Wolf-Moose Spatial Dynamics in Alberta's Athabasca Oil Sands Region

by

Eric William Neilson

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Department of Biological Sciences
University of Alberta

Abstract

The degree to which predator and prey distributions overlap in space influences the probability of encounters between predator and prey, kills of prey, and consequently, how each species' abundance varies in time and in space. Predator and prey attempt to increase or decrease overlap respectively through movement and habitat selection, processes that are sensitive to habitat heterogeneity. If predator and prey respond differently to novel habitat heterogeneity such as a zone of influence in and around human disturbance, it may provide prey with a refuge or facilitate predator hunting efficiency. Alberta's Athabasca oils sands region (AOSR) is a region of boreal forest with extensive mining developments and overlapping wolf (*Canis lupus*) and moose (*Alces alces*) populations. To assess whether the human disturbance in AOSR has affected wolf-moose spatial overlap, I quantified the degree to which both wolves and moose avoid human disturbance across my study area. I hypothesized that wolves would avoid areas disturbed by human developments and activity, and that this avoidance would be used by moose as a refuge. Wolves and moose both used and selected areas near human disturbance such that no refugia for moose was available due to human disturbance. Further, I found that a higher proportion of moose were killed as the distance to oil sands mines decreased. I also found that wolves selected to move on linear features associated with oil extraction and such selection facilitated faster movement. Wolves did select to move farther away from human habitation and oil sands facilities, but only during the day. There was no relationship between wolf movement speed and proximity to industrial facilities, urban area or oil sands mines. Moose cows, particularly those with calves, strongly avoided areas within their home ranges with a high intensity of wolf use. In addition, moose altered their behaviour both within and between individuals as a function of the local intensity of use by wolves, but only with respect to natural features. Rivers and streams were avoided in areas with more wolf use. Overall, I conclude that human disturbance in AOSR has not generated prey refugia for moose, rather it has provided a marginal advantage for wolves while hunting in proximity to mines.

Preface

This thesis is an original work by Eric W. Neilson. Field methods were approved by the University of Alberta (Animal Care and Use Committee Protocol #761, Study Id. AUP00000040 and Study Id. AUP00000102). I conducted all data management, analysis, and manuscript writing. Dr. Stan Boutin facilitated access to data and assisted in conception of the research questions, analysis and writing.

A version of Chapter 3 has been published in *Ecosphere* as Neilson, E. W., and S. Boutin. 2017. Human disturbance alters the predation rate of moose in the Athabasca oil sands. *Ecosphere* 8(8):e01913. 10.1002/ecs2.1913. I was responsible for the analysis as well as the manuscript composition. Dr. Stan Boutin was the supervisory author, was involved with concept formation and contributed to manuscript edits.

Acknowledgements

This thesis was made possible through the mentorship, teaching, collaboration and support of many people. First and foremost, I would like to thank my supervisor, Dr. Stan Boutin. Without a doubt, the most important thing I'll take from this degree is the critical approach to science that prioritizes logic, evidence and rigor, which I learned from Stan. Thank you to my committee, Dr. Mark Boyce and Dr. Erin Bayne, who provided excellent feedback and creative ideas for testing my hypotheses. Mark was helpful is navigating difficulties concerning resource selection and Erin was a great guide for ensuring the analysis was to the point and on track. Other faculty members including Dr. Mark Lewis, Dr. Scott Nielsen, Dr. Andrew Derocher, and Dr. Colleen Cassidy St. Clair have provided guidance on everything from the philosophy of science to details of statistics and mathematics. In particular, I would like to extend my gratitude to Dr. Evelyn Merrill. From the content of her Landscape Ecology course, to the many conversations about how large mammals use a landscape across scales and contexts, Evie was an invaluable resource for this thesis. I can go no farther without extending extra thanks to Ainsley Sykes, whose helpful organization and management has certainly made this entire process possible.

Upon finishing my MSc I started working with the Alberta Biodiversity Monitoring Institute, an experience that provided essential training and connections with colleagues essential for my PhD. Working with Dr. Jim Schieck cemented how to manage a large project and the team to get it done. Dr. Daiyuan Pan helped me to really see the potential of GIS and Haitao Li first showed me how to work with spatial data in R. Dr. Ermias Azeria helped through some difficult R coding that opened up the possibility of the software. Dr. Tyler Muhly provided me the opportunities both to really dig into a large spatial dataset and simulate spatial data. Dr. Cole Burton brought me in on a research program that first demonstrated to me the effectiveness of

remote cameras, as wells as the advancing my understanding of occupancy, data collection and conservation biology in general. Working with Cole has made me better at answering applied ecological and methodological questions. And collecting camera data with ABMI introduced me to Alex MacPhail and Logan McLeod; great field technicians, and many new habitats in Alberta.

I can't imagine a better place to study ecology than the wildlife biology labs at the University of Alberta. The Boutin lab teems with critical thinking, engaging discussions and laughs. In particular I would like to thank Amanda Droghini, with whom I learned how to navigate the formidable dataset we both used for our graduate degrees. Also, I'd like to thank Dr. Dario Moreira, Dr. Jess Haines, Clayton Lamb, Kate Broadley, Darcy Doran-Meyers, Yasmine Majchrzak, Mike Peers, Laura Garland, Sean Konkolics and April Martinig. I'd like to extend extra thanks to Melanie Dickie. Mel and I have worked through many of the same issue concerning wolf ecology and the analysis needed to understand it and it was easier doing so as a team. Interaction with members of other labs in the wildlife world made working at the U of A all the better. Thanks to Christina Prokopenko, Dr. Andrea Morehouse, Dr. Andrew Ladle, Jodi Berg, Eric Spilker, Shantel Sparkes, Dr. Robin Steenweg, Dr. Nick Pilfold, Jody Reimer, Janet Ng, Julia Shonfield, Michelle Knaggs, Dan Yip, Cam Nordell, Jesse Watson and Natasha Annich. Thanks to Aaron Bell (U of S!), with whom I conducted my first ecological experiment at the Bamfield Marine Sciences Centre.

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investigate it, as well as his patience for entertaining questions from grad students were incredibly helpful.

The data used in this thesis were collected by the Wildlife Habitat Effectiveness and Connectivity working group (WHEC). Thanks to WHEC's government and industry partners. I commend the companies involved in this project as well as the University of Alberta and government of Alberta for pooling resources to more effectively answer questions in an area important to Alberta's environment, people and economy. Thanks to Corey De La Mare for getting the ball rolling for WHEC and for the help with the habitat analysis. Thanks to Dr. Joanna Burgar for the help she provided with data and questions while at the AEP office in Fort McMurray. Thank you to WHEC's funders; Syncrude Canada Ltd., Suncor Energy, Imperial Oil, Total, Canadian Natural Resources Ltd., BP Canada, Cenovus Energy Ltd., Devon Canada Corporation, Teck Resources Ltd. and Shell. Thank you to my PhD funders; the University of Alberta and the Natural Sciences and Engineering Research Council of Canada.

Working with WHEC provided me with essential and immersive experience with the habitat and conditions of the Athabasca oil sands. Thank you to Holger Bohm, for bringing me on board and facilitating the collection of such a wonderful dataset. Thanks to Brynlee Thomas and Emily Chow, who not only managed the WHEC field staff, while themselves canoeing down a spring river or sledding down seismic lines, but also conducted the wolf scat processing and analysis to inform what we know about wolf diets in the oil sands. Thanks to all the technicians with whom I worked and provided all the data for my thesis; Kevin Coates, Adam Hope and Kristin Van Katwyk. Of critical importance, thank you to Clay Wilson and Bighorn Helicopters for expertly capturing and collaring the moose and wolves used to answer the questions in this thesis.

Finally, and most importantly, thank you to my family. When I think about how I got to where I am today, my interest in the natural world, my desire to be out in it, I think of my two wonderful parents Myrna and Walter Neilson and my two brothers Alex and John. To each member of my family. Thank you.

To my dearest Harmony, without you this whole endeavor would have stalled before it ever got going. You keep me grounded, you keep me moving forward. Thank you sweetie.

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Chapter 1. General Introduction

Predator-Prey Spatial Distributions

The degree to which species distributions overlap in space has long been understood to be critical in determining co-existence between predator and prey (Huffaker 1958, Holling 1959). For predators, the importance of overlap is intuitive; it is required for the encounters with prey and subsequent kills needed by predators for survival (Sih 2005). For prey, reducing overlap may be important for escaping predation, thereby allowing prey, and subsequently predator, persistence (Gause 1934, Huffaker 1958). Two predictions follow from considerations of predator-prey overlap. Firstly, the distributions and resulting overlap between predators and prey determine how species abundances vary in time (Holling 1959, Sinclair 1989, Messier 1994) and in space (Huffaker 1958, Sih 2005, Kauffman et al. 2007). Secondly, for mobile predators and prey a behavioural response race, or ‘space race’ (Sih 2005), in which predators attempt to maximize spatial overlap with their prey and prey attempt to minimize it, emerges (Sih 1984, Lima and Dill 1990). These two predictions are not exclusive. Spatial and temporal variation in predator and prey abundance determine the extent of spatial overlap and the importance of behavioural responses to it, and vice versa.

In the absence of predation, prey should be distributed according to the distribution of their food (Sih 2005) with interacting effects of intraspecific competition and attraction (Fretwell and Lucas 1969). Predators are therefore expected to aggregate in areas of high prey density or prey resources (Lima 2002, Flaxman and Lou 2009) but may be constrained by conspecifics in the same ways as prey (Hassell 1978), in particular by territoriality (Maher and Lott 2000). Prey are expected to respond to predators through the use of refugia, defined as any prey strategy that reduces the probability of mortality due to predation (McNair 1986, Sih 1987a, Sih et al. 1988). Refugia include avoidance of areas with higher predator densities (Sih 1987b) or higher predator hunting efficiency (Lima and Dill 1990, Lima 1998). Without refugia therefore, the correlation between the predator and prey distributions may decrease if predator and prey responses to one another are of equal strength, i.e. predator work to increase overlap and prey do the opposite (Sih 1984). With the introduction of refugia, prey begin to 'win' the space race, and the correlation may become negative (Huffaker 1958, Sih 1984, Muhly et al. 2011).

The degree of spatial overlap between predators and prey varies across different ecological scales (Sih 2005, Courbin et al. 2013) and as the importance of predation increases, species select for overlap at broader scales (DeCesare et al. 2012). Two ecological scales are of interest; the population-range scale, at which individuals in the population select areas for their entire home-range, and the home-range scale, at which individuals choose patches of resources within their home-range (Johnson 1980). By selecting habitat avoided by predators at the population-range scale, prey can more effectively avoid predation than by doing so at finer scales (Rettie and Messier 2000). However, given the importance of overlap from the perspective of the predator, finer scale overlap is expected, particularly for single prey systems. Predator and prey spatial overlap translates into encounters and kills within the home-range scale and varies through selection of patchy refugia by prey (Caley and John 1996) and both predator and prey movement. Movement rates of both species partially determined by the movement rate of the other such that reduced prey movement may lead to increased predator movement (Sih 1984).

Because selection, or disproportionate use (Lele et al. 2013), of habitat partially determines spatial overlap between predator and prey, overlap is a function of spatial heterogeneity. Heterogeneity is the axis along which refugia are generated and so, novel sources of heterogeneity influence overlap, behavioural response races and ultimately, predator and prey abundances (Huffaker 1958). The sensitivity of a predator-prey space race to novel sources of landscape heterogeneity is expected to depend on both the strength of and the difference between predator and prey responses to that heterogeneity. When predator prey responses differ in magnitude, direction or both, spatial overlap shifts. One critical source of novel heterogeneity, is human disturbance.

Human Disturbance

Species responses to humans and human disturbance vary according to level of habituation (Mattson et al. 1992, Frid and Dill 2002), the cost to other important life-history requirements or any advantages presented by association with human disturbance features (Hebblewhite et al. 2002, Latham et al. 2011b). The range of responses to disturbance determines whether a species can cope with the new environments created by human disturbance (Sih 2013). If a species is able to response to disturbance behaviourally (Frid and Dill 2002) or through phenotypic plasticity (Crews 2005, Hendry et al. 2008), they may cope without demographic changes. When behavioural/phenotypic responses are insufficient or maladaptive (DeWitt et al. 1998) then the species may experience demographic consequences (Dwernychuk and Boag 1972) and increased natural selection pressure.

Such responses to human alters species distribution in two principal ways. When the area of the disturbance is not used by a species, that area is removed from the landscape, reducing or displacing the space over which species are distributed with potential reductions in abundance being the end results (Gaston et al. 2000). Alternatively, if the disturbance alters the quality of the habitat in proximity to it, the number of individuals that can occupy or use that habitat changes. This effect has been called a ‘zone of influence’ (Dyer and Schneider 2006) and ranges from edge effects at the boundary between disturbed and undisturbed habitat (Bayne et al. 2005), to noise or risk effects reaching for kilometers away from a disturbance itself (Francis et al. 2009), to constraints on animal movement (Muhly et al. 2015). When a zone of influence decreases habitat quality, it leads to functional habitat loss, with potential demographic costs (Dyer et al. 2001) vs increased habitat quality, which leads to increased occupancy (Chace and Walsh 2006), improved foraging efficiency (Dickie et al. 2017) and/or improved vital rates. As human impacts to natural systems and habitats increase, it is important to assess the population consequences of human mediated changes to species interactions.

The effect of human disturbance on predator-prey overlap varies due to differences between predator and prey response to human disturbance. When novel heterogeneity creates habitat for either predator or prey leading to higher abundance or increased use, the other species may shift its space use in response. For instance, songbird densities increased along novel cutblock edges elicited an aggregative response from predators to those edges (Gates and Gysel 1978). Predator use of areas opened up after human disturbance may lead to prey avoidance and functional habitat loss for the prey (James and Stuart-Smith 2000). Conversely, when predators avoid human disturbance and prey do not, refugia are created near the disturbance (Hebblewhite et al. 2005b, Berger 2007, Muhly et al. 2011).

Alberta's Athabasca Oil Sands

Alberta's Athabasca oils sands region (AOSR) is a region of boreal forest in the Canadian boreal plains ecozone with extensive deposits of bitumen, a viscous form of hydrocarbon or crude oil (Alberta Biodiversity Monitoring Institute 2014). Development of the area for bitumen extraction began in the 1960's with accelerated development beginning in the early 2000s (Hauge and Keith 1981, Schindler 2010). Currently, the AOSR is characterized by extensive human disturbance including open pit mines, tailings ponds and industrial facilities (Fig 1.1, Schindler 2010). In 2014, the total footprint of the mines was approximately 650 km^2. Because bitumen in the AOSR is extracted using pit mining, such disturbances completely remove habitat from the landscape for most species. However, indirect habitat loss also occurs due to species avoidance of the areas in proximity to mining features or a zone of influence due to noise, wildlife-human conflict, hunting and traffic (Dyer and Schneider 2006). Spatial refugia will occur if such avoidance varies between predator and prey in the AOSR.

Oil sands extraction activities in the AOSR are distributed close to several major rivers (Fig 1.2). To investigate the importance of riparian habitat and connectivity along rivers, and the utility of setback distances between rivers and industrial development, the Wildlife Habitat Effectiveness and Connectivity (WHEC) working group, which included representatives from the oil sands industry and the Alberta government, and scientists from the University of Alberta was formed (Boutin et al. 2015). WHEC deployed GPS collars on moose between 2010 and 2012 and wolves between 2012 and 2014 in the AOSR to examine movement and habitat selection with respect to rivers of the two species.

Wolf distribution and abundance is closely related to those of moose across North America (Messier 1994). Wolves maximize home-range scale overlap with moose by selecting habitats preferred by moose (Kittle et al. 2017). However, the correlation between the distribution of moose and wolves does not equal one for several reasons. At the population scale, moose avoid predation by selecting home-ranges with low overlap with wolves (Dussault et al. 2005). At the home-range scale, wolves select habitat that facilitates hunting behaviour (Kunkel and Pletscher 2000), allowing moose to reduce overlap by avoiding those habitats. Human disturbance further allows moose to reduce overlap with moose. Wolf respond to human disturbance varies with the types and intensity/frequency of use of the disturbance. When the intensity of use by humans is low, wolves use human disturbance such as linear features but reduce their use with increasing human use (Whittington et al. 2005, Hebblewhite and Merrill 2008, Houle et al. 2010, Rogala et al. 2011, Lesmerises et al. 2012). Moose also exhibit a mixed response to human disturbance. In some cases, moose select disturbances with a high intensity of human use that are avoided by predators, presumably to reduce predation risk (Stephens and Peterson 1984, Berger 2007).

The GPS telemetry data collected by WHEC suggested that wolves and moose exhibit disparate and variable responses to oil sands mining activities, with concentrations of both species near mines in some areas and avoidance by one, the other, or both species in other areas. The question was raised; does differential response to human activity by wolves and moose in the AOSR result in disruption to wolf-moose spatial overlap, generating prey refugia for moose? In this thesis, I utilized a multi-scale predator-prey space race conceptual framework to investigate whether the imposition of large human disturbance alters the spatial dynamics of a predator-prey system.

Thesis Structure

I structured this these as a series of stand-alone but inter-related chapters. In *Chapter 2*, I test the prediction that wolves are distributed farther away from mines than would be expected randomly at the population scale, which is necessary for refugia for moose near mines. The chapter investigates population scale selection of both wolves and moose allowing direct comparison. In this chapter I also calculate the latent selection difference (Latham et al. 2011a) between the two species, the coefficients from which I used to map areas across the study area predicted to provide refugia for moose.

In *Chapter 3*, I extended the analysis of the second chapter to assess how wolf and moose distributions and proximity mines and other human disturbance determine the distribution of locations at which wolves killed moose. To estimate the location of wolf kills of moose across the study area, I developed an algorithm in the R programming language (R Core Team 2016) to summarize clusters in the wolf GPS telemetry data. A sub-set of these clusters were visited in the field in order to estimate a predictive model based on cluster characteristics. The resulting distribution of kill locations was compared to an independent spatial index of moose density to assess changes to the proportion of moose killed near and far from human disturbance.

Both predator hunting behaviour and anti-predation behaviour by prey contribute to the predator space race. Therefore, in *Chapters 4* and *5* I investigated the behaviour of wolves and moose respectively to further understand how wolves and moose and kills of moose are distributed in the AOSR. In *Chapter 4*, I used integrated step selection analysis (iSSA), a novel analysis method that estimates and controls for changes in movement behaviour in habitat selection analysis (Avgar et al. 2016), to investigate changes to wolf movement and home-range scale selection as a function of proximity to human disturbance. By then comparing movement locations to kill locations, I elaborated on how wolf hunting determines kill location. Finally, in *Chapter 5*, I analyzed moose habitat selection across gradients of wolf presence both within and between moose individuals, when accompanied or not, by calves. By parsing the effects of habitat and the presence of an important predator, I used this chapter to demonstrate the capacity of moose to respond spatially to predators and whether the presence of human disturbance provides them with an advantage in doing so.

In the final chapter, I summarized the main findings of my thesis and suggested both management implications for both wolf moose populations in the AOSR and, more generally, for large mammals living in proximity to large polygonal disturbances. I also discuss directions for future research.

Throughout the thesis, I concentrated on the winter season. I did so for two reasons; firstly, scat analysis from the WHEC project indicated that the majority of wolf predation on adult moose is in the winter (unpublished data, Thomas 2013) and secondly, we only visited kill locations in winter.

Study System

As written in Neilson and Boutin (2017); the study area (Fig 1.2) is comprised of the area surrounding the Athabasca Oil Sands. The mines lie along the Athabasca River approximately 20 km north of the town of Ft. McMurray between 56.9 and 57.4 degrees north and -111.0 and -112.0 degrees east. The forested areas surrounding the mines are moderately disturbed by linear features with few cut blocks of various ages. Topographic heterogeneity is contained largely within steep and deep river valleys and a broad, decreasing elevation gradient (860m to 250m) from north to south. Low, peat (*Sphagnum sp.*) forming wet areas with variable black spruce (*Picea mariana*) and tamarack (*Larix laricina*) forest dominates the area (33%), followed by uplands of aspen (*Populus tremuloides*), white spruce (*Picea glauca*) and jackpine (*Pinus banksiana*) (together 30%). Forest understories contain willow (*Salix sp.*) dogwood (*Cornus stolonifera*), blueberry (*Vaccinium myrtilloides*), cranberry (*Vaccinium sp.*) and alder (*Alnus sp.*).

Moose densities are low in the AOSR, ranging between 0.04 and 0.15/km2 in the three Wildlife Management Units overlapping our study area as measured between 2008 and 2013 (Morgan and Powell 2008, 2009, 2010, Sustainable Resource Development 2013). Wolves and black bear prey on moose in the AOSR (Hauge and Keith 1981). Human hunting of moose is also an important source of moose mortality (Hauge and Keith 1981). Reported hunter harvest of moose was below the allocated quota for two and similar to the allocated quota in one of the wildlife management units in the study area (Morgan and Powell 2008, 2009, 2010). Moose are the most frequent source of prey for wolves in the winter in AOSR although wolves switch to beaver in the summer (Thomas 2013, unpublished data). Wolf trapping rates are between 0.5-3/1000 km^2 annually in the area (Robichaud and Boyce 2010).

Study area size and shape varied for the various chapters but inference from my thesis does not extend beyond the extent of all the wolf pack territories and moose home ranges (Fig 1.2). Kernel density estimates were created using the distribution of moose individual and wolf pack GPS locations in Geospatial Modeling Environments (Beyer 2012).

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Figure 1.1 Photos of oil sands mines in the Athabasca oil sands region, taken from helicopter. *Photo credits: Eric W. Neilson*

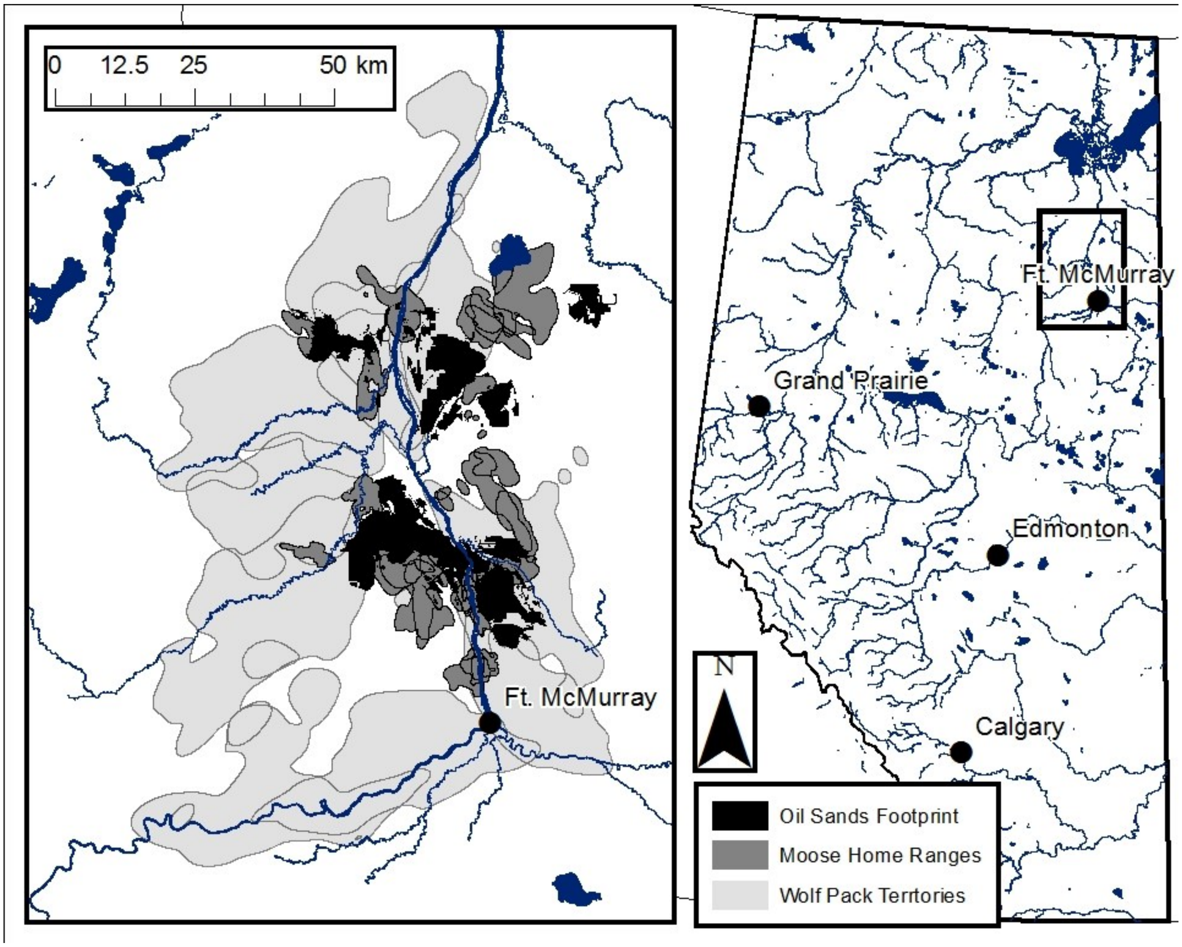

Figure 1.2 Moose home ranges and wolf pack territories in the Athabasca oil sands region. Home ranges and territories were estimated using kernel density estimates.

Chapter 2. Differential responses to disturbance alters spatial overlap of predators and prey in the Athabasca oil sands

Introduction

Predator-prey relationships are characterized by competing strategies in which predators attempt to maximize and prey attempt to minimize spatial overlap (Sih 2005). In the absence of predators, prey use space according to the distribution of important resources and the degree of intraspecific competition (Kacelnik et al. 1992, Hammond et al. 2007). Therefore, predators can track the distribution of their prey's resources to maximize spatial overlap (Flaxman and Lou 2009). Consequently, prey use of space can shift to reflect the distribution of food as well as areas offering spatial refugia from predation (Sih 1987a, Hammond et al. 2007). Refugia are any space used by a prey species to reduce the probability of mortality due to predation (Sih 1987a). Novel refugia can arise due to differences between predator and prey response to human disturbance (Hebblewhite et al. 2005b, Berger 2007, Muhly et al. 2011).

When predation is an important limiting factor, prey selection for areas and habitats that facilitate reduced overlap with predators should be prioritized at broad scales (Rettie and Messier 2000). An individual prey that has selected an area avoided by predators at the landscape scale (the second order of selection defined by Johnson (1980)) experiences an overall reduction in risk such that it can prioritize selecting habitat to mitigate other limiting factors at finer scales (Hebblewhite and Merrill 2009). For instance, caribou (*Rangifer turandus*) select habitat that minimizes overlap with moose (*Alces alces*) which consequently minimizes overlaps with wolves (*Canis lupus*) at broad scales, thereby limiting their need to avoid predation within their seasonal home ranges (Rettie and Messier 2000, DeCesare et al. 2012). Therefore, whereas refugia can be present at multiple scales (Brown and Kotler 2004), the most effective refugia from predation are those that allow prey to select areas for their entire home that exhibit low predator use or hunting efficiency. In addition, broad-scale refugia that maintain little to zero overlap between predators and prey can be more safely inferred to be an effective refuge when data are collected over a short period. A smaller scale refuge must consider prey movement in and out of a refuge in order to make conclusions about that refuge's effectiveness because intermittent exposure to predation will determine the longer term predation rate (Sih et al. 1988).

Investigations of prey refugia have tended to focus on the effect of refugia on predator and prey population stability and interactions (McNair 1986, Sih 1987a), trophic cascades (Hebblewhite et al. 2005b, Finke and Denno 2006) and community richness and diversity (Hixon and Beets 1993, Caley and John 1996). These studies assume that a refuge is present and seek to measure its impact. Determining the presence of spatial refugia for large wide-ranging vertebrates (Hebblewhite et al. 2005a, Muhly et al. 2011) is equally important, particularly when novel human disturbance may disrupt the overlap between predator and prey.

