return from all feeding sites available to the animal (Charnov 1976). However, the information animals use to determine foraging strategies can extend beyond the biomass currently available (Valone and Brown 1989). Time spent at a feeding site could be a function of competition or missed-opportunity costs (Brown 1988; Stewart et al. 2016). For example, one would expect an animal to reside at a feeding site longer if there was competition for forage from conspecifics (Schrader et al. 2006). The time an animal takes to leaves a patch, or it's quitting-harvest rate (Mukherjee et al. 2009), should be when the sum of costs associated with foraging exceed the energy gained from the site. Optimal foraging strategies also should also be reflected in the recursion rates to feeding sites. The time it takes for an animal to return to a site should be a function of the resources available at the site. For example, large herbivores will make quick returns to highly productivity feeding sites (Siedel and Boyce 2015; Van Moorter et al. 2016) or recently grazed areas to use regrowth (Bar-David et al. 2009). As with time at the site, variables such as opportunity costs and competition should influence the return interval (e.g., Siedel and Boyce 2015).

We defined a large-feeding site for a wolverine as a site where a wolverine has either scavenged the remains of an ungulate or killed a medium- to large-bodied prey (e.g., beaver). GPS clustering techniques developed for large carnivores have proven successful at identifying kill sites (Webb et al. 2008; Knopff et al. 2009). However, it is uncertain whether these techniques are sufficient for quantifying foraging of facultative scavengers or mesocarnivores because of their unique behaviors at feeding sites, such as caching (Ebinger et al. 2016), relative to more pure predators such as cougars (*Puma concolor*) (Knopff et al. 2009) or wolves (Webb et al. 2008). Instead of attempting to differentiate kills from scavenging events for grizzly bears (*Ursus arctos*), Ebinger et al. (2016) used clustering algorithms to differentiate small- from large-biomass carcasses. One first aim was to examine the predictive ability of the cluster algorithm created by Knopff et al. (2009) for identifying large-feeding sites found by wolverines.

We then used these large-feeding sites to acquire a better understanding of the foraging ecology of wolverines. Our first set of competing hypotheses was that the time-to-encounter of large-feeding sites by wolverines were random, or that encounters were influenced by season and satiation. Wolverines rely on scavenging ungulates for food during the winter (Lofroth et al. 2007; van Dijk et al. 2008; Inman and Packilia 2015; Mattison et al. 2016). This may be due to the increased mortality of ungulates during winter through starvation and increased predation (Coulson et al. 2001; Hebblewhite 2005), and because wolves often leave more meat at carcasses in the winter (Metz et al. 2012). These factors provide an increased availability of ungulate carcasses to be scavenged in the winter. In summer, however, it is believed that wolverines switch to predation on small mammals (Magoun 1987; Inman and Packilia 2015), and we therefore predict that encounter rates with large-feeding sites will increase in winter when scavenging opportunities are plentiful. We also would predict the time-to-encounter is negatively related to the amount of time spent at the previous feeding site because of satiation (e.g., Whittington et al. 2011).

Next, we examined wolverine behaviours at feeding sites by using residency time (RT) in a patch and return time after departing a patch (TtoR) metrics (Courant and Fortin 2012; Seidel and Boyce 2015; Van Moorter et al. 2016). Our first hypothesis was that RT and TtoR are best explained by the cumulative time a wolverine spent at a feeding site. We assume that time spent within a patch is a surrogate for the effort required to acquire resources. Therefore, we predict the law of diminishing returns will cause a decay in RT and TtoR as the cumulative time spent by a wolverine within a large-feeding site increases. Our competing hypothesis was that TtoR and RT are related to variables in addition to time spent in a patch including competition, opportunity costs, and seasonality. Competition for resources is likely greatest when there are proximate competitors (Schrader et al. 2006). Therefore, as a form of exploitive competition, we would predict that RT will increase and TtoR will decrease when other wolverines also are detected at the site. We expect that a wolverine should leave a feeding site when the opportunity costs of staying increase above the value of the available biomass (Brown 1988). Because wolverines are territorial (Persson et al. 2010), they will likely move quickly between their feeding sites to reduce kleptoparasitism from conspecifics or other scavengers and facilitate first access to the most accessible meat. Therefore, we would predict that RT decreases and TtoR increases when there are multiple large-feeding sites being used concurrently by the wolverine. Seasonality is also likely to affect wolverine foraging behavior because it influences food availability throughout the landscape. Although winter is a time when wolves are killing more ungulates and providing increased numbers of carcasses for scavenging, it is overall a time of resource scarcity. During the summer months wolverines have access to a wider variety of small prey (Magoun 1987; Inman and Packilia 2015). Therefore, we would expect TtoR to decrease and RT to increase in winter to maximize energy gain from large-feeding sites.

Previous studies have investigated factors influencing the kill rates of wolverines on reindeer in Scandinavia (Mattison et al. 2016), and wolverine foraging at bait sites (Heim 2015; Stewart et al. 2016), but we are unaware of research on RT and TtoR at natural-feeding sites. Our data provide insight into the adoption of foraging behaviors by wolverines and the importance of large-feeding events to the overall diet of wolverines.

5.2 Methods

Study Area and animal handling

Our research took place in the boreal forest surrounding the town of Rainbow Lake, Alberta (population 870, elevation 500m) (119°28'18.705"W, 58°32'22.361"N). Rainbow Lake is within the central mixedwood subregion of the boreal forest. Upland forests in this subregion are comprised of aspen (*Populous tremuloides*). white spruce (*Picea glauca*), and jackpine (*Pinus banksiana*). Wetlands comprise 30% of the landscape and include peatlands (bogs and fens) with black spruce (*Picea mariana*) forests. Topography in the Rainbow Lake area is relatively flat except for narrow river valleys and an escarpment on the northern border of the study area. 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 1950's, and includes the oil, gas, mining, and forestry industries. Non-linear industrial developments include cutblocks, well sites, processing plants, and industrial camps. Linear developments include roads, seismic lines, transmissions lines, and pipeline rights-of-ways. The predator community in the Rainbow Lake area includes the grey wolf (*Canis lupus*), black bear (*Ursus americanus*), lynx (*Lynx canadensis*), fisher (*Martes pennanti*), pine martin (*Martes americana*), and ravens (*Corvus corax*). The potential large prey of wolverines in Rainbow Lake include moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), caribou (*Rangifer tarandus*), and beaver (*Castor canadensis*).

We used 22 live-traps to capture and radiocollar wolverines over three-winters (Nov. 2013 to Apr. 2016). Livetraps were placed across a range of road densities and separated by approximately 10 km. We captured and collared at least one wolverine in each of our live-traps. Wolverines were fitted with Telemetry Solutions store-on-board (Quantum 4000) or Tellus Ultralight satellite-Global Positioning System (GPS) radiocollars programmed to take GPS fixes every two hours. 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**.**

Event modeling

We visited GPS clusters in the field to identify feeding events by wolverines. We deemed a cluster worth visiting if two consecutive GPS relocations were within 200m of each other (Knopff et al. 2009). We searched the area for prey remains or bed sites. If the wolverine was at a site where there was a fresh-killed ungulate, either from wolves or hunters, it was designated a large event. Likewise, we would designate a predation event on a beaver as large event. If there were minimal prey remains (e.g., a femur) it was identified as a small event. Moreover, bed sites and kill sites of small prey (e.g., snowshoe hare, grouse) were designated as small events.

We then used a cluster algorithm, developed for identifying kill sites of cougars in southwest Alberta (Knopff et al. 2009), to give spatial and temporal attributes to clusters visited in the field. These attributes included the cluster radius (distance from geometric center of cluster to further GPS relocation), actual points (the number of GPS relocations within 200 m of the geometric center of the cluster), away points (the number of points outside of 200 m of the geometric center of the cluster), distance (average distance of each GPS relocation to the geometric center of the cluster) and total points (away points + actual points) (Knopff et al. 2009). If there were multiple clusters created by the algorithm within proximity (500 m) of the observed event, we used the cluster created by the algorithm that was initialized earliest.

We next used logistic regression to distinguish the attributes of small (designated as a “0”) versus large (designated as a “1”) events. We created candidate models with explanatory variables that were not correlated ($r^2 \leq 0.70$) (Table 5.1). We used Akaike Information Criterion adjusted for small sample size (AIC_c) to evaluate competing models and designated the top model as the one with the greatest AIC_c weight. We report coefficient estimates and 95% confidence intervals for variables within the top model. We evaluated the accuracy of the model with a receiver operator curve (ROC) and the predictive capacity of the model with k-fold cross validation. The top model was then used to identify clusters from the rest of the GPS relocations that were likely to be large events. The probability cutoff used to designate a large event was determined after investigating specificity and sensitivity curves.

Time to new event

We used a mixed-effects model of Cox proportional hazards (CPH) to identify explanatory variables related to the time to a new event (TTNE). The CPH model measures the risk that an event will occur at any given time, with an increase in the relative risk corresponding to a decreased time to a new event. TTNE was the time (days) between events. The time of origin was the first event and TTNE was calculated through the last event. Therefore, an animal had to have at least two events over the course of GPS monitoring to be included in the analysis. Many wolverines had periods of monitoring separated by periods without monitoring because the GPS radiocollar was not operational. When there was a gap in monitoring, the time or origin was based on the beginning of the new monitoring period.

A list of candidate models can be seen in Table 5.2. The hypothesis that TTNE is random is represented with model #1 which only includes an intercept term. Model #2 represents the hypothesis that TTNE is not random and instead varies based on season [1 = winter (Nov. 1 to Apr. 1), 0 = summer (Apr. 2 to Oct. 31)] and previous time (PT), which is the amount of actual points (see event modeling above) in the prior event (*t-1*). We used individual wolverine as a random intercept to account for pseudo-replication and we used AIC_c for model selection. We designated the top model as the one with the greatest AIC_c weight and report the relative hazard of explanatory variables from the top model.

Residency time

We model residency time (RT) at a large event using a mixed-effects CPH. An increase in the risk of an event occurring translates to a reduction in RT. We used the first GPS relocation of the event as the time of origin. We then identified all GPS relocations that were within the radius of the event (identified with cluster algorithm, Knopff et al. 2009) but after the time of origin. We included GPS relocations until 90 days after detection of the event. Using these GPS relocations, we identified separate visits to a cluster if a wolverine was outside the radius of the cluster for ≥ 1.90 days, which corresponds to the average duration that a wolverine was at a site during its first visit. We calculated RT as the time from the first GPS relocation of a visit to the last GPS relocation (e.g., relocation before animal left for ≥ 1.90 days). Candidate models for explaining RT can be seen in Table 5.2. Model #1 has only an intercept term. Model #2 represents the hypothesis that RT is best explained by the sum of the wolverine's times spent at the feeding site [cumulative time spent at a feeding site (CT)]. Model #3 represents the hypothesis that RT might best be explained by variables in addition to CT including competition, opportunity costs, and seasonality. The number of concurrent events (CE) is a count of the number of times the range of dates (minimum and maximum date of an event) that the wolverine visited the feeding site intersected the range of dates of all other events visited by that wolverine. We also included season (based on start time of RT) and "wolverine". The explanatory variable "wolverine" indicates if another wolverine was found at the event based on radiotelemetry relocations (1 = wolverine, 0 = no wolverine). Random effects included a random intercept for the event nested within a term for individual wolverines. Candidate models can be seen in Table 5.2 and top models were determined using AIC_c.

Time to return

We modeled time to return to an event (TtoR) with a mixed-effects CPH. An increase in the risk of an event occurring translates to a reduction in TtoR. TtoR was calculated by subtracting the date and time of the last GPS relocation before departing the event from the date and time of the first GPS relocation in the following revisit. A list of candidate models can be seen in Table 5.2. Model #1 included only an intercept term. Model #2 included only CT whereas model #3 included CT, CE, wolverine, and season, with winter or summer based on the month that that wolverine left the feeding site.

Random effects included a random intercept for the event nested within a term for individual wolverines. Top models were identified using AIC_c.

5.3 Results

Event modeling

We found evidence of 21 clusters where a wolverine killed a beaver, 12 clusters where a wolverine was scavenging on the remains of a large-ungulate carcass, 48 clusters that were bed sites without prey remains, 2 grouse kills, 9 hare kills, and 15 small-scavenge events (e.g., single bone, skull). We calculated the averages of the attributes of clusters using a non-parametric bootstrap (Table 5.3). We found significant overlap in the characteristics of events associated with beaver and ungulates (Table 5.3). Therefore, we suggest that combining beaver and ungulate events into a single "large event" category is justified to increase the sample size of large events for modeling purposes.

