# IMPACTS OF INDUSTRIAL DEVELOPMENTS ON THE DISTRIBUTION AND MOVEMENT ECOLOGY OF WOLVES (Canis lupus) AND WOODLAND CARIBOU (Rangifer tarandus caribou) IN THE SOUTH PEACE REGION OF BRITISH COLUMBIA

by

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# THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE IN NATURAL RESOURCES AND ENVIRONMENTAL STUDIES (BIOLOGY)

UNIVERSITY OF NORTHERN BRITISH COLUMBIA

April 2012

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#### Abstract

Habitat alterations from anthropogenic disturbances across northeastern British Columbia have resulted in large-scale modifications to predator-prey dynamics. I used GPS collar locations and field data to quantify the responses of wolves (*Canis lupus*) and woodland caribou (*Rangifer tarandus caribou*) to the cumulative effects of industrial disturbance. I developed seasonal resource selection functions for caribou and count models of habitat occupancy for wolves. I also related wolf movements to caribou habitat and industrial features. Caribou occupying the boreal forest likely are more at risk from industrial developments. My results suggest that caribou occupying these ecosystems are subject to disturbance by human activity and a greater risk of spatial interactions with wolves. However, these relationships are complicated by the positive and negative responses of wolves to landscape change and the distribution of other prey and predator species.

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#### Acknowledgements

The completion of this project would not have been possible without the considerable help and support from multiple organizations and people along the way. The Habitat Conservation Trust Foundation (HCTF), Canadian Association of Petroleum Producers (CAPP), the BC Ministry of Forests, Lands and Natural Resource Operations, UNBC, West Fraser Timber Company Ltd., Peace River Coal Ltd., and Western Coal (now under Walter Energy, Inc.) provided funding for this project.

I thank Dr. Chris Johnson first and foremost, for his confidence, friendship, guidance, patience, and constant unselfishness that will continue to guide my professional and personal life. Chris inspired, heightened, and broadened my appreciation and application of conservation ecology, writing, statistics and academics, all while demonstrating a passion for loving what you do and the importance of balancing everything in life. I am grateful for the opportunity to have been a part of his research group and to have learned from such a talented conservationist. In addition, my advisory committee members, Dr. Dale Seip and Dr. Kathy Parker, provided me with constructive comments and advice throughout the duration of my degree. Dale's expertise on caribou ecology was supreme, as well as his ability to search for and secure funding to make this project possible. I also thank Dale for opportunities to go to Kennedy Siding and re-connect with caribou after long hours on the computer. Kathy Parker's office was always open; her warmth, expert advice, friendship and remarkable teaching ability will always be remembered and appreciated (not to mention our many discussions focused on our mutual love for Jasper and introducing me to the best cinnamon rolls ever).

I am very fortunate to have experienced caribou and wolf capture and handling with a truly special and highly respectful trio. Brad and Diane Culling's passion, trust, organization, courteous and meticulous capture and handling skills, wit, positive energy and coaching were impressive during our times in the field. I am grateful for their friendship and ability to treat me like family during visits to FSJ; their zealous commitment to conservation is contagious and our winter field days together in the South Peace will never be forgotten. Greg Altoft's exceptional piloting skills are unsurpassed. Greg's excitement for wildlife and the places outside our backyard of Prince George were infectious and I always felt safe flying into the Rockies and into often challenging (in my mind at least) landing spots. Thank you Greg for going out of your way to help with personal endeavours, including helping Nick plan one of the most memorable experiences in our lives; we are happy to share so many fond memories with you.

The UNBC chapter of The Wildlife Society welcomed my background and provided me with the opportunity to stay involved and excited about the field of wildlife outside my thesis. Members of the executive board (2010 - 2011) were great to work with and made my involvement in the chapter meaningful. Ping Bai, Scott Emmons, and Roger Wheate endured my challenges and accommodated my struggles along the way pertaining to GIS. Doug

Heard (BC Ministry of Environment), Brian Pate (West Fraser Timber Co.) and Mark Sharrington (Shell) were willing and eager to help answer any questions I threw their way. I also want to thank Dr. Mike Gillingham and Elena Jones for their willingness to help me with statistics and data management.