Alberta's Athabasca oils sands region (AOSR) is a region of boreal forest in the Canadian boreal shield ecozone with extensive deposits of bitumen. Development of the area for bitumen extraction began in the 1960's with accelerated development beginning in the early 2000s (Schindler 2010). Currently, the AOSR is characterized by extensive human disturbance including open pit mines, tailings ponds and industrial facilities (Schindler 2010). Because bitumen in AOSR is extracted using pit mining, such disturbances completely remove habitat for many species from the landscape. However, indirect habitat loss also may occur due to species avoidance of the areas in proximity to mining features or a "zone of influence" caused by noise, wildlife-human conflict, hunting and traffic (Dyer and Schneider 2006).

Wolf responses to human disturbance vary with the types and intensity/frequency of use of the disturbance. When the intensity of use by humans is low, wolves use human disturbance such as linear features but reduce their use with increasing human use (Whittington et al. 2005, Hebblewhite and Merrill 2008, Houle et al. 2010, Rogala et al. 2011). Moose also exhibit a mixed response to human disturbance. In some cases, moose select disturbances with a high intensity of human use that are avoided by predators to reduce predation risk and avoidance of low or unknown intensity of use human linear features, which have shown to be selected by wolves (Stephens and Peterson 1984, James and Stuart-Smith 2000, Berger 2007, Wasser et al. 2011). Whereas moose home ranges do not always strongly overlap those of wolves, the link between selection for large human disturbance providing refugia and reduced overlap with wolves has not been demonstrated (Dussault et al. 2005). We investigated the hypothesis that wolf avoidance of human disturbance in AOSR creates prey refugia for moose in winter. Specifically we predicted that wolves avoid human disturbance more than moose and this discrepancy increases with the intensity of use of disturbances by humans.

Methods

Study Area

The AOSR is comprised of the broader Athabasca watershed surrounding the Athabasca oil sands. The mines lie along the Athabasca River approximately 20 km north of the town of Ft. McMurray between 56.9 and 57.4 degrees north and -111.0 and -112.0 degrees east. Topographic heterogeneity is contained largely within steep and deep river valleys and a broad, decreasing elevation gradient (860m to 250m) from north to south. Low, peat (*Sphagnum sp.*) forming wet areas with variable black spruce (*Picea mariana*) and tamarack (*Larix laricina*) forest dominates the area (33%), followed by uplands of aspen (*Populus tremuloides*), white spruce (*Picea glauca*) and jackpine (*Pinus banksiana*) (together 30%). Forest understories contain willow (*Salix* spp.) dogwood (*Cornus stolonifera*), blueberry (*Vaccinium myrtilloides*), cranberry (*Vaccinium* spp.) and alder (*Alnus* spp.).

The area is characterized by extensive mining footprints consisting of large extraction pits (325 km^2), tailings ponds (248 km^2) and associated large facilities (66 km^2). The area surrounding the mines has linear densities as high as 18 km/km^2. Forestry is minimal in AOSR. Moose densities are low in the AOSR, ranging between 0.04 and 0.15/km^2 in the three Wildlife Management Units overlapping our study area as measured between 2008 and 2013 (Morgan and Powell 2008, 2009, 2010, Sustainable Resource Development 2013). The Alberta provincial government estimated the moose population declined by 60% between 1994 and 2009 in the management unit west of the Athabasca river (Morgan and Powell 2010). Wolves and black bear prey on moose in the AOSR (Hauge and Keith 1981). Human hunting of moose is also an important source of moose mortality (Hauge and Keith 1981). Reported hunter harvest of moose was below the allocated quota for two and similar to the allocated quota in one of the wildlife management units in the study area (Morgan and Powell 2008, 2009, 2010). Moose are the most frequent source of prey for wolves in the winter in AOSR although wolves switch to beaver in the summer (Thomas 2013, unpublished data). Wolf trapping rates are between 0.5-3/1000 km^2 annually in the area (Robichaud and Boyce 2010).

Moose and Wolf Location Data

As written in Neilson and Boutin (2017); We collared 25 individual moose cows throughout the study area in February 2010 and outfitted each with a GPS (Lotek 7000MU) collar (University of Alberta, ACUC Study Id. AUP00000102). GPS collars were programmed to fix the moose's location every three hours and continued collecting data until October 2012. The presence of calves with moose cows was ascertained during the collaring in March of 2010 and using aerial surveys in December of 2010, January of 2012 and December of 2012. All flights were conducted using a Jet Ranger helicopter flying between 80 and 100 km/h. Collared moose were relocated using radio telemetry and the presence and number of young of the year were recorded.

We collared at least two wolves in every pack in the area covered by moose GPS telemetry and equipped each with Iridium GPS collars (Lotek Inc., Newmarket, ON) in winter of 2011/12 using aerial net-gunning (University of Alberta, ACUC Study Id. AUP00000040). A total of 41 wolves from 10 packs were captured and collared. Wolf collars were programmed to fix the wolf's location every three hours. In the winter of 2012/13, collars were replaced where they had failed and new wolves were captured where individuals had died. In the second winter, GPS locations of the previous year were used to establish pack boundaries to assess whether or not all packs in the area had a collared wolf. We discovered 2 distinct gaps; one situated between Fort McMurray town site and an oil sands mine west of the Athabasca River and the second south of oil sands mines and east of the Athabasca River. Both areas were searched using two helicopters for a full day. We did find limited wolf tracks indicating that wolves had moved through the area but could not find any signs of wolves using this habitat as territory, such as kill sites or large groups of tracks. Based on our extensive efforts we are confident that we placed collars on wolves from all 10 packs in our study area.

We conduced all spatial and statistical analysis on moose and wolf winter locations (October to March) because in summer wolf predation of moose is low (Thomas 2013) due to wolf switching to consuming more beaver in the denning period than in the winter. We only estimated resource selection for the area common to the distribution of GPS telemetry for both species (Fig 2.1). Critically, because the wolf GPS data extended much farther from the human footprint than for moose (Fig 1.2), we did not want to bias our estimate of wolf selection for areas near human footprint compared to that of moose. We used the minimum convex polygon (MCP) or the smallest possible shape surrounding a set of locations or shapes, enclosing the all individual moose 95% utilization distributions (UD) (Fig 2.1), calculated using kernel density estimation (kde) and the least squares cross validation smoothing factor (Seaman et al. 1999). The moose MCP was used to clip wolf 95% UDs calculated for each individual. The resulting polygons were the utilization distributions for each wolf that overlapped the area covered by the moose GPS data. We then calculated the 95% MCP of the resulting wolf polygons, producing a 2967 km^2 polygon (Fig 2.1, 2.2). All GPS telemetry from both species falling outside this polygon was then removed. The effect is to not compare the species in areas where we only had information from one of them.

Environmental Covariates

As written in Neilson and Boutin (2017); We used Alberta Vegetation Inventory data (AVI; Alberta Environment and Sustainable Resource Development 2011) to classify land cover into five classes: fen, bog, mixedwood, deciduous and coniferous based on the Alberta Ecosites definitions (Beckingham and Archibald 1996) for uplands and the Alberta Wetland Inventory Classification System (Halsey et al. 2003) for wetlands (Table 2.1). Fen was used as a reference category for analysis of land cover. We calculated the distance to major rivers and the density of streams using the Inland Waterway Base Hydrology layer (Table 2.1) (Alberta Environment and Parks 2004). We calculated the distance to major rivers and the density of streams using the

Inland Waterway Base Hydrology layer (Table 2.1) (Alberta Environment and Parks 2004). Stream density was calculated as km per km^2.

As written in Neilson and Boutin (2017); we defined the mine footprint as any area where excavation had occurred including pit mines and tailings ponds. Facilities were defined as the mining footprint associated with oil sands operations; upgraders, processing plants, work camps and parking lots. Cleared areas were any area adjacent to mines that had been cleared of forest cover for future pit mining (Table 2.1). To delineate the borders of mines and facilities, we modified 2009 land use shapefiles supplied by the Regional Aquatics Monitoring Program (2011) using SPOT satellite imagery for 2010 and 2012, the earliest years for which we had GPS telemetry for moose and wolves respectively. We only included facilities that were larger than one km^2 for analysis and clipped facility polygons from mines. Because we were interested in a zone of influence around the mining footprint, we removed locations falling inside mines and facilities for analysis and calculated the Euclidean distance to mines and facilities. To account for an attenuating effect of distance to mines and facilities as well as the collinearity between mines and facilities at far distances, we used an exponential decay transformation of the shortest distances to mines and facilities for each GPS location. The decay we chose reduced our transformed distance to zero approximately past distance of 8 km (Table 5.1), the approximate mean diameter of a moose home range in AOSR. Consequently, coefficients estimated the effect of the transformed distance to mines and facilities that are negative indicate avoidance and are predict effects that go to zero at approximately 8 km from either mines or facilities.

As written in Neilson and Boutin (2017); the distribution of linear features was delineated by the Alberta Biodiversity Monitoring Institute (ABMI) at a 1:15 000 scale using 2012 SPOT imagery. We used proximity to the city of Ft. McMurray, located in the south of our study area, as a surrogate for intensity of human recreational use on linear features. Using network analyst in ArcMap 10.1 (ESRI 2011), we calculated the density of seismic, transmission and pipelines as km/km^2 weighted with network distance to Ft. McMurray. We re-calculated the network distances as their difference from the maximum distance such that the largest values were closest to the Ft. McMurray. The resulting density values were a composite of linear feature density and proximity to Ft. McMurray, with larger values indicating higher densities or closer proximity to Ft. McMurray.

Distribution of moose and wolves in AOSR

To test our predictions we modelled moose and wolf resource selection at the population scale, or second order (Johnson 1980) to determine the extent to which wolves avoid establishing territories in areas near human disturbance, thereby providing a refuge zone available to moose. Second order selection is estimated by comparing the locations used by an animal to random locations available to it sampled from across a study area (Boyce et al. 2003). We sampled availability of resources using a distribution of points randomly generated at a density of 50 points/km^2. Second order selection analysis assumes that all individuals are exposed to the same availability (Manly et al. 2002). Due to pack territoriality (Peters and Mech 1975), the area occupied by adjacent packs is not available to all individual wolves, so we included a variable indicating whether a used or random location is in or out of the area occupied by neighboring packs, calculated as the summed 90% utilization distribution for all other packs. We used 90% UDs rather than 95% to allow for a greater degree of overlap at territory edges. We fit a model including distance to facilities, mines and rivers, the density of streams, weighted linear feature density (WLD), a categorical landcover factor for each individual moose and wolf. Individual models were used to account for spatial auto-correlation within and sample size differences among individuals (Fieberg et al. 2010). We fit logistic regression models with the function glm in R, with the bias reduction fitting method. Bias reduction was used to estimate finite standard errors (Firth 1993) because some individual moose or wolves had nearly complete use/availability in distance to mines or facilities due to the distance exponential decay transformation. We centered all continuous variables on zero by subtracting the variable mean from each value and dividing by the standard deviation.

We inferred moose and wolf selection for human disturbance variables in two ways. Firstly, we calculated a population mean and confidence interval (CI) by bootstrapping the distribution of coefficients per species for each model covariate, weighted by the inverse of the standard error for each coefficient per moose or wolf. Wolf bootstrap means were calculated among individuals within packs and then across packs. Pack bootstrapping was weighted with the inverse of the variance between individuals from the same pack. We inferred that moose or wolves selected or avoided a landscape feature when its CIs did not overlap zero and that the species differed from one another when each species' CIs did not overlap the other's mean. We then calculated the proportion of individuals with coefficients in agreement with the bootstrapped population mean.

To spatially visualize areas providing possible refugia for moose, we calculated the latent selection difference (LSD) between moose and wolf selection in winter for both habitat and disturbance variables using logistic regression, coding moose as 1 and wolves as 0 (Latham et al. 2011a). We then calculated and mapped the predicted relative latent selection distance value for all pixels in the study area. Because the LSD was solely for spatial prediction, we did not make inferences from the model coefficients. All mapping and spatial analysis was conducted in ArcGIS 10.1 (ESRI 2011). All other analysis was conducted in R 3.2.3 (R Core Team 2015).

Results

Between 2010 and 2012 we collected 58,323 moose locations in winter, which after clipping to our study area left 56,193 locations. We collected 146,590 wolf locations in winter between 2012 and 2014. After rarefying to a three hour fix rate and clipping data by the study area common to both species, we retained 10,575 locations of wolves from eight packs that we used in modeling. The large reduction in wolf GPS locations is due to removal of points outside the study area common to the moose GPS data.

As predicted, moose selected home ranges closer to human disturbances than wolves (Fig 2.3). However, the difference between the species was not due to wolf avoidance of the mining footprint. Rather, both moose and wolves selected home ranges and territories on average closer to facilities than expected by chance, moose selected home ranges closer to mines and wolves were indifferent to mines (Fig 2.3). Further, the probability of selecting territories increased for a majority of wolf packs with decreasing distance to facilities (63%, Fig 2.4) and mines (63%, Fig 2.4). A majority of moose selected home ranges near mines (64%, Fig 2.4) but were completely equivocal in their response to facilities (48%, Fig 2.4). Moose and wolves did not differ in their selection of home ranges and territories with respect to weighted linear feature density or cleared areas (Fig 2.3).

Rivers emerged as an important predictor of overlap between wolves and moose. Wolves strongly selected territories near rivers whereas moose selected home ranges farther away (Fig 2.3). The probability of selection for territories only increased with increasing distance from rivers for only 25% of wolf packs (Fig 2.4). Moose individuals varied with response to rivers such that there was no clear majority of selection for rivers (Fig 2.4). Among other natural landscape features, moose and wolves did not demonstrate differences in their second order selection. Wolves exhibited territoriality. The boostrapped mean selection coefficient for areas occupied by neighboring packs was - 1.89, (-2.67,-1.55) and was negative for every pack.

The spatially mapped LSD demonstrates the importance of natural habitat for reducing overlap between moose and wolves. Areas far from rivers and east of the Athabasca River comprised of high density conifer and fen complexes exhibit relatively large LSD values (Fig. 2.2). Areas very closed to oil sands facilities also exhibited relative high LSD values (Fig. 2.2).

Discussion

We tested a spatial refugia hypothesis for a moose-wolf system in the heavily disturbed Athabasca oil sands. Our prediction that moose select areas closer to human disturbance than wolves for their home ranges was supported. However, by modeling individuals of each species we determined that the difference in moose and wolf selection was not due to wolf avoidance as we predicted. Therefore, any refugia experienced by moose in the oil sands is due to the strength of their own selection for human areas, not wolf avoidance.

Our results differ from earlier studies examining the variation in the response of wolves and their ungulate prey to human disturbance. Broadly, large carnivores in western North America avoid humans and human disturbance, whereas prey species do not such that human areas provide ‘shields’ that protect prey from predation (Berger 2007, Muhly et al. 2011). In particular, wolves have been shown to avoid human disturbance ranging from human settlement (Hebblewhite et al. 2005b) to forestry (Houle et al. 2010), to linear feature density (Whittington et al. 2005). Much of this previous work has demonstrated that the driver of wolf avoidance is not the disturbance itself but increased presence of humans on the disturbance (Whittington et al. 2005, Hebblewhite and Merrill 2008, Houle et al. 2010). We conclude that the mines, facilities and linear features in AOSR are simply not used intensely enough by humans to provoke wolf avoidance.

Wolf selection for areas near human disturbance may be due to constraints in space use. Three of the eight packs considered have had recent mining developments within their territories such that large portions of their available space has recently been removed by human footprint. Wolves may continue using their territory after it is reduced or compromised and we speculate that loss of territory to mines results in higher intensity of use by wolves near mine edges, particularly in important hunting habitats such as along rivers (Lesmerises et al. 2012). Therefore, far from providing refugia, proximity to mines likely generates increased risk of predation for moose in AOSR.

Strikingly, rivers emerged as an important predictor of relative predation risk for moose. Wolves strongly selected pack territories near rivers and we found that on average moose selected home ranges farther from rivers than expected by chance. Consequently, areas far from rivers, particularly those cut off from access to a river by mining developments presented areas with large ratios of moose to wolf selection as demonstrated by our mapped LSD values (Fig 2.2). The accumulation of these impacts resulted in a large area in the southwest corner of the study area, lying between Ft. McMurray and the oldest mines in the area in which no wolves were detected throughout the study period. The use of areas near human disturbance with low wolf presence by moose was most pronounced in this hole in the wolf distribution.

Because we examined the broad distribution of moose data as opposed to individual movement and fine scale habitat selection, it is not possible to say whether moose move into areas of low wolf use (Sih 1984) or simply exhibit higher recruitment there (McNair 1986, Caley and John 1996). Further, the increased selection for areas near human disturbance by moose compared to wolves is not due to wolf avoidance. Wolf use of the area may be sufficient to maintain a constant predation rate across the study area. Examining the distribution of locations of moose killed by wolves is an important next step in determining the magnitude of the refugia.

Before the population consequences of a prey refugia can be measured, observations of predator and prey behaviour in the field are needed to establish the existence of refugia. Here, we demonstrate that relatively novel human disturbance in the Athabasca oil sands has disrupted the overlap between moose and wolves. However, disturbance does not create refugia for moose in all areas of the region because while moose select areas closer to the oil sands footprint than wolves, wolves do not avoid it. Only in areas far from rivers near oil sands facilities is there a refugia for moose, indicating that natural drivers of the wolf distribution may be more important than human disturbance for structuring the distribution and population of moose in northeastern Alberta.

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Table 2.1 Explanatory variables used in analysis of wolf and moose selection and latent selection difference in winter in the Athabasca oil sands region, northeastern Alberta, 2010-2014.

Variable	Description	Model Units
Landcover	bog, conifer, mixedwood, deciduous, fen used as reference category	In=1, out=0
Rivers	Distance to nearest river	m
Streams	Density of streams	km/km^2
Facilities	Distance (*d*) to oil sands facilities	exp(-0.001 x *d*)
Mines	Distance (*d*) to oil sands pits, tailings ponds	exp(-0.001 x *d*)
Linear features	Density of trails, seismic, transmission, pipelines weighted by the network distance to Ft. McMurray	weighted km/km^2

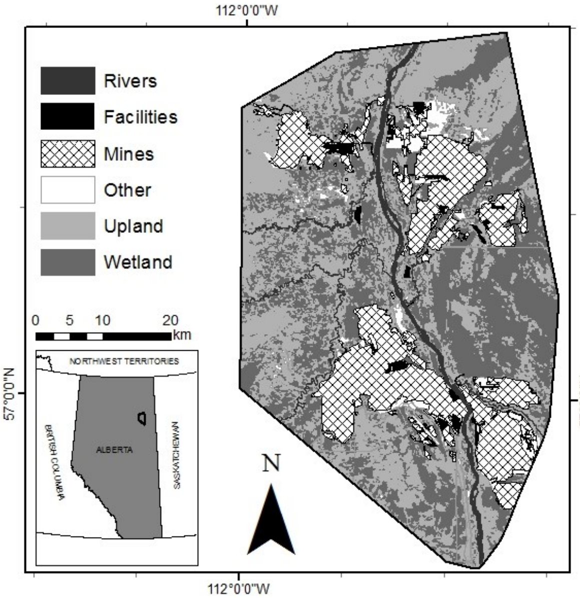

Figure 2.1 The study area polygon was created by intersecting the MCP of individual moose and wolf pack 95% kernel density estimates. Uplands are a combination of deciduous, coniferous and mixedwood landcover defined using the Alberta Ecosites. Wetlands are a combination of bogs and fen defined using the Alberta Wetlands Inventory Classification System. Other is a combination of cleared areas near mines, open water and other forest cover types.

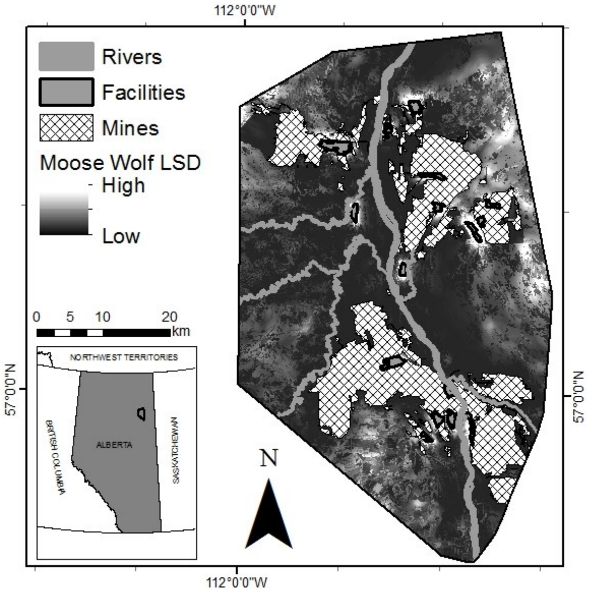

Figure 2.2 The model estimated ratio of the probability of a moose selecting a given pixel to the ratio of the probability of wolf selecting the same pixel, predicted across the Athabasca oil sand study area. Ratios were estimated using latent selection difference (LSD) analysis which assumes each species had all areas available to it. The resulting raster image (Moose Wolf LSD) was brightened by 50%.

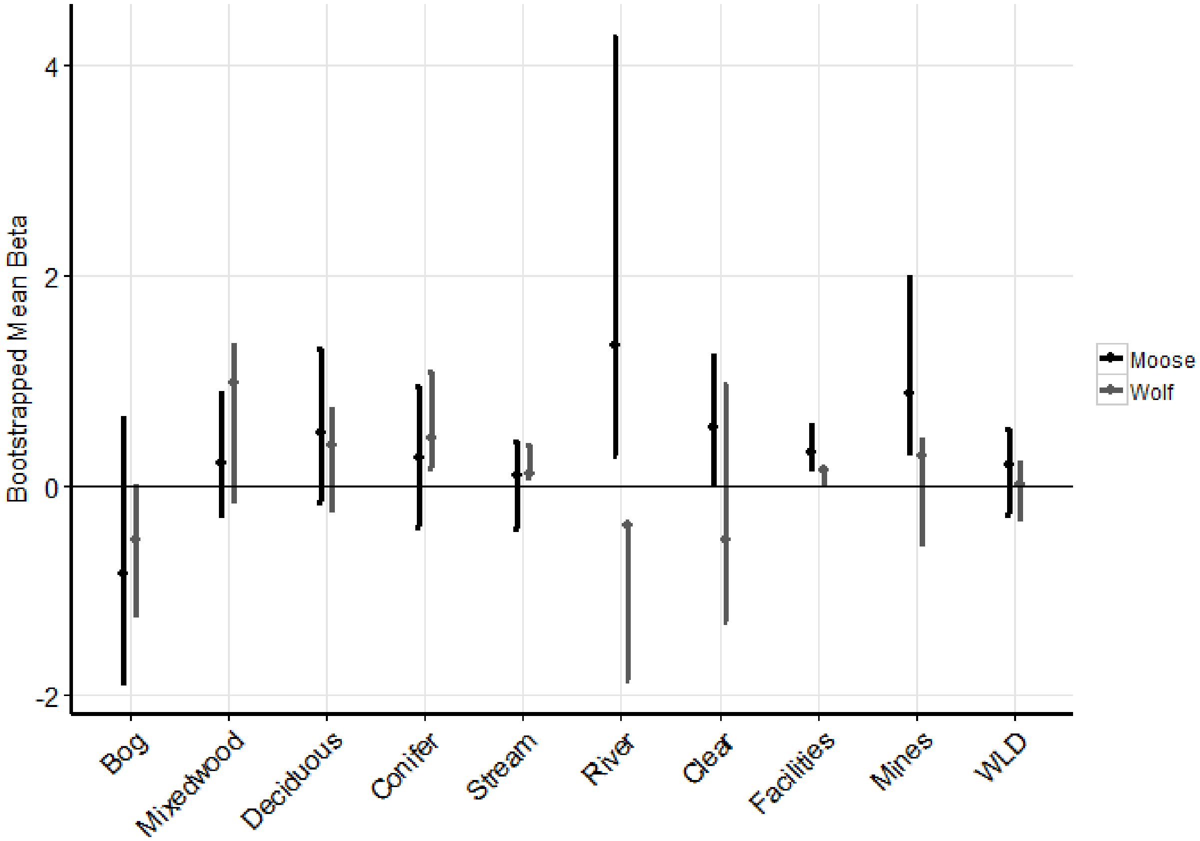

Figure 2.3 Bootstrapped beta coefficients and 95% confidence intervals of moose and wolf selection for landscape features in the Athabasca oil sands. Coefficients were estimated with logistic regression comparing individual moose and wolf GPS locations to random locations generated across the study area. Bootstrapping weighted the beta value from each individual moose and wolf by the inverse of the model estimated variance for each covariate. Wolf values were bootstrapped across all individuals in a pack and then packs were bootstrapped weighting using the inverse of the per pack estimated variance. Note: positive coefficients estimating the effect of selection along a gradient of distance to rivers indicate avoidance.

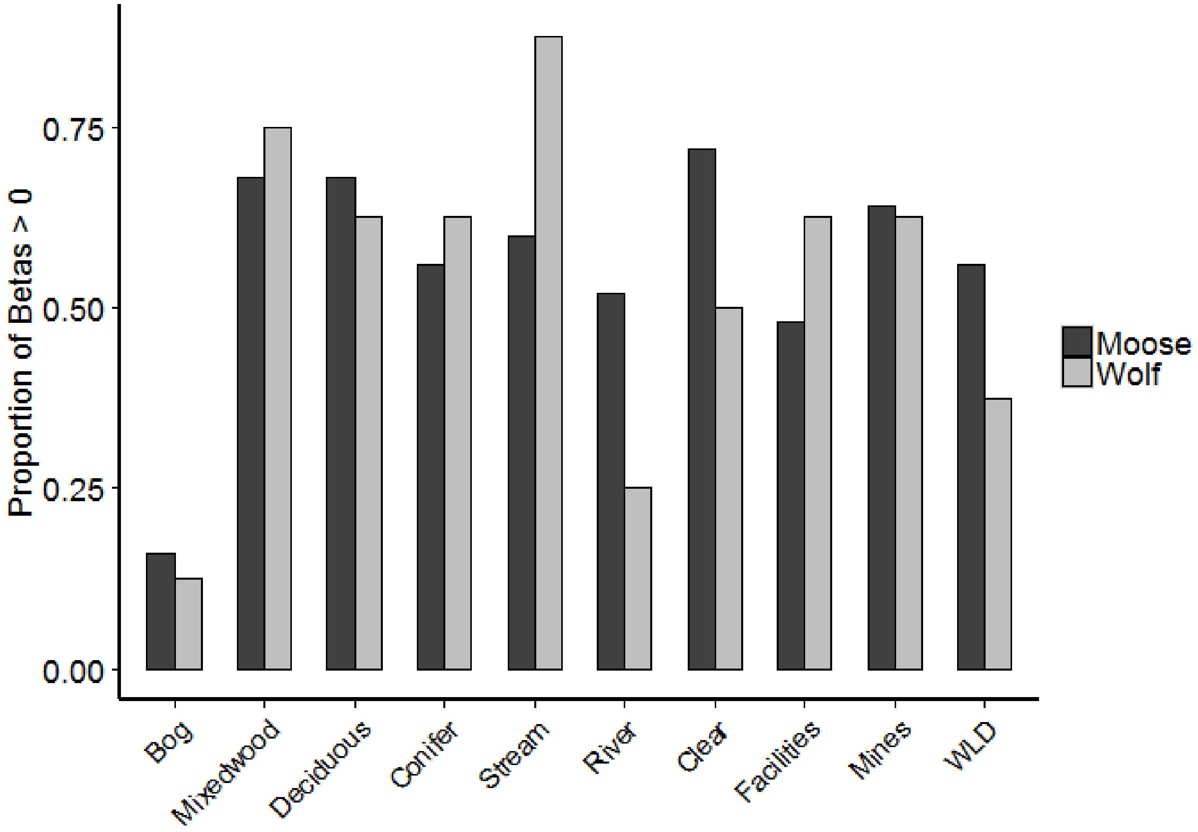

Figure 2.4 Proportion of moose or wolf packs with beta coefficients estimating selection for various landscape features larger than zero. Coefficients were estimated with logistic regression comparing individual moose and wolf GPS locations to random locations generated across the study area. Note: positive coefficients estimating the effect of selection along a gradient of distance to rivers indicate avoidance.