We used a logistic regression model (binomial family, log-link) to differentiate large ($n = 33$) from small clusters ($n = 74$). The top model included the number of away and actual GPS relocations (AIC_c weight = 0.90). The next best model, including only the total number of GPS relocations associated with the cluster, had minimal support from the data (AIC_c weight = 0.07, Table 5.1). Large clusters had a greater number of actual points ($\beta = 0.181$, $SE = 0.041$) and away points ($\beta = 0.734$, $SE = 0.020$) (Fig. 5.1). The 10-fold cross validation prediction error for the top model was 0.12 and the ROC score was 0.94, indicating excellent predictive capacity and accuracy, respectively.

We used the top model to predict large events throughout the GPS data of all wolverines. We only considered a cluster to be a large event if it's probability was greater than ≥ 0.7. Using this probability cut-off, the top model identified 115 large-feeding sites in the winter and 135 large-feeding sites in the summer. Females had 64 events ($n = 12$ females) in winter and 65 events ($n = 11$ females) in summer whereas males had 71 events ($n = 13$) in winter and 50 events ($n = 11$ males) in summer.

Time to new event

The average TTNE in winter ($n = 92$ events, $n = 22$ wolverines) was 19.46 (95th percentile = 16.07−23.13 days) and in summer ($n = 109$ events, $n = 19$ wolverines) was 12.82 (95th percentile =

10.04−15.99 days) (Fig. 5.3). We found support for the hypothesis TTNE is not random for wolverines. Model #1 assumed TTNE was random and had an AIC$_c$ weight of 0.02. Model #2 was our top model (AIC$_c$ weight = 0.98) and included the explanatory variables PT and season (Table 5.2). Contrary to our prediction, the relative risk of TTNE decreased in winter versus the summer. The top model also indicated that the relative risk of TTNE decreased with increasing PT, however, the confidence interval for PT crossed zero which indicates variation in its effects (Table 5.2).

Residency time

The average RT per visit in summer (n = 415 visits, n = 22 wolverines) was 0.74 (95th percentile = 0.61−0.88 days) and in winter (n = 235 visits, n = 24 wolverines) was 1.50 (95th percentile = 1.24−1.77 days) (Fig. 5.3). The average total time (RT summed across all visits) spent at large-feeding site in winter was 3.27 (95th percentile = 2.74−3.84 days) and 2.03 (95th percentile = 1.69−2.41 days) in summer (Fig. 5.3). The average number of visits by a wolverine per large-feeding site was 2.18 (95th percentile = 2.06−2.27 days) and the average number of concurrent events visited was 3.25 (95th percentile = 3.07−3.44 days). The average RT during a visit with another wolverine at the feeding site (n = 248) was 1.12 (95th percentile = 0.99−1.45 days) and without a wolverine (n = 402) was 0.89 (95th percentile = 0.73−1.06 days). We found support for the hypothesis that RT and TtoR are best explained by variables in addition to CT. Model #2 included only CT and had no support from the data (AIC$_c$ weight = 0.00, Table 5.2). Model #3 was most supported by the data (AIC$_c$ weight = 1.00) and included the explanatory variables CT, CE, season, and wolverine. As predicted, the relative risk of RT increased with CT (Fig. 5.3) and CE and decreased with season and wolverine (Table 5.2).

Time to return

The average TtoR after each visit in summer (n = 264, n = 22 wolverines) was 8.39 (95th percentile = 7.18−9.74 days) and in winter (n = 138 events, n = 24 wolverines) was 10.12 (95th percentile = 7.99−12.56 days) (Fig. 5.3). The average number of departures from a large-feeding site was 2.89 (95th percentile = 2.77−3.01 days) and the average number of concurrent events visited per large-feeding site was 3.55 (95th percentile = 3.31−3.78 days). We found support for the hypothesis that TtoR is better explained by variables in addition to CT. Model #2 included only CT and was not supported by the data (AIC_c weight = 0.00). Model #3 was the top model (AIC_c weight = 1.00) and included CT, CE, season, and wolverine. As predicted, the relative risk of TtoR decreased with CT (Fig. 5.3), CE, and season. The confidence interval for wolverine crossed zero indicating a variable effect on RT (Table 5.2).

5.4 Discussion

We identified the behaviours of wolverines at large-feeding sites in the boreal forest of northwest Alberta. We provide evidence that foraging strategies are not dictated singularly by time spent at the feeding site and that wolverines take into consideration numerous other factors, such as competition and opportunity costs, when making foraging decisions. These foraging strategies are likely critical to ensure wolverines fully utilize the scant resources available in the low-productivity niche they inhabit (Inman et al. 2012).

We found that models created to detect kill sites by cougars (Knopff et al. 2009) successfully differentiated and predicted large-feeding sites (beaver kill sites, ungulate scavenging sites) of wolverines from smaller events such as resting or killing small prey. The use of these algorithms for identifying large-foraging events by facultative scavengers has been questioned because of their diverse behaviours and prey types (Ebinger et al. 2016). However, wolverine behaviour at kill sites appears comparable to an apex predator, in that they stay proximal to feeding sites during foraging events. Moreover, relative to grizzly bears, wolverines rarely forage herbaceous vegetation within patches which might inaccurately appear as a kill site. Therefore, these methods offer opportunities to learn about variations in the availability of large-feeding sites to wolverines.

We found support for the hypothesis that wolverine encounter-rates with large-feeding sites are not random but change seasonally. However, TTNE decreased in the summer rather than in the winter as we had predicted. Increased rates of predation are common for terrestrial predators when their prey is abundant (Scheel 1992; Adams et al. 1995; Knopff et al. 2010; Matz et al. 2012). For example, the increased availability of reindeer calves in summer caused wolverines to switch from scavenging in the winter to predation in the summer (Mattison et al. 2016). We suspect wolverines in our study switched from scavenging and some predation on beaver in the winter to mostly predation on beaver in the summer. The reduced TTNE in summer is likely because beavers are more available to wolverines in summer when they are out of their lodges (e.g., Gable et al. 2016). Some of the events we predicted in summer could be scavenging. However, wolves often prey switch from ungulates to beavers in summer which means ungulate carcasses are less available to wolverines in summer (Peterson and Page 1988, Latham et al. 2013).

The reduction in TTNE in summer is also likely related to prey size. We found that the total handling time (sum of RT across all visits) at a large-feeding site was lower in the summer versus the winter. A potential explanation for this pattern is that it takes less time to handle a beaver in summer than to dig into a beaver lodge and kill a beaver in winter. Moreover, it likely takes longer to scavenge an ungulate carcass in winter than kill and consume a beaver in summer. Likewise, cougars in southwest Alberta had lower handling times in the summer because their prey were more often ungulate neonates rather than adults and were therefore quick to consume (Knopff et al. 2010).

We interpret our encounter rate similarly to a kill rate for an apex predator in that it relates how often wolverines finds a substantial energy source. For ease of comparison with Mattison et al. (2016), we put our TTNE into encounters per 30 days (1.54/30 days in winter and 2.34/30 days in summer). This rate aligns very closely with kill rates on reindeer in Scandinavia (1-2 reindeer/30 days, Mattison et al. 2016). The average cougar kill rate of ungulates was 0.8 ungulates/week which is approximately 3.2 kills/30 days (Knopff et al. 2010) and Amur tigers (*Panthera tigris*) made 4.54 kills/30 days (Miller et al. 2013). Wolverines do not encounter large-feeding sites as often as more pure predators such as cougars and tigers. However, wolverines are opportunists and can fill the void between large-feeding events with small prey such as snowshoe hare or grouse.

When a large-feeding site was first discovered by a wolverine they spent a considerable amount of time feeding within the vicinity. As predicted, the RT at a feeding site decreased and TtoR increased as the cumulative time (CT) spent at the feeding site increased. This pattern is likely driven by available biomass, with wolverines decreasing RT and increasing TtoR as biomass becomes harder to acquire from the feeding site. We suggest this result provides evidence that wolverine foraging strategies at large-feeding sites conform to the law of diminishing returns that forms the basis of the marginal value theorem (Charnov 1976). This strategy has the added benefit of reducing competition at feeding sites by ensuring that easily-accessible meat is consumed before competitors can detect and feed at the site.

We found support for the hypothesis that wolverine behaviour at large-feeding sites was explained by more than simply the cumulative time they had spent at the site. Our finding of an increase in RT if there were other wolverines present at the site demonstrates exploitive competition by wolverines to maximize current gain when there are proximate competitors. This strategy also has been detected for group-living goats (*Capra hircus*) (Shrader et al. 2007). Wolverines are likely able to detect other wolverines that have visited feeding sites because they have scent marked the area (Pulliainen and Ovaskainen 1975; Koehler et al. 1980). This might trigger a response by wolverines to reside in the area longer to protect the kill, consume more, or to cache food items in the surrounding area.

Besides competition, variables important to explaining wolverine behaviours at feeding sites included opportunity costs and seasonality. The opportunity costs associated with residing at a large-feeding site for an extended period are likely high for wolverines because it reduces time that could be used for patrolling home ranges for conspecifics (Persson et al. 2010; Inman et al. 2012). We found evidence that wolverines often are visiting numerous large-feeding sites throughout their home range at any time. Wolverines probably revisit these sites during routine patrols of their home range. We found that how long a wolverine stays at one of these feeding sites is negatively related to how many other sites the wolverine is currently visiting. Wolverines decreased RT at sites as the number of concurrent sites they also visited increased. This behaviour might reflect a trade-off wolverines make to reduce their time at feeding sites so that they are still able to visit all sites, procuring the easiest meat from carcasses, while also having time to patrol their home range. The ability to cache or consume the most easily accessible meat is likely critical because we found evidence that when a wolverine has multiple large-feeding sites it takes the wolverine longer to return, giving an opportunity to competitors to feed at these sites (Heim 2015).

The seasonal difference in wolverine behaviour at large-feeding sites might be related to energy-availability on the landscape. Wolverines increased their RT and decreased their TtoR in winter. Taken together, this result could indicate that the environment in the winter has less available energy for wolverines to use which causes them to reduce energy expenditure. For example, the cost of leaving a large-feeding site might be high in winter because of the effort required to move on the landscape when there is deep snow (Crete and Lariviere 2003; Wright and Ernst 2004). Many wildlife species show similar patterns of reduced energy expenditure, or torpor, when available energy decreases (Aleksiuk and Cowan 1969; Renecker and Hudson 1986; Parker et al. 1996).

Our study highlights the availability of large-feeding sites in the lowland boreal forest and the strategies wolverines use to maximize energy gain at these sites while minimizing opportunity costs and competition. We suggest these methods could be used to quantify wolverine foraging behaviour at large-feeding sites throughout their circumpolar range. We expect that the availability of large-feeding sites and wolverine behaviour at these sites will vary among ecosystems. For example, availability of feeding sites could vary based on the size or migration patterns of local ungulate populations (Henden et al. 2014) or on the contribution of small prey to diets (Magoun 1987; Inman and Packilia 2015). We suggest the consistent availability of large-feeding sites across seasons is an indication of a highly-productive ecosystem for wolverines.

Although wolverines will leave feeding sites for periods of time (8-10 days) between foraging bouts, potentially to defend territorial boundaries, the low abundance of competitors combined with a wolverine's ability to cache (Inman et al. 2012), allow these food resources to be preserved in their absence. The alteration of ecosystems by industrial development can increase the abundance of mesocarnivores that ultimately will also scavenge at large-feeding sites. A reduction in the availability of cached and stored food could be the reason for population decline in some areas of North America (Heim 2015; Stewart et al. 2016).

Table 5.1. Candidate models for the logistic regression analysis of the difference in attributes of small (n = 48, designated as “0”) versus large (n = 33, designated as “1”) foraging events. Also included is the support for candidate models through AIC_c. The prediction error for the top model (AIC_c weight = 0.90) was 0.12 and its Receiver Operator Score was 0.93.

Model	K	AIC_c	ΔAIC_c	AIC_c weight	Log Likelihood
Away + actual	3	74.89	0.00	0.90	-34.33
Total	2	80.10	5.21	0.07	-37.99
Total + distance	3	81.56	6.67	0.03	-37.66
Actual	2	89.05	14.16	0.00	-42.47
Away + radius	3	94.08	19.19	0.00	-43.92
Intercept only	1	134.25	59.37	0.00	-66.11

Table 5.2. Candidate CPH models used to explain time to new event (TTNE), residency time (RT), and time to return (TtoR) at large events. Also included is the support for candidate models through AIC_c and hazard ratios of the top model.