To the many wonderful people on campus that made my personal life at UNBC and around Prince George fun, entertaining and rewarding, I will always be thankful. The Committee of Life (COL) on campus kept life exciting beyond the office and provided hours of laughter, adventure and knowledge of Canadian culture. The memories of sushi nights, curling, coffee hours, backcountry cabins, potlucks, brewing beer, winter fires, floating the Nechako, wasting time, playing music and living life to its fullest with great friends in PG will last a lifetime! Leslie Witter, my only lab mate, made our windowless lab bright by filling it with talk about the amazing-ness of caribou and the north, a great cup (ok, lots of pots) of coffee, the love of the trails in the Forest for the World and keeping the Bread Guy in business together; I'm excited for our friendship and adventures to continue. I also thank all my fellow graduate friends who helped provide great care for my best friends during times I was called into the field. Furthermore, I want to thank the Yellowstone Wolf Project for being such a dedicated, strong and respectable organization that provided me with the handson research and observational experience I needed to be competitive for this project. A special thank you goes out to one YWP friend and colleague in particular, who was largely responsible for saving my life, that fine July day back in 2007; cheers to all our miles, memories and conversations in the backcountry of one of the greatest places on Earth.

I thank my incredible posse of fur balls for walking into my life; Koya, Tiger, and Takla. Thank you for your continued ability to make me laugh, your constant reminders that snuggle and play sessions, walks, jogs, hikes, swims and skis are a far superior alternative to working and your lifelong dedication to teaching me about the unparalleled bonds shared between humans and animals. You all make my world a happy place everyday.

For their extraordinary support, I share this success with my parents (Stan and Catharine Williamson), my sisters (Sarah and Kate) and their husbands and families (Russ, Sadie, James, and Dave, Elle and Sydney). I thank my parents for encouraging me that anything and everything is possible and for instilling in me an enormous appreciation for music, nature, travel and beautiful places rooted at an early age from a life full of visits to our beautiful cabin in northern Minnesota (in addition to many other places around the world).

My most heartfelt and sincere thank you goes out to my partner in life, Nick. I could not have completed this project without his support, humour, understanding, patience, and undivided love at the end of each day (not to mention his excitement to move to Canada). Nick was the most paramount and knowledgeable field assistant I could have asked for and made exploring the backcountry of the South Peace region and our time living in Prince George, truly unique and unforgettable. I very much look forward to sharing our life and our love of adventures, wild places, family, friends, education, good food, travelling, and creatures big and small, for all our years to come. ¡La salud y el amor a mi alma gemela! Chapter 1: General Research Introduction

Woodland caribou (*Rangifer tarandus caribou*) populations across North America have declined since European advancement and colonization (Bergerud 1974). In some locations, caribou range has contracted northward by roughly 35 km each decade since the late 1880s (Edmonds 1991, Schaefer 2003, Hummel and Ray 2008). Woodland caribou now receive considerable conservation attention across the western provinces, and throughout much of boreal Canada. Habitat alteration and disturbance resulting from human developments and predation, as an indirect effect of development activities, are thought to contribute to the cross-continent decline of this *Rangifer* subspecies (Fuller and Keith 1981, James et al. 2004, Johnson et al. 2004a, Weclaw and Hudson 2004, Wittmer et al. 2007, St-Laurent et al. 2009, Vors and Boyce 2009, DeCesare et al. 2010, Festa-Bianchet et al. 2011, Hebblewhite 2011, Latham et al. 2011a, b). Anthropogenic disturbances are widespread across portions of eastern British Columbia (BC) and caribou herds in these regions are listed as threatened under the federal Species at Risk Act (SARA; Festa-Bianchet et al. 2011).

In BC, biologists and resource managers recognize three ecotypes of woodland caribou: mountain, northern and boreal (Heard and Vagt 1998). Mountain caribou range across forests in subalpine and alpine habitats in the central and southeastern portions of the province. During winter, these caribou forage on abundant arboreal lichens (*Bryoria* spp. and *Alectoria sarmentosa*) as deep snow restricts access to terrestrial lichens or vascular plants (Stevenson and Hatler 1985, Jones et al. 2007). For these caribou, moving to higher elevations in winter is an effective strategy for accessing forage and avoiding predators (Seip 1991, Seip and Cichowski 1996).