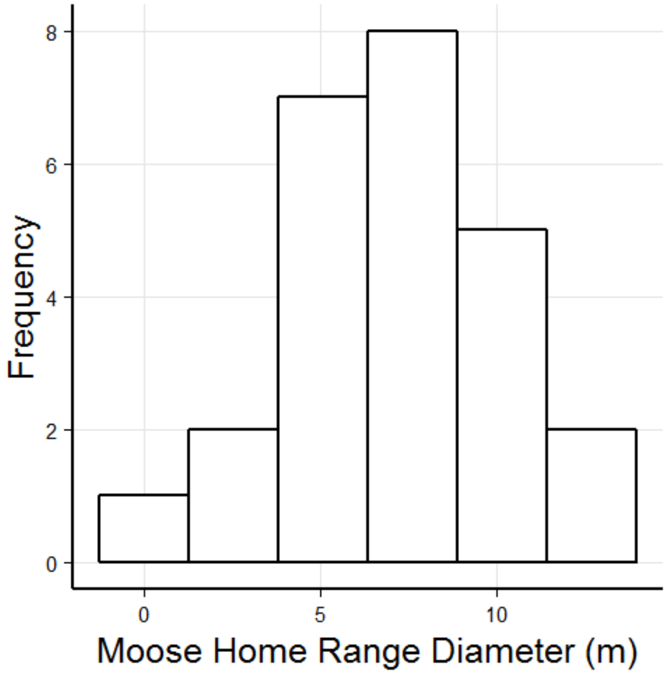

Figure 2.S1 Distribution of 25 cow moose home range diameters in winter. Home ranges areas were calculated for each moose from 95% isopleths of kernel density estimates using all years of data per individual.

Chapter 3. Human disturbance alters the predation rate of moose in the Athabasca oil sands

Introduction

Predation rate, or the proportion of prey killed by a predator per unit time, is a fundamental component of understanding the effect of predation on prey population dynamics (Messier 1994). Predation rate varies when predator abundance (numerical response), per predator kill rate (functional response) or both vary with prey density (Solomon 1949, Holling 1959, Vucetich et al. 2011). Predator abundance changes temporally in response to prey density via predator reproduction and spatially due to a predator's aggregative response, by which individual predators hunt more in some areas than others in response to prey clumping (Holling 1959, Hassell 1978). Therefore, landscape heterogeneity causes predation rate to vary spatially when prey aggregate in habitat with increased access to food or mates and predators allocate disproportionately more hunting effort there than other areas.

Both predators and prey can respond to spatial heterogeneity caused by novel human disturbance such that the proportion of prey killed by predators is a function of proximity to human disturbance. However, the direction and magnitude of such effects are not always predictable. Increased prey density at human-made forested edges can elicit an increased predator functional response leading to increased predation rate (Gates and Gysel 1978). Predators use areas disturbed by humans such as along linear features to increase movement rates (Dickie et al. 2017), potentially increasing predation rates in the absence of prey density changes (James and Stuart-Smith 2000, Decesare 2012). When a predator avoids human disturbance (Frid and Dill 2002) more than their prey, predation rates will be decreased near disturbance due to a prey refuge effect (Hebblewhite et al. 2005b, Berger 2007). When predation influences prey population dynamics, it is important to assess if and how predation rates vary with novel human disturbance.

Alberta's Athabasca oils sands region (AOSR) is a region of boreal forest in the Canadian western sedimentary basin with extensive deposits of bitumen. The AOSR is characterized by extensive human disturbance (Schindler 2010) and is home to spatially overlapping moose (*Alces alces*) and wolf (*Canis lupus*) populations (Fuller and Keith 1980, Wasser et al. 2011). Wolves respond to human disturbance depending on the types and intensity/frequency of use of the disturbance. When the intensity of use by humans is low, wolves use human disturbance such as linear features but reduce their use with increasing human use (Whittington et al. 2005, Hebblewhite and Merrill 2008, Houle et al. 2010, Rogala et al. 2011). Several studies have shown that moose use areas avoided by their predators near human disturbance to reduce the probability of predation (Edwards 1983, Stephens and Peterson 1984, Dussault et al. 2005, Berger 2007, Latombe et al. 2014).

We used the locations of moose killed by wolves and a spatial index of moose density to calculate a relative predation rate in a spatially heterogeneous and highly disturbed landscape. We tested whether wolves kill a larger proportion of moose by estimating the relationship between relative moose density and the frequency of kills across gradients of natural and anthropogenic landscape features. By including both natural and anthropogenic features we were able to compare the strength of each source of spatial heterogeneity on predation rate dynamics. Human induced rapid ecological change (HIREC) can disrupt predator-prey spatial interactions by adjusting either the type or behavior of predator (Latham et al. 2011b, Sih et al. 2011). We therefore predicted that because human disturbance is a novel source of heterogeneity, disruption to the wolf aggregative response would lead to stronger changes in predation rate near oil sands mining features than near or in natural habitats.

Methods

Study Area

The AOSR is comprised of the broader Athabasca watershed surrounding the Athabasca oil sands mines (Fig 3.1). The mines lie along the Athabasca River approximately 20 km north of the town of Ft. McMurray between 56.9 and 57.4 degrees north and -111.0 and -112.0 degrees east. The mining footprints consists of large extraction pits (325 km^2), tailings ponds (248 km^2) and associated large facilities (66 km^2). The area surrounding the mines has densities of linear features including seismic, transmission and pipe lines as high as 18 km/km^2. Forest surrounding the mines is made up of peat (*Sphagnum sp.*) forming wet areas with variable black spruce (*Picea mariana*) and tamarack (*Larix laricina*) (33%), uplands of aspen (*Populus tremuloides*), white spruce (*Picea glauca*) and jackpine (*Pinus banksiana*) (together 30%). Forestry is minimal in AOSR. Moose densities, estimated with random block surveys are low in the AOSR, but vary spatially between 0.04 and 0.15/km^2 (90% CI ranged from 21 to 41% of the estimate) in the three Wildlife Management Units overlapping our study area as measured between 2008 and 2013 (Morgan and Powell 2008, 2009, 2010, Sustainable Resource Development 2013).

Wolf Telemetry Data

We attempted to collar at least two wolves in every pack in the area covered by moose GPS telemetry. Wolves were captured and equipped with Iridium GPS collars (Lotek Inc., Newmarket, ON) in winter of 2011/12 using aerial net-gunning following the Wildlife Animal Care Committee Class Protocol #761 (Study Id. AUP00000040). A total of 41 wolves were captured and collared. Wolf collars were programmed to fix the wolf's location at variable intervals depending on the time of year. In winter the fix rates varied from 10 min to three hours. We estimated the number of wolves in the pack using counts of unique individuals during the collaring process.

In the winter of 2012/13, collars were replaced where they had failed and new wolves were captured where individuals had died. In the second winter GPS locations of the previous year were used to establish pack boundaries to assess whether or not all packs in the area had a collared wolf. We discovered 2 distinct gaps; one situated between Fort McMurray and the oil sands mines west of the Athabasca River, and the second south of oil sands mines and north of the Steepbank river on the east side of the Athabasca River. Both areas were searched using two helicopters for a full day. We did find limited wolf tracks indicating that wolves had moved through the area but could not find any sign of wolves using this habitat as territory. Based on our extensive efforts we are confident that we placed collars on wolves from all packs in our study area.

Locations of moose killed by wolves

We estimated the potential locations of wolf-caused moose mortalities using GPS clusters in wolf telemetry (Webb 2007). We followed the method developed by Knopff *et al.* (2009), which established GPS cluster centroids as the geometric mean of points within a space-time window. Seed centroids were established when a minimum of three points and three hours (given variable fix rates) had past. Once a single centroid was established, points were added chronologically and the centroid mean was adjusted. As the centroid moved, we corrected which points were included in the GPS cluster using the space-time window. When two centroids from the same wolf fell inside the sampling window, they were combined into a new GPS cluster centroid using all points from each. We used a 300-m radius and four day space-time window (Webb et al. 2008, Lake et al. 2013). We allowed GPS cluster durations to extend beyond the four day temporal sampling window to a maximum of thirty days (Webb et al. 2008) as long as points added chronologically were not more than four days past the end of the GPS cluster (Knopff et al. 2009).

We measured a suite of variables at each GPS cluster (Table 3.1). The duration was calculated as the sum of all times between locations less than six hours at a GPS cluster. We tallied the number of returns to a GPS cluster as the number of consecutive locations separated by more than 6 hours. The mean and maximum (radius) distance between all points and the GPS cluster centroid were calculated. We tallied the number of times the wolf returned and created a new cluster within the space window (300-m) of another cluster within 30 days. We attributed the pack size and the latitude to each GPS cluster.

We visited 49 GPS clusters in the field in the winters of 2013 and 2014. At each, we searched for a prey carcass, blood or other remains and then scored whether the location was a kill or a bed distinguished by areas in the snow where wolves had rested. At kills, we scored the species, sex, age class and condition of the prey. As we were interested only in the components of GPS clusters when wolves were at a prey carcass, we did not distinguish between kills and scavenge locations. However, only two carcasses near roads appeared to have been caused by means other than wolves.

We plotted the location of these ground-truthed (GT) GPS clusters and selected from the full set of summarized GPS clusters the closest centroid in space and time so long as the GPS cluster began before our GT visit. When two wolves were present at the same GPS cluster, we selected the summarized GPS cluster from the first individual present to maintain a single wolf sampling unit for modeling. Using this subset of 49 summarized GPS clusters, we modelled the effect of GPS cluster characteristics on whether the GPS clusters were beds or kills (kill model), and among kill clusters whether the prey was deer or moose (species model) using a two-step model selection (Webb et al. 2008, Knopff et al. 2009). We coded GPS clusters known to be beds as 0 and kills as 1, then subset the kills from the GT GPS clusters and coded deer as 0 and moose as 1. We developed a candidate set of models with all combinations of GPS cluster characteristics (Table 3.1) using logistic regression modelling. We excluded any models containing covariates with a correlation coefficient > 0.7. Latitude was included in the species model selection because deer densities are expected to decrease with latitude (Dawe and Boutin 2016). For both the kill and species models, we selected the most parsimonious model within 2 delta AICc of the top ranking model.

We assessed the ability of the selected kill and species model to distinguish among kills and beds, and species, using k-fold cross validation (Boyce et al. 2002), for which we re-fit the model to a 60% subset of the data, then calculated predicted values from the remaining 40%. From the predictions we calculated the area under the receiver operator characteristic (ROC) curve (AUC) and optimal threshold to maximize both the model classifier specificity and sensitivity as the point on the curve furthest from the diagonal line where AUC = 0.5. We bootstrapped the above evaluation 1000 times. Using the mean optimal cutoff for both the kill and species models we predicted first whether each GPS cluster from the full dataset of clusters summarized between November and March, 2012-2014, was a kill and then among the kills, the prey species. Once GPS clusters were predicted for each wolf, we combined GPS cluster centroids from different wolves within the 300-m and within a max of thirty days by retaining only the first GPS cluster of the first wolf at the GPS cluster.

Relative Moose Density

We calculated a spatial index of moose density using Alberta Environment and Parks (AEP) moose surveys of our study area. AEP conducts ungulate surveys using a random stratified block survey in which they fly initial surveys along lines of latitude (approx. 1.8 km spacing) to stratify the area by moose density. We used the sightings from these initial stratification flights in order to capture uniform survey effort over our entire study area. Stratification flights are flown with a Cessna 206 fixed-wing aircraft at 100 km/h allowing sightings of moose 250-300-m on either side of the aircraft (Morgan and Powell 2010). The four wildlife management units (WMU) in our study area were flown in the winters of 2013, (WMU 518), 2010 (WMU 530), 2009 (WMU 531) and 2008 (WMU 519).

We calculated the kernel density of moose sightings using kernel density in ArcGIS 10.1 The kernel density estimator was weighted by the number of moose sighted at each location, used a pixel size of 1 km^2 and a search radius of 8 km, corresponding to the average moose home range diameter (7.15 $\pm$ 0.55 SE km) in our study area. We rounded the search radius to 8 km to be more inclusive of the moose in our study area and to create a smoother density surface. Moose home ranges areas were calculated using moose GPS telemetry from collared moose. We collared moose throughout the study area in February 2010. Twenty-five moose were captured and outfitted with a GPS (Lotek 7000MU) collar. Moose GPS collars were programmed to fix the moose's location every three hours. We calculated each moose home range area from the 95% isopleth of a kernel density estimate (kde) using the least squares cross validation (LSCV, Seaman et al. 1999) smoothing factor in Geospatial Modeling Environments (Beyer 2012).

Measuring Environmental Variables

We defined the mine footprint as mining excavation including pit mines and tailings ponds, and the facilities footprint as buildings, oil sands upgraders, processing plants, work camps and parking lots. To delineate the borders of mines and facilities in AOSR, we modified 2009 landuse shapefiles supplied by the Regional Aquatics Monitoring Program (2011) using 2012 SPOT satellite imagery. We only used facilities that were larger than one km^2 for analysis and clipped facility polygons from mines. Because we were interested in a zone of influence around the mining footprint, we removed locations falling inside mines and facilities for analysis and calculated the Euclidean distance to mines and facilities.

The distribution of linear features was delineated by the Alberta Biodiversity Monitoring Institute (ABMI) at a 1:15 000 scale using 2012 SPOT imagery. We used proximity to the city of Ft. McMurray, located in the south of our study area, as a surrogate for intensity of human recreational use on linear features. Using network analyst in ArcMap 10.1 (ESRI 2011), we calculated the density of seismic, transmission and pipelines as km/km^2 weighted with network distance to Ft. McMurray. We re-calculated the network distances as their difference from the max distance such that the largest values were closest to the Ft. McMurray.

We used data from the Alberta Vegetation Inventory data (AVI; Alberta Environment and Sustainable Resource Development 2011) to classify land cover into wetlands (fens and bogs) based on the Alberta Wetland Inventory Classification System (Halsey et al. 2003) and uplands (mixedwood, deciduous and coniferous) based on the Alberta Ecosites definitions (Beckingham and Archibald 1996). We calculated the distance to major rivers using the Inland Waterway Base Hydrology layer (Table 3.2) (Alberta Environment and Parks 2004).

Statistical Analysis

We calculated a study area as a minimum convex polygon (MCP) calculated for the 95% isopleth of summed KDEs for each wolf pack. This generated an 8122 km^2 study area polygon used for modeling. We compared the locations of kills to random locations (10 per km^2) in the study area using mixed effects logistic regression with a random intercept for wolf pack to account for varying GPS data collection durations. We fit multiple models containing all combinations of five variables (Table 3.2) interacted with moose density such that interaction coefficients estimated how predation rate changes with each natural and anthropogenic variable. For our inference, we selected the top model using AIC. No covariates were collinear > 0.7 and we scaled all continuous variables so they were centered on zero. For ease of interpretation we re-calculated the distances to disturbance variables as their difference from the max distance such that the largest values were closest to the disturbance. We compared the odds ratios of interaction terms (predation rate) in the top model. All modeling was conducted in R 3.3.0 (R Core Team 2016).

Results

Locations of Wolf Kills of Moose

Of the 49 GPS clusters visited in the field, 29 were beds. Twelve of the 20 kill GPS clusters were of moose and 7 of deer, with one large-bodied carcass un-identified. In the selected kill model (Table 3.S1), GPS clusters defining locations of ungulates killed by wolves were distinguished from locations of wolf beds by longer durations and larger mean distance of points to the GPS cluster centroid. The bootstrapped mean AUC ROC score was 0.87 yielding an optimal classifying cutoff of 0.42. The kill model successfully classified an average 84% of kill clusters and 89% of bed clusters in bootstrapped k-fold evaluation. The selected species model (Table 3.S2) distinguished clusters of moose kills from those of deer kills by longer durations and smaller mean distance of points to the GPS cluster centroid. The model with equal parsimony to our selected species model, which contained duration and cluster radius was also within two AICc of the top model (Table 3.S2). To maintain a more general model for predicting kill type, we selected the model with the higher likelihood as opposed to model averaging. With a bootstrapped mean AUC ROC score of 0.85 and an optimal classifying cutoff of 0.49, the species model successfully classified 85% deer kill clusters and 90% of moose kill clusters.

Using the top kill model, we distinguished between bed and kill GPS clusters across our entire GPS dataset, yielding 988 kills. From this subset we applied our species model, yielding 199 moose kills. After combining GPS clusters from wolves at the same kill we were left with 153 unique GPS clusters describing moose kills across the 10 wolf packs. After sub-setting to our study area polygon, we were left with 129 locations of moose killed by wolves (Fig 3.2). The average home range area of moose was 46 km^2. We therefore used an 8-km search radius to calculate relative moose density using kernel density estimation (Fig 3.2).

Relative Predation Rate

Our top ranked predation rate model (Table 3.S3) contained interactions between moose density and rivers, distance to mines, weighted linear feature density and forest cover type (Table 3.3). Wolves killed moose more frequently with decreasing distance to mines and rivers (Table 3.3) such that the relative predation rate increased significantly near mines (Fig 3.3) and rivers (Fig 3.4). Wolves killed moose more frequently in upland forest than wetland forest (Table 3.3). Fifty-nine percent of kills occurred in upland forest, which only made up 45 % of the available area, whereas only 19 % of kills occurred in wetland forest, which made up 43% of the study area. Frequency of kills also decreased with increasing density of weighted linear feature density (Table 3.3). However, when compared to moose density, the number of kills in upland forest and along the linear feature gradient translated into only weak changes to the relative predation rate.

Discussion

Comparing locations of moose killed by wolves to an index of moose density revealed dynamics in the relative predation rate of moose driven by natural and anthropogenic landscape features. Our approach allowed inference concerning both the distribution of kills, which revealed areas where wolves are aggregating while hunting, and how that distribution contributes to the relative predation rate in space. Our results indicate that the influence of predation on the moose population is not uniform across the Athabasca oil sands, with areas of relatively high and low rates of predation and that these areas have changed with building of mining features. Whereas the wolf aggregative response demonstrated avoidance of high density of linear features near Ft. McMurray but not to the extent that the predation rate was altered in these areas. On the other hand, areas in proximity to oil sands mines and tailings ponds exhibited increased wolf kills above that predicted by moose density.

As predicted, variation in the predation rate was better explained by gradients in anthropogenic than natural landscape features. Predators and prey compete in an evolutionary arms race to maximize or minimize spatial overlap (Sih 2005). In a system with relatively stable population dynamics, such as wolves and moose in AOSR (Fuller and Keith 1980, Hauge and Keith 1981, Wasser et al. 2011) it is unlikely that either species wins the race over long time spans. Long standing features such as forest cover and rivers are likely therefore to exhibit relatively uniform predation rates across space. For instance, despite the strong increased frequency of moose kills in upland forest cover over wetlands, the predation rate was not different between these two forest types. The two landscape gradients over which predation rate did vary spatially, distance to rivers and mines, had comparable effect sizes but the effect on distance to mines on predation rate dynamics was mines was stronger. The imposition of oil sands mines may have provided wolves with an advantage in the arms race with potential population consequences for moose.

Previous work has demonstrated that human disturbance increases wolf hunting efficiency. Wolves use linear features (James and Stuart-Smith 2000) to move faster and further in a day (Dickie et al. 2017). The edges of mines are similar to linear features in that they are open and can be long and straight, characteristics previously shown to facilitate wolf movement (Dickie et al. 2017). For a coursing predator that uses a large area to encounter prey, such features facilitate movement and should increase encounters. For moose living near a mine, the edge of a pit, tailings pond or fence presents a consistent feature past which there are reduced escape opportunities. We speculate that the large barriers such as mines provide a hunting advantage to wolves because unlike the edge of a territory, which is a boundary to wolves (Mech 1977) but not their prey, mines constrain the movement and space use both species thereby increasing overlap near mines. This effect has been observed in hunting by African wild dogs (van Dyk and Slotow 2003, Davies-Mostert et al. 2013) and demonstrated experimentally with predatory shrimp in which co-aggregation with their prey along microcosm walls increased predator attack rates (Bergstrom and Englund 2004). Muhly et al. (2015) speculated that restriction to the movement of woodland caribou (*Rangifer tarandus*) due to impermeability of human disturbance increased the probability of encounter with predators. Additional work examining predator and prey movement along boundaries is needed to understand this effect in vertebrate systems.

Predicting the relative predation rate as a function distance to mines demonstrated increased frequency of kills with increasing moose density within several km of mines. Given that, on average, a moose home range in our area is approx. 8 km in diameter, individual moose near mines will experience increased exposure to predation across their entire home range. Increased predation rates near mines will reduce moose densities there, driving dispersal of juvenile moose to the area (Pulliam 1988). Such a novel source-sink would be unsustainable if mortality near mines is higher than can be replaced by dispersal, putting downward pressure on the moose population in AOSR. Consequences for the moose population may be particularly concerning considering the large footprint of the mine edge (975 km). However, compensation could mitigate the increased predation rate near mines. The top predation model demonstrated that wolves are killing fewer moose than expected given moose density in areas with high relative moose density away from mines and rivers (Fig 3.3, 3.4). It is possible that the imposition of the mines has further aggregated wolves in some areas of the AOSR, decreasing the relative predation rate in others. Our results do not predict specific changes to the absolute predation rate of moose in AOSR over time and additional work is needed to assess moose population dynamics over longer time periods.

Wolves may be trading off food and perceived risk in areas near high intensity human disturbances. Overall, there were fewer kills in areas of high linear feature density near the city of Ft. McMurray, but wolves were killing moose there in proportion to other areas. We speculate that wolves use areas near human disturbance in AOSR despite the human presence where moose density is highest. Avoidance of human disturbance by predators can be thought of as anti-predator behavior (Frid and Dill 2002). However, the benefits of such behavior will be weighed against costs (Fryxell 1991). If moose near human disturbance are unavailable to wolves, they potentially incur reduced access to food. If that loss limits wolf survival for packs near Ft. McMurray, they would likely begin using areas near human disturbance because the advantage of avoiding the disturbance does not outweigh the disadvantage of lost hunting opportunities (Hebblewhite and Merrill 2009). Our results demonstrate that for wolves, access to prey is more important than avoiding human disturbance.

The aggregative response of wolves is an important component of predation rates and measuring how it varies in space provides a deeper understanding of how the total proportion of wolves' prey are killed. Several recent studies have demonstrated that wolves adjust aggregation behavior in response to human disturbance by either avoiding (Hebblewhite et al. 2005b, Rogala et al. 2011, Muhly et al. 2011) or using (James and Stuart-Smith 2000, Latham et al. 2011b, Dickie et al. 2017) human disturbance, particularly linear features. By estimating the relative predation rate of wolves on moose in the Athabasca oil sands region, we have illustrated that removal of large areas of habitat, which creates boundaries and alters the amount of space available to wolves and their prey, facilitates wolf predation with potential prey population and trophic consequences. Considering that oils sands mines are large and in places, used intensely by humans, the expected outcome may be wolf avoidance of mining features that creates refugia for moose. Our results highlight the un-predictability of the effects of human disturbance and the importance of investigating novel types and magnitudes of disturbances on predator-prey interaction.

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Table 3.1. Variables measured at clusters in the wolf GPS data. Clusters were estimated using a 300-m and 4 day space time window.

Variable	Units
Duration	min.
Mean Distance	m
Radius	m
Returns	count
Pack Size	count
Latitude (species model only)	weighted km/km^2

Table 3.2 Covariates used to model the dynamics in the relative predation rate of moose in the Athabasca oil sands. Each variable was interacted with relative moose density to estimate its effect on the relationship between the distribution of location of kills of moose and moose density.

Covariate	Units
Landcover: Upland, Wetland, Other	0/1
Distance to rivers	m
Distance to mines	m
Distance to facilities	m
Linear feature density	weighted km/km^2
Rel. Moose Density	kde

Table 3.3 Top model output testing for changes in predation risk to moose in the Athabasca oil sands. Effects were estimated with logistic regression with random intercept for each wolf pack. Landcover Wetlands was the reference category for Landcover categorical variable. Covariates with : indicate an interaction between relative moose density. WLD = weighted linear feature density. Moose refers to relative moose density.

Covariate	Estimate	SE
Distance to Rivers	0.4420	0.1051
Moose	0.0035	0.2123
Cover Uplands	0.9409	0.2300
Landcover Other	1.0417	0.2823
Distance to Mines	0.5683	0.1197
WLD	-0.2770	0.1145
Moose:Rivers	0.2664	0.1208
Moose:Cover Uplands	-0.1585	0.2275
Moose:Landcover Other	-0.2012	0.2728
Moose:Mines	0.4245	0.1146
Moose:WLD	-0.0072	0.0996

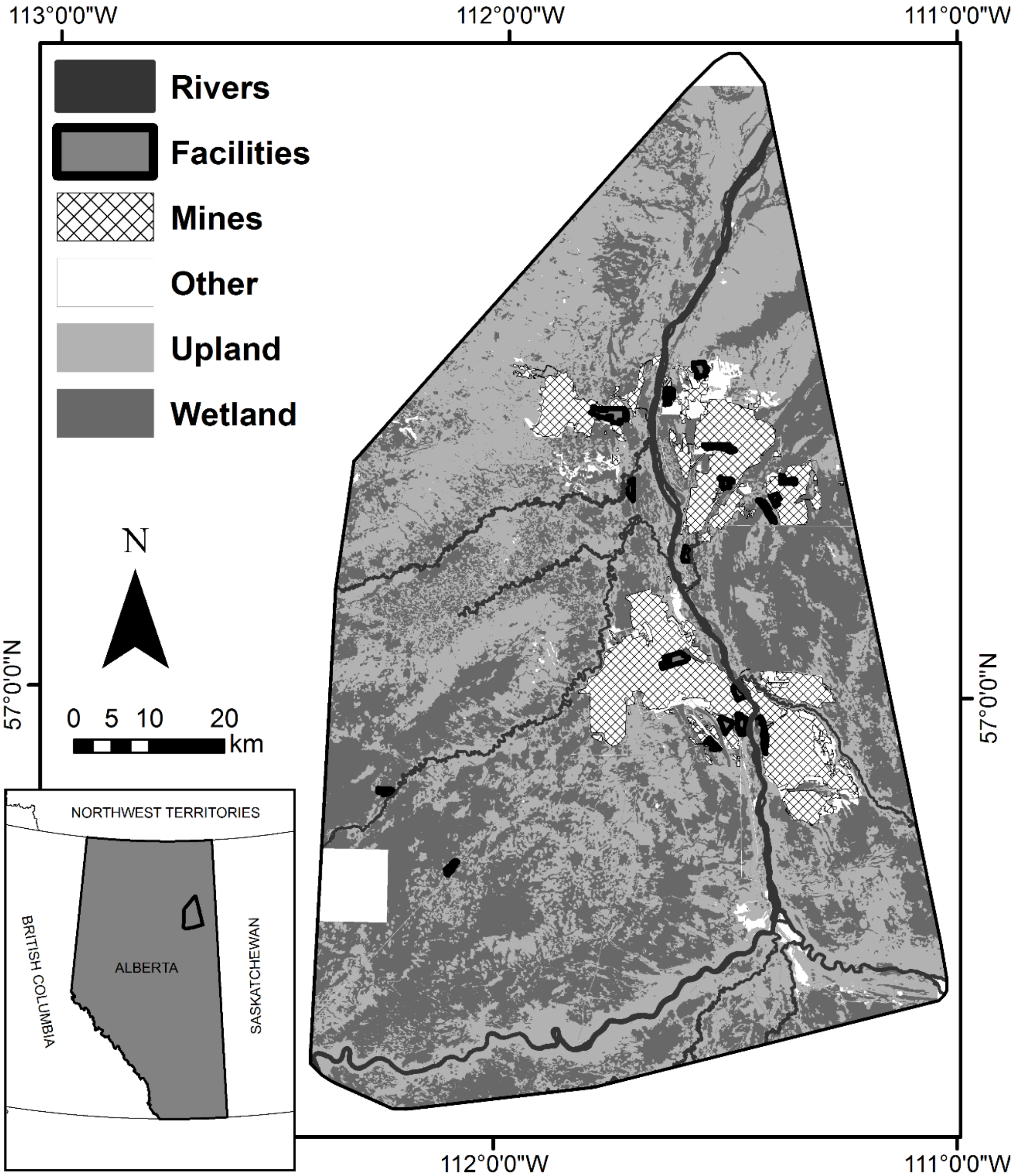

Figure 3.1 Map of the Athabasca oil sands clipped by our study area. We calculated a study area as a minimum convex polygon (MCP) calculated for the 95% isopleth of summed KDEs for each wolf pack.