Model	Response	Explanatory variables	ΔAIC_c	AIC_c weight	Log Likelihood
#2	TTNE ~	PT + Season	0.00	0.98	-849.33
#1		Intercept only	7.37	0.02	-857.69
#3	RT ~	CT + CE + Season + Wolverine	0.00	1.00	-3372.03
#2		CT	25.58	0.00	-3362.08
#1		Intercept only	97.87	0.00	-3459.27
#2	TtoR ~	CT + CE + Season + Wolverine	0.00	1.00	-1999.59
#2		CT	12.61	0.00	-2008.97
#1		Intercept only	17.59	0.00	-2012.45
			Hazard ratio	LCL	UCL
#2	TTNE ~	PT	0.900	0.750	1.080
		Season	0.630	0.470	0.850
#3	RT ~	CT	1.362	1.204	1.541
		CE	1.483	1.182	1.862
		Season	0.732	0.571	0.939
		Wolverine	0.788	0.629	0.985
#3	TtoR ~	CT	0.820	0.709	0.948
		CE	0.695	0.588	0.821
		Season	0.806	0.650	0.999
		Wolverine	1.000	0.813	1.229

Table 5.3. Non-parametric bootstrap of the attributes of beaver, ungulate, and resting clusters. Not included are clusters from small scavenging and predation events (n = 26) (e.g., grouse, snowshoe hare).

Explanatory variable	Beaver (n=21)	Ungulate (n=12)	Resting (n=48)
Actual relocations	23.13 (16.81, 30.19)	20.25 (12.50, 29.08)	7.31 (5.94, 8.92)
Away relocations	14.28 (5.62, 24.47)	36.40 (25.17, 47.17)	4.15 (1.69, 7.10)
Total relocations	37.26 (25.57, 51.90)	56.59 (43.50, 68.83)	11.46 (8.27, 15.08)
Event radius	134.29 (106.00, 165.10)	157.30 (118.80, 194.60)	72 (58.94, 84.92)
Event distance	51.9 (38.90, 65.71)	71.57 (56.75, 84.92)	35.46 (29.21, 42.42)

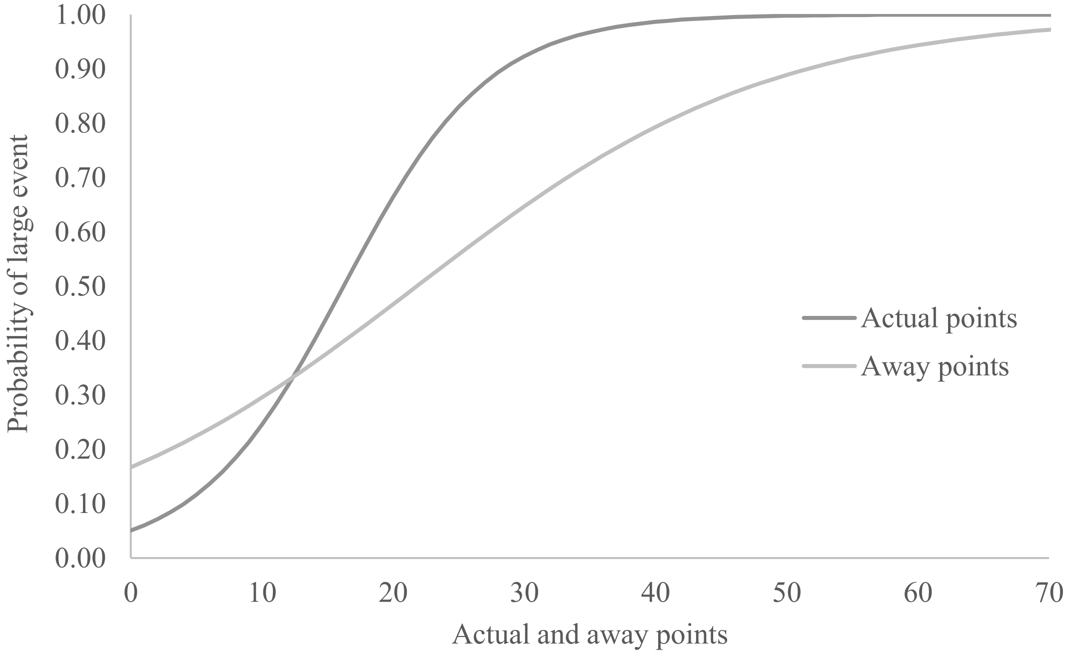

Fig. 5.1. Predicted effect of an increasing number of actual and away points on whether an event would be considered a large-feeding site (ungulate carcass or beaver kill site).

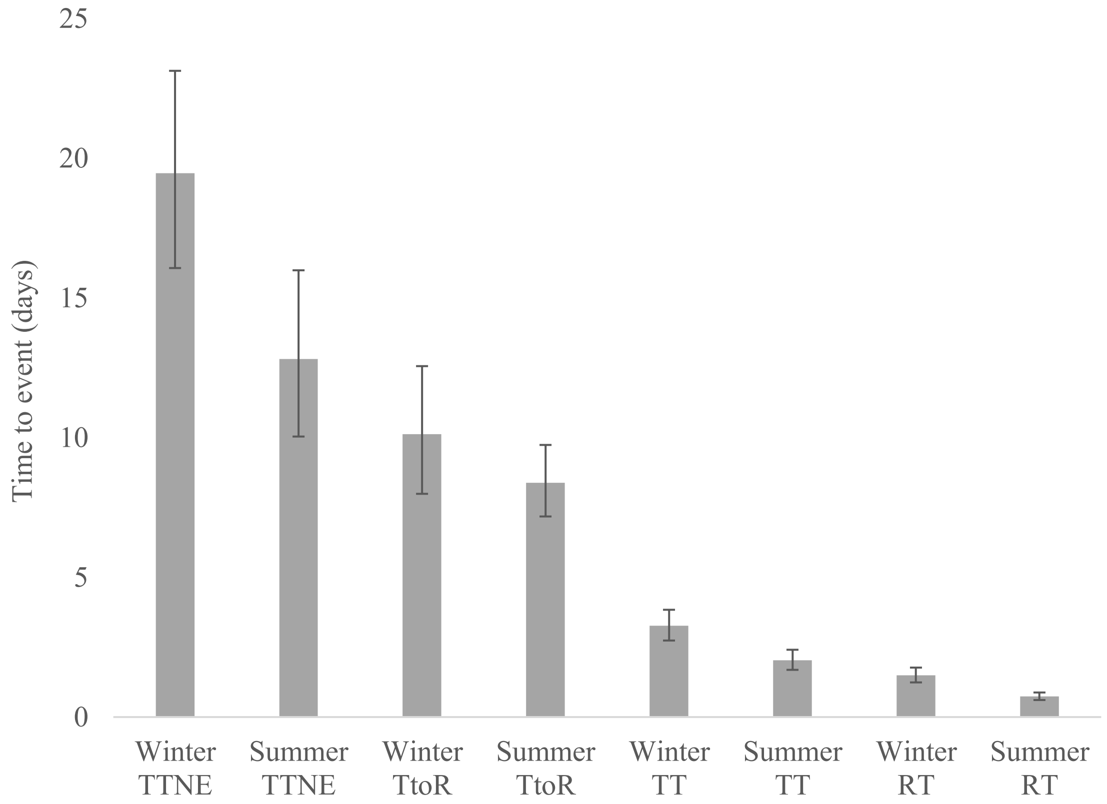

Fig. 5.2. Seasonal averages of time to new event (TTNE) or large-feeding site, time to return to a large-feeding site (TtoR), total time at a large-feeding site (TT), and residency time at a large-feeding site (RT). Averages were calculated based on a non-parametric bootstrap (10,000 iterations).

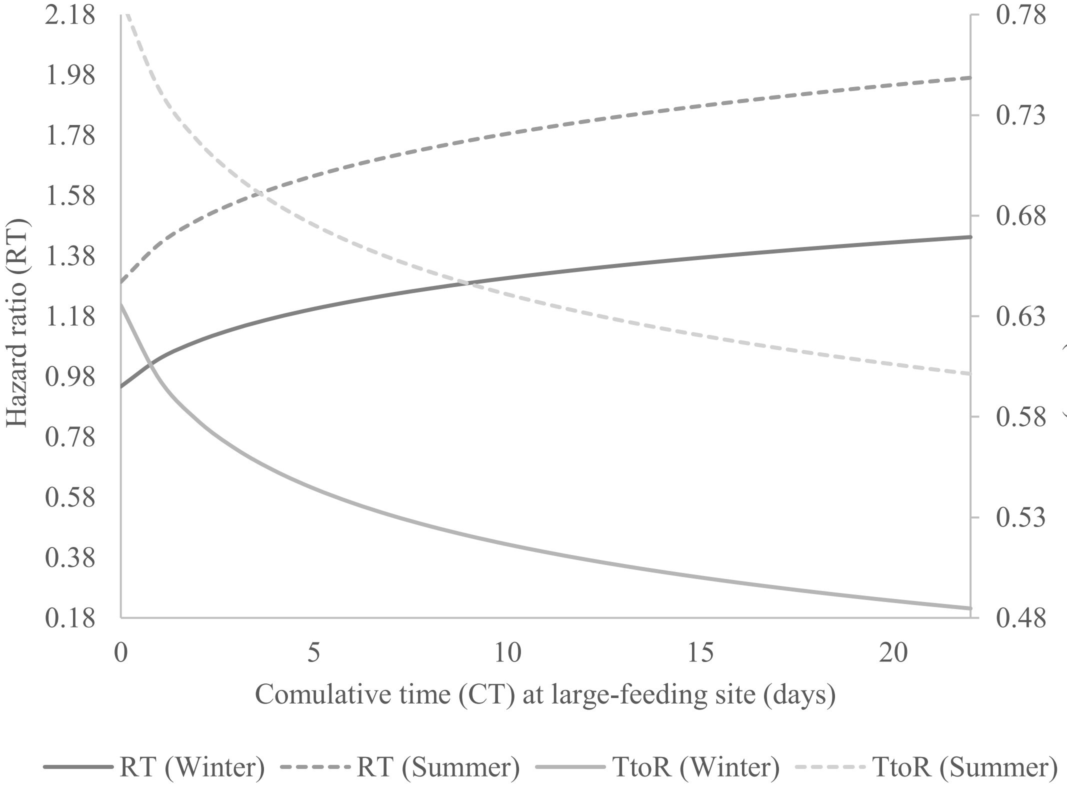

Fig. 5.3. Cumulative time (days) spent at a large-feeding site in relation to residency time (RT) and time to return (TtoR) in winter and summer seasons.

6 General conclusions

My graduate work brought together multiple stakeholders to study wolverine populations in the northern boreal forest of Alberta. Contributions from the Alberta Trappers Associations and Dene Tha First Nation were critical in the success of this study. Trappers helped me with placement of traps and in understanding the behaviours of wolverines that we tracked in the field. Before our work, there was not a detailed understanding of the ecology of wolverines in the northern boreal forest of North America save for work in Ontario (Bowman et al. 2010; Dawson et al. 2010). Over three years, we tracked with GPS radiocollars 44 wolverines in summer and winter seasons. These data allowed for a fine-scale analysis of the movement, habitat selection, and foraging of wolverines on an industrial landscape. We believe these data can be used to better manage populations of wolverines in industrial landscapes.

The effects of industrial development on wildlife populations has received wide-spread attention from ecologists (Wasser et al. 2011; Lesmerises et al. 2012; Tigner et al. 2015; Latham and Boutin 2015) because of its expansive effects on the composition of environments (Schneider 2002; Pickell et al. 2013). Although there are wildlife species that benefit from resource extraction [e.g., wolves (Whittington et al. 2011)] there are others that are displaced (Prokopenko et al. 2017) or suffer increased mortality (Nielsen et al. 2004). Proper management of wildlife populations requires that winners and losers from industrial development are identified so that steps can be taken to mitigate negative effects. I found situations where industrial infrastructure both improved and degraded wolverine habitats. I also found that human activity can have variables effects on wolverine space use. Therefore, I suggest that the paradigm that wolverines avoid anthropogenic developments and disturbance is too simplistic for proper management.

I investigated wolverine habitat selection in relation to an active-logging program in Chapter 2. I also investigated wolverine habitat selection relative to roads, borrow pits, seismic lines, and cutblocks. Surprisingly, I found support for the hypothesis that wolverines were attracted to areas of active logging. I speculated that this attraction could be because wolverines are curious of a novel disturbance within their range, that wolverines use logging roads as movement corridors, or that there are foraging opportunities for wolverines near cutblocks from displaced prey from the areas logged (Ferron et al. 1998;

Potvin et al. 1999; Turcotte et al. 2000). This was the first time an analysis was conducted of wolverine habitat selection relative to a novel disturbance in the home range. Potentially, the paradigm that wolverines avoid anthropogenic features is rooted in a learned avoidance of features that wolverines have long associated with predation risk because of human or predator activity. For example, I also found that wolverines avoided winter roads which I speculated is because wolves use these roads for movement (Whittington al. 2011; Dickie et al. 2016). However, I also found evidence that wolverines selected features that have been on the landscape for long periods of time such as intermediate-aged cutblocks, seismic lines, and road sections with borrow pits. I suggested that low-predation risk and large-potential gain from foraging drives the use of these features by wolverines. For example, borrow pits along roads might be attractive to wolverines because these pits are inhabited by beaver (*Castor canadensis*) that wolverines kill. These pits also are on all-season roads that wolves might avoid (Latham et al. 2013) which creates a predator shield for wolverines (Berger 2007). Further research should aim to understand the reasons why wolverines appear attracted to some of these features.