Caribou of the northern ecotype are found in mountainous and valley habitats throughout central and northern BC. Northern caribou have highly variable wintering

strategies between years, populations and individuals; some caribou winter on high, windswept alpine ridges, while others winter in lower-elevation pine-lichen forests (Bergerud 1978, Terry and Wood 1999, Johnson et al. 2002b). During winter, these caribou forage on terrestrial lichens (*Cladina mitis, Cetraria* spp. and *Cladonia* spp.) that are found in pine forests or wind-swept alpine habitats (Heard and Vagt 1998, Johnson et al. 2004a, Jones et al. 2007). Depending on snow conditions, northern caribou also forage on arboreal lichens (*Bryoria* spp.) during the winter months (Johnson et al. 2004a).

The boreal ecotype of caribou is found in the northeastern portion of the province and prefers black spruce (*Picea mariana*) fen/bog complexes, and tends to avoid well-drained areas (Bradshaw et al. 1995, Stuart-Smith et al. 1997, Rettie and Messier 2000, Dzus 2001, Culling et al. 2006). A lack of topographic relief prevents boreal caribou from making elevational migrations as demonstrated by the mountain and northern ecotypes (Stuart-Smith et al. 1997, Culling et al. 2006). Ground lichens (*C. stellaris, C. mitis* and *C. rangiferina*) are the dominant food source in winter (Bradshaw et al. 1995). Boreal caribou now occupy less than half of their historical range across the continent (Schaefer 2003).

Gray wolves (*Canis lupus*) once ranged throughout the northern hemisphere at latitudes north of  $15^{\circ} - 20^{\circ}$ N (Young and Goldman 1944, Nowak 1983, Mech and Boitani 2003, Paquet and Carbyn 2003). An increasing human population and the expansion and advancement of agriculture in the late 1800s served as the catalyst for the general decline of the gray wolf in North America. During that time, increased harvest of ungulates also contributed to reductions in the distribution of wolf populations (Paquet and Carbyn 2003). In addition, predator control was implemented in the early 1900s, which led to wolf eradication and extirpation from the western United States and neighbouring locations in

Canada (Paquet and Carbyn 2003). In southwestern Canada, wolves increased in number between 1930 and 1950 as they responded to relaxed predator control programs and more restrictive regulations for big game hunting which led to an expansion of ungulate populations (Nowak 1983, Gunson 1995).

Recent studies in BC and Alberta have demonstrated that roads, trails, geophysical exploration lines, pipelines, electrical right-of-ways, cutblocks and oil and gas wells can alter the movements, distributions and population dynamics of both caribou and wolves. Timber harvesting is one of the primary agents of habitat change. Large-scale harvesting reduces the amount of habitat for caribou and increases the area of early-succession forests favoured by moose and other ungulate species (Fuller and Keith 1981, Rempel et al. 1997, Schaefer 2003, Johnson et al 2004a, Nitschke 2008). Linear features have resulted in negative impacts for caribou, including increased human hunting, vehicle collisions, habitat reduction and predation from enhanced encounter opportunities (Thurber et al. 1994, James and Stuart-Smith 2000, Dyer et al. 2002, Latham et al. 2011c). Linear features have the ability to change predator-prey dynamics by creating efficient travel routes for wolves and increasing access to habitats used by caribou (Dyer et al. 2002, McCutchen 2007, Rinaldi 2010).

Landscape change and an increase in the abundance of other ungulate species now limit the ability of caribou to effectively space-away from predators such as the wolf (Rempel et al. 1997, Wittmer 2004, Latham 2009). Since the early 1900s, moose (*Alces alces*) have expanded their distribution throughout BC resulting in a numerical and distributional response by wolves (Bergerud and Elliot 1986, Spalding 1990, Seip 1992). Known as "apparent competition", deer and moose do not compete directly with caribou for forage or space, but support larger numbers of wolves that prey on caribou opportunistically

(Holt 1977, DeCesare et al. 2010). Apparent competition is an important limiting factor for many populations of woodland caribou in BC (Seip 1992, Hatter et al. 2002, Wittmer et al. 2005).