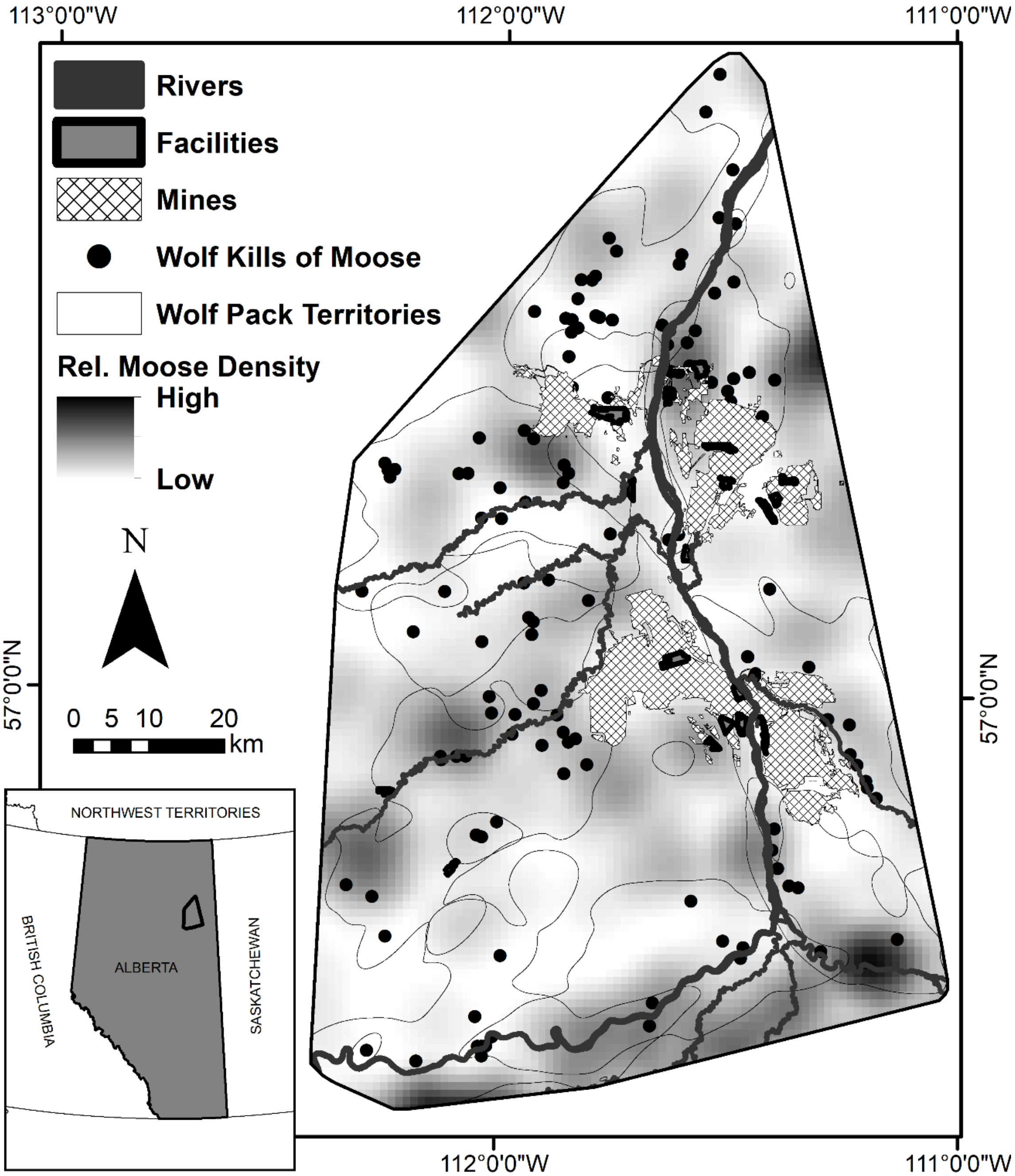

Figure 3.2 Map of the Athabasca oil sands clipped by our study area. Locations of moose killed by wolves were estimated from wolf GPS data and ground truthed kill locations. The relative density of moose was calculated as a kernel density estimate (KDE) of sightings from Alberta Environment and Parks moose density stratification flights. The KDE was calculated with an 8 km search radius to match the mean moose home range diameter in our study area.

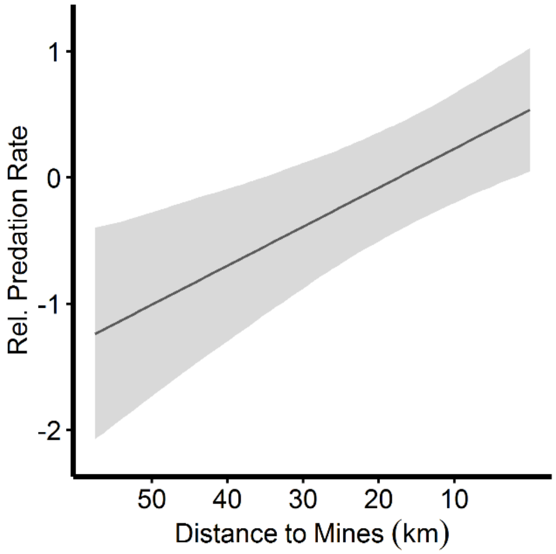

Figure 3.3 Model predicted effect of relative moose density on the frequency of kills (Rel. Predation Rate) as a function of distance to mines. Effects were estimated using logistic regression that compared the locations of kills to random available locations across the study area against an interaction of distance to mines and a spatial index of moose density. Distances were transformed such that close distances had the largest values. Grey areas are 95% confidence intervals.

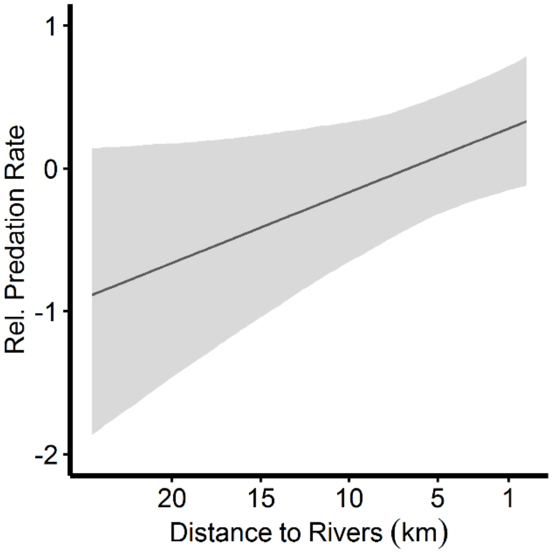

Figure 3.4 Model predicted effect of relative moose density on the frequency of kills (Rel. Predation Rate) as a function of distance to rivers. Effects were estimated using logistic regression that compared the locations of kills to random available locations across the study area against an interaction of distance to mines and a spatial index of moose density. Distances were transformed such that close distances had the largest values. Grey areas are 95% confidence intervals.

Supplemental Material

Table 3.S1 Model ranking information for selection of model distinguishing kill clusters from beds in wolf GPS clusters. Duration = sum of all intervals between locations less than six hours at a GPS cluster. Returns = the number of consecutive locations separated by more than 6 hours. MonthReturns = number of subsequent GPS clusters created with 300-m and 30 days at GPS cluster. MeanDist, Radius = mean and maximum distance between all points and the GPS cluster centroid. PS = number of wolves in pack for each cluster.

ModelName	df	logLik	AICc	delta	weight
Duration+Returns+MonthReturns	4	-17.00	42.90	0.00	0.14
Duration+Returns+MeanDist+MonthReturns	5	-16.16	43.72	0.82	0.09
Duration+MeanDist+MonthReturns	4	-17.51	43.92	1.02	0.08
Duration+MeanDist	3	-18.88	44.30	1.40	0.07
Duration+MeanDist+PS+MonthReturns	5	-16.71	44.82	1.92	0.05
Duration+Returns+PS+MonthReturns	5	-16.77	44.94	2.04	0.05
Duration+Returns+MeanDist	4	-18.09	45.10	2.20	0.05
Duration+Returns+MeanDist+PS+MonthReturns	6	-15.57	45.13	2.23	0.05
Duration+Returns+Radius+MonthReturns	5	-17.00	45.39	2.49	0.04
Duration+Returns	3	-19.49	45.50	2.60	0.04
Duration+MeanDist+PS	4	-18.48	45.87	2.97	0.03
Duration+MeanDist+Radius+MonthReturns	5	-17.32	46.04	3.14	0.03
Duration+Returns+MeanDist+Radius+MonthReturns	6	-16.03	46.05	3.15	0.03
Duration+MonthReturns	3	-19.81	46.15	3.25	0.03
Duration+MeanDist+PS+Radius+MonthReturns	6	-16.32	46.64	3.74	0.02
Duration+MeanDist+Radius	4	-18.88	46.67	3.77	0.02
Duration+Returns+MeanDist+PS+Radius+MonthReturns	7	-15.23	47.18	4.28	0.02
Duration+Returns+Radius	4	-19.16	47.23	4.33	0.02
Duration+Returns+MeanDist+PS	5	-17.93	47.25	4.35	0.02
Duration+Returns+PS+Radius+MonthReturns	6	-16.77	47.54	4.64	0.01
Duration+Returns+MeanDist+Radius	5	-18.09	47.57	4.67	0.01
Duration+Returns+PS	4	-19.47	47.85	4.95	0.01
Duration	2	-21.81	47.88	4.98	0.01
Duration+PS+MonthReturns	4	-19.59	48.08	5.18	0.01
Returns+MeanDist+MonthReturns	4	-19.65	48.21	5.31	0.01
Duration+MeanDist+PS+Radius	5	-18.48	48.35	5.45	0.01

Duration+Radius+MonthReturns	4	-19.77	48.46	5.56	0.01
Returns+MonthReturns	3	-21.05	48.63	5.73	0.01
Duration+Radius	3	-21.26	49.05	6.15	0.01
Duration+Returns+PS+Radius	5	-19.14	49.67	6.77	0.00
Duration+Returns+MeanDist+PS+Radius	6	-17.92	49.85	6.95	0.00
Duration+PS	3	-21.70	49.94	7.04	0.00
Returns+MeanDist	3	-21.73	49.99	7.09	0.00
Returns+MeanDist+PS+MonthReturns	5	-19.46	50.31	7.41	0.00
Returns+MeanDist+Radius+MonthReturns	5	-19.52	50.43	7.53	0.00
Duration+PS+Radius+MonthReturns	5	-19.54	50.48	7.58	0.00
Returns+Radius+MonthReturns	4	-21.05	51.00	8.10	0.00
Returns+PS+MonthReturns	4	-21.05	51.01	8.11	0.00
Duration+PS+Radius	4	-21.09	51.10	8.20	0.00
Returns	2	-23.96	52.18	9.28	0.00
Returns+MeanDist+PS	4	-21.65	52.21	9.31	0.00
Returns+MeanDist+Radius	4	-21.68	52.28	9.38	0.00
Returns+MeanDist+PS+Radius+MonthReturns	6	-19.30	52.61	9.71	0.00
MeanDist+MonthReturns	3	-23.26	53.05	10.15	0.00
Returns+Radius	3	-23.36	53.26	10.36	0.00
Returns+PS+Radius+MonthReturns	5	-21.05	53.49	10.59	0.00
MeanDist+PS+MonthReturns	4	-22.44	53.79	10.89	0.00
MeanDist	2	-24.77	53.80	10.90	0.00
Returns+PS	3	-23.90	54.34	11.44	0.00
Returns+MeanDist+PS+Radius	5	-21.61	54.62	11.72	0.00
MeanDist+PS	3	-24.13	54.78	11.89	0.00
MeanDist+Radius+MonthReturns	4	-23.19	55.28	12.38	0.00
Returns+PS+Radius	4	-23.34	55.59	12.69	0.00
MeanDist+Radius	3	-24.72	55.98	13.08	0.00
MeanDist+PS+Radius+MonthReturns	5	-22.33	56.05	13.15	0.00
MeanDist+PS+Radius	4	-24.07	57.06	14.16	0.00
MonthReturns	2	-28.85	61.96	19.06	0.00
Radius+MonthReturns	3	-28.45	63.42	20.52	0.00
PS+MonthReturns	3	-28.62	63.77	20.87	0.00

PS+Radius+MonthReturns	4	-28.16	65.23	22.33	0.00
Radius	2	-30.72	65.69	22.79	0.00
PS+Radius	3	-30.37	67.27	24.37	0.00
Null	1	-33.13	68.35	25.45	0.00
PS	2	-32.96	70.18	27.28	0.00

Table 3.S2 Model ranking information for selection of model distinguishing the species of prey at GPS cluster predicted to be kills. Duration = sum of all intervals between locations less than six hours at a GPS cluster. Returns = the number of consecutive locations separated by more than 6 hours. MonthReturns = number of subsequent GPS clusters created with 300-m and 30 days at GPS cluster. MeanDist, Radius = mean and maximum distance between all points and the GPS cluster centroid. PS = number of wolves in pack for each cluster. LAT = latitude at the GPS cluster centroid.

ModelName	df	logLik	AICc	delta	weight
Duration+Returns+Radius	4	-6.21	23.27	0.00	0.12
Duration+PS+Radius	4	-6.57	24.01	0.74	0.08
Duration+MeanDist	3	-8.29	24.18	0.91	0.08
Duration+Radius	3	-8.55	24.70	1.43	0.06
Duration+MeanDist+Radius	4	-7.32	25.49	2.22	0.04
Duration+MeanDist+PS	4	-7.36	25.57	2.30	0.04
Duration	2	-10.44	25.62	2.35	0.04
Duration+Returns+MeanDist+Radius	5	-5.70	26.02	2.75	0.03
Duration+MeanDist+PS+Radius	5	-5.74	26.09	2.82	0.03
Duration+Returns	3	-9.27	26.14	2.87	0.03
Duration+Returns+MeanDist	4	-7.79	26.44	3.17	0.03
LAT	2	-10.94	26.63	3.36	0.02
Duration+MeanDist+LAT	4	-8.06	26.97	3.70	0.02
Duration+Returns+Radius+MonthReturns	5	-6.21	27.03	3.76	0.02
null	1	-12.50	27.24	3.97	0.02
Duration+PS	3	-9.86	27.31	4.04	0.02
Duration+MeanDist+MonthReturns	4	-8.27	27.41	4.14	0.02
Duration+PS+Radius+LAT	5	-6.44	27.51	4.24	0.01
Duration+Radius+LAT	4	-8.36	27.57	4.30	0.01
Duration+LAT	3	-10.01	27.61	4.34	0.01
Duration+PS+Radius+MonthReturns	5	-6.54	27.70	4.43	0.01
Duration+Radius+MonthReturns	4	-8.55	27.95	4.68	0.01
Duration+MonthReturns	3	-10.19	27.98	4.71	0.01
Radius+LAT	3	-10.21	28.02	4.75	0.01
Radius	2	-11.71	28.17	4.90	0.01
MeanDist+LAT	3	-10.37	28.34	5.07	0.01
Duration+Returns+PS	4	-8.99	28.84	5.57	0.01
Duration+Returns+MonthReturns	4	-8.99	28.84	5.57	0.01
Duration+MeanDist+Radius+MonthReturns	5	-7.17	28.96	5.69	0.01
PS+LAT	3	-10.68	28.97	5.70	0.01
MeanDist	2	-12.11	28.97	5.70	0.01
Duration+Returns+MeanDist+PS	5	-7.19	29.00	5.73	0.01

Duration+MeanDist+Radius+LAT	5	-7.20	29.01	5.74	0.01
PS	2	-12.18	29.12	5.85	0.01
Duration+MeanDist+PS+LAT	5	-7.28	29.18	5.91	0.01
Duration+MeanDist+PS+MonthReturns	5	-7.36	29.33	6.06	0.01
Duration+Returns+LAT	4	-9.25	29.35	6.08	0.01
Returns+LAT	3	-10.93	29.47	6.20	0.01
LAT+MonthReturns	3	-10.94	29.48	6.21	0.01
MonthReturns	2	-12.41	29.57	6.30	0.01
Duration+PS+MonthReturns	4	-9.43	29.71	6.44	0.00
Returns	2	-12.50	29.76	6.49	0.00
Duration+PS+LAT	4	-9.56	29.97	6.70	0.00
Duration+Returns+MeanDist+Radius+MonthReturns	6	-5.50	29.99	6.72	0.00
PS+Radius	3	-11.21	30.02	6.75	0.00
Duration+Returns+MeanDist+LAT	5	-7.78	30.17	6.90	0.00
Duration+Returns+MeanDist+MonthReturns	5	-7.79	30.20	6.93	0.00
PS+Radius+LAT	4	-9.67	30.21	6.94	0.00
Duration+MeanDist+PS+Radius+MonthReturns	6	-5.65	30.31	7.04	0.00
Duration+MeanDist+PS+Radius+LAT	6	-5.69	30.39	7.12	0.00
Duration+MeanDist+LAT+MonthReturns	5	-7.97	30.56	7.29	0.00
Duration+LAT+MonthReturns	4	-9.93	30.72	7.45	0.00
Returns+MeanDist+LAT	4	-10.01	30.88	7.61	0.00
MeanDist+Radius	3	-11.65	30.89	7.62	0.00
MeanDist+Radius+LAT	4	-10.04	30.94	7.67	0.00
Returns+Radius	3	-11.68	30.95	7.68	0.00
MeanDist+PS+LAT	4	-10.07	31.00	7.73	0.00
Radius+MonthReturns	3	-11.71	31.01	7.74	0.00
MeanDist+PS	3	-11.71	31.02	7.75	0.00
Radius+LAT+MonthReturns	4	-10.09	31.05	7.78	0.00
Returns+Radius+LAT	4	-10.15	31.15	7.88	0.00
Duration+Radius+LAT+MonthReturns	5	-8.35	31.31	8.04	0.00
MeanDist+LAT+MonthReturns	4	-10.25	31.35	8.08	0.00
Returns+MeanDist	3	-11.96	31.52	8.25	0.00
PS+MonthReturns	3	-12.05	31.69	8.42	0.00
MeanDist+MonthReturns	3	-12.11	31.82	8.55	0.00
Duration+Returns+PS+MonthReturns	5	-8.62	31.85	8.58	0.00
Duration+PS+Radius+LAT+MonthReturns	6	-6.44	31.89	8.62	0.00
Returns+PS	3	-12.16	31.93	8.66	0.00

Returns+PS+LAT	4	-10.65	32.15	8.88	0.00
PS+LAT+MonthReturns	4	-10.68	32.22	8.95	0.00
Returns+MonthReturns	3	-12.41	32.41	9.14	0.00
Duration+Returns+LAT+MonthReturns	5	-8.98	32.57	9.30	0.00
Duration+Returns+PS+LAT	5	-8.98	32.57	9.30	0.00
Returns+LAT+MonthReturns	4	-10.93	32.72	9.45	0.00
Duration+MeanDist+Radius+LAT+MonthReturns	6	-6.93	32.85	9.58	0.00
Returns+PS+Radius	4	-11.04	32.93	9.66	0.00
MeanDist+PS+Radius	4	-11.16	33.19	9.92	0.00
PS+Radius+MonthReturns	4	-11.21	33.28	10.01	0.00
Duration+PS+LAT+MonthReturns	5	-9.35	33.32	10.05	0.00
Duration+Returns+MeanDist+PS+LAT	6	-7.19	33.38	10.11	0.00
Returns+PS+Radius+LAT	5	-9.38	33.38	10.11	0.00
Duration+Returns+MeanDist+PS+MonthReturns	6	-7.19	33.38	10.11	0.00
Returns+MeanDist+PS	4	-11.33	33.52	10.25	0.00
Duration+MeanDist+PS+LAT+MonthReturns	6	-7.26	33.52	10.25	0.00
Returns+MeanDist+PS+LAT	5	-9.48	33.59	10.32	0.00
PS+Radius+LAT+MonthReturns	5	-9.53	33.68	10.41	0.00
MeanDist+PS+Radius+LAT	5	-9.59	33.80	10.53	0.00
Returns+MeanDist+Radius	4	-11.53	33.92	10.65	0.00
Returns+MeanDist+Radius+LAT	5	-9.73	34.07	10.80	0.00
MeanDist+Radius+MonthReturns	4	-11.63	34.11	10.84	0.00
MeanDist+Radius+LAT+MonthReturns	5	-9.79	34.20	10.93	0.00
Returns+Radius+MonthReturns	4	-11.67	34.21	10.94	0.00
Returns+MeanDist+LAT+MonthReturns	5	-9.80	34.22	10.95	0.00
MeanDist+PS+MonthReturns	4	-11.70	34.27	11.00	0.00
MeanDist+PS+LAT+MonthReturns	5	-9.95	34.51	11.24	0.00
Duration+Returns+MeanDist+LAT+MonthReturns	6	-7.77	34.54	11.27	0.00
Returns+Radius+LAT+MonthReturns	5	-10.03	34.68	11.41	0.00
Returns+MeanDist+MonthReturns	4	-11.96	34.78	11.51	0.00
Returns+PS+MonthReturns	4	-12.00	34.86	11.59	0.00
Duration+MeanDist+PS+Radius+LAT+MonthReturns	7	-5.41	35.00	11.73	0.00
Returns+PS+LAT+MonthReturns	5	-10.64	35.90	12.63	0.00
Duration+Returns+PS+LAT+MonthReturns	6	-8.55	36.11	12.84	0.00
Returns+MeanDist+PS+Radius	5	-10.81	36.24	12.97	0.00
Returns+PS+Radius+MonthReturns	5	-11.04	36.69	13.42	0.00
MeanDist+PS+Radius+MonthReturns	5	-11.15	36.93	13.66	0.00

Returns+MeanDist+PS+Radius+LAT	6	-9.01	37.01	13.74	0.00
Returns+MeanDist+PS+MonthReturns	5	-11.33	37.27	14.00	0.00
Returns+PS+Radius+LAT+MonthReturns	6	-9.23	37.46	14.19	0.00
Returns+MeanDist+PS+LAT+MonthReturns	6	-9.23	37.46	14.19	0.00
Returns+MeanDist+Radius+MonthReturns	5	-11.50	37.62	14.35	0.00
MeanDist+PS+Radius+LAT+MonthReturns	6	-9.33	37.66	14.39	0.00
Returns+MeanDist+Radius+LAT+MonthReturns	6	-9.35	37.70	14.43	0.00
Duration+Returns+MeanDist+PS+LAT+MonthReturns	7	-7.19	38.56	15.29	0.00
Returns+MeanDist+PS+Radius+MonthReturns	6	-10.79	40.58	17.31	0.00
Returns+MeanDist+PS+Radius+LAT+MonthReturns	7	-8.48	41.15	17.88	0.00

Table 3.S3. Model ranking information for selection of model best describing the change in wolf predation rate of moose in the Athabsca oil sands. All included variables were interacted with relative moose density. WLD = weighted linear feature density. Fac (facilities), mine and river are all 'distance to' variables.

ModelName	df	logLik	AIC	delta	weight
river+cover+mine+WLD	13	-897.70	1821.39	0.00	0.63
river+cover+mine	11	-901.02	1824.04	2.64	0.17
river+cover+fac+mine+WLD	15	-897.11	1824.23	2.83	0.15
river+cover+fac+mine	13	-900.17	1826.34	4.95	0.05
river+mine+WLD	9	-908.66	1835.31	13.92	0.00
river+cover+fac	11	-907.63	1837.25	15.86	0.00
river+fac+mine+WLD	11	-907.68	1837.37	15.97	0.00
river+cover+fac+WLD	13	-907.19	1840.39	18.99	0.00
river+mine	7	-913.36	1840.72	19.33	0.00
river+fac+mine	9	-911.89	1841.78	20.38	0.00
cover+mine+WLD	11	-910.33	1842.66	21.27	0.00
cover+mine	9	-912.79	1843.58	22.19	0.00
cover+fac+mine+WLD	13	-909.64	1845.29	23.90	0.00
cover+fac+mine	11	-911.82	1845.64	24.24	0.00
cover+fac	9	-916.76	1851.52	30.12	0.00
river+fac	7	-922.20	1858.40	37.01	0.00
mine+WLD	7	-923.52	1861.05	39.66	0.00
river+fac+WLD	9	-921.71	1861.43	40.04	0.00
fac+mine+WLD	9	-922.32	1862.64	41.25	0.00
cover	7	-924.57	1863.15	41.76	0.00
mine	5	-927.33	1864.67	43.28	0.00
fac+mine	7	-925.52	1865.04	43.65	0.00
cover+WLD	9	-923.77	1865.54	44.15	0.00
river	5	-932.32	1874.64	53.25	0.00
fac	5	-933.10	1876.21	54.82	0.00
river+WLD	7	-931.32	1876.65	55.25	0.00
fac+WLD	7	-932.76	1879.52	58.13	0.00
null	2	-941.57	1887.13	65.74	0.00
WLD	5	-939.74	1889.47	68.08	0.00

Chapter 4. Separating the effects of predator movement and habitat selection on predation risk to prey in a highly disturbed landscape

Introduction

Anthropogenic landscape disturbance affects the abundance and distribution of species because it can remove or create habitat. Behaviourally, a species can be attracted to newly created habitat, avoid areas rendered inhospitable by habitat removal or avoid or select areas due to human activity (Sih et al. 2014). Animal space use is a function of habitat use and movement because an individual might move differently while in a certain habitat and select habitat based on how quickly or directionally it moves (Avgar et al. 2016). Therefore, without considering movement behaviour, inference concerning the spatial response to anthropogenic disturbance will be biased (Sih 1984).

When effects beyond the response to human disturbance are of interest, such as the resulting changes in the distribution of predation risk to a prey species, inferring movement behaviour is critical because predators can increase encounters with prey by covering space quickly (Holling 1959, Sih 1984). Anthropogenic landscape disturbance might act to decrease predation risk because predators move more slowly there, or because they avoid it. On the other hand, it might act to increase predation risk, because predators move more near landscape features or utilize human-made feature to search faster. When a predator spends less time near a disturbance (i.e. spatial avoidance), one might infer that predation is reduced there when in actuality, increased movement rates compensate for time spent such that predation rates do not change. Further, if human disturbance facilitates increased movement rates (Dickie et al. 2017), they may be associated with increased risk to prey.