The aim of Chapter 3 was to evaluate the effects of traffic volume on wolverine movement and habitat selection. I found support for the hypothesis that wolverine space use was best explained by models that included variables for both wolverine movement and habitat selection. These results provide evidence that wildlife space use near roads should be viewed as a continuum between distinct behavioural categories proposed by Jacobson et al. (2016) (e.g., pausers, speeders, avoiders, nonresponders). As predicted for a low-density and wide-ranging carnivore with a low-reproductive rate (Rytwinski and Fahrig 2009), wolverines generally avoided roads, increased their movement near roads, and increased their movement even more as traffic volume on the road increased. We suggest these results provide evidence that wolverines view roads as areas of high-predation risk, and that this perception of predation risk increases with greater-traffic volume (Frid and Dill 2002).

Chapter 4 compared the movement and habitat selection of wolverines in the home range versus during dispersal. The behavior of male wolverines during dispersal supported the hypothesis that they follow optimal strategies for dispersal as outlined by Zollner et al. (2005), including, decreased movement and increased foraging rates (when compared with these metrics in the home range). Large movements in the home range by males might be important for patrolling territories and moving between food patches in an expansive area (Van Moorter et al. 2016). Lower movement rates by males during dispersal might be to detect predators. Males might forage more often during dispersal to take advantage of unpredictable food sources in a new landscape. Females, however, had similar dispersal and home-range behaviours. I suspect that females move cautiously both within and outside the home range and that their smaller home ranges mean that there is less disparity between dispersal and home-range movements. The similar movement rate between male and female dispersers suggests that this rate might be optimal for foraging and predator detection during dispersal movements. As reported by other researchers (Killeen et al. 2014), I found some support for the hypothesis that wolverines select more strongly for linear features during dispersal than during home-range movements. This result might indicate that wolverines are using linear features during dispersal, such as roads and streams, to increase their movement efficiency. The increased attraction to roads during dispersal (when compared within the home range) indicates that wolverines, and especially males, might take more risks during dispersal (e.g., Elliot et al. 2014; Gaston et al. 2016).

In Chapter 5 I evaluated hypotheses regarding wolverine detection of prey and movements at large-feeding sites (ungulate scavenging and beaver-kill sites). I found that the time between detection of large-feeding sites was not random but instead decreased during summer months. This is likely because wolverines are feeding on beavers that are emerging from their over-winter lodges. This result corroborates findings that predation rates of carnivores are driven by biomass availability (Knopff et al. 2010; Metz et al. 2012). I also found that wolverine residence and return time at large-feeding sites adheres to ideas put forward in the marginal value theorem (Charnov 1976). Aligned with the law of diminishing returns, I found a decrease in residency time and an increase in return time as the cumulative time a wolverine spent at a large-feeding site increased. This result is likely because biomass becomes depleted at large-feeding sites overtime. However, I also found that other factors, such as competition, opportunity costs, and seasonality influenced a wolverine's residency and return time to large-feeding sites (Brown 1988). Wolverines spent more time at feeding sites if there were other wolverines detected at the site, likely as a form of exploitive competition (Schrader et al. 2006). Wolverines also increased residency time during visits in winter, likely because there is less available energy on the landscape and the cost of movement in snow is high (Wright and Ernst 2004). Wolverines also spent less time at a large-feeding site if they were visiting other feeding sites concurrently. I would suggest these data provide a better understanding of the energetic constraints of wolverine populations in the northern boreal forest.

Management implications

I provided evidence that industrial infrastructure and activity can both attract and repel wolverines. Attraction of wolverines to industrial areas could mean these areas enhance wolverine habitats by providing cover or foraging opportunities. We found some strong evidence of wolverines using these areas for foraging (killing beavers at borrow pits) and cover (denning within slash piles and log-decks), but additional research should attempt to better understand these relationships. Conversely, attraction of wolverines to areas with human activity could increase their mortality (Battin 2004). For example, over a 1.5 year-period during my study nine wolverines were struck and killed by vehicles in the Hay-Zama region of northern Alberta (data provided by the government of Alberta). Mortality likely could be diminished if speeds on roads were reduced and enforced to ensure that drivers have time to avoid hitting wolverines.

How roads and other industrial features impact wolverine abundance on the landscape is critical to the management of populations. For a species such as a wolverine, the greatest effect of human activity and infrastructure should be displacement from habitats near industrial features (Rytwinski and Fahrig 2012) which ultimately reduces available habitats (e.g., Beyer et al. 2016; D'Amico et al. 2016). The industrial feature that we found wolverines avoided most were winter roads. We speculated this avoidance was from wolf activity and therefore predation risk on these roads. Although there is the potential that displacement has negatively affected wolverines at the population level in some regions (Bowman et al. 2010; Fisher et al. 2013; Heim 2015), wolverine populations in Rainbow Lake appear robust based on our capture history of individuals. This likely means that the threshold of road density, or the magnitude of human use of roads, necessary to illicit negative effects at the population level has not yet occurred in our study area.

The synergism between climate, industrial development, and the decline of wolverine populations should be explored more thoroughly. I believe another reason wolverines populations are robust in Rainbow Lake, in-spite of widespread industrial development, is because there is a low-density of wolves that can kill wolverines (Krebs et al. 2004). Wolf populations are likely limited by low-ungulate populations in Rainbow Lake because of the effects of harsh-winter climates on ungulates (Dawe et al. 2014). Wolf and ungulate populations thrive in southern boreal habitats, where less severe climates and industrial development foster large populations (Latham et al. 2011), which can increase the mortality of wolverines (Krebs et al. 2004) and cause their displacement (Bowman et al. 2010). Therefore, managers should be aware of how industrial developments can interact with climate to influence wolverine populations.

Finally, the importance of a reliable food source leading up to and during denning is critical to the reproductive success of female wolverines (Persson 2005). The Rainbow Lake landscape has abundant beaver populations because of both natural habitats and borrow pits. There are over 1,400 borrow pits in the immediate Rainbow Lake area and our sampling indicated that 16-23% of these borrow pits have active beaver colonies. Therefore, beaver populations inhabiting borrow pits, in combination with those inhabiting natural wetlands, likely provide a large and stable food source for wolverines. Moreover, the food habits data from Rainbow Lake indicate that beaver and snowshoe hare are much more common in the scat of wolverines than ungulate. The reliability of these prey items for reproductive females, relative to the inconsistency and risk of scavenging, might be an important reason wolverine populations are robust in Rainbow Lake.

References

Abrahms, B., Sawyer, S.C., Jordan, N.R., McNutt, J.W., Wilson, A.M., and J.S. Brashares. 2016. Does wildlife resource selection accurately inform corridor conservation? Journal of Applied Ecology 54:412−422.

Adams, L.G., Singer, F.J., and D.W. Dale. 1995. Caribou calf mortality in Denali National Park, Alaska. Journal of Wildlife Management 59:584−594.

Alberta Forest Management Planning Standard. 2006. Alberta Sustainable Resource Development, Edmonton.

Aleksiuk, M., and I.M. Cowan. 1969. Aspects of seasonal energy expenditure in the beaver (*Castorcanadensis Kuhl*) at the northern limit of its distribution. Canadian Journal of Zoology 47: 471–481.

Avgar, T., Lele, S.R., Keim, J.L., and M.S. Boyce. Under review. Relative Selection Strength: quantifying effect size in habitat- and step-selection inference. Ecology and Evolution.

Avgar, T., Potts, J.R., Lewis, M.A., and M.S. Boyce. 2016. Integrated step selection analysis: bridging the gap between resource selection and animal movement. Methods of Ecology and Evolution 7:619−630.

Balzquez-Cabrera, S., Gaston, A., Beier, P., Garrote, G., Simon, M.A., and S. Saura. 2016. Influence of separating home range and dispersal movements on characterizing corridors and effective distances. Landscape Ecology 31:2355−2366.

Banci, V. 1987. Ecology and behavior of the wolverine in the Yukon. Thesis. Simon Fraser University, Burnaby, British Columbia, Canada.

Bar-David, S., Bar-David, I., Cross, P.C., Ryan, S.J., Knechtel, C.U., and W.M. Getz. 2009. Methods for assessing movement path recursion with application to African buffalo in South Africa. Ecology 90: 2467−2479.

Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology 18:1482–1491.

Bellefeuille, S., Belanger, L., Huot, J., and A. Cimon. 2001. Clear-cutting and regeneration practices in Quebec boreal balsam fir forest: effects on snowshoe hare. Canadian Journal of Forest Research 31:41–51.

Benz, R.A., Boyce, M.S., Thurjell, H., Paton, D.G., Musiani, M., Dormann, C.F., and S. Ciuti. 2016. Dispersal ecology informs design of large-scale wildlife corridors. PLoS ONE 11: e0162989.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letter 3:620–623.

Beyer, H.L., Gurari, E., Borger, L., Panzacchi, M., Basille, M., Herfindal, I., Van Moorter, B., Lele, S.R., and J. Matthiopoulos. 2016. 'You shall not pass': quantifying barrier permeability and proximity avoidance by animals. Journal of Animal Ecology 85:43−53.

Bowler D.E., and T.G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behavior to spatial dynamics. Biological Review 80:205–225.

Bowman, J., Ray, J.C., Magoun, A.J., Johnson, D.S., and F.N. Dawson. 2010. Roads, logging, and the large-mammal community of an eastern Canadian boreal forest. Canadian Journal of Zoology 88:454−467.

Boyce, M.S., and L.L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trend in Ecology and Evolution 14:268−272.

Boyle, S.A., and F.B. Samson. 1985. Effects of nonconsumptive recreation on wildlife: a review. Wildlife Society Bulletin 13:110−116.

Brown, J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology 22:37−47.

Buech, R.R. 1995. Sex difference in behavior of beavers living in near-boreal lake habitat. Canadian Journal of Zoology 73:2133−2143.

Bunnefeld N., Borger L., van Moorter B., Rolandsen C.M., Dettki H., Solberg E.J., and G. Ericsson. 2011. Journal of Animal Ecology 80:466−476.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach, second ed. Springer Science, New York.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346−352.

Carbone, C., Teacher, A., and M. Rowcliffe. 2007. The costs of carnivory. PloS Biology 5:363−368.

Carroll, C., Noss, R.F., and P.C. Paquet. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. Ecological Applications 11:961−980.

Charnov, E.L. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9:129−136.

Chen, L.A., and J.L. Koprowski. 2016. Differential Effects of Roads and Traffic on Space Use and Movements of Native Forest-Dependent and Introduced Edge-Tolerant Species. PLoS ONE 11: e0148121.

Chetkiewicz, C.L., St. Clair, C.C. and M.S. Boyce. 2006. Corridors for conservation: structure versus function. Annual Review of Ecology and Evolutionary Systematics 37:317–42.

Chetkiewicz, C.B., and M.S. Boyce. 2009. Use of resource selection functions to identify conservation corridors. Journal of Applied Ecology 46:1036−1047.

Clobert J., Galliard J., Cote J., Meylan S., Masson M. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12:197−209.

Committee on the Status of Endangered Wildlife in Canada. 2014. COSEWIC Assessment and Update Status Report on the Wolverine *Gulo gulo* in Canada. In: Committee on the Status of Endangered Wildlife in Canada. Department of Environment and Climate Change, Ottawa

Conroy, M.J., Gysel, L.W., and G.R. Dudderar. 1979. Habitat components of clear-cut areas for snowshoe hares in Michigan. Journal of Wildlife Management 43:680–690.

Cook, T.C., and D.T. Blumstein. 2013. The omnivore's dilemma: Diet explains variation in vulnerability to vehicle collision. Biological Conservation 167:310−315.

Copeland J.P., Cesar E., Peek J.M., Haris C.E., Long C.D., and D.L. Hunter. 1995. A live trap for wolverine and other forest carnivores. Wildlife Society Bulletin 23:535−538.

Copeland, J.P., Peek, J.M., Groves, C.R., Melquist, W.E., McKelvey, K.S., McDaniel, G.W., Long, C.D., and C.E. Harris. 2007. Seasonal habitat associations of the wolverine in central Idaho. Journal of Wildlife Management 71:2201–2212.