To conserve declining populations and manage the predators that historically coexisted with caribou, land-use planners, biologists, and resource managers require information that reveals how landscape change influences predator-prey dynamics. Such information is essential in the South Peace region where there are increasing rates of development for timber and coal reserves, natural gas deposits and wind energy. In addition, there have been few studies of woodland caribou or gray wolves across that region. My study investigated both the spatial dynamics and movement ecology of wolves in relation to caribou and the presence and density of industrial developments. I focused my research on two broad themes. First, I investigated the spatial co-occurrence of collared wolves and caribou relative to habitat and disturbance factors. Second, I explored how wolves used industrial features and disturbances when moving across the South Peace landscape. In the context of those themes, I addressed two specific study objectives:

- to quantify seasonal selection or avoidance of habitat and disturbance features for two herds of woodland caribou using resource selection functions (RSFs) and four packs of wolves using a count model based on biological sampling units, and
- 2) to quantify movement parameters for wolves as they relate to a) cumulative effects from human-caused disturbances at two scales, and b) the inferred distribution of caribou.

### Organization of Thesis

I organized the thesis as two separate chapters to be submitted for journal publication, followed by a final chapter summarizing the implications of my study findings. The portion of my research that addressed resource selection by caribou and spatial dynamics of wolves across landscapes modified by human-caused developments (Objective 1) is presented in Chapter 2. In Chapter 3, I present methods and results that relate the presence and density of industrial features and caribou habitat to seasonal movement behaviours of wolves. For those analyses, movement behaviour is represented by the rate and sinuosity of the movement paths of monitored wolves (Objective 2). In the final chapter (Chapter 4), I summarize findings and present the implications of my research for the conservation of woodland caribou in the context of wolf distribution, predation behaviour, and development practices across the South Peace region of northeastern BC.

#### Study Area

The study area is located on the eastern slopes of the Rocky Mountains and encompasses approximately 12,000 km<sup>2</sup> (Figure 1). Tumbler Ridge is located near the center of the study area, which then extends northwest towards the town of Mackenzie, northeast towards Dawson Creek and south along the Alberta border. Four Biogeoclimatic Ecosystem Classification (BEC) zones occur within that area (Sopuck 1985, Meidinger and Pojar 1991). The Boreal White and Black Spruce (BWBS) zone is found at elevations ranging between 230 – 1300 m, with the majority of the BWBS occurring above 600 m (DeLong et al. 1991). Air masses from the Arctic occur in frequent bursts, accounting for long, cold winters.



Figure 1. Locations from GPS collared wolves (symbols) and minimum convex polygons (95% MCPs) for woodland caribou representing their current distribution across the South Peace region of northeastern British Columbia. Distribution of caribou includes all locations from members of the Quintette (n = 22) and Bearhole/Redwillow (BHRW; n = 5) herds collected between April 2003 and August 2009. Wolf distribution includes all locations collected from wolves in five packs (n = 16) between December 2007 and March 2010.

In the southern range of the BWBS zone, annual precipitation averages between 330 – 570 mm; snowfall accounts for approximately 45% of the annual total (DeLong et al. 1991). Prominent tree species within the BWBS include lodgepole pine (*Pinus contorta*), black spruce (*Picea mariana*), white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*) and cottonwood (*Populus balsamifera*). Fire disturbance occurs frequently in the BWBS and therefore, these forests are characterized by a range of age classes (DeLong et al. 1991).

The Sub-Boreal Spruce (SBS) zone is found throughout the low-elevation valley bottoms and extends upwards into areas 1200 m in elevation (Meidinger et al. 1991). The SBS zone receives 600 – 1000 mm of annual precipitation, where 35% falls as snow (Meidinger et al. 1991). Dominant tree species include subalpine fir (*Abies lasiocarpa*), hybrid white spruce (*P. engelmannii* x glauca), lodgepole pine, trembling aspen, paper birch (*Betula papyrifera*) and Douglas-fir (*Pseudotsuga menziesii*; Meidinger et al. 1991).