The gray wolf (*Canis lupus*) is a coursing predator that uses long distance movements to encounter prey, leading to chases and kills (Mech and Boitani 2010, Vander Vennen et al. 2016) such that where wolves killed their prey is conditional on where they travel. Therefore, landscape features that increase wolf movement efficiency have the potential to increase hunting success leading to numerical increases of wolves (Kittle et al. 2017). Previous work has demonstrated that wolves both avoid human disturbances (Hebblewhite et al. 2005b, Muhly et al. 2011) and select them (Latham et al. 2011b), typically depending on the intensity of human use of those features (Whittington et al. 2005, Rogala et al. 2011). Wolves avoid large areas with human habitation that provide their prey with refugia from predation (Rogala et al. 2011). Avoidance of human areas is due to avoidance of intense human use of these features and has been shown to vary temporally with human activity patterns (Hebblewhite and Merrill 2008). In addition to avoidance or selection, wolves have been shown to use human disturbance to alter their movement rate. Of particular concern in Alberta's boreal forest region is the use of anthropogenic linear features (LF) by wolves, which increases both a wolf's speed and distance traveled (Dickie et al. 2017), potentially increasing encounters with prey such as the threatened woodland caribou (*Rangifer tarandus*) (James and Stuart-Smith 2000, Decesare 2012).

The Athabasca oil sands region (AOSR) in northeastern Alberta is a large expanse of boreal plains forest characterized by extensive human disturbance of varying types and intensities. Large areal disturbances such as pit mines, tailings ponds and processing centers remove habitat from the landscape and influence adjacent areas due to noise and human presence. Linear exploration and transportation features extend outward from central developments and fragment the surrounding forest cover. The forest around the oil sands mines in AOSR is also home to several packs of wolves. We examined how natural and anthropogenic features in AOSR are selected, affect wolf movement and how each affect the probability of wolves having lethal encounters with prey. Specifically, we evaluated the following hypotheses. First, while traveling, wolves select linear features, rivers and streams in AOSR because these features allow wolves to increase their movement rates. Here we predicted wolves to move on, toward and more quickly while on linear features, streams and rivers. Secondly, wolves avoid towns and mining facilities while traveling but this avoidance varies with time of day due to temporal variation in human activity. We predicted wolves to move away from urban areas and facilities but for this avoidance to be less at night. We also predicted wolves to move more quickly near mines, facilities and urban areas. Finally, wolves kill prey where they travel and the frequency of kill events increases where wolves move faster. We predicted that the distribution of kills does not differ from where wolves select to travel except for near features that facilitate increased wolf movement.

Methods

Study Area

As written in Neilson and Boutin (2017); the AOSR is comprised of the broader Athabasca watershed surrounding the Athabasca oil sands. The mines lie along the Athabasca River approximately 20 km north of the town of Ft. McMurray between 56.9 and 57.4 degrees north and -111.0 and -112.0 degrees east. Topographic heterogeneity is contained largely within steep and deep river valleys and a broad, decreasing elevation gradient (860m to 250m) from north to south. Low, peat (*Sphagnum sp.*) forming wet areas with variable black spruce (*Picea mariana*) and tamarack (*Larix laricina*) forest dominates the area (33%), followed by uplands of aspen (*Populus tremuloides*), white spruce (*Picea glauca*) and jackpine (*Pinus banksiana*) (together 30%). Forest understories contain willow (*Salix* spp.) dogwood (*Cornus stolonifera*), blueberry (*Vaccinium myrtilloides*), cranberry (*Vaccinium* spp.) and alder (*Alnus* spp.). The area is characterized by extensive mining footprints consisting of large extraction pits (325 km^2), tailings ponds (248 km^2) and associated large facilities (66 km^2). The area surrounding the mines has linear densities as high as 18 km/km^2. Forestry is minimal in AOSR.

Telemetry Data

We used GPS positional data to investigate both wolf movement and the distribution of wolf kill sites. As written in Neilson and Boutin (2017); we attempted to collar at least two wolves in every pack surrounding the mines in AOSR. Wolves were captured and equipped with Iridium GPS collars (Lotek Inc., Newmarket, ON) in winters of 2011 2012 using aerial net-gunning following the Wildlife Animal Care Committee Class Protocol #761. A total of 41 wolves from 10 packs were captured and collared. Wolf collars were programmed to fix the wolf's location at intervals of 10, 15, 30 min and three hours in winter. For analysis we removed periods over which the fix interval was 3 hours and rarefied the 10 and 15 min interval data to 30 min, leaving positional data from 30 wolves from the winters of 2012, 2013 and 2014. We used our wolf GPS telemetry to calculate a study area polygon. For each wolf pack, we calculated a utilization distributions using kernel density estimation (kde) and the least squares cross validation smoothing factor (Seaman et al. 1999). We calculated the minimum convex polygon (MCP) containing the sum of the 95% contours from each pack UDs. This generated an 8122 km^2 study area polygon used for modeling (Fig 4.1, 4.2).

We conducted our analysis during winter only for two reasons 1) our positional data were collected with higher temporal precision in winter allowing better estimation of both moving behaviour and the position of kill clusters in the GPS data (see below) and 2) scat analysis from the study area indicated that the majority of wolf predation on adult moose is in the winter (unpublished data, Thomas 2013).

We tested our hypotheses using two subsets of the wolf positional data. Moving locations (hereafter, 'steps') were those not associated with a cluster in the GPS telemetry. Clusters were defined as times when the wolf was either resting or at a kill and identified as three or more points within a space (300 m) and time (4 days) window for at least three hours (Knopff et al. 2009). Kill sites were defined as the centroid (geometric mean) of clusters identified as a kill site, predicted by comparing cluster types (kill site, bed site) against cluster attributes measured in the field at GPS clusters at kill sites of moose and deer (for details of assigning clusters as kill sites or resting see chapter 3, this volume).

Habitat Description

We predicted snow depth to be an important predictor of wolf habitat selection while moving. We used a binary classifier to capture broad forest patch scale differences in snow depth using Alberta Vegetation Inventory data (AVI; Alberta Environment and Sustainable Resource Development 2011). We used forest cover as a proxy for snow depth (D'Eon 2004) and classified shallow snow patches as those with at least 30% coniferous tree mean percent cover based on the Alberta Ecosites definitions (max conifer cover = 51%, Beckingham and Archibald 1996) for uplands and 70% mean percent cover for wetlands using the Alberta Wetland Inventory Classification System (Halsey et al. 2003) for wetlands (Table 4.1).

As written in Neilson and Boutin (2017); we calculated the distance to major rivers and the density of streams using the Inland Waterway Base Hydrology layer (Table 4.1) (Alberta Environment and Parks 2004). Rivers were delineated as polygons and streams were delineated as lines. We therefore buffered streams by 2.5 m and then calculated the distance to all wolf GPS and kill sites for rivers and streams separately. The distribution of linear features was delineated by the Alberta Biodiversity Monitoring Institute (ABMI) at a 1:15 000 scale using 2012 SPOT imagery. We buffered linear features with a distances assigned by ABMI during delineation (trail=0 m, seismic line=5 m, low use roads, pipelines and transmission lines = 10:20 m). From the edge of the resulting buffers we calculated the distance to all locations used for analysis. We classed GPS locations as on a linear features when they were within 5 m of a frozen river or an anthropogenic linear feature and within 10 m of a stream. We used a wider buffer for streams because there was more uncertainty about the edge of streams, which were delineated as lines and buffer by a standard width, as opposed to rivers and linear features which were assigned widths during delineation.

As written in Neilson and Boutin (2017); we defined the mine footprint as any area where excavation had occurred including pit mines and tailings ponds. Facilities were defined as the city of Ft. McMurray and the mining footprint associated with oil sands operations; upgraders, processing plants, work camps and parking lots (Table 4.1). To delineate the borders of mines, Ft. McMurray and facilities, we modified 2009 land use shapefiles supplied by the Regional Aquatics Monitoring Program (2011) using SPOT satellite imagery for 2012, the earliest year for which we had GPS telemetry for wolves. We only included facilities that were larger than one km^2 for analysis and clipped facility polygons from mines. Because we were interested in a zone of influence around the mining footprint, we removed steps ending inside mines and facilities for analysis and calculated the Euclidean distance to mines and facilities from wolf GPS and kill sites.

Because we expected wolf space use while traveling near areas used by humans to vary between night and day, we calculated a binary night/day variable (NT) using the National Research Council Canada sun rise sun set calculator ("National Reseach Council Canada Sunrise/Sunset Calculator" 2017).

Statistical Analysis

We used integrated step selection analysis (iSSA, (Avgar et al 2016)) to test our first two hypotheses. Similar to step selection functions (Fortin et al. 2005, Duchesne et al. 2010, Thurfjell et al. 2014), iSSA estimates coefficients proportional to the relative probability of selecting landscape features or other habitat resources while accounting for animal movement characteristics; displacement and directionality. Therefore, iSSA directly acknowledges the extent to which habitat selection and movement are non-independent while simultaneously estimating coefficients for both. Animal movement steps, the unit of analysis of iSSA, are described by step lengths, the straight line distance between consecutive steps, and turning angles, the change in bearing between consecutive steps. Integrated step selection analysis compares the distribution of observed steps to a set of available steps. Available steps are generated for each observed step by sampling a step length and turning angle from theoretical distributions such that including both step length and turning angle in modeling provides estimates of how animal movement deviates from a theoretical movement model (Avgar et al. 2016). We generated a random gamma distribution of step lengths using the shape (0.62) and scale (1368.89 m) parameters from the a gamma distribution of fit to our observed wolf moving steps using the *fitdistr* function from the MASS package in R (R Core Team 2016). For calculating our shape and scale parameters, we removed 190 steps corresponding to a speed of over 10km/h from our observed step length distribution. We generated a von Mises turning angle distribution using the mu (0.01) and kappa (0.69) from a von Mises distribution fit to our observed wolf moving steps using the *circ.summary* function from DIRECTIONAL package in R. From our theoretical step length and turning angle distributions, we drew 10 step lengths and turning angles and generated random end points for each observed step. The movement characteristics and end point habitat features of each available step were then compared to the associated observed step using conditional logistic regression.

Our first two hypotheses proposes that wolves select to move on or toward features that allow them to increase their speed, and move away from and increase their speed near large-area anthropogenic features exhibiting higher intensity of human use. We tested our first two hypothesis by fitting a single iSSA to our movement data subset with the form

$$W(x) = \frac{exp[B * H(x)]}{\int_0^\Omega \exp[B * H(x)]}$$

where B is a vector of parameters and H(x) (Table 4.1) is a vector of attributes of the step ending in position x the spatial domain Ω. *W(x)* is proportional to the probability of observing the wolf at location x conditional on the availability of habitat at that location. Wolf step selection was modeled for the locations at the end of steps for the log distances to streams, rivers, linear features, facilities and mines, and areas with shallow snow (Table 4.1). The log distance to facilities was interacted with the binary night/day term to examine whether wolves selected to move near facilities more during the night than during the day. We estimated a coefficient for the cosine of the turning angle at subsequent wolf steps. The iSSA framework evaluates animal movement speed as both a determinant and function of step selection by interacting the term for a landscape variable at the beginning of a step with the log step length. We compared the movement speed of wolves on and off linear features, frozen rivers and streams, and near and far from mines, and urban areas and facilities. We fit our iSSA models using the function *clogit* from the package *survival* in R (version 3.3.3) (R Core Team 2016), with the end point ID as the strata of comparison.

We calculated predicted movement rates from our model output by multiplying the scale and shape parameter values from the gamma distribution form which we sampled our available steps.

We first modified the shape parameter using the iSSA log step length beta from each habitat interacted with log step length (Avgar et al. 2016). We calculated the predicted movement rate for each wolf then calculated mean and 95% confidence intervals using bootstrapping.

We tested our third hypothesis with a latent selection difference (LSD) model that differentiated the distribution of wolf steps from the distribution of wolf kill sites (Latham et al. 2011a). Because the movement location came from wolf GPS data not at wolf GPS clusters, whereas the kill sites were a subset of clusters, our LSD model is a used/unused selection function (Lele et al. 2013). Covariate labels from our LSD correspond to those use in iSSA analysis (Table 4.1). Sites where wolves killed moose and deer were extracted from the full distribution of kills summarized in Chapter 3 for the wolves with steps included in the above step selection analysis.

We fit the iSSA and LSD models to data for each wolf separately then calculated the bootstrapped mean and confidence intervals for each beta coefficient to make inferences about the population of wolves in AOSR. Bootstrap sampling was weighted by the inverse of the standard error for each coefficient.

Results

Wolf Movement

After rarefying all steps to 30 min and removing steps longer than 30 min, 12,710 steps from 30 wolves were obtained and used for modeling (Fig 4.2). As predicted, wolves selected to move toward both linear features and frozen streams and rivers (Fig 4.3, 4.4). Wolves did not increase their speed on streams but increased their speed on linear features and frozen rivers compared to when not on these features (Fig 4.5). On average, wolves moved fastest on linear features, for which their predicted movement rate (2.13 km/h, 95% CI =1.07, 3.58) was 63% faster than off linear features (1.31 km/h, 95% CI =0.43, 2.59). Wolves moved 45% faster on frozen rivers (1.90 km/h, 95% CI =0.76, 3.56) than off frozen rivers. However, the confidence intervals of these predicted movement rates included the means of the movement off linear features and frozen rivers, indicating high variation between wolves.

Wolf responses to large human disturbances varied by the time of day and the intensity of use of those disturbances by humans. Neither wolf step selection nor speed varied with proximity to mines (Fig 4.3). However, wolves selected to mover farther from facilities during the day than compared to random whereas at night, wolves selected to move closer to facilities and urban areas (Fig 4.3, 4.6). Wolf speed did not vary as a function of distance to mines or facilities/urban areas (Fig 4.7). As predicted, wolves selected to move in forest patches assumed to have shallower snow (Fig 4.8) but this did not translate into faster speeds while traveling in these patches (Fig 4.5).

Kill Sites

We identified 372 kills of ungulates by the 30 wolves included in our step selection dataset (Fig 4.2). The distribution of wolf kill sites was proportionally to the distribution of steps with respect to streams mines and facilities at night (Fig 4.9). Contrary to predictions however, the distribution of kill sites increased with increasing distance from rivers and linear features when compared to distribution of steps (Fig 4.9). However, during the day, wolf kills of prey were closer to facilities than wolf travel steps (Fig 4.9). Wolves killed a higher proportion of ungulate prey in closed canopy forest cover than their use of those patches for traveling (Fig 4.8).

Discussion

Predators can only kill prey where they hunt. However, whereas encounters between predators and prey are determined by where predators move, kill events are also functions of prey density (Bergman et al. 2006), behaviour (Sih 1984, Laundré et al. 2001, Middleton et al. 2013) and vulnerability (Hebblewhite et al. 2005a). Our results indicate that, without comparing kill locations to movement locations directly, assuming the two do not differ will bias inference about predator behaviour and predation risk to prey. We found that wolf use of particular features while traveling, even when allowing wolves to move more quickly, did not necessarily translate into increased kills near those features. Important effects of anthropogenic features on the relationship between wolf movement and kill locations were also revealed. We found that wolves generally kill prey in the natural habitats where they hunt but this is not the case for anthropogenic habitats. For instance, whereas wolves avoided travelling near facilities during the day, this avoidance did not translate into fewer kills near facilities. Further, linear features were strongly used for traveling quickly, but kills were farther away from linear features than movement locations.

Overall, wolves responded to human disturbances as predicted. Linear features were selected and increased wolf movement, whereas intensely used facilities and the city of Ft. McMurray were avoided while moving except at night when they were selected. By parsing the effect of day and night periods on movement, we revealed a subtle response of wolves to intensely used human disturbance. Wolf packs in AOSR are distributed randomly with respect to facilities (Chapter 2). Our work corroborates previous work demonstrating that when a wolves lives in proximity to human areas they only travel near cities and facilities at night (Hebblewhite and Merrill 2008). Further, separating wolf movement from killing locations established that wolf avoidance of areas near facilities and cities during the day was not sufficient to generate refugia for their ungulate prey. Wolf use of areas near human settlements may become problematic for both the city of Ft. McMurray and oil sands work areas and camps if wolves become habituated, which can lead to use of garbage dumps (Fuller and Keith 1980) human-wolf conflict and human injury (McNay 2002).

The discrepancy between where wolves select to travel and the locations where they kill prey has important implications for understanding the effect of human disturbance on wolf prey. Because wolves use long distance movements to increase encounter rates with their prey (Vander Vennen et al. 2016), the high density of linear features in Alberta'a boreal forest has been hypothesized to influence both wolf movement (Latham et al. 2011b) and consequently, the population dynamics of their prey (Hervieux et al. 2013). Corroborating other recent work (Dickie et al. 2017), we provide evidence that wolves select to move on or near linear features and move more quickly there. However, the distribution of kills was on average farther from linear features than movement steps. Moose in AOSR avoid linear features of low or unknown use (Wasser et al. 2011), meaning that whereas use of linear features may facilitate wolf movement between patches of higher moose density (Kittle et al. 2017), movement off linear features is required for a wolves to encounter and kill prey (Decesare 2012).

As predicted wolves selected natural linear features while moving in winter. Neither frozen rivers nor streams remain as linear and unidirectional as anthropogenic linear features however, and the increase of movement speed on frozen rivers was lower than for LF and there was no increase in speed while traveling on streams. Wolves did not kill ungulate prey near rivers as much as they traveled there, indicating that similar to LF, frozen rivers provide a means for wolves to cover large areas but do not increase encounters with prey. On the other hand, the distribution of kill locations was proportional to movement with respect to distance to streams.

Use of the tortuous configuration of streams in AOSR likely provide wolves with effective searching patterns through habitat used by their prey. When not accompanied by a calf, moose in AOSR select areas near streams in winter (Chapter 5).

Closed canopy areas exhibited both increased movement and increased kill locations compared to movement locations. Our results corroborate previous work that reported increased wolf use of areas with shallow snow (Droghini and Boutin 2017). However, we did not find that speed was increased in covered forest areas, indicating that wolves select forest cover for ease of movement, not to facilitate higher speeds. Use of covered forest could allow wolves to cover more area, necessary for searching for prey, with the same effort as open areas. In addition to movement considerations, our results indicate that closed canopy areas facilitate the kill component of predation. Hebblewhite et al (2005a) found that open areas such as grasslands and open conifer are important for encounters between wolves and elk, but that kills occurred more frequently in pine forests, which they attributed to increased downed woody debris (see also Kunkel and Pletscher 2000). We speculate that whereas open areas may advantage wolves in detecting ungulate prey, in winter the shallower snow in conifer forest cover provides an advantage in killing prey.

Previous work has demonstrated that wolves kill ungulate prey where they travel (Hebblewhite et al. 2005a, Bergman et al. 2006, Decesare 2012) but here we do so in the context of changes to the efficiency with which wolves move. In addition, we directly compare the location of kills to locations selected by wolves when moving, providing use with analytical power to compare the two. Our results indicate the wolves utilize landscape features like seismic lines and frozen rivers for traversing the landscape quickly but then move off these features to search for prey in areas that allow them to search more local area such as streams and in closed canopy forest cover where snow is shallow.

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Table 4.1 Variables (h(X))used to model wolf selection and movement characteristics while moving and the latent selection difference between wolf movement and kill locations

Variable	Description	Model Covariate	Model
Linear Features	Trails, Seismic, Transmission, Pipe (various buffers, see text)	log Distance	iSSA, LSD
		On=1, Off=0 ; step start location	iSSA
Rivers	delineated river polygons	log Distance	iSSA, LSD
		On=1, Off=0 ; step start location	iSSA
Streams	buffered streams, 2.5 m buffer	log Distance	iSSA, LSD
		On=1, Off=0; step start location	iSSA
Facilities	Delineated oil sands facilities and Ft. McMurray	log Distance	iSSA, LSD
Mines	Delineated oil sands pits, tailings ponds	log Distance	iSSA, LSD
Snow Cover	Forest cover patches at least 30% coniferous tree mean percent for uplands and 70% mean percent cover for wetlands	In cover=1, out of cover = 0	iSSA, LSD
Night	Temporal, day or night	Day=0, Night=1	iSSA, LSD
Step Length	euclidean distance between sequential 30 min wolf locations (m)	log step length	iSSA
Turning Angle	Difference in bearing between current step and previous step	cosine turning angle	iSSA

Varables used in iSSA model were measured at the end of each step except those with the prefix ST_ for which the covariate was measured at the beginning of each wolf step.

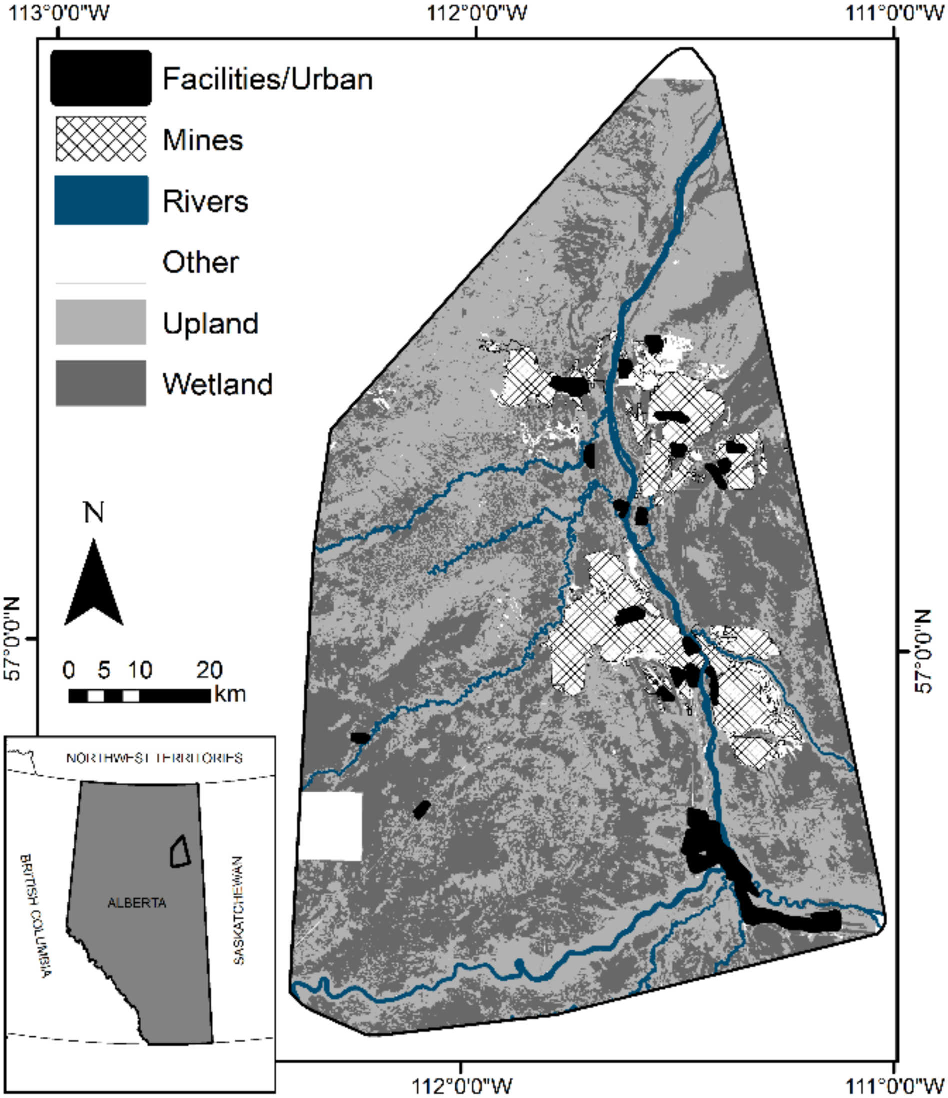

Figure. 4.1 Map of the Athabasca oil sands. The study area polygon was calculated as the minimum convex polygon of all wolf pack 95% kernel density esimates. Uplands are a combination of deciduous, coniferous and mixedwood landcover defined using the Alberta Ecosites. Wetlands are a combination of bogs and fen defined using the Alberta Wetlands Inventory Classification System. Other is a combination of cleared areas near mines, open water and other forest cover types.

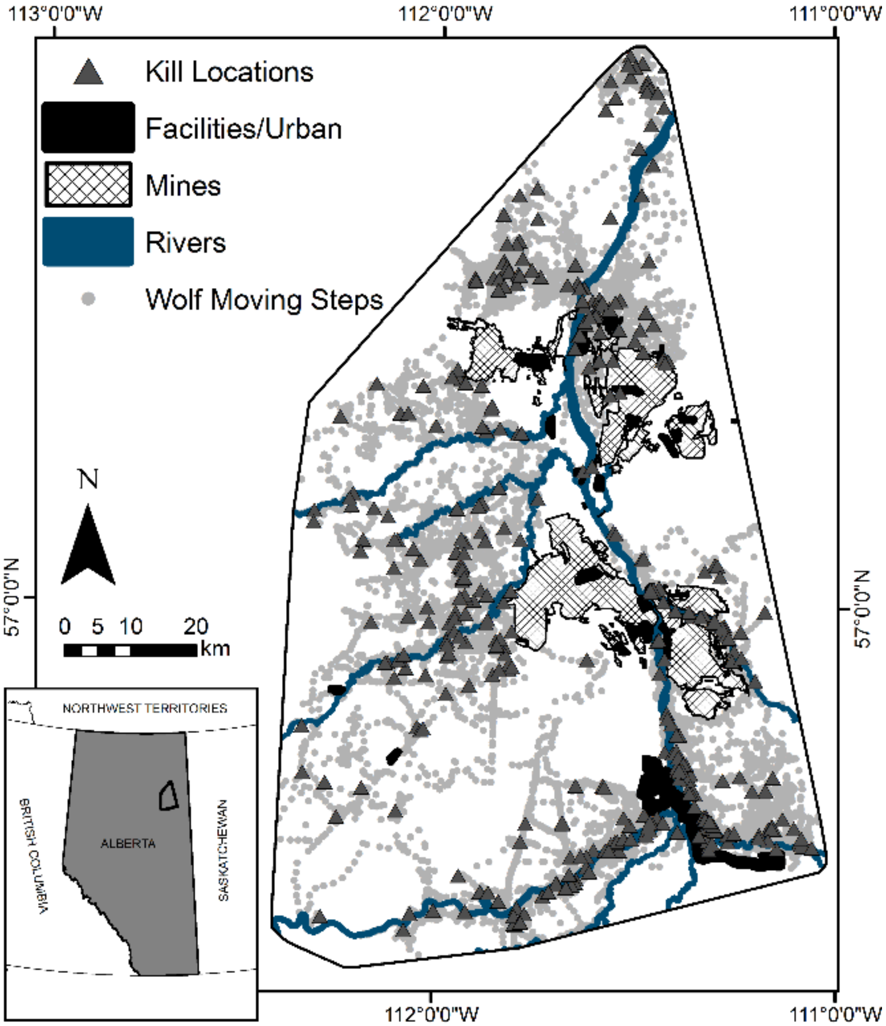

Figure 4.2 Wolf movement locations, isolated from all wolf GPS locations as those not associated with clusters of data where wolves spent at least three hours within a 300 m radius and 4 days. Kill locations are of deer and moose prey and are a subset of clusters with attributes matching those of ungulate kills visited in the field.