Copeland J.P., McKelvey K.S., Aubry K.B., Landa A., Persson J., Inman R.M., Krebs J., Lofroth E., Golden H., Squires J.R., Magoun A., Schwartz M.K., Wilmot J., Copeland C.L., Yates R.E., Kojola I., and R. May. 2010. The bioclimatic envelope of the wolverine (*Gulo gulo*): do climatic constraints limit its geographic distribution? Canadian Journal of Zoology 88:233–246.

Coulson, T., Catchpole, S.D., Albon, D., Morgan, J.T., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J., and B.T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:1528−1531.

Courant, S. and D. Fortin. 2012. Time allocation of bison in meadow patches driven by potential energy gains and group size dynamics. Oikos 121:1163−1173.

Courbin, N., Fortin, D., Dussault, C., and R. Courtois. 2009. Landscape management for woodland caribou: the protection of forest blocks influences world-caribou co-occurrence. Landscape Ecology 24:1375–1388.

Cox, E.W., Garott, R.A., and J.R. Cary. 1997. Effect of supplemental cover on survival of snowshoe hares and cottontail rabbits in patchy habitat. Canadian Journal of Zoology 75:1357–1363.

Craiu, R.V, Duchesne, T., Fortin, D., and S. Baillargeon. 2011. Conditional logistic regression with longitudinal follow-up and individual-level random coefficients: A stable and efficient two-step estimation method. Journal of Computational and Graphical Statistics 20:767–784.

Crete, M., and S. Lariviere. 2003. Estimating the costs of locomotion in snow for coyotes. Canadian Journal of Zoology 81:1808–1814.

Cristescu, B. 2015. Predicting multiple behaviors from GPS radiocollar cluster data. Behavioral Ecology 26:452−464.

Dall, S.R.X., and R.S. Johnstone. 2002. Managing uncertainty: information and insurance under the risk of starvation. Philosophical Transactions of the Royal Society B 357:1519–1526.

D'Amico, M., Periquet, S., Roman, J., and E. Revilla. 2016. Road avoidance responses determine the impact of heterogenous road networks at a regional scale. Journal of Applied Ecology 53: 181−190.

Dawe, K.I., Bayne, E.M., and S. Boutin. 2014. Influence of climate and human land use on the distribution of white-tailed deer (*Odocoileus virginianus*) in the western boreal forest. Canadian Journal of zoology 92:353–363.

Dawson, F.N., Magoun, A.J., Bowman, J., and J.C. Ray. 2010. Wolverine, *Gulo gulo*, home range size and denning habitat in the lowland boreal forest in Ontario. Canadian Field Naturalist 124:139−144.

Da Rosa, C.A., and A. Bager. .2013. Review of the factors underlying the mechanisms and effects of roads on vertebrates. Oecologia Australis 17:6−19.

Dickie, M., 2015. The use of anthropogenic linear features by wolves in northeastern Alberta. MSc Thesis, University of Alberta, Edmonton.

Dickie, M., Serrouya R., McNay R.S., and S. Boutin. 2016. Faster and farther: wolf movement on linear features and implications for hunting behavior. Journal of Applied Ecology 54:253−263.

Dyck, A.P., and R.A. MacArthur. 1992. Seasonal patterns of body temperature and activity in free ranging beaver (*Castor canadensis*). Canadian Journal of Zoology 70:1668−1672.

Ebinger, M.R., Haroldson, M.A., van Manen, F.T., Costello, C.M., Bjornlie, D.D., Thompson, D.J., Gunther, K.A., Fortin, J.K., Teisberg, J.E., Pils, S.R., White, P.J., Cain, S.L., and P.C. Cross. 2016. Detecting grizzly bear use of ungulate carcasses using global positioning system telemetry and activity data. Oecologia 181:695−708.

Elliot, N.B., Cushman, S.A., Macdonald, D.W., and A.J. Loveridge. 2014. The devil is in the dispersers: predictions of landscape change with demography. Journal of Applied Ecology 51:1169−1178.

Fahrig, L. 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology 21:1003−1015.

Fahrig, L., and T. Rytwinski. 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecology and Society 14:1–20.

Ferron, J., Potvin, F., and C. Dussault. 1998. Short-term effects of logging on snowshoe hares in the boreal forest. Canadian Journal of Forest Research 28:1335–1343.

Fieberg, J., Matthiopoulos, J., Hebblewhite, M., Boyce, M.S., and J.L. Frair. 2010. Correlation and studies of habitat selection: problem, red herring or opportunity? Philosophical Transactions of The Royal Society B 363:2233−2244.

Fisher, J.T., and L. Wilkenson. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mammal Review 35:51–81.

Fisher, J.T., Bradbury, S., Anholt, B., Nolan, L., Roy, L., Volpe, J.P., and M. Wheatley. 2013. Wolverines (*Gulo gulo luscus*) on the Rocky Mountain slopes: natural heterogeneity and landscape alteration as predictors of distribution. Canadian Journal of Zoology 91:706–716.

Ford, A.T., and L. Fahrig. 2007. Diet and body size of North American mammal road mortalities. Transportation Research Part D 12:498−505.

Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, and J.S. Mao. 2005. Wolves influence elk movements: behaviour shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320−1330.

Forman, R.T.T., and L.E. Alexander. 1998. Roads and Their Major Ecological Effects. Annual Review of Ecology and Systematics 29:207−231.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11.

Gable, T.D., Windels, S.K., Bruggink, J.G., and A.T. Homkes. 2016. Where and how wolves (*Canis lupus*) kill beavers (*Castor canadensis*). PloS ONE 11: e0165537.

Gaston, A., Blazquez-Cabreara, S., Garrote, G., Mateo-Sanchez, M.C., Beier, P., Simon, M.A., and S. Saura. 2016. Response to agriculture by a woodland species depends on cover type and behavioural state: insights from resident and dispersing Iberian lynx. Journal of Applied Ecology 53:814−824.

Gillies, C.G., Hebblewhite, M., Nielsen, S.E., Krawchuk, M.A., and C.L. Aldridge. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887 898.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., and R.G. Townshend. 2013. High-Resolution Global Maps of 21st-Century Forest Cover Change. Science 342:850−853.

Hebblewhite, M. 2005. Predation by wolves interacts with the North Pacific Oscillation (NPO) on a western North American elk population. Journal of Animal Ecology 74: 226−233.

Hebblewhite, M. 2017. Billion dollar boreal woodland caribou and the biodiversity impacts of the global oil and gas industry. Biological Conservation 206:102−111.

Heim, N.A. 2015. Complex Effects of Human-Impacted Landscapes on the Spatial Patterns of Mammalian Carnivores. University of Victoria, Victoria, British Columbia.

Henden, J., Stien, A., Bardsen, B., Yoccoz, N.G., and R.A. Ims. 2014. Community-wide mesocarnivore response to partial ungulate migration. Journal of Applied Ecology 51: 1525−1533.

Hilty, J.A., Lidicker, W.Z., Merenlender, A.M. 2012. Corridor ecology: The science and practice of linking landscapes for biodiversity conservation. Washington, D.C: Island Press.

Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. The Canadian Entomologist 7:385−398.

Hornocker, M.G., and H.S. Hash. 1981. Ecology of the wolverine in northwestern Montana. Canadian Journal of Zoology 59:1286–1301.

Houle, M., Fortin, D., Dussault, C., Courtois, R., and J. Ouellet. 2009. Cumulative effects of forestry on habitat use by gray wolf (*Canis lupus*) in the boreal forest. Landscape Ecology 25:419–433.

Inman. R., Packila, M., Inman, K., Aber, B., Spence, R., and D. McCauley. 2009. Greater Yellowstone Wolverine Program – Progress Report December 2009. Wildlife Conservation Society.

Inman, R.M., Magoun, A.J., Persson, J., and J. Mattisson. 2012. The wolverine's niche: linking reproductive chronology, caching, competition, and climate. Journal of Mammalogy 94:633−644.

Inman, R.M., Packila, M.L., Inman, K.H., McCue, A.J., White, G.C., Persson, J., Aber, B.C., Orme, M.L., Alt, K.L., Cain, S.L., Fredrick, J.A., Oaklead, B.J., and S.S. Sartorius. 2012. Spatial ecology of wolverines at the southern periphery of distribution. Journal of Wildlife Management 76:778−792.

Inman, R.M., Brock, B.L., Inman, K.H., Sartorius, S.S., Aber, B.C., Giddings, B., Cain, S.L., Orme, M.L., Fredrick, J.A., Oakleaf, B.J., Alt, K.L., Odell, E., and G. Chapron. 2013. Developing priorities for metapopulation conservation at the landscape scale: Wolverines in the Western United States. Biological Conservation 166:276−286.

Inman, R.M. and Packila, M.L. 2015. Wolverine (*Gulo gulo*) food habits in greater Yellowstone. American Midland Naturalist 173:156−161.

Jackson, C.R., Marnewick, K., Lindsey, P.A., Roskaft, E., and M.P. Robertston. 2016. Evaluating habitat connectivity methodologies: a case study with endangered African wild dogs in South Africa. Landscape Ecology 31:1433−1447.

Jacobson, S.L., Bliss-Kletchum, L., de Rivera, C.E., and W.P. Smith. 2016. A behavior-based framework for assessing barrier effects to wildlife from vehicle traffic volume. Ecosphere **7**: e01345. 10.1002/ecs2.1345

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, C.J., Boyce, M.S., Chase, R.L., Dean, C., Gau, R.J., Gunn, A., and R. Mulders. 2005. Cumulative effects of human developments on arctic wildlife. Ecology 70:164−168.

Keeley, A.T.H., Beier, P., Keeley, B.W., and M.C. Fagan. 2017. Habitat suitability is a poor proxy for landscape connectivity during dispersal and mating movements. Landscape and Urban Planning 161:90−102.

Killeen, J., Thurfjell, H., Ciuti, S., Paton, D., Musiani, M., and M.S. Boyce. 2014. Habitat selection during ungulate dispersal and exploratory movement at broad and fine scale with implications for conservation management. Movement Ecology 2:15.

Kite, R., Nelson, T., Stenhouse, G., and C. Darimont. 2016. A movement-driven approach to quantifying grizzly bear (*Ursus arctos*) near-road movement patterns in west-central Alberta, Canada. Biological Conservation 195:24–32.

Knopff, K.H, Knopff, A.A., Warren, M.B., and M.S. Boyce. 2009. Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. Journal of Wildlife Management 73:586−597.

Knopff, K.H., Knopff, A.A., Kortello, A., and M.S. Boyce. 2010. Cougar kill rate and prey composition in a multiprey system. Journal of Wildlife Management 74:1435–1447.

Knopff, A.A., Knopff, K.H., Boyce, M.S., and C.C. St. Clair. 2014. Flexible habitat selection by cougars in response to anthropogenic development. Biological Conservation 178:136–145.

Koehler, G. M., Hornocker, M.G. and H.S. Hash. 1980. Wolverine marking behavior. Canadian Field Naturalist 94:339−341.

Krebs, J., Lofroth, E., Copeland, J., Banci, V., Cooley, D., Golden, H., Magoun, A., Mulders, R., and B. Shultz. 2004. Synthesis of survival rates and causes of mortality in North American wolverines. Journal of Wildlife Management 68:493–502.

Krebs, J., Lofroth, E.C., and I. Parfitt. 2007. Multiscale habitat use by wolverines in British Columbia, Canada. Journal of Wildlife Management 71:2180−2192.

Kyle, C.J., and C. Strobeck. 2002. Connectivity of peripheral and core populations of North American wolverines. Journal of Mammalogy 83:1141−1150.

Ladle, A. 2017. Grizzly bear response to linear features and human recreational activity. PhD Dissertation, University of Alberta, Edmonton.

Latham, A.D.M., Latham, M.C., McClutchen, N.A., and S. Boutin. 2011. Invading white-tailed deer change wolf-caribou dynamics in northeastern Alberta. Journal of Wildlife Management 75:204−212.

Latham, A.D.M., Latham, M.C., Boyce, M.S., and S. Boutin. 2011. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. Ecological Applications 21:2854−2865.

Latham, A.D.M., Latham, M.C., Boyce, M.S., and S. Boutin. 2013. Spatial relationships of sympatric wolves (*Canis lupus*) and coyotes (*C. latrans*) with woodland caribou (*Rangifer tarandus caribou*) during the calving season in a human-modified boreal landscape. Wildlife Research 40:250–260.

Latham, A.D., Latham, M.C., Knopff, K.H., Hebblewhite, M., and S. Boutin. 2013. Wolves, white-tailed deer, and beaver: implications of seasonal prey switching for woodland caribou declines. Ecography 36:1276−1290.

Latham, A.D., and S. Boutin. 2015. Impacts of utility and other industrial linear corridors on wildlife. In: Handbook of Road Ecology. Eds: van der Ree, R., Smith, D.J. & Grilo, C. John Wiley & Sons.

Lee, P., and S. Boutin. 2005. Persistence and development transition of wide seismic lines in the western Boreal Plains of Canada. Journal of Environmental Management 78:240–250.

Lele, S.R., Merrill, E.H., Keim, J., and M.S. Boyce. 2013. Selection, choice, use, and occurrence: clarifying concepts in resource selection studies. Journal of Animal Ecology 82:1183–1191.

Lesmerises, F., Dussault, C., and M. St-Laurent. 2012. Wolf habitat selection is shaped by human activities in a highly managed boreal forest. Forest Ecology and Management 276:125−131.

Lidicker, W. 1999. Response of mammals to habitat edges: an overview. Landscape Ecology14:333–343.

Lofroth, E.C., Krebs, J.A., Harrower, W.L., and D. Lewis. 2007. Food habits of wolverine *Gulo gulo* in montane ecosystems of British Columbia, Canada. Wildlife Biology 13:31–37.

Lovallo, M.J., and E.M. Anderson. 1996. Bobcat movements and home ranges relative to roads in Wisconsin. Wildlife Society Bulletin 24:71–76.

Magoun, A.J., 1985. Population characteristics. Ecology and Management of wolverines in northwestern Alaska. PhD Thesis, University of Alaska, Fairbanks.

Magoun, A. 1987. Summer and winter diets of wolverines, *Gulo gulo*, in arctic Alaska. Canadian Field Naturalist 101:392−397.

Magoun, A.J., and J.P. Copeland. 1998. Characteristics of wolverine reproductive den sites. Journal of Wildlife Management 62:1313−1320.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., and W.P. Erickson. 2002. Resource Selection by Animals: Statistical Design and Analysis for Field Studies. 2nd edition. Kluwer Academic Publishers, Nordrect, The Netherlands.

Mattison, J., Andren, H., Persson, J., and P. Segerstrom. 2010. Effects of species behavior on global positioning system collar fix rates. Journal of Wildlife Management 74:557−563.

Mattison, J., Rauset, G.R., Odden, J., Andren, H., Linnell, J.D.C., and J. Persson. 2016. Predation or scavenging? Prey body condition influences decision-making in a facultative predator, the wolverine. Ecosphere 7:1−14.

May, R., Landa, A., van Dijk, J., Linnell, J.D.C., and R. Andersen. 2006. Impact of infrastructure on habitat selection of wolverines *Gulo gulo*. Wildlife Biology 12:285−295.

McClintock, B.T., Russell, D.J.F., Matthiopoulos, J., and R. King. 2013. Combining individual animal movement and ancillary biotelemetry data to investigate population-level activity budgets. Ecology 94:838−849.

McClure, M.L., Hansen, A.J., and R.M. Inman. 2016. Connecting models to movements: testing connectivity model predictions against empirical migration and dispersal data. Landscape Ecology 31:1419−1432.

McKelvey, K.S., Aubry, K.B., Anderson, N.J., Clevenger, A.P., Copeland, J.P., Heinemeyer, K.S., Iman, R.M., Squires, J.R., Waller, J.S., Pilgrim, K.L., and M.K. Schwartz. 2014. Journal of Wildlife Management 78:325−334.

McKenzie, H.W., Merrill, E.H., Spiteri, R.J., and M.A. Lewis. 2012. How linear features alter predator movement and the functional response. Interface Focus 2:205–216.

Meade, R.A., Rector, M., Starypan, G., Neirinckx, S., Jones, M., and M.N. DonCarlos. 1991. Reproductive biology of captive wolverines. Journal of Mammalogy 72:807−814.

Mech, D.L., Heezen, K.L., and D.B. Siniff. 1966. Onset and cessation of activity in cottontail rabbits and snowshoe hares in relation to sunset and sunrise. Animal Behavior 14:410−413.

Merrill, E., Sand, H., Zimmermann, B., McPhee, H., Webb, N., Hebblewhite, M., Wabakken, P., and J.L. Frair. 2010. Building a mechanistic understanding of predation with GPS-based movement data. Philosophical Transactions of the Royal Society B 36:2279−2288.

Metz, M.C., Vucetich, J.A., Smith, D.W., Stahler, D.R., and R.O. Peterson. 2011. Effect of sociality and season on gray wolf (*Canis lupus*) foraging behavior: implications for estimating summer kill rate. PloS ONE 6:1−10.

Miller, C.S., Hebblewhite, M., Petrunenko, Y.K., Seryodkin, I.V., DeCesare, N.J., Goodrich, J.M., and D.G. Miquelle. 2010. Estimating Amur tiger (*Panthera tigris altaica*) kill rates and potential consumption rates using global positioning system collars. Journal of Mammalogy 94: 845−855.

Morrison, C.D., Boyce, M.S., and S.E. Nielsen. 2015. Space-use, movement and dispersal of sub-adult cougars in a geographically isolated population. PeerJ 3: e1118; DOI 10.7717/peerj.1118.

Mukherjee, S., Zelcer, M., and B.P. Kotler. 2009. Patch use in time and space for a meso-predator in a risky world. Oecologia 159: 661−668.

Murray, D.L., Steury, T.D., and J.D Roth. 2008. Assessment of Canada lynx research and conservation needs in the southern range: another kick at the cat. Journal of Wildlife Management 72:1463−1472.

Nielsen, S.E., Boyce, M.S., and G.B. Stenhouse. 2004. Grizzly bears and forestry I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada. Forest Ecology and Management 199:51–65.

Nielsen, S.E., Herrero, S., Boyce, M.S., Mace, R.D., Benn, B., Gibeau, M.L., and S. Jevons. 2004. Modeling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. Biological Conservation 120:101−113.

Niemi, M., Rolanden, C.M., Neumann, W., Kukko, T., Tiilikainen, R., Pusenius, J., Solberg, E.J., and G. Ericsson. 2017. Temporal patterns of moose collisions with and without personal injury. Accident Analysis and Prevention 98:167−173.

Niemuth, N., and M.S. Boyce. 1997. Edge-related nest losses in Wisconsin pine barrens. Journal of Wildlife Management 61:1234–1238.

Northrup, J.M., Pitt, J., Muhly, T.B., Stenhouse, G.B., Musiani, M., and M.S. Boyce. 2012. Vehicle traffic shapes grizzly bear behavior on a multiple-use landscape. Journal of Applied Ecology 49: 1159−1167.

Parker, G.R. 1984. Use of spruce plantations by snowshoe hare in New Brunswick. The Forestry Chronicle 60:162–166.

Parker, K.L., Gillingham, M.P., Hanley, T.A., and C.T. Robbins. 1996. Foraging efficiency: energy expenditure versus energy gain in free-ranging black-tailed deer. Canadian Journal of Zoology 74: 442-450.

Pattison, C.A., Quinn, M.S., Dale, P., and C.P. Catterall. 2016. The landscape impact of linear seismic clearings for oil and gas development in boreal forest. Northwest Science 90:340–354.

Pereira, L.M., Owen-Smith, N., and M. Moleon. 2014. Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. Mammal Review 44: 44−55.

Persson, J., Landa, A., Andersen, R., and P. Segerstronm. 2006. Reproductive characteristic of female wolverines (*Gulo gulo*) in Scandinavia. Journal of Mammalogy 87:75–79.

Persson, J., Wedholm, P., and P. Segerstrom. 2010. Space use and territoriality of wolverines (*Gulo gulo*) in northern Scandinavia. European Journal of Wildlife Research 56:49−57.

Peterson, R.O., and R.E. Page. 1988. The rise and fall of Isle Royal Wolves, 1975-1986. Journal of Mammalogy 69:89−99.

Pickell, P. D., Andison, D.W., and N.C Coops. 2013. Characterizations of anthropogenic disturbance patterns in the mixedwood boreal forest of Alberta, Canada. Forest Ecology and Management 304:243–253.

Pickell, P. D., Hermosilla, T., Coops, N.C., Masek, J.G., Franks, S., and C. Huang. 2014. Monitoring anthropogenic disturbance trends in an industrialized boreal forest with Landsat time series. Remote Sensing Letters 5:783–792.

Pickell, P.D., Coops, N.C., Gergel, S.E., Andison, D.W., and P.L. Marshall. 2016. Evolution of Canada's Boreal Forest Spatial Patterns as Seen from Space. PLoS ONE 11: e0157736.

Pigeon, K.E., Anderson, M., MacNearney, D., Cranston, J., Stenhouse, G., and L. Finnegan. 2016. Towards the restoration of caribou habitat: understanding factors associated with human motorized use of legacy seismic lines. Environmental Management 58:821–832.

Potvin, F., Courtois, R., and L. Bélanger. 1999. Short-term response of wildlife to clear-cutting in Quebec boreal forest: multiscale effects and management implications. Canadian Journal of Forest Research 29:1120–1127.

Potvin, F., Breton, L., and R. Courtois. 2005. Response of beaver, moose, and snowshoe hare to clear cutting in a Quebec boreal forest: a reassessment 10 years after cut. Canadian Journal of Forest Research 35:151–160.

Powell, R.A., Zimmerman, J.W., and D.E. Seaman. 1997. Ecology and Behaviour of North American Black Bears. Chapman and Hall, London, UK.

Prokopenko, C.M., Boyce, M.S., and T. Avgar. 2017. Characterizing wildlife behavioral response to roads using integrated step selection analysis. Journal of Applied Ecology 54:470–479.

Pulliainen, E., and P. Ovaskainen. 1975. Territory marking by a wolverine (*Gulo gulo*) in northeastern Lapland. Annales Zoologici Fennici 12:268–270.

Pyke, G.H. 1984. Optimal foraging theory: a critical review. Annual Review of Ecology, Evolution, and Systematics 15:523−575.

Renecker, L.A., and R.J. Hudson. 1986. Seasonal energy expenditures and thermoregulatory responses o moose. Canadian Journal of Zoology 64:322−327.

Roemer, G.W., Gomper, M.E., and B. Van Valkenburgh. 2008. The ecological role of the mammalian mesocarnivore. BioScience 59:165−173.

Roever, C.L., Boyce, M.S., and G.B. Stenhouse. 2010. Grizzly bear movements relative to roads: application of step-selection functions. Ecography 33:985−1156.

Rowland, M.M., Wisdom, M.J., Johnson, D.H., Wales, B.C., and J.P. Copeland. 2003. Evaluation of landscape models for wolverines in the interior Northwest, United States of America. Journal of Mammalogy 84:92−105.

Ruggiero, L.F., McKelvey, K.S., Aubry, K.B., Copeland, J.P., Pletscher, D.H., and M.G. Hornocker. 2007. Wolverine conservation and management. Journal of Wildlife Management 71: 2145−2146.

Rytwinski, T., and L. Fahrig. 2012. Do species life-history traits explain population responses to roads? A meta-analysis. Biological Conservation 147:87−98**.**

Scheel, D. 1993. Profitability, encounter rates, and prey choice of African lions. Behavioural Ecology 4:90−97.

Schneider, R. R. 2002. Alternative futures: Alberta's boreal forest at the crossroads. Federation of Alberta Naturalists, Edmonton, Alberta, Canada.

Schrader, A.M., Kerley, G.I.H., Kotler, B.P., and J.S. Brown. 2006. Social information, social feeding, and competition in group-living goats (*Capra hircus*). Behavioral Ecology 18:103−107.

Schtickzelle, N., Mennechez, G., Baguette, M., and G. Mennechez. 2006. Dispersal depression with habitat fragmentation in the bog fritillary butterfly. Ecology 87:1057−1065.

Schwartz, M.K., Copeland, J.P., Anderson, N.J., Squires, J.R., Inman, R.M., McKelvey, K.S., Pilgrim, K.L., Waits, L.P., and S.A. Cushman. 2009. Wolverine gene flow across and narrow climatic niche. Ecology 90:3222−3232.

Scrafford, M.A., Avgar, T., Abercrombie, B., Tigner, J., and M.S. Boyce. 2017. Wolverine habitat selection in response to anthropogenic disturbance in the western Canadian boreal forest. Forest Ecology and Management 395:27−36.

Seidel, D.P., and M.S. Boyce. 2015. Patch-use dynamics by a large herbivore. Movement Ecology 3: 7.

Shannon, G., Angeloni, L.M., Wittemyer, G., Fristrup, K.M., and K.R. Crooks. 2014. Road traffic noise modifies behaviour of a keystone species. Animal Behaviour 94:135−141.

Smith, K.G., Ficht, E.J., Hobson, D., Sorensen, T.C., and D. Hervieux. 2000. Winter distribution of woodland caribou in relation to clear-cut logging in west-central Alberta. Canadian Journal of Zoology 78:1433–1440.