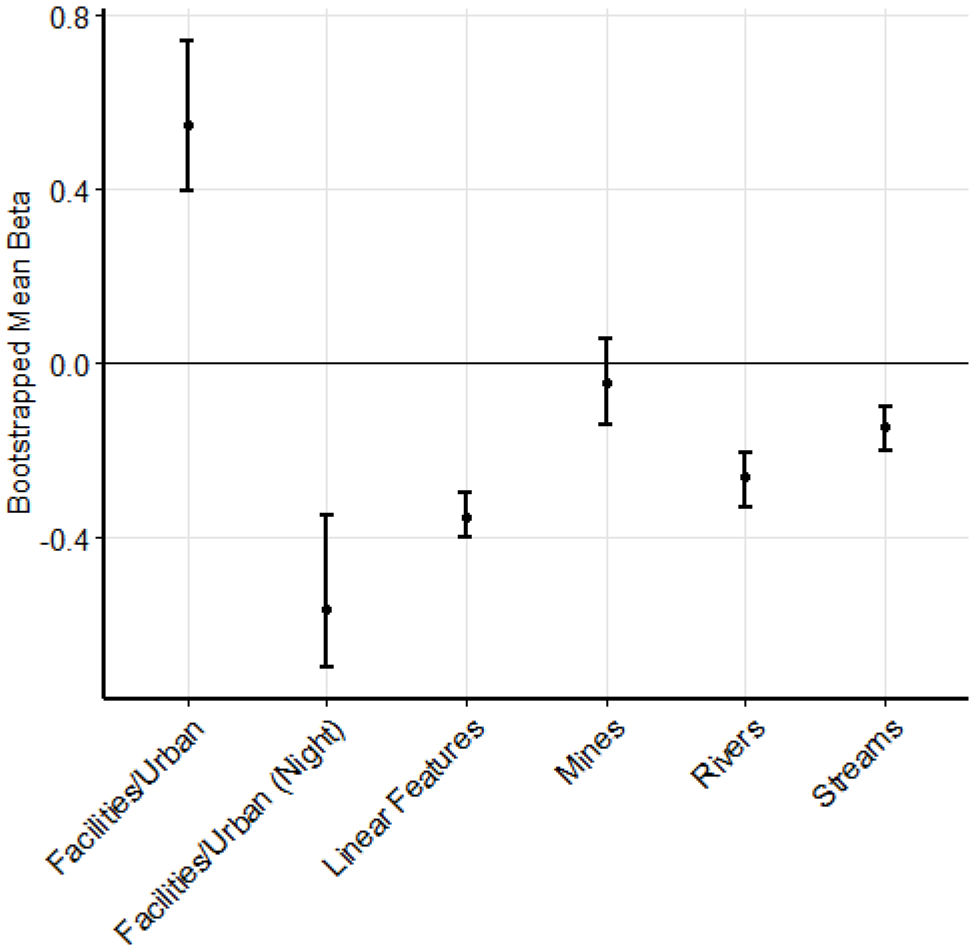

Figure 4.3 Bootstrapped mean and 95% confidence intervals for coefficients of wolf step selection for log distance to linear features, mines, facilities and the city of Ft. McMurray, rivers and streams. Coefficients were estimated using integrated step selection analysis that compared the end point of observed wolf steps to conditional available points sampled from theoretical gamma step length and von Mises turning angle distributions. Coefficients were calculated for each wolf using conditional logistic regression. Note: for distance to feature coefficients, negative values indicate selection.

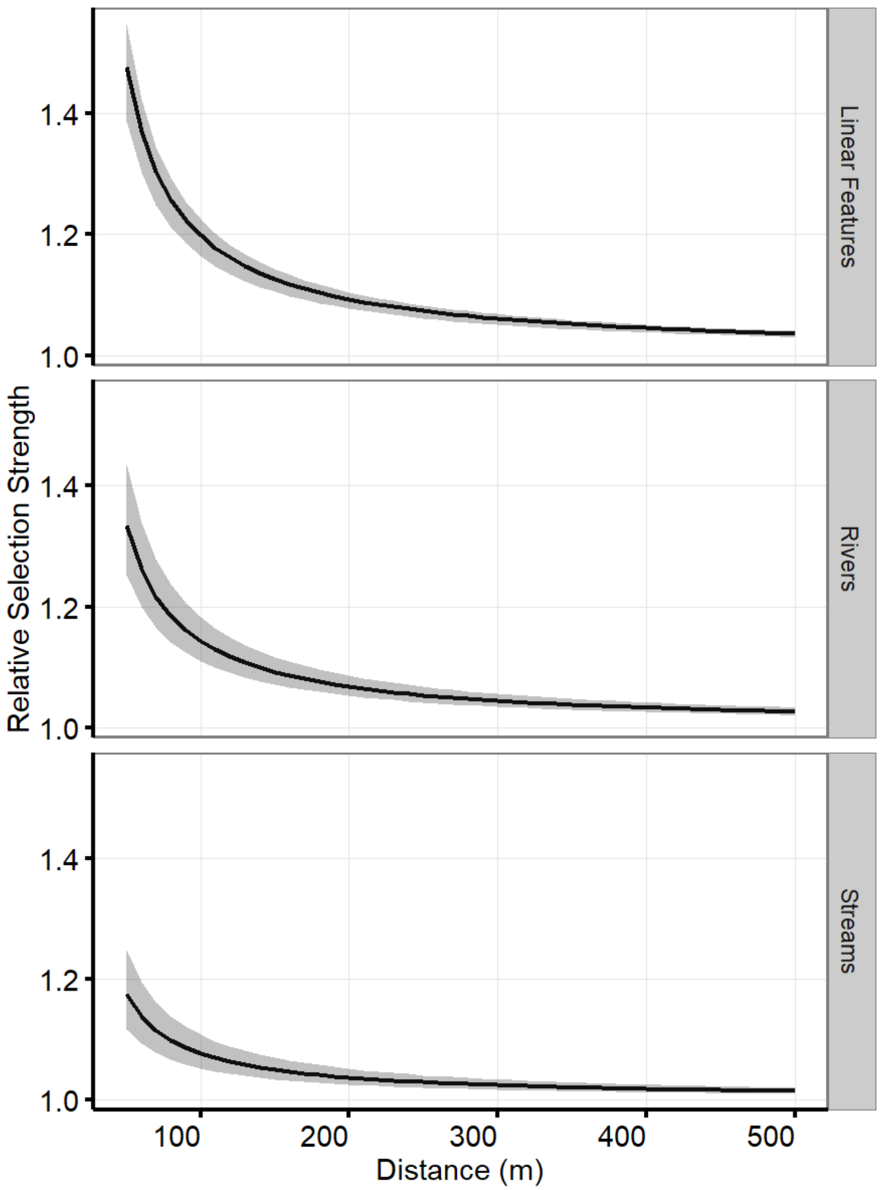

Figure 4.4 Relative selection strength of wolves selecting to move closer to human linear features, rivers and streams. Relative selection strength is the difference in selection between two locations (Avgar et al. 2017), separated here by 25 m. The calculation assumes that the effects of all covariates other distance to linear features, rivers or streams are the same. Coefficients were calculated for each wolf using conditional logistic regression. Grey areas are 95% confidence limits.

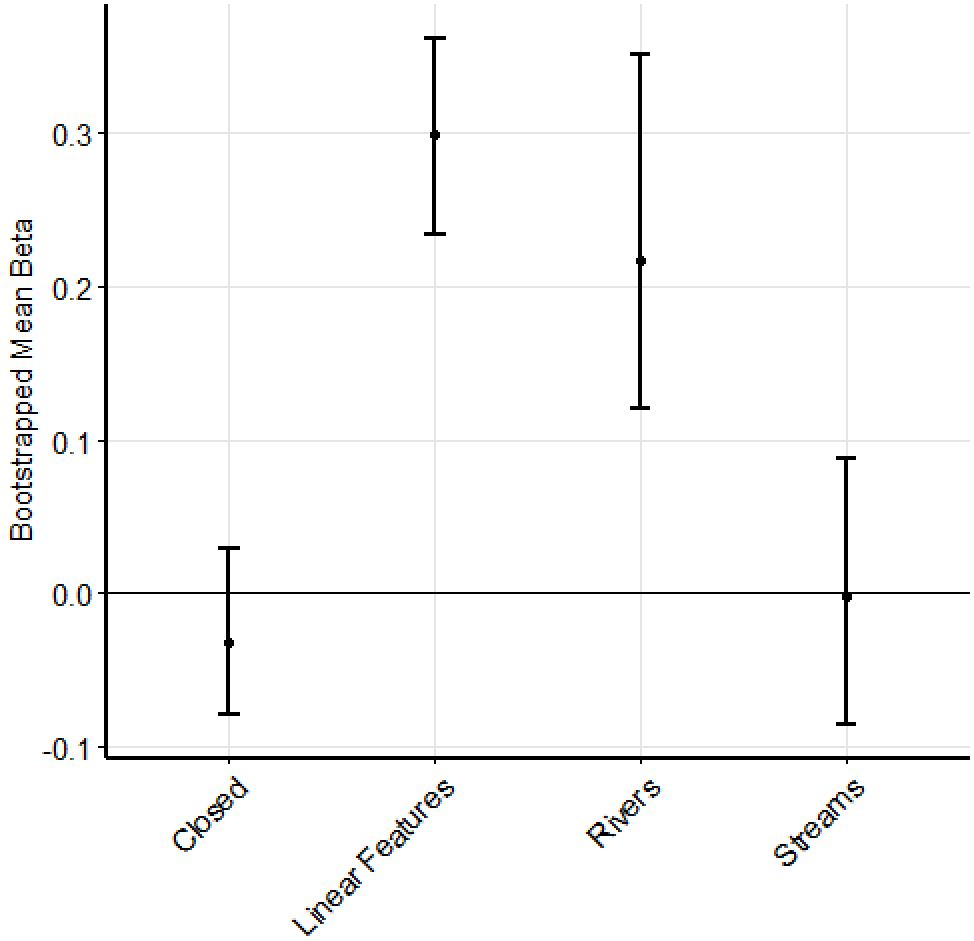

Figure 4.5 Bootstrapped mean and 95% confidence intervals for coefficients of wolf speed on linear features, frozen rivers and streams and in closed forest cover. Coefficients were estimated using integrated step selection analysis that interacted the log step with the habitat characteristics at the beginning of wolf steps in comparison to available points sampled from theoretical gamma step length and von Mises turning angle distributions.

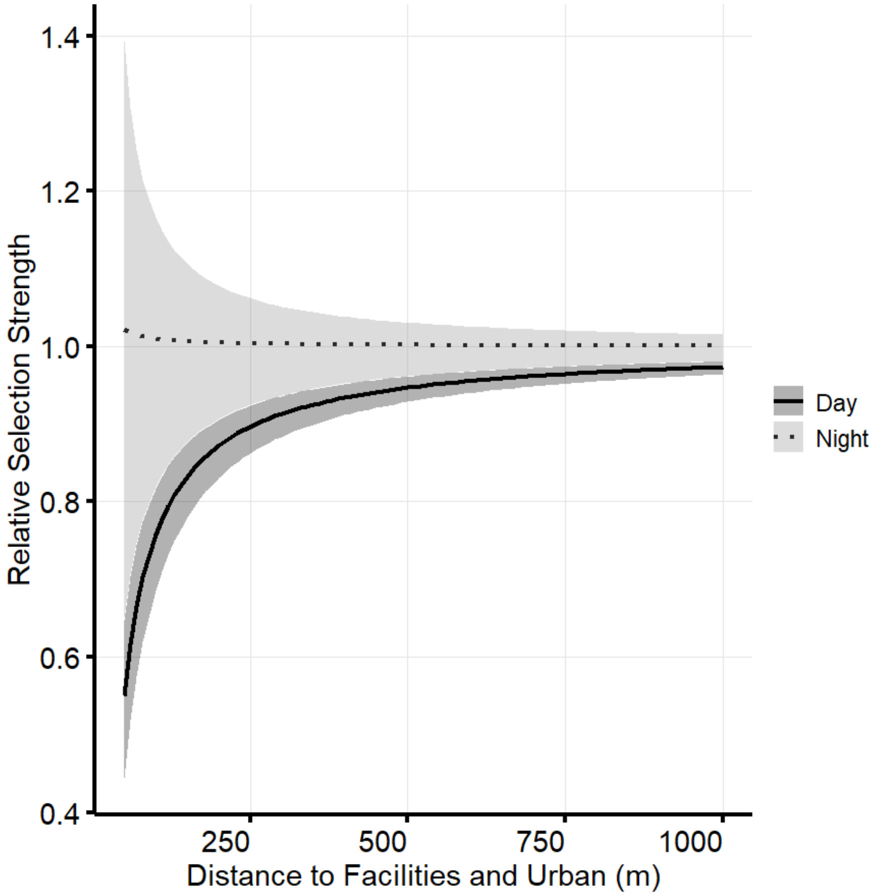

Figure 4.6 Relative selection strength of wolves selecting to move closer to facilities and urban areas at night and day. Relative selection strength is the difference in selection between two locations (Avgar et al. 2017), separated here by 25 m. The calculation assumes that the effects of all covariates other than the Night/Day and distance to facilities/urban are the same. Coefficients were calculated for each wolf using conditional logistic regression. Grey areas are 95% confidence limits.

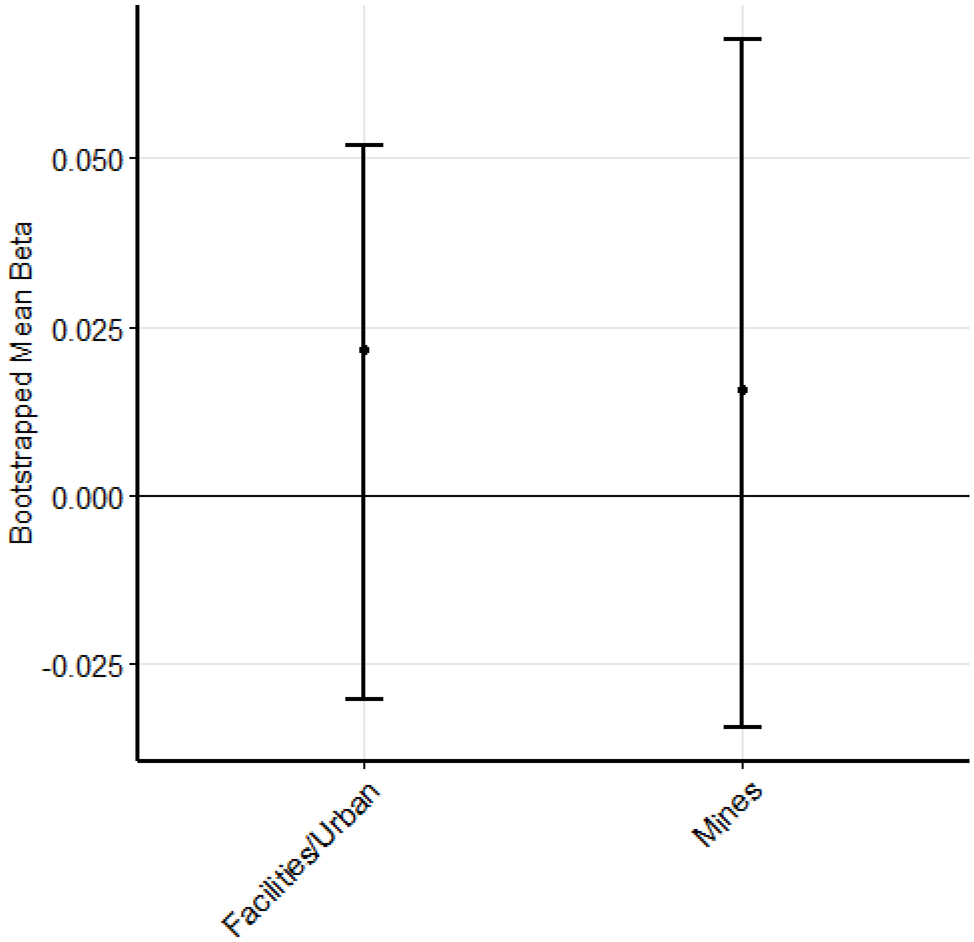

Figure 4.7 Bootstrapped mean and 95% confidence intervals for coefficients of wolf speed as a function of log distance to facilities and the city of Ft. McMurray, and mines. Coefficients were estimated using integrated step selection analysis that interacted the log step with the habitat characteristics at the beginning of wolf steps in comparison to available points sampled from theoretical gamma step length and von Mises turning angle distributions. Coefficients were calculated for each wolf using conditional logistic regression.

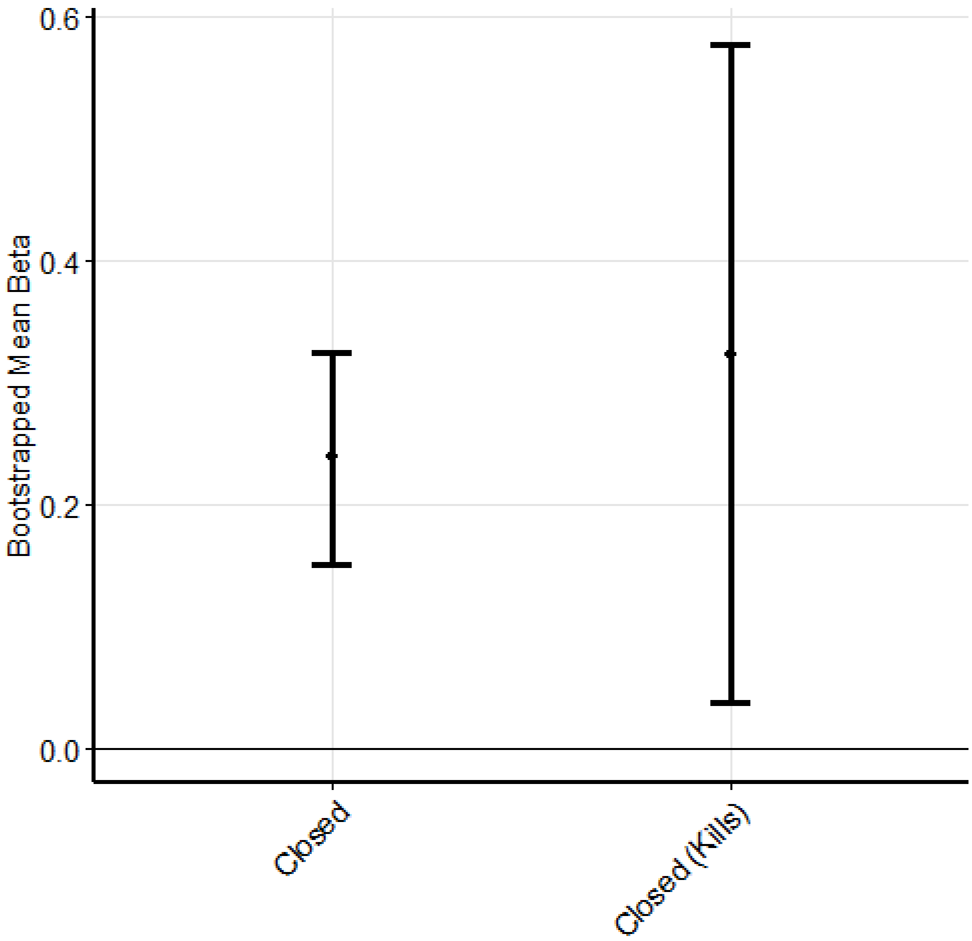

Figure 4.8 Bootstrapped mean and 95% confidence intervals for coefficients of wolf step selection for closed forest cover and the latent selection difference between between the distribution of locations where wolves kill prey and wolf steps in closed habitat . Step selection coefficients were estimated using integrated step selection analysis that compared the end point of observed wolf steps to conditional available points sampled from theoretical gamma step length and von Mises turning angle distributions. Latent selection difference coefficients were calculated using logistic regression that coded kills as 1 and steps as 0. Coefficients were calculated for each wolf using conditional logistic regression.

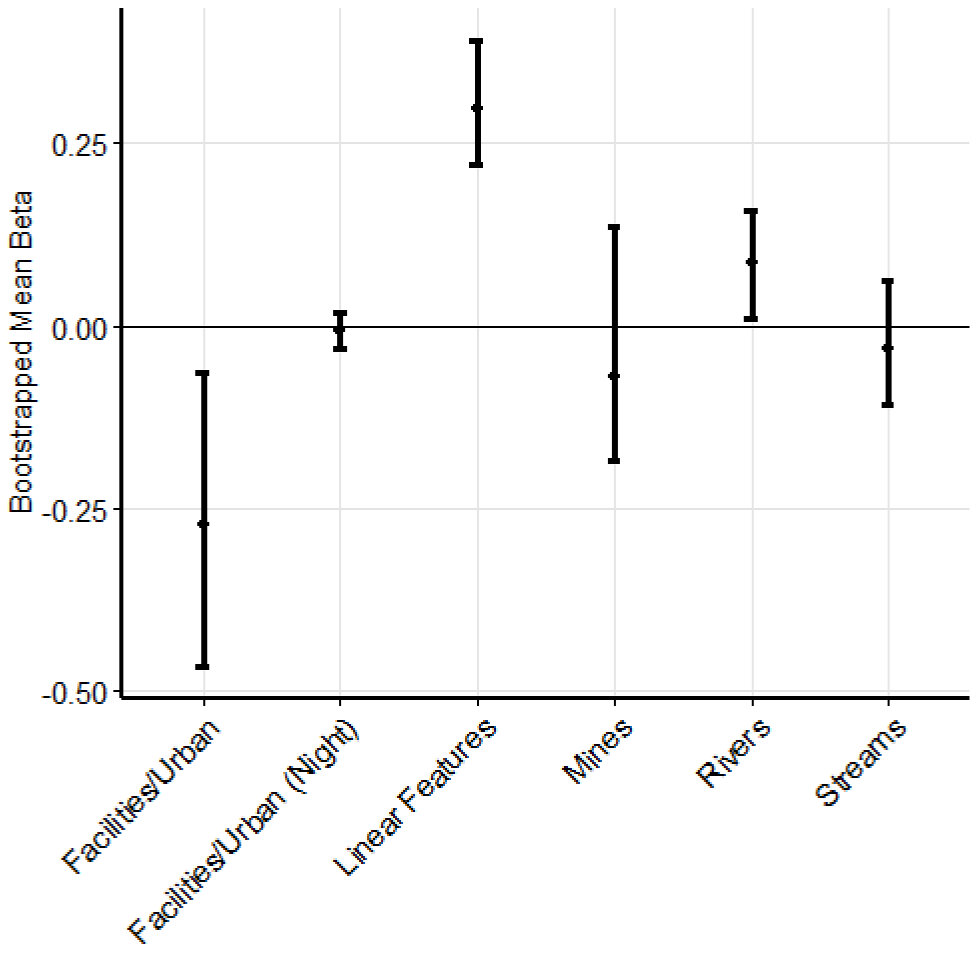

Figure 4.9 Bootstrapped mean and 95% confidence intervals for coefficients estimating the latent selection difference between the distribution of locations where wolves kill prey and wolf steps at the log distance to linear features, mines, facilities and the city of Ft. McMurray, rivers and streams. Coefficients were calculated for each wolf using logistic regression that coded kills as 1 and steps as 0. Note: for distance to feature coefficients, negative values indicate selection.

Chapter 5. The direct and indirect effects of predation structuring the distribution of moose (*Alces alces*) in the Athabasca oil sands

Introduction

Predator-prey relationships involve competing strategies in which predators attempt to maximize and prey attempt to minimize spatial overlap (Sih 2005). Predators are principally distributed by their prey such that predation pressure should be highest where prey are most abundant (Hassell 1978). However, predator distributions vary in space and time as functions of alternative prey species (Rettie and Messier 2000), territoriality (Maher and Lott 2000), competitors and predation, abiotic limitations (Connell 1970) and avoidance of anthropogenic disturbance (Frid and Dill 2002). This variation in the predator distribution affects the prey distribution through two pathways. First, the relative abundance of prey is reduced by direct killing of prey in areas where predation pressure is high (Huffaker 1958, Kauffman et al. 2007) and second, prey can respond behaviourally to variation in predation pressure by altering their space use (Schmitz et al. 2004, Sih 2005).

The landscape of fear predicts that prey respond to predation pressure in a variety of ways to reduce the probability of lethal encounters with predators (Laundré et al. 2001, Stankowich and Blumstein 2005, Creel and Christianson 2008). Where predation pressure is highest, individual prey avoid areas used by predators (Fortin et al. 2005, Sih 2005), avoid specific habitats or features used by predators (Berger 2007), and increase vigilance (Brown et al. 1999). Because anti-predator behaviour (APB) can incur costs to foraging, finding mates and avoiding competitors (Sih 1982, Relyea 2001), it should be proportional to predation pressure. Investment in APB is also a function of individual status. For instance, prey accompanied by offspring may engage in APB more readily than otherwise (Clark 1994). Conversely, where predation pressure is reduced, prey may not exhibit APB and be in higher abundance (McNair 1986, Sih 1987a).

Thus, variation in predation pressure can determine the prey distribution through direct killing of prey and indirectly by influencing prey behaviour. Investigating the relative strength of direct and indirect predation allows for better predictions of future space use under alteration of habitat through human disturbance (Sih et al. 2014).

Alberta's Athabasca oils sands region (AOSR) is a region of boreal forest in the Canadian western sedimentary basin with extensive deposits of bitumen. The AOSR is characterized by extensive human disturbance (Schindler 2010) and is home to spatially overlapping moose (*Alces alces*) and wolf (*Canis lupus*) populations (Fuller and Keith 1980, Hauge and Keith 1981, Wasser et al. 2011). Wolves respond to human disturbance depending on the types and intensity/frequency of use of the disturbance. When the intensity of use by humans is low, wolves use human disturbance such as linear features but reduce their use with increasing human use (Whittington et al. 2005, Hebblewhite and Merrill 2008, Houle et al. 2010, Rogala et al. 2011). Several studies have shown that moose use areas near human disturbance (Stephens and Peterson 1984, Berger 2007) and natural habitats (Edwards 1983, Latombe et al. 2014) that decreased the probability of lethal encounters with predators particularly when with a calf. However, previous work has focused on the spring calving or summer periods and has typically not directly examined how moose behaviour varies with the wolf use to determine the distribution of moose in winter, a period when wolves primarily hunt moose (Thomas 2013, unpublished data).

Throughout much of the boreal forest of Canada, moose are the primary prey of wolves (Hayes et al. 2000) and wolves are largely distributed according to the distribution of moose. However, wolves are also constrained in their space use by territoriality (Mech 1977, White et al. 1996). In AOSR, wolf packs strongly select territories near rivers (Chapter 2), creating areas far from rivers exhibiting low wolf intensity of use where moose might experience reduced predation pressure. Within their territories, individual wolves move along human made linear features, which increases their speed, and streams, which increases the probability of lethal encounters with prey (Chapter 4). Given the resulting non-uniform distribution of wolves, we hypothesized that the distribution of moose in winter in AOSR is a function of wolf killing of moose and moose behavioural responses to wolf predation pressure. We first predicted that due to direct killing, moose are relatively more abundant where wolf use is lower. We then established predictions testing the degree to which moose respond behaviourally to wolves. Specifically we predicted that within their home ranges individual moose would avoid areas with high wolf use, irrespective of habitat. Where moose are exposed to a higher wolf use, we predicted that moose habitat selection would vary both within individual moose across a gradient of wolf use and across individuals by their overall exposure to wolves. Finally, we predicted that any behavioural responses to wolves would be increased for moose accompanied by a calf.

Methods

Study Area

As written in Neilson and Boutin (2017); the AOSR is comprised of the broader Athabasca watershed surrounding the Athabasca oil sands. The mines lie along the Athabasca River approximately 20 km north of the town of Ft. McMurray between 56.9 and 57.4 degrees north and -111.0 and -112.0 degrees east. Topographic heterogeneity is contained largely within steep and deep river valleys and a broad, decreasing elevation gradient (860m to 250m) from north to south. Low, peat (*Sphagnum sp.*) forming wet areas with variable black spruce (*Picea mariana*) and tamarack (*Larix laricina*) forest dominates the area (33%), followed by uplands of aspen

(*Populus tremuloides*), white spruce (*Picea glauca*) and jackpine (*Pinus banksiana*) (together 30%). Forest understories contain willow (*Salix* spp.) dogwood (*Cornus stolonifera*), blueberry (*Vaccinium myrtilloides*), cranberry (*Vaccinium* spp.) and alder (*Alnus* spp.). The area is characterized by extensive mining footprints consisting of large extraction pits (325 km^2), tailings ponds (248 km^2) and associated large facilities (66 km^2). The area surrounding the mines has linear densities as high as 18 km/km^2. Forestry is minimal in AOSR.

Moose densities are low in the AOSR, ranging between 0.04 and 0.15/km2 in the three Wildlife Management Units overlapping our study area as measured between 2008 and 2013 (Morgan and Powell 2008, 2009, 2010, Sustainable Resource Development 2013). The Alberta provincial government estimates the moose population declined by 60% between 2004 and 2009 in the management unit west of the Athabasca river (Morgan and Powell 2010). Wolves and black bear prey on moose in the AOSR (Hauge and Keith 1981). Human hunting of moose is also an important source of moose mortality (Hauge and Keith 1981). Reported hunter harvest of moose was below the allocated quota for two and similar to the allocated quota in one of the wildlife management units in the study area (Morgan and Powell 2008, 2009, 2010). Moose are the most frequent source of prey for wolves in the winter in AOSR although wolves switch to beaver in the summer (Thomas 2013, unpublished data). Wolf trapping rates are between 0.5-3/1000 km^2 annually in the area (Robichaud and Boyce 2010).

Moose and Wolf Location Data

As written in Neilson and Boutin (2017); we collared 25 individuals moose cows throughout the study area in February 2010 and outfitted each with a GPS (Lotek 7000MU) collar (University of Alberta, ACUC Study ID. AUP00000102) GPS collars were programmed to fix the moose's location every three hours and continued collecting data until October 2012. The presence of calves with moose cows was ascertained during the collaring in March of 2010 and using aerial surveys in December of 2010, January of 2012 and December of 2012. All flights were conducted using a Jet Ranger helicopter flying between 80 and 100 km/h. Collared moose were relocated using radio telemetry and the presence and number of young of the year were recorded.

We collared at least two wolves in every pack in the area covered by moose GPS telemetry and equipped each with Iridium GPS collars (Lotek Inc., Newmarket, ON) in winter of 2011/12 using aerial net-gunning (University of Alberta, ACUC Study Id. AUP00000040). A total of 41 wolves from 10 packs were captured and collared. Wolf collars were programmed to fix the wolf's location every three hours. In the winter of 2012/13, collars were replaced where they had failed and new wolves were captured where individuals had died. In the second winter, GPS locations of the previous year were used to establish pack boundaries to assess whether or not all packs in the area had a collared wolf. We discovered 2 distinct gaps; one situated between Fort McMurray town site and an oil sands mine west of the Athabasca River and the second south of oil sands mines and east of the Athabasca River. Both areas were searched using two helicopters for a full day. We found limited wolf tracks indicating that wolves had moved through the area but could not find any sign of wolves using this habitat as territory. Based on our extensive efforts we are confident that we placed collars on wolves from all 10 packs in our study area.

We conduced all spatial and statistical analysis on moose and wolf winter locations (October to March) because in summer wolf predation of moose is low (Thomas 2013) due to wolf switching to consuming more beaver in the denning period than in the winter. We only estimated resource selection for the area common to the distribution of GPS telemetry for both species (Fig 2.1). Critically, because the wolf GPS data extended much farther from the human footprint than for moose (Fig 1.2), we did not want to bias our estimate of wolf selection for areas near human footprint compared to that of moose. We used the minimum convex polygon (MCP) or the smallest possible shape surrounding a set of locations or shapes, enclosing the all individual moose 95% utilization distributions (UD) (Fig 2.1), calculated using kernel density estimation (kde) and the least squares cross validation smoothing factor (Seaman et al. 1999). The moose MCP was used to clip wolf 95% UDs calculated for each individual. The resulting polygons were the utilization distributions for each wolf that overlapped the area covered by the moose GPS data. We then calculated the 95% MCP of the resulting wolf polygons, producing a 2967 km^2 polygon (Fig 2.1, 2.2). All GPS telemetry from both species falling outside this polygon was then removed. The effect is to not compare the species in areas where we only had information from one of them.

Environmental Covariates

As written in Neilson and Boutin (2017); we predicted that moose respond to the wolf use by altering their selection of closed conifer forest cover, which have shallower snow (D'Eon 2004) and reduced lateral cover compared to open deciduous and mixedwood stands in winter (Dussault et al. 2005). Using the Alberta Vegetation Inventory (AVI; Alberta Environment and Sustainable Resource Development 2011), we classified closed forest patches as those with at least 30% coniferous tree mean percent cover based on the Alberta Ecosites definitions (max conifer cover = 51%, Beckingham and Archibald 1996a) for uplands and 70% mean percent cover for wetlands using the Alberta Wetland Inventory Classification System (Halsey et al. 2003) for wetlands (Table 5.1).

As written in Neilson and Boutin (2017); we calculated the distance to major rivers and the density of streams using the Inland Waterway Base Hydrology layer (Table 5.1) (Alberta

Environment and Parks 2004). We calculated the distance to major rivers and streams using the Inland Waterway Base Hydrology layer (Table 5.1) (Alberta Environment and Parks 2004). Rivers were delineated as polygons and streams were delineated as lines, which we buffered by 2.5 m. The distribution of linear features was delineated by the Alberta Biodiversity Monitoring Institute (ABMI) at a 1:15 000 scale using 2012 SPOT imagery. We calculated the distance to the edge of linear features buffered with distances corresponding to classes assigned by ABMI (trail=0 m, seismic line=5 m, low use roads, pipelines and transmission lines = 10:20 m). We log transformed the distance to linear features, rivers and streams.

As written in Neilson and Boutin (2017); we defined the mine footprint as any area where excavation had occurred including pit mines and tailings ponds. Facilities were defined as the mining footprint associated with oil sands operations; upgraders, processing plants, work camps and parking lots. Cleared areas were any area adjacent to mines that had been cleared of forest cover for future pit mining (Table 2.1). To delineate the borders of mines and facilities, we modified 2009 land use shapefiles supplied by the Regional Aquatics Monitoring Program (2011) using SPOT satellite imagery for 2010 and 2012, the earliest years for which we had GPS telemetry for moose and wolves respectively. We only included facilities that were larger than one km^2 for analysis and clipped facility polygons from mines. Because we were interested in a zone of influence around the mining footprint, we removed locations falling inside mines and facilities for analysis and calculated the Euclidean distance to mines and facilities. To account for an attenuating effect of distance to mines and facilities as well as the collinearity between mines and facilities at far distances, we used an exponential decay transformation of the shortest distances to mines and facilities for each GPS location. The decay we chose reduced our transformed distance to zero approximately past distance of 8 km (Table 5.1), the approximate mean diameter of a moose home range in AOSR. Consequently, coefficients estimated the effect of the transformed distance to mines and facilities that are negative indicate avoidance and are predict effects that go to zero at approximately 8 km from either mines or facilities.

We calculated a spatial index of wolf abundance using kernel density estimation (kde) and the least squares cross validation smoothing factor (Seaman et al. 1999). We calculated a kde utilization distribution (UD) for each wolf pack, standardized each so UD values ranged from 0 to 1, then summed the packs to create a study area wide surface of wolf use. We transformed the UD such that the higher values were prioritized by first subtracting all values from the max value, log transformed the result and then subtracting from the max again (Table 5.1). From this UD we also calculated contour polygons corresponding to the 100%, 50% and top 10% of wolf use (Table 5.1).

Statistical Analysis

We separated analyses of moose by winters for which they were accompanied by a calf and those when they were not, while maintaining the individual moose as the unit of analysis. Data from some moose were therefore split into two sets. We tested our predictions using resource selection analysis that compares the habitat at locations used by a species to those at locations available to them (Manly et al. 1992). We first predicted that moose are more abundant where the intensity of wolves is lower. For each moose we calculated the ratio of locations in each contour of wolf use to random locations in the study area in each contour, predicted the mean selection ratio be highest at the lowest level of wolf use. These selection ratios are proportional to each moose selection for wolf areas at the population scale or second order (Johnson 1980). Availability was calculated by randomly generating 50 points/km^2 in the study area polygon and dividing them into the wolf levels of use. We bootstrapped mean and confidence intervals for the selection ratio in each wolf level of use. We also calculated the proportion of moose with any locations in each level of wolf use.

Our remaining predictions were that within their home ranges, moose would avoid areas with high wolf use, modify their behaviour in areas of high wolf use and that moose individuals would vary behaviourally as a function of mean wolf use. We tested these prediction using resource selection functions that compared resources at used GPS locations to random locations sample within each moose home range using logistic regression. We calculated a kde and 95% contour polygon for each individual moose in winter for each year then sampled availability of resources using a distribution of points randomly generated at a density of 50/km^2. Used and available data from each year were then combined for each moose into a calf or no-calf dataset. We fit a model that estimated selection for closed forest cover, and the log distance to rivers, streams, and linear features. All variables were interacted with the log transformed wolf UD to examine both whether moose avoided wolves and how their selection changed as a function of wolf use. The log distance to mines and linear features was collinear with one another so transformed each with an exponential decay such that transformed distances went to zero approximately past 8 km, the approximate mean diameter of a moose home range in AOSR (Table 5.1).

Our model was fit to each individual moose to address spatial autocorrelation within and sample size differences among individuals (Fieberg et al. 2010). We bootstrapped mean and confidence intervals for each beta coefficient and made population inferences by examining confidence intervals that did not overlap zero. Bootstrap sampling was weighted by the inverse of the variance for each coefficient per moose. We tested the prediction that moose do not alter their behaviour but various across individuals as a function of wolf use by regressing the distribution of moose selection coefficients against the mean wolf UD, interacted with a binary variable indicating whether that moose was accompanied by a calf. We weighted each regression with the inverse of the standard error for each coefficient per moose.

Results

Across the study area, moose selection ratios decreased as wolf use increased from the total 100% of use to the top 10% of use but this effect was dependent on the presence of a calf. Moose with calves demonstrated a clear reduction in any use of the top 50% and top 10% levels of wolf use, with the bootstrapped mean value decreasing significantly with each level of use wolf use (Fig 5.3). The proportion of moose with calves exposed to various levels of wolf use matched the mean selection ratios, decreasing from 0.79 to 0.16 (Fig 5.4). On average, solitary cow moose were also distributed away from wolves but with more variation than cows with calves (Fig 5.3). The mean selection ratio decreased from significantly positive to negative from the total 100% of wolf use to the top 50%. The response was highly variable and insignificant for the top 10% of wolf use (Fig 5.3). However, this variation was likely driven by few moose as only 30% of moose had any exposure to the top 10% wolf level of use (Fig 5.4).

We split the data for 14 moose because they varied by whether they were accompanied by a calf resulting in models for 18 moose cows with no calf (25,645 locations) and 19 models for cow with a calf (28,904 locations). We found that moose habitat selection at the home range scale varied both by the local level of wolf use and the presence of a calf. Solitary cows were characterized by variation among individuals such that the only clear signal was selection of areas near streams (Table 5.2, Fig 5.5). Habitat selection by cows with calves was more sensitive to wolf use (Table 5.2). Overall, they strongly avoided areas used intensely by wolves, irrespective of habitat, a signal not observed for solitary cows (Fig 5.6). Cows with calves also selected rivers but as the wolf use increased they switched to avoiding rivers (Fig 5.5, 5.7). The interactions between wolf use and the transformed distance to facilities was negative for cows with calves such that these cows responded to increasing wolf use by selecting away from human disturbance (Fig 5.6).

Variation between individual moose responses to both natural and anthropogenic landscape features was not well predicted by the mean availability of wolves per individual moose. We observed two variables that were weakly correlated with the interaction of wolf exposure and the presence of a calf (Table 5.S1). Increasing average exposure to wolves per moose, predicted increases selection for both closed forest cover (Fig 5.8) and areas farther from linear features (Fig 5.9), irrespective of the presence of a calf.

Discussion

We examined how the direct consumption of moose by predators and indirect effects of fear of predation distributes moose in the Athabasca oil sands. Moose in AOSR were strongly distributed away from areas where wolf use is highest but when exposed to wolves, cow moose adjust their behaviour according to the level of wolf use, particularly when accompanied by a calf. The relatively higher densities of moose on the periphery of wolf territories and farther from wolf use could arise due to moose selection of home ranges away from relatively higher predation risk or irrespective of moose behaviour, wolves could have reduced moose abundance in their core territory via hunting. Our results indicate that both of these processes work to shape the distribution of moose in AOSR and are a function of the presence of a calf.

Because wolves in AOSR select territories around rivers (Chapter 2), moose abundance becomes relatively higher in areas farther from river. As moose density in these refugia increases toward carrying capacity, dispersal to riskier areas (McNair 1986) could maintain the wolf pack distribution because dispersers are naïve to predation risks and are more easily killed. Previous work examining moose responses to predation found moose more likely to avoid predators or adjust their habitat selection when pregnant or accompanied by a calf (Dussault et al. 2005, Berger 2007). The lack of both avoidance of wolves and behvioural plasticity in habitat selection in response to wolves among solitary cows suggests direct predation may be reducing moose densities in the core of wolf territories.

Antipredator behaviour comes with fitness costs through reductions in foraging and changes to movement and habitat selection. Prey should therefore only engage in APB as much as is necessary to reduce direct predation. Variation in the distribution of wolves in AOSR potentially allows moose to balance the effect of direct and indirect effects away from costly indirect effects by utilizing area with lower intensity of use by wolves. Cows with calves strongly avoided the area with the highest wolf use at the population-range scale and within their home range. We conclude that moose respond to wolf predation as a function of their vulnerability. Such a strategy allows prey to mitigate the costs of anti-predator behaviour (Creel and Christianson 2008).

Moose with calves demonstrated plasticity in their selection for both natural habitat features and human disturbance features as a function of the wolf use. Rivers are selected by wolves at pack territory scale and by individual wolves while moving (Chapter 2, 4), leading to an increased relative predation rate of moose in areas near rivers in AOSR (Chapter 3). By modifying their habitat selection, moose make their location less predictable to wolves, thereby decreasing the chance of predation (Mitchell and Lima 2002, McPhee et al. 2012). However, because moose with calves select areas near rivers but plastically respond to the wolf use by switching to river avoidance where wolf use is highest indicates that increased predation risk near rivers has potential foraging costs for moose. Previous work has reported avoidance of heavily used human disturbances such as oil sands facilities by wolves, such that in around these features prey are partially released from predation pressure (Hebblewhite et al. 2005b). However, in winter in AOSR, while wolves do avoid traveling near facilities and urban areas during the day, they continue to use these areas during the night such that kill are not less frequent there (Chapter 4). Cows with calves may respond to this by avoiding areas near facilities where wolf use is high.

In addition to exhibiting behavioural plasticity, individual moose exhibited antipredator strategies commensurate with the average wolf use available in their home range. Irrespective of the presence of a calf, selection for closed forest cover increased as the moose's average exposure to wolves increased. In winter, closed forest stands provide the most amount of lateral visual cover in comparison with mixedwood, deciduous and open forest stands (Beckingham and Archibald 1996, Dussault et al. 2005). Switching to use of closed forest cover could decrease the probability of wolves detecting the moose, thereby decreasing the probability of lethal encounters with wolves (Stephens and Peterson 1984, Mysterud and Ostbye 1999, Hebblewhite et al. 2005a). However, moose selection for closed areas may not provide an advantage once an encounter has occurred as closed and conifer forest cover has been associated with higher probabilities of wolves killing prey (Hebblewhite et al 2005, Chapter 4). Selection for areas near linear features also decreased among moose depending on their overall exposure to wolves. Wasser et al. (2011) found a positive association between moose and linear feature density and argued that linear features are used for forage but also demonstrated that moose avoid linear features of low or unknown intensities of human use. We conclude that because linear features are more likely to be used by wolves (James and Stuart-Smith 2000, Chapter 4) moose avoid linear features when exposed to a higher intensity of wolf use. It is not possible from our results to assert whether the variation in habitat selection among moose individuals is due to indirect predation (moose learning) or simple removal of individual moose not exhibiting sufficient APB by wolves. Further work examining cause-specific mortality for moose with known behavioural patterns is needed to parse these effects.

Studies of animal habitat selection as a function of predation do not in themselves reveal how predation drives population dynamics. However, examining behavioural responses like habitat selection in the context of predation at multiple scales provides insight into the effects of predation on the distribution of prey. We compared the broad distribution of moose to their primary predator wolves, in winter, to better understand how wolves both numerically and behaviourally limit moose across space in a highly developed landscape. Our results indicate that moose only respond to wolves when wolf use is most intense and when moose are most vulnerable. Where wolf use is highest moose are less abundant but in these areas, moose with calves exhibit both avoidance of wolves in their home ranges and behavioural plasticity allowing them to switch habitat selection and reduce their vulnerability.

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Table 5.1 Variables used to model moose selection and anti-predator behavioural responses.

Variable	Description	Model Units
Linear Features	Trails, Seismic, Transmission, Pipe	log Distance
Rivers	delineated river polygons	log Distance
Streams	buffered streams, 2.5 m buffer	log Distance
Facilities	Delineated oil sands facilities	exp(-0.001*distance)
Mines	Delineated oil sands pits, tailings ponds	exp(-0.001*distance)
Land cover	Closed forest cover patches at least 30% coniferous tree mean percent for uplands and 70% mean percent cover for wetlands	in/out
Wolf Level of use	Logged sum of a single kde utilization distribution per wolf pack. Each pack UD calculated with the least squares cross validation smoothing parameter.	log(probability of use)
	polygons enclosing contours of wolf use calculated from the summed pack UD, top 50% and 10% compared against 100% (all wolf use)	in/out

Table 5.2 Mean beta coefficient values and 95% CIs from models of moose cows with calves. Population means and CIs were calculated by bootstrapping coefficients from each moose, weighted by the inverse model estimated variance. Variables with “:” indicates an interaction. ‘Closed’ refers to closed forest cover.

Variable	With Calf				No Calf			
	Beta	SE	Lower CI	Upper CI	Beta	SE	Lower CI	Upper CI
Closed	-0.08	0.05	-0.43	0.38	-0.1	0.05	-0.66	0.15
Wolf	-13.92	1.25	-26.11	-3.1	2.98	1.68	-20.46	3.43
Lines Distance	0.06	0.02	-0.08	0.22	0	0.01	-0.08	0.12
Rivers Distance	-0.3	0.03	-0.53	-0.01	0.09	0.05	-0.18	0.65
Streams Distance	-0.34	0.04	-0.69	0.06	-0.24	0.03	-0.54	-0.03
Facilities Distance	0.53	0.81	-4.85	9.23	1.18	0.48	-2.97	3.1
Mines Distance	-1.24	0.25	-2.94	1.11	0.02	0.15	-0.94	1.56
Closed:Wolf	-0.37	0.17	-1.91	1.07	-0.25	0.17	-0.99	1.89
Lines Distance:Wolf	-0.19	0.12	-0.51	1.41	-0.2	0.07	-0.3	0.45
Rivers Distance:Wolf	1.44	0.06	1.01	2.08	-0.14	0.08	-0.14	0.78
Streams Distance:Wolf	0.36	0.11	-0.49	1.28	0.05	0.13	-0.02	1.51
Facilities Distance:Wolf	-8.44	18.82	-137.82	-3.9	-1.71	24.17	-120.5	162.69
Mines Distance:Wolf	4.64	2.62	-30.27	16.99	-0.17	2.32	-20.75	5.43

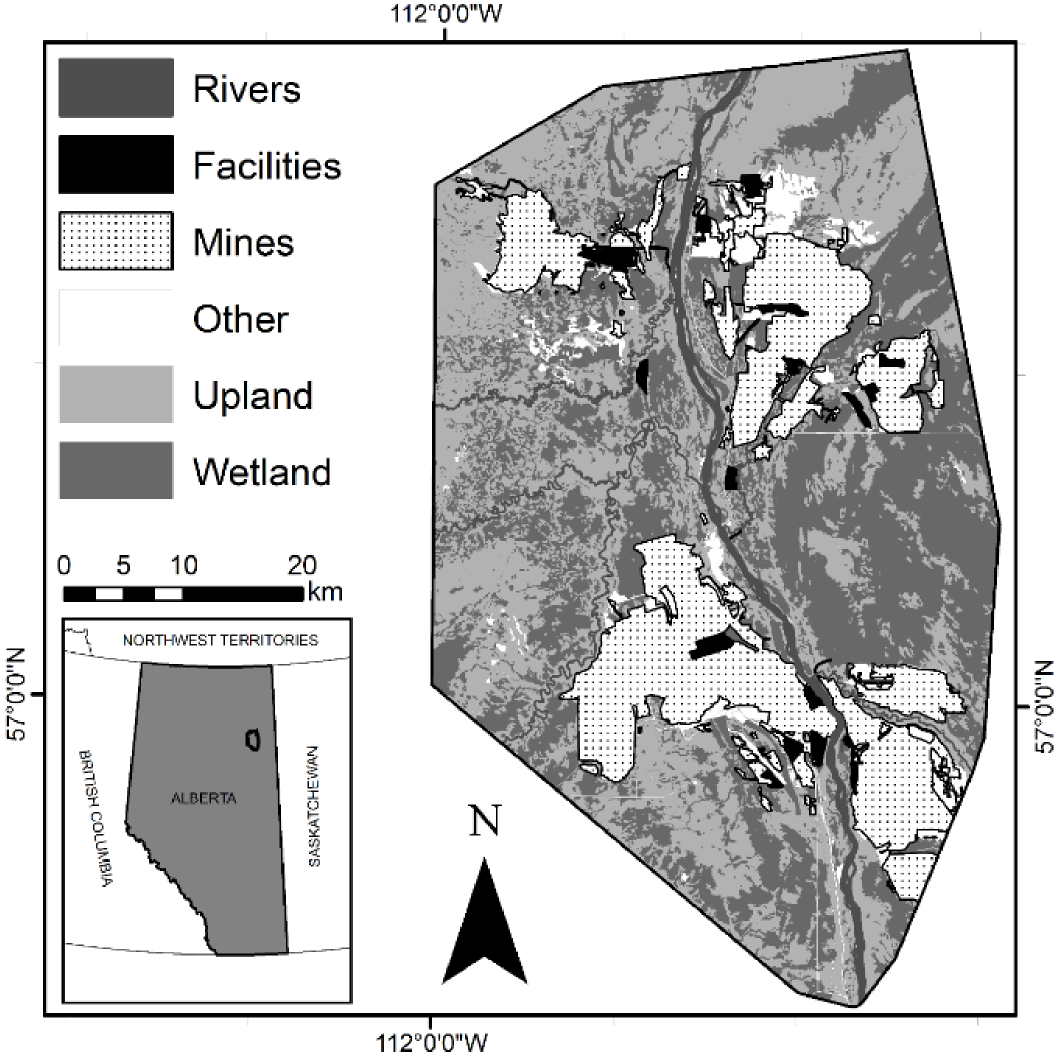

Figure 5.1 The study area polygon was created by intersecting the MCP of individual moose and wolf pack 95% kernel density estimates. Uplands are a combination of deciduous, coniferous and mixedwood landcover defined using the Alberta Ecosites. Wetlands are a combination of bogs and fen defined using the Alberta Wetlands Inventory Classification System. Other is a combination of cleared areas near mines, open water and other forest cover types.

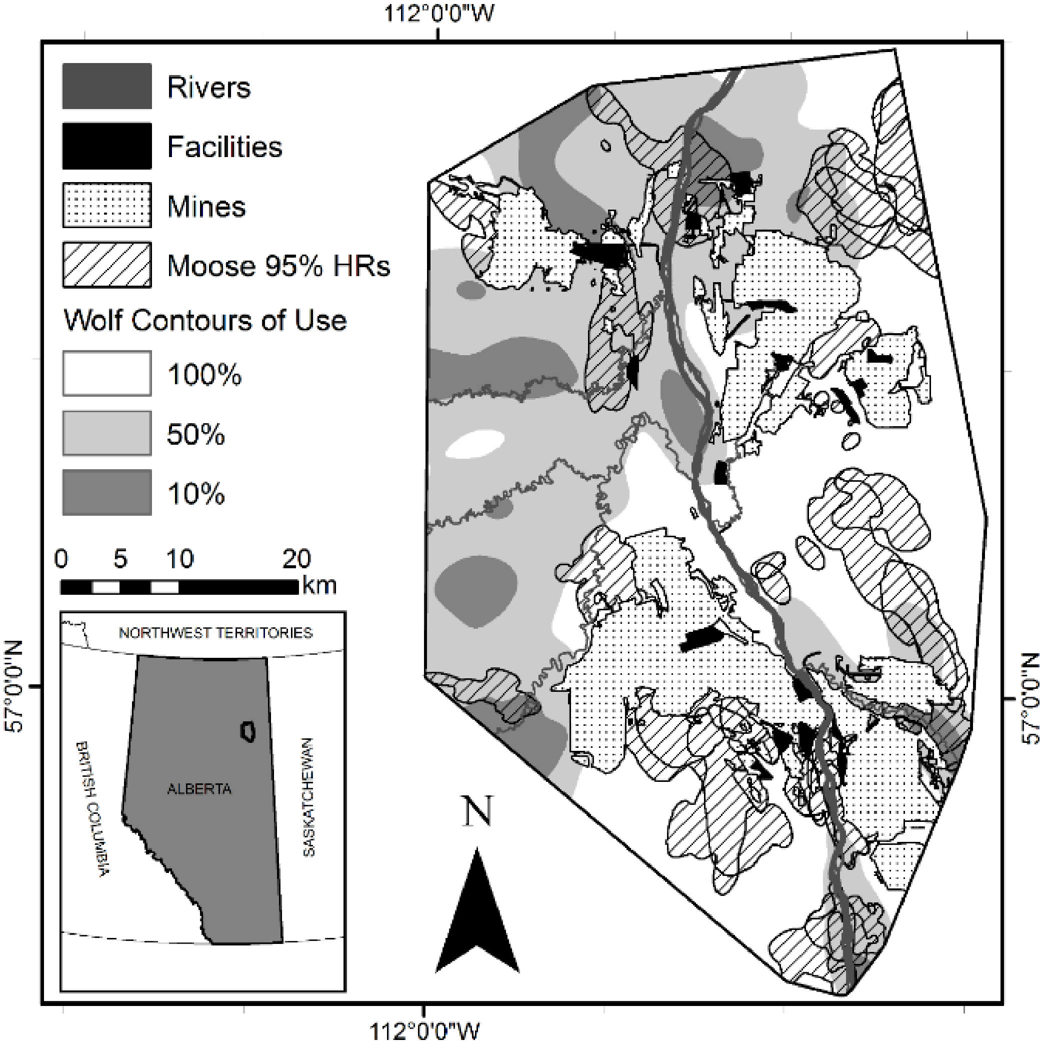

Figure 5.2 The study area polygon was created by intersecting the MCP of individual moose and wolf pack 95% kernel density estimates. Wolf levels of use were calculated as utilization distributions (UD) using kernel density estimates of each pack. Each pack was UD was standardized and then summed together, from which contours of wolf use were calculated. Moose 95% home ranges (HR) are the 95% contour of use calculated from the UD of individual moose GPS data.