Soulsbury, C.D., Iossa, G., Baker, P.J., White, P.C.L., and S. Harris. 2011. Behavioral and spatial analysis of extraterritorial movements in red foxes (*Vulpes vulpes*). Journal of Mammalogy 92:190−199.

Squires, J.R., DeCesare, N.J., Olson, L.E., Kolbe, J.A., Hebblewhite, M., and S.A. Parks. 2013. Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. Biological Conservation 157:187−195.

Stewart, F.E.C., Heim, N.A., Clevenger, A.P., Paczkowski, J., Volpe, J.P., and J.T. Fisher. 2016. Wolverine behaviour varies spatially with anthropogenic footprint: implications for conservation and inferences about declines. Ecology and Evolution 6:1493–1503.

Strong, W., and K.R. Leggat. 1981. Ecoregions of Alberta. Alberta Energy and Natural Resources, Resource Evaluation and Planning Division, Edmonton.

Sweanor, L.L., Logan, K.A., and M.G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. Conservation Biology 14:798−808.

Thurfjell, H., Spong, G., Olsson, M., and G. Ericsson. 2015. Avoidance of high traffic levels results in lower risk of wild boar-vehicle accidents. Landscape and Urban Planning 133:98−104.

Tigner, J., Bayne, E., and S. Boutin. 2014. Black bear use of seismic lines in northern Alberta. Journal Wildlife Management 78: 282–292.

Tigner, J., Bayne, E.M., and S. Boutin. 2015. American marten respond to seismic lines in northern Canada at two spatial scales. PLoS ONE 10: e0118720.

Trakhtenbrot, A., Nathan, R., Perry, G., and D.M. Richardson. 2005 The importance of long-distance dispersal in biodiversity conservation. Diversity and Distributions 11:173−181.

Travis, J.M.J., Delgado, M., Bocedi, G., Baguette, M., Barton, K., Bonte, D., Boulangeat, I., Hodgson, J.A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V.M., and J.M. Bullock. 2013. Dispersal and species' response to climate change. Oikos 000:001–009.

Turchin, P. 1998. Quantitative analysis of movements: measuring and modeling population redistribution in animals and plants. Sunderland, Mass.: Sinauer.

Turcotte, F.R., Courtois, R., Couture, R., and J. Ferron. 2000. Impact à court terme de l'exploitation forestière sur le tétras du Canada (*Falcipennis canadensis*). Canadian Journal of Forest Research 30:1–9.

Valone, T.J., and J.S. Brown. 1989. Measuring patch assessment abilities of desert granivores. Ecology 70:1800−1810.

Van Dijk, J., Gustavsen, L., Mysterud, A., May, R., Flagstad, O., Broseth, H., Andersen, R., Andersen, R., Steen, H., and A. Landa. 2008. Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. Journal of Animal Ecology 77:1183−1190.

Van Moorter, B., Rolandsen, C.M., Basille, M., and J. Galliard. 2016. Movement is the glue connecting home ranges and habitat selection. Journal of Animal Ecology 85:21−31.

Van Rensen, C.K., Nielsen, S.E., White, B., Vinge, T., and V.J. Lieffers. 2015. Natural regeneration of forest vegetation on legacy seismic lines in boreal habitats in Alberta's oil sands region. Biological Conservation 184:127–135.

Vangen, K.M., Persson, J., Landa, A., Andersen, R., and P. Segerstrom. 2001. Characteristics of dispersal in wolverines. Canadian Journal of Zoology 79:1641–1649.

Wasser, S.K., Keim, J.L., Taper, M.L., and S.R. Lele. 2011. The influences of wolf predation, habitat loss, and human activity on caribou and moose in the Alberta oil sands. Frontiers in Ecology 9: 546−551.

Waser, P.M., Nichols, K.M., and J.D. Hadfield. 2013. Fitness consequences of dispersal: Is leaving home the best of a bad lot? Ecology 94:1287−1295.

Webb, N.F., Hebblewhite, M., and E.H. Merrill. 2008. Statistical methods for identifying wolf kill sites using global positioning system locations. Journal of Wildlife Management 72:798–807.

White, T.H, Bowman, J.L., Jacobson, H.A., Leopold, D.B., and W.P. Smith. 2001. Forest management and female black bear denning. Journal of Wildlife Management 65:34–40.

Whittington, J., St. Clair, C.C., and G. Mercer. 2005. Spatial response of wolves to roads and trails in mountain valleys. Ecological Applications 15:543–553.

Whittington, J., Hebblewhite, M., DeCesare, N.J., Neufeld, L., Bradley, M., Wilmshurst, J., and M. Musiani. 2011. Caribou encounters with wolves increase near roads and trails: a time-to-event approach. Journal of Applied Ecology 48:1535–1542.

Wilson, G.M., van Den Bussche, R.A., Kennedy, P.K., Gunn, A., and K. Poole. 2000. Genetic variability of wolverines (*Gulo gulo*) from the Northwest Territories, Canada: conservation implications. Journal of Mammalogy 81:186−196.

Wright, J.D., Ernst J., 2004. Effects of mid-winter snow depth on stand selection by wolverines, *Gulo gulo luscus*, in the boreal forest. Canadian Field Naturalist 118:56–60.

Zollner, P.A., and S.L. Lima. 2005. Behavioural tradeoffs when dispersing across a patchy landscape. Oikos 108:219−230.

Appendices

Table S2.1. 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 the logging program. We modeled wolverine habitat selection with a mixed-effects generalized linear model (binomial family, logit link) with the individual as a random intercept.

Model	Explanatory variable	β	SE	LCL	UCL	Model	β	SE	LCL	UCL
Winter before	Intercept	-3.854	0.435	-4.708	-3.001	Summer before	-5.231	0.631	-6.467	-3.994
	Stream	-0.100	0.012	-0.125	-0.076		-0.075	0.012	-0.098	-0.052
	Broadleaf	-0.123	0.011	-0.144	-0.102		0.058	0.009	0.041	0.076
	Coniferous	-0.147	0.011	-0.168	-0.125		-0.033	0.009	-0.050	-0.016
	Mixed	-0.116	0.010	-0.136	-0.096		0.046	0.010	0.027	0.065
	Bog or fen	-0.060	0.008	-0.076	-0.043		-0.067	0.007	-0.081	-0.053
	Seismic	-0.034	0.010	-0.054	-0.014		-0.030	0.009	-0.047	-0.013
	All-season	0.220	0.020	0.180	0.259		0.168	0.017	0.135	0.201
	Winter	0.188	0.018	0.153	0.224		0.073	0.015	0.043	0.103
	Cutblock	-0.052	0.015	-0.080	-0.023		0.136	0.014	0.109	0.162
Winter during	Intercept	-3.044	0.398	-3.825	-2.263	Winter interim	-0.653	0.396	-1.429	0.122
	Stream	-0.141	0.013	-0.166	-0.116		-0.123	0.018	-0.158	-0.088
	Broadleaf	-0.131	0.012	-0.154	-0.108		-0.040	0.015	-0.071	-0.010
	Coniferous	-0.104	0.012	-0.128	-0.081		-0.078	0.016	-0.109	-0.047
	Mixed	-0.051	0.012	-0.075	-0.028		-0.033	0.016	-0.064	-0.002
	Bog or fen	-0.030	0.010	-0.049	-0.011		-0.060	0.012	-0.084	-0.036
	Seismic	-0.029	0.011	-0.051	-0.008		-0.019	0.015	-0.048	0.010
	All-season	0.004	0.019	-0.034	0.042		-0.137	0.022	-0.181	-0.094
	Winter	0.310	0.022	0.268	0.353		-0.026	0.023	-0.071	0.020
	Cutblock	-0.086	0.015	-0.116	-0.057		-0.075	0.024	-0.121	-0.028
Summer after	Intercept	-1.368	0.364	-2.082	-0.654	Winter after	-0.820	0.241	-1.293	-0.347
	Stream	-0.100	0.008	-0.116	-0.083		-0.024	0.009	-0.042	-0.005
	Broadleaf	0.045	0.007	0.032	0.058		-0.104	0.007	-0.117	-0.090
	Coniferous	-0.046	0.007	-0.059	-0.032		-0.108	0.007	-0.122	-0.094
	Mixed	0.000	0.007	-0.013	0.014		-0.043	0.007	-0.057	-0.029
	Bog or fen	-0.035	0.006	-0.046	-0.024		-0.064	0.006	-0.075	-0.053
	Seismic	-0.029	0.007	-0.042	-0.016		0.014	0.007	0.001	0.028
	All-season	-0.018	0.011	-0.041	0.004		-0.026	0.011	-0.048	-0.005
	Winter	0.041	0.011	0.020	0.062		-0.001	0.011	-0.022	0.020
	Cutblock	-0.091	0.008	-0.107	-0.076		-0.060	0.010	-0.080	-0.041

Table S2.2 Occurrence of prey items at GPS clusters visited by field crews between November 2013 and March 2016 (n = 116). We determined the food habits of wolverines using clusters and scats. Scats (n = 128) were used to identify prey at 56 clusters whereas visible prey remains were used to identify prey at the remaining clusters (n = 60). When visiting a GPS cluster, there either was obvious prey remains or scat left at the site or both prey remains and scat. Our analysis made clusters the sample unit. For clusters that had obvious prey remains that could be identified in the field, the cluster was designated as 100% whatever the species. If field technicians were unsure of the origin of prey remains, scat was collected, analyzed, and used to represent the prey within the cluster where it was collected. We then used cluster as the sample unit for occurrence calculations.

Species	Population	*n* = 116	Male	*n* = 41	Female	*n* = 75
Rabbit	31.90	37	26.83	11	34.67	26
Beaver	30.17	35	43.90	18	22.67	17
Moose	15.52	18	17.07	7	14.67	11
Small Rodent	8.62	10	2.44	1	12.00	9
Caribou	4.31	5	4.88	2	4.00	3
Deer	2.59	3	0.00	0	4.00	3
Grouse	2.59	3	4.88	2	1.33	1
Marten	2.59	3	0.00	0	4.00	3
Cricetidae	1.72	2	0.00	0	2.67	2

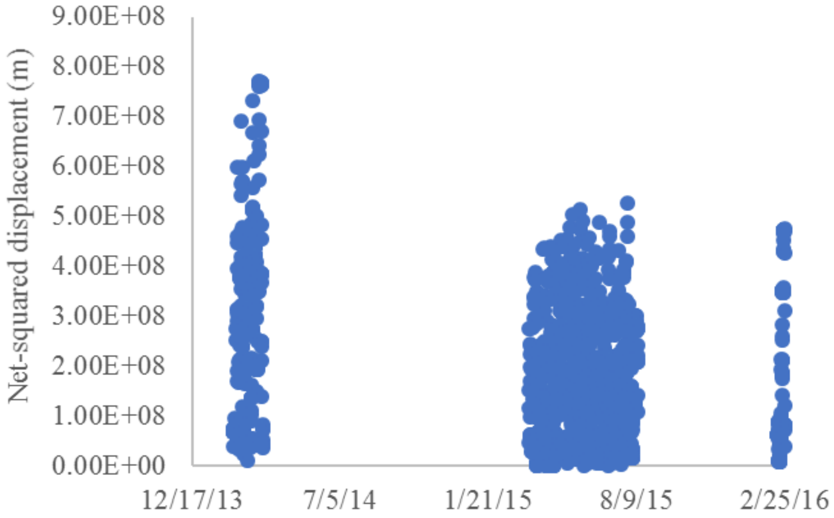

Fig. S4.1. Net-squared displacement (m) of M07 from his first GPS relocation recorded. M07 was considered to display exploratory movements.

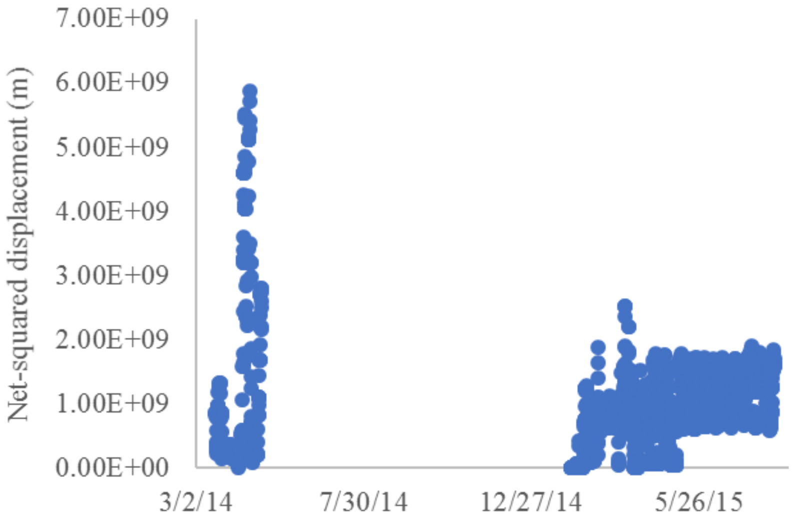

Fig. S4.2. Net-squared displacement (m) of M10 from his first GPS relocation recorded. M10 was considered to display exploratory movements.