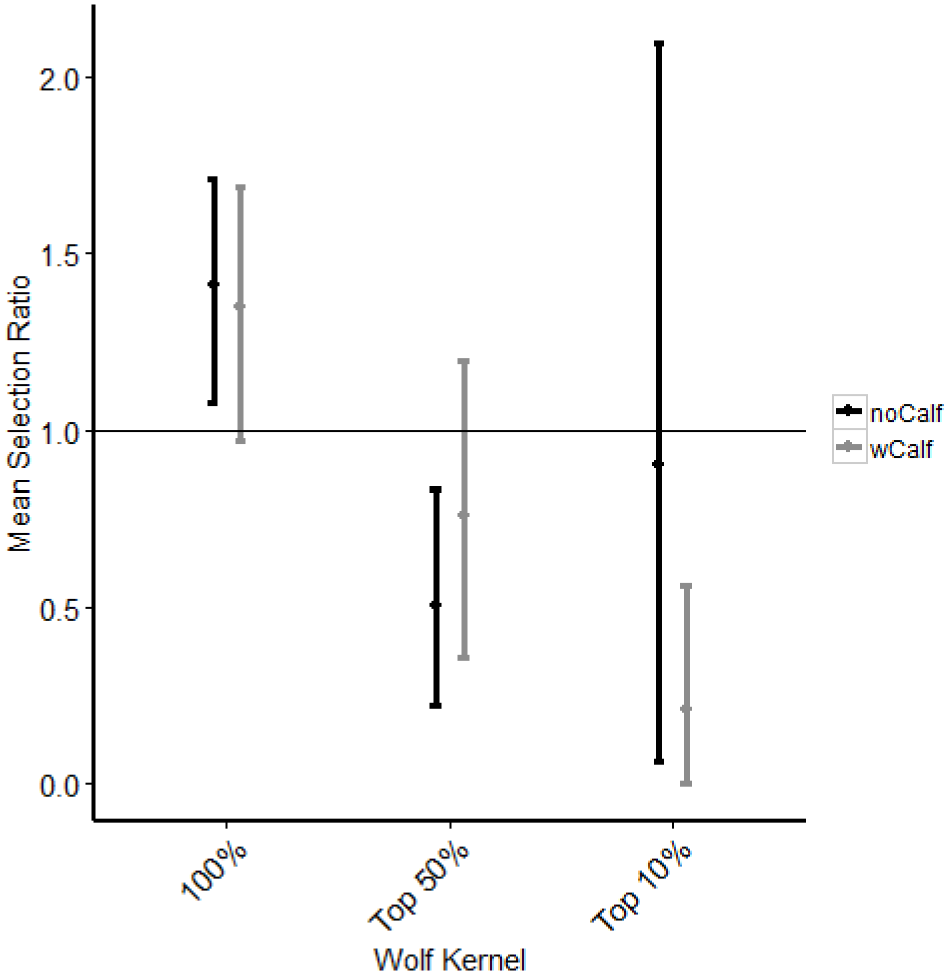

Figure 5.3 Bootstrapped mean and 95% confidence intervals of moose selection ratios for contours of wolf use for moose cows with and without calves. Contours of wolf use were calculated from a sum of utilization distribution from each wolf pack. We transformed the UD such that the higher values were prioritized by first subtracting all values from the max value, log transformed the result and then subtracting from the max again. From this UD we calculated contour polygons corresponding to the 100%, 50% and top 10% of wolf use.

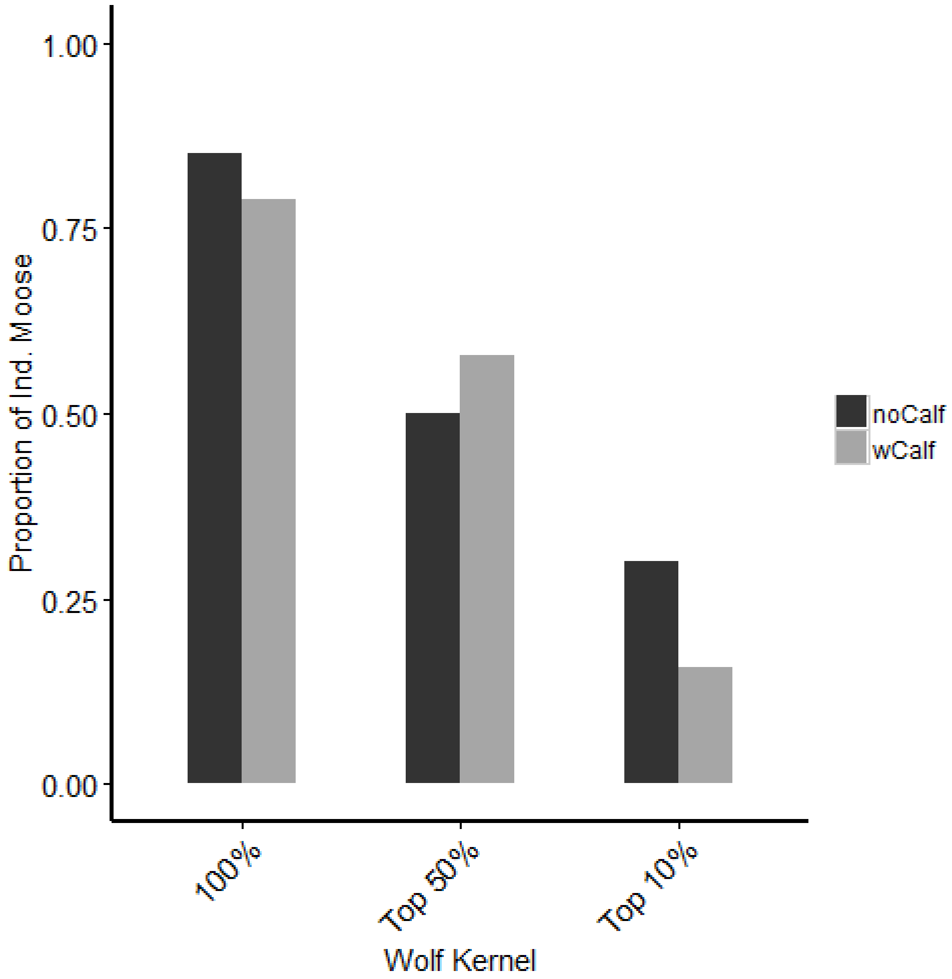

Figure 5.4 Proportion of individual moose with any locations inside contours of wolf use for moose cows with and without calves. Contours of wolf use were calculated from a sum of utilization distribution from each wolf pack. We transformed the UD such that the higher values were prioritized by first subtracting all values from the max value, log transformed the result and then subtracting from the max again. From this UD we calculated contour polygons corresponding to the 100%, 50% and top 10% of wolf use.

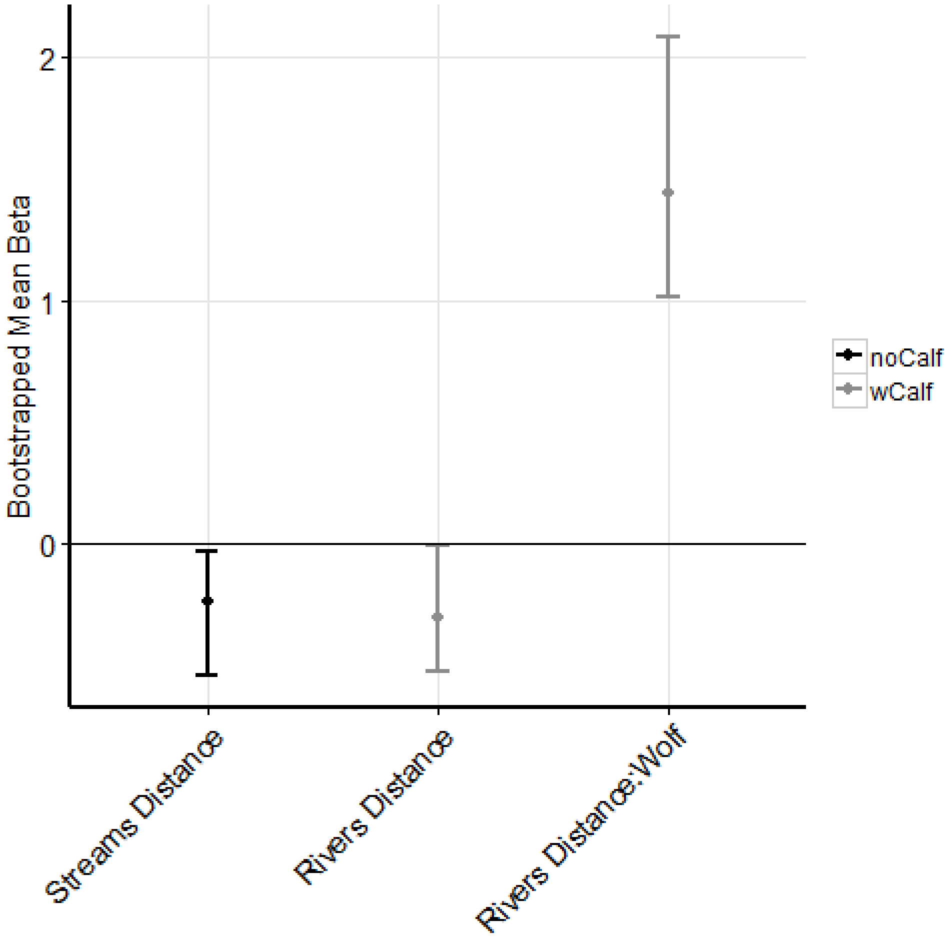

Figure 5.5 Bootstrapped mean and 95% confidence intervals for coefficients of moose selection for the log distance to rivers and streams. Coefficients were estimated using logistic regression. The distance to rivers and streams were log transformed, such that negative coefficient values indicate selection.

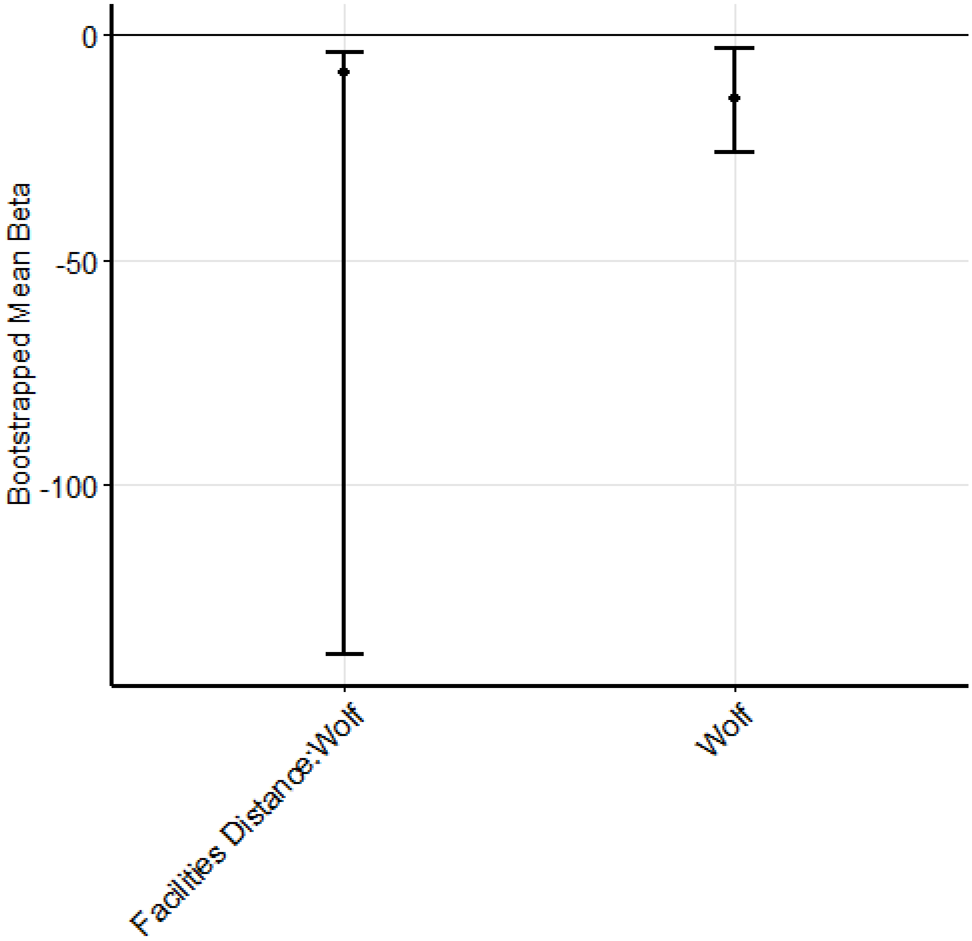

Figure 5.6 Bootstrapped mean and 95% confidence intervals for coefficients of moose selection for the transformed level of wolf use (Wolf), the interaction coefficient between selection for areas closer to facilities as wolf use increases and for areas farther from rivers as wolf use increases. Coefficients were estimated using logistic regression. The distance to facilities (d) was transformed using exp(-0.001*d), such that negative coefficient values indicate avoidance.

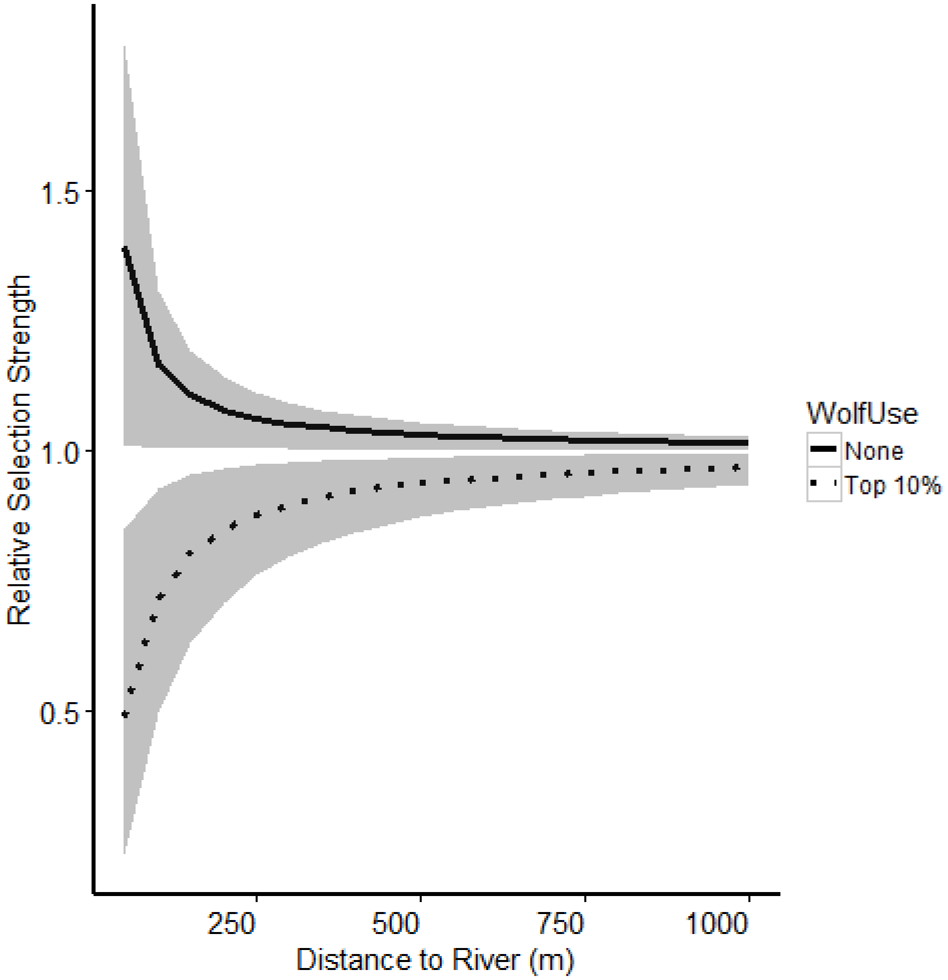

Figure 5.7 The relative selection strength of moose with calves selecting to move closer to, rivers. Relative selection strength is the difference in selection between two locations (Avgar et al. 2017), separated here by 25 m. The calculation assumes that the effects of all covariates other distance to linear features, rivers and streams are the same.

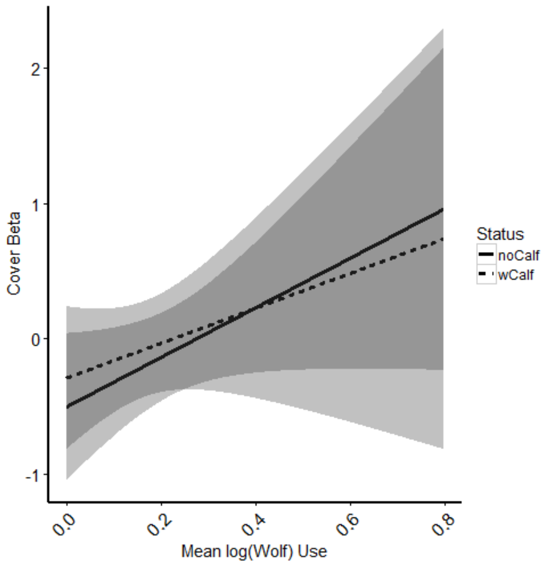

Figure 5.8 Predicted effect of increasing wolf use on individual moose selection for closed forest cover. Individual selection for closed cover was estimated using resource selection functions for each moose. Coefficients from each individual were then regressed against the mean log wolf use, using linear regression weighted by the inverse variance from individual models.

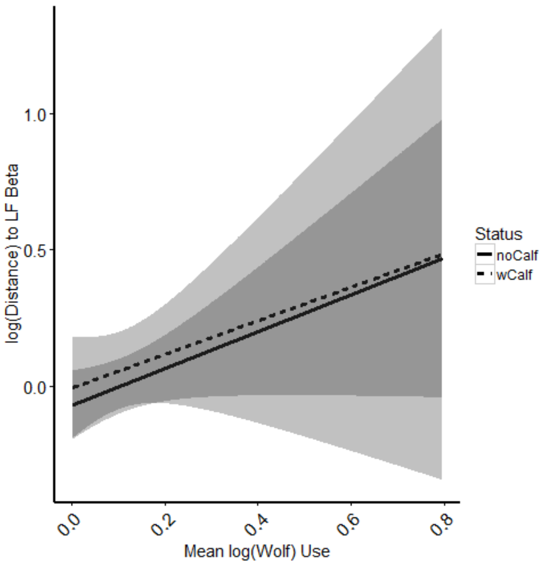

Figure 5.9 Predicted effect of increasing wolf use on individual moose selection for areas farther from linear features (LF). Individual selection for linear features was estimated using resource selection functions for each moose. Coefficients from each individual were then regressed against the mean log wolf use, using linear regression weighted by the inverse variance from individual models.

Supplementary Material

Table 5.S1 Effect of the wolf presence and reproductive status per moose on moose selection for natural and anthropogenic habitat features. Each response was predicted with the same model: y~Wolf*Calf, where Wolf is the mean log(wolf) use and Calf is a binary variable indicating whether a cow moose accompanied by a calf. The table was sorted by ascending p values to highlight significant effects. Closed = closed forest cover.

Response	Predictor	Beta	Standard Error	p value
Closed	Wolf	1.965	0.993	0.056
Lines Distance	Wolf	0.681	0.358	0.066
Wolf	Wolf:Calf	-77.424	48.2	0.118
Mines Distance	Wolf	-3.577	2.993	0.241
Wolf	Wolf	36.924	31.456	0.249
Facilities Distance	Wolf	10.451	8.94	0.251
Streams Distance	Calf	-0.203	0.224	0.372
Rivers Distance	Calf	-0.405	0.455	0.38
Rivers Distance	Wolf	-0.784	1.051	0.461
Streams Distance	Wolf:Calf	1	1.375	0.472
Closed	Calf	0.252	0.374	0.506
Wolf	Calf	10.467	17.53	0.555
Lines Distance	Calf	0.066	0.112	0.564
Mines Distance	Wolf:Calf	-3.016	6.319	0.636
Closed	Wolf:Calf	-0.697	1.566	0.659
Rivers Distance	Wolf:Calf	-0.613	1.39	0.662
Streams Distance	Wolf	0.254	0.629	0.689
Mines Distance	Calf	-0.376	1.581	0.814
Lines Distance	Wolf:Calf	-0.058	0.699	0.934
Facilities Distance	Calf	-0.133	3.794	0.972
Facilities Distance	Wolf:Calf	-0.167	14.41	0.991

Chapter 6. General Discussion

The energy provided by crude oil makes it one of the most highly commodified substances on the planet, and developments for its extraction, refinement and consumption abound wherever it is available. Between 2014 and 2017 (completion year of this thesis), the global price of a barrel of oil had reduced to approximately $40US/barrel, its lowest since the early 2000's, partially due to reduced consumption (IEA 2016). However, despite political and economic shifts away from the use of hydrocarbons as an energy source, oil remains an economically important industry for the countries in which it occurs. Canada's Athabasca oil sands are no different, with increased extraction expected in the AOSR (IEA 2017).

The large open pit mining used to extract bitumen and the tailings ponds required for its upgrade in the AOSR produce a large polygonal disturbance that remove habitat from the landscape. The effect of such habitat loss on a species that occupies the disturbed area is, in part, straight forward; the percentage of habitat lost provides the percentage reduction in the species population (Bender et al. 1998). However, habitat surrounding polygonal disturbances may also increase or decrease in quality due to a zone of influence (Gates and Gysel 1978, Dyer et al. 2001). In such cases, the effect for populations is less clear and estimating the magnitude of direction of habitat quality change is needed to predict population outcomes. In this thesis I explored one realm in which habitat quality might change for two large mammals linked by predation: predator-prey spatial overlap.

Overall, I detected only small effects of the Athabasca oil sands footprint on wolf (*Canis lupus*) moose (*Alces alces*) spatial overlap. In *Chapter 2*, I investigated the broad scale distributions of wolves and moose in the AOSR. The goal was to assess the degree to which moose may be avoiding encounters with wolves by avoiding areas wolves occur by using areas near oil sands developments. Whereas wolves and moose did not demonstrate complete overlap in their distributions, this disparity was not largely driven by the proximity of oil sands mines. Wolves in the AOSR selected territories near rivers but were largely insensitive to the presence of mines. However, when mining developments generated isolated areas far from rivers, moose in the area were less exposed to wolves due to reduced wolf use.

The insensitivity of wolves to oil sands mines themselves was further supported in *Chapter 3*, for which I studied the distribution of locations where wolves kill moose. Kill locations regressed against a spatial index of moose abundance revealed that a higher proportion of moose were killed as the distance to mines decreased. I speculated that two effects drive this relationship. Firstly, when a new development removes a portion of a wolf pack's territory, they maintain the shape of their territory as much as possible, i.e. they do not move away, forcing them to spend more time near mine edges. Moose in these areas will therefore be subject to increased predation pressure. Secondly, the edge of the mines present a barrier that both provides coursing predators like wolves with a means to increase encounters with prey and reduces moose options for escape (Husseman et al. 2003, Davies-Mostert et al. 2013).

In the final two chapters, I investigated wolf and moose behaviour to assess how the mines may disrupt their spatial relationship beyond simply shifting the areas over which each occurs. Wolves are a coursing predator that uses long distance movements to both encounter and chase down prey (Mech and Boitani 2010, Vander Vennen et al. 2016). Therefore, any relationship between mines and wolf movement has the potential to shift predation rates of wolf prey. *Chapter 4* examined whether proximity to oil sands mines and associated features alter where and how wolves move. Corroborating previous work (Dickie et al. 2017), I found that wolves select to move on linear features associated with oil extraction and such selection facilitates faster movement. In addition, wolves selected to move farther away from human habitation and oil sands facilities, but only during the day. By comparing these movement locations to where wolves kill ungulate prey, I demonstrated that whereas wolf movement changed in relation to some oil sands features, the distribution of kills did not match this change. Wolf selection or avoidance of the human features they to move did not alter their kill rate. No relationship between movement and distance to the mines themselves was detected, suggesting that the increased predation rates near mines observed in *Chapter 3* are simply due to increased use of those areas.

Finally, by estimating moose selection for both natural and home features as a function of the intensity of use of wolves across AOSR, I investigated how moose respond to predation and whether human features may provide moose with advantages for escape in *Chapter 5*. Moose cows, particularly those with calves, did alter their behaviour both within and between individuals as a function of the local intensity of use by wolves, but only with respect to natural features. Rivers and streams, features wolves selected for hunting, were avoided in areas with more wolf use.

In general, this thesis demonstrates that there is only a marginal zone of influence around the footprint of oil sands mines with respect to wolf-moose spatial dynamics. The habitat at the mine boundaries appears to be of equal quality of that farther away from mines for both species. Wolves and moose use areas near the mine boundaries and only with careful analysis of selection differences, movement and the distribution of kills, were any effects concerning how wolves and moose overlap found. I conclude that the mines themselves do not generate refugia for moose and marginal advantages for wolves while hunting in proximity to mine boundaries.

Management Implications and Recommendations for Future Research

Predation by wolves limits moose population size (Messier and Crête 1985, Boutin 1992, Hayes et al. 2000) but there is debate as to whether wolf predation can regulate moose populations (Messier and Crête 1984, Boutin 1992, Ballenberghe and Ballard 1994). Regulation through predation occurs when the proportion of prey killed is a function of prey density (Sinclair 1989, Messier 1991). Density dependent predation is due to the relationship between prey density and both predator behaviour (the per predator kill rate or functional response) and number of predators (the numerical response) (Solomon 1949, Holling 1959, Messier 1994). After examining wolf predation rates of moose across several moose densities, Messier (Messier 1994) concluded that wolf predation of moose is regulator at low moose density ($<0.65/km^2$) due to both a functional and numerical response. Moose densities range between 0.04 and 0.15/km2 in the AOSR (Morgan and Powell 2008, 2009, 2010, Sustainable Resource Development 2013), indicating that the predation should respond quickly to changes in moose density.

In *Chapter 3*, I observed that the reduced space within wolf pack territories and hard boundaries produced by oil sands mines facilitated increased predation rates of moose AOSR. This is a form of aggregative response, in which predator densities changed spatially not temporally (Holling 1959, Decesare 2012) in response to prey density. I demonstrated that the oil sands footprint allow an aggregative response from wolves such that wolves are killing more moose in areas of relatively high moose density near mines. Such a response could both facilitate wolf population growth and down-regulate moose populations. However, in chapters 2 and 4, I show that this response is due to wolf selection for mine edges, which increases the amount of time wolves spend near mines, not increased kill rates near mines. Therefore, moose farther from mines may be experiencing less exposure to wolves such that over the entire study area there is no change in the absolute predation rate.

Before making recommendations for mitigating the effects of mines observed in this thesis, several follow-up questions require answers.

1. Have the increased predation rates near mines observed in this thesis lead to an increased proportion of moose killed across the entire oil sands region? A GPS collaring program that follows a subset of moose until they die would allow cause specific mortality to be estimated. The GPS data collected by WHEC only followed moose cows for a maximum of three years and only 7 mortalities out of 50 collared individuals were observed. A mortality study would provide insight onto how often moose mortality is caused by wolves.
2. Are the edges of mines the mechanism causing the increased predation rates? The study in number 1 (above) would illustrate the proximity of wolf caused moose mortalities to the mine edges, allowing inference concerning how wolves are killing more moose near mines.
3. What is the effect of alternative prey sources on wolf predation rates of moose? If moose population is reduced due to increased predation pressure from wolves, wolves are expected to respond numerically with decreased abundance, through regulatory feedback. However, with additional prey in the system, this may not occur due to prey switching (Murdoch 1969). White-tailed deer are an alternative prey for wolves in the AOSR (Chapter 3) and they are increasing in the Athabasca oil sands region (Latham et al. 2011c, Dawe and Boutin 2016). Wolf and moose populations should be monitored as deer increase in the AOSR to determine whether deer can supplement wolves allowing increased predation pressure on moose, irrespective of moose density (Serrouya et al. 2015).

The above research could be conducted by monitoring the moose-wolf-deer system in the AOSR with remote cameras and GPS collars deployed at regular intervals. Such a study would provide demographic, behavioural and population data. Once the proceeding questions are answered, two avenues of interventions could be considered. Firstly, if wolf predations rates of moose are sensitive to the presence of barriers such as mine edges, oil sands mines should be developed to minimize the edge to area ratio (Davies-Mostert et al. 2013). However, considerations of cost may make such interventions unfeasible. Secondly, human hunting of moose in the AOSR could be curtailed and hunting of white-tailed deer increased, if moose densities become unsustainable.

In Chapter 2, I provided evidence that wolves in the AOSR selected territories near rivers and that areas isolated from rivers. Because the bitumen deposits are most easily accessed near rivers in the AOSR, I recommend that future mining develops maintain undisturbed areas near rivers large enough to accommodate access and occupancy of wolf pack territories, which average 648 km^2 ($\pm$ 60 km^2, SE). Despite the large mining footprint in the area, the majority of river access remains, but as developments move forward, it is important to consider wolf use of rivers.

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