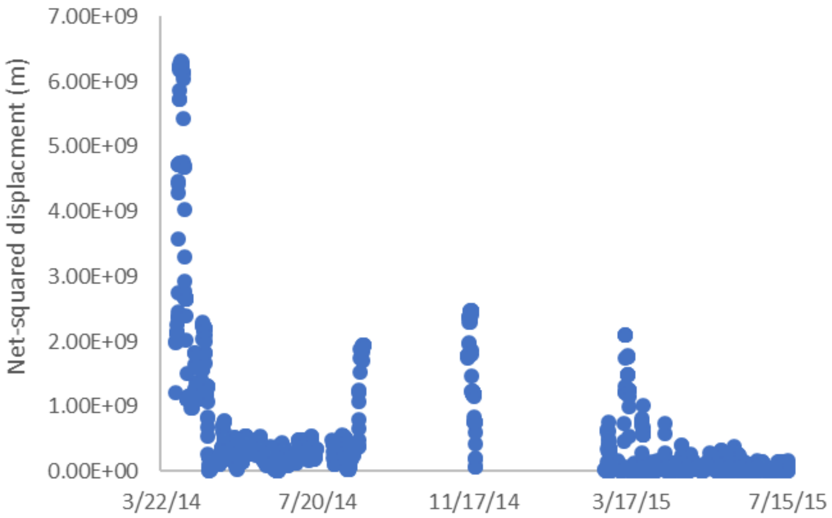

Fig. S4.3. Net-squared displacement (m) of M11 from his first GPS relocation recorded. M11 was considered to display exploratory movements.

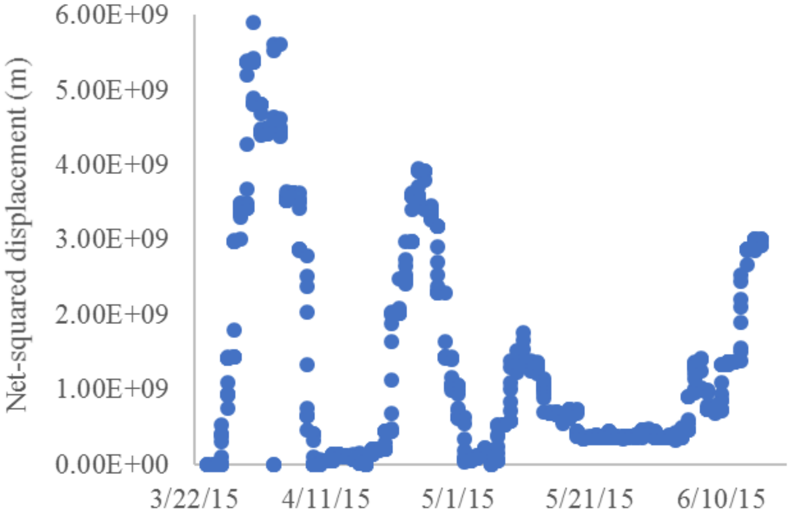

Fig. S4.4. Net-squared displacement (m) of M17 from his first GPS relocation recorded. M17 was considered to display nomadic movements.

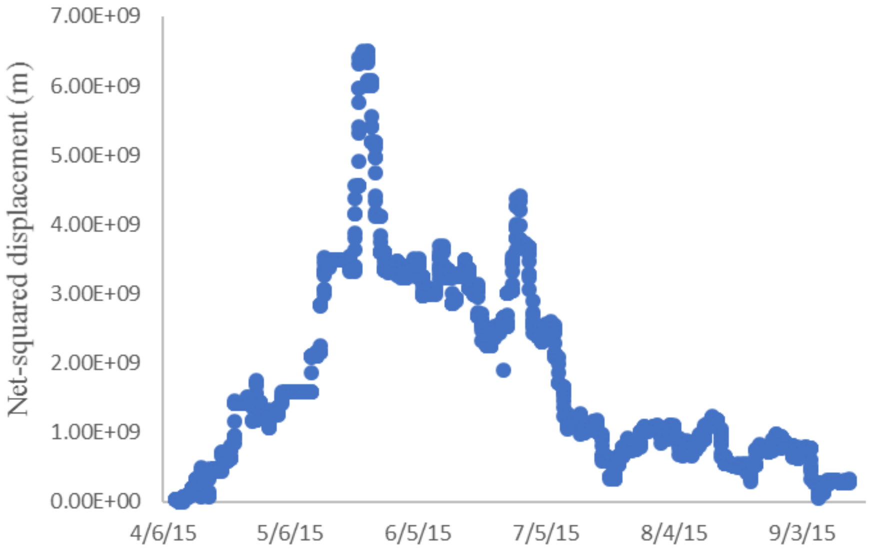

Fig. S4.5. Net-squared displacement (m) of M18 from his first GPS relocation recorded. M18 was considered to display nomadic movements.

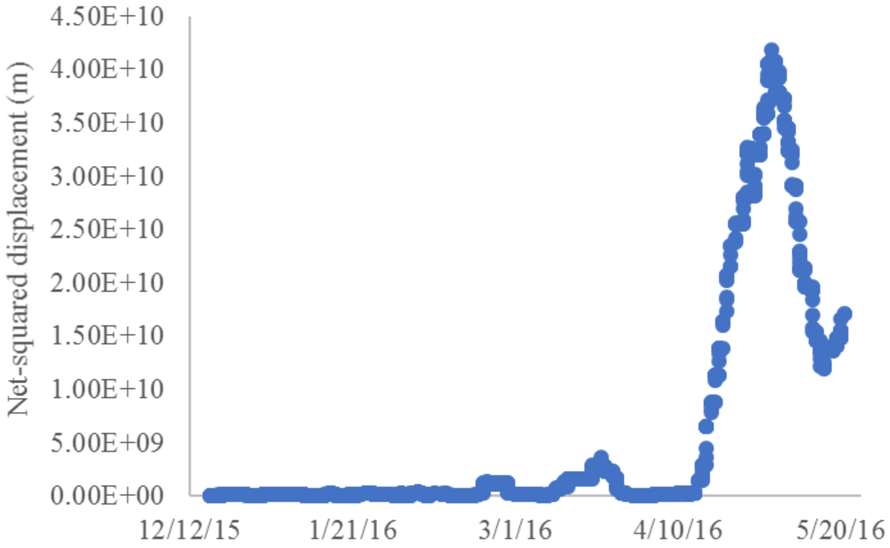

Fig. S4.6. Net-squared displacement (m) of M20 from his first GPS relocation recorded. M20 was considered to display exploratory movements.

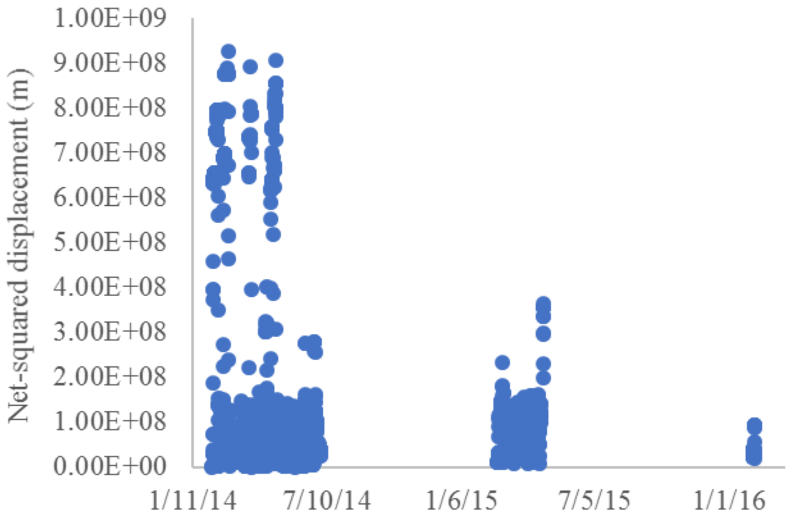

Fig. S4.7. Net-squared displacement (m) of F07 from his first GPS relocation recorded. F07 was considered to display exploratory movements.

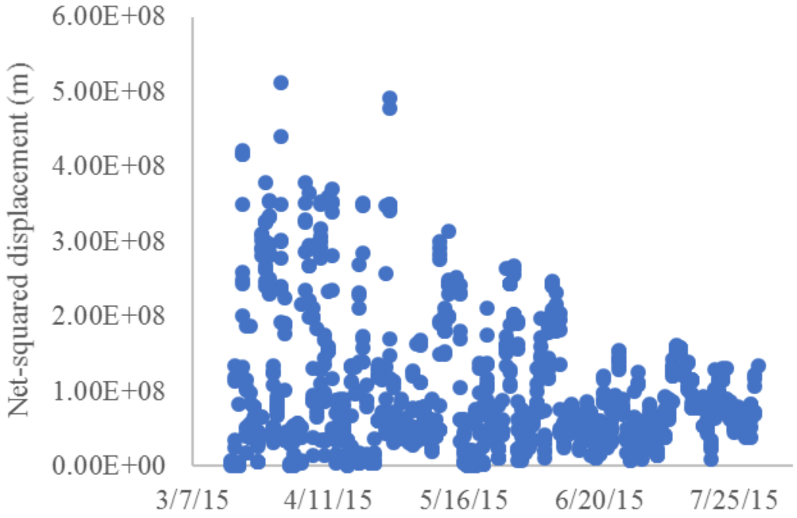

Fig. S4.8. Net-squared displacement (m) of F13 from his first GPS relocation recorded. F13 was considered to display exploratory movements.

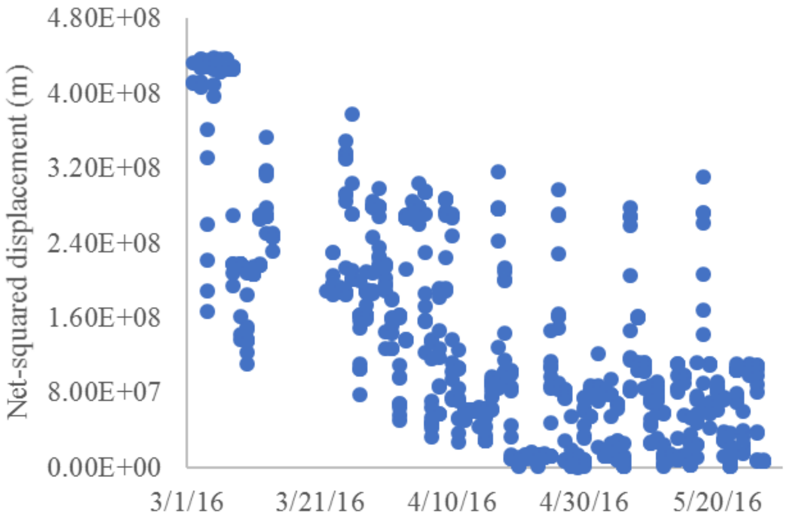

Fig. S4.9. Net-squared displacement (m) of F17 from his first GPS relocation recorded. F17 was considered to display nomadic movements.

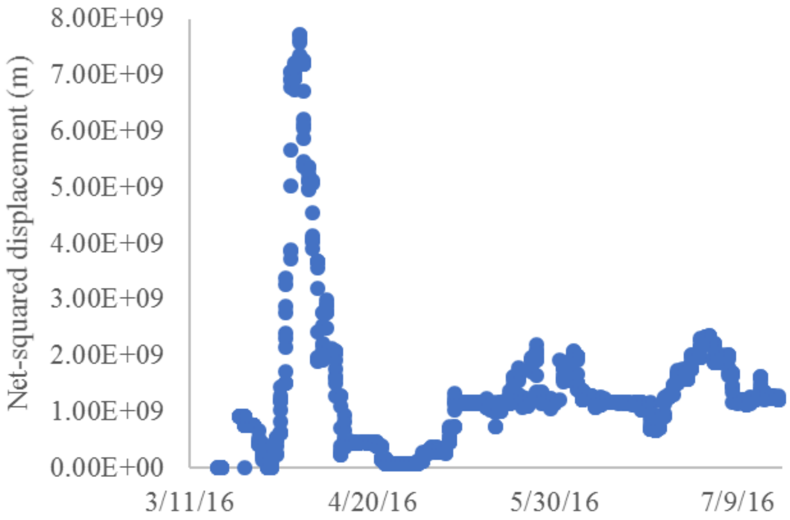

Fig. S4.10. Net-squared displacement (m) of F20 from his first GPS relocation recorded. F20 was considered to display nomadic movements.