The Engelmann Spruce-Subalpine Fir (ESSF) zone occurs across mountainous areas with elevations between 900 – 1700 m (Coupé et al. 1991). Prominent tree species include Engelmann spruce (*Picea engelmannii*) and subalpine fir; as elevation increases, the ESSF transitions into the Alpine Tundra (AT) zone. At this junction, the ESSF forests become more open and are characterised by stunted subalpine fir intermixed with alpine meadow. Because of a lower fire frequency at higher elevations within the ESSF zone, older age classes of forest prevail (Coupé et al. 1991).

The AT zone is usually treeless and occurs above the ESSF. Prominent vegetation includes ground lichens, sedges, mosses, grasses, dwarf shrubs and forbs (Pojar and Stewart 1991). The AT generally occurs at elevations above 2250 m in the southeastern portion of the province and receives 700 - 3000 mm of precipitation annually, which mostly (70 - 80%)

falls in the form of snow (Pojar and Stewart 1991). Despite the heavy amounts of snowfall, wind blows snow off alpine ridgelines leading to high variability in snow depth.

#### Woodland Caribou and Wolf Location Data

The analyses I developed for this study were dependent on location data collected from individual woodland caribou and wolves. I collected GPS location data from caribou located in the Quintette and Bearhole/Redwillow (BHRW) herds. The Quintette herd is found at higher elevations to the west of the boreal forest and winters primarily on windswept ridgelines in the alpine (Figure 2). Seip and Jones (2011) classified the population as 'increasing' due to low adult mortality (9%) and high calf recruitment (20%). The Quintette herd of caribou is estimated at 173 – 218 individuals (Seip and Jones 2011).

The BHRW herd remains in the low-elevation boreal forests during winter (Figure 3). From this point forward, I use the term "boreal" to broadly refer to the portion of lowelevation habitat occupied by caribou in the BHRW herd (although located on the same latitude, this landscape lies just beyond the western edge boundary classified as the boreal zone and is therefore, classified as hemiboreal; Brandt 2009). Seasonal movements of caribou in the BHRW herd into the western and southwestern mountains suggest that seasonally, some caribou may use mountainous habitats typically associated with the Quintette herd (Figure 3, Appendix A). Unlike the Quintette herd, the BHRW herd is classified as 'declining' due to high adult mortality (25%) and a low level of calf recruitment (10%); in 2008, the BHRW population was estimated at a minimum of 49 individuals (Seip and Jones 2011).



Figure 2. Seasonal distribution of Quintette caribou (2003 – 2009) across the South Peace region of northeastern British Columbia.



Figure 3. Seasonal distribution of Bearhole/Redwillow (BHRW) caribou (2007 – 2009) across the South Peace region of northeastern British Columbia.

I collected location and kill-site data from individual wolves within five packs (Figure 1). The Lower Sukunka pack does not have territory overlap with caribou in either study herd, whereas the Upper Sukunka pack resides further southeast and has a territory that coincides with the annual range of the Quintette caribou herd (e.g., Figure 4, Appendix A). The distribution of the Upper Murray and Onion Creek packs overlaps with habitats used by both Quintette and BHRW caribou (Appendix A). The range of the Chain Lakes pack overlaps completely with caribou in the BHRW herd (Appendix A). The BHRW and Quintette herds of caribou, in addition to each pack of wolves across the study area, are exposed to various levels of disturbance resulting from logging, mining, extensive oil and gas (and currently wind) exploration and extraction.

### Anthropogenic Disturbances in the South Peace Region of British Columbia

Since the early 1990s, eastern BC and western Alberta have experienced rapid landuse change from resource extraction activities, such as the exploration and development of oil and gas reserves, in addition to large-scale commercial forestry, agriculture, mining, and most recently, wind power (Sopuck 1985, Schneider et al. 2003). The cumulative effects from these activities have produced forested landscapes that are progressively younger and increasingly fragmented (Schneider et al. 2003). Nitschke (2008) reported that resource development accounted for an 89% increase in edge habitats, a 67% increase in areas containing habitats of early seral stages, and a 47% increase in the amount of open landscapes.

The Tumbler Ridge area has served as the center of the expanding energy sector in central BC.



Figure 4. Distribution of Quintette caribou (2003 - 2009) and three packs of wolves (Upper Sukunka, Upper Murray and Onion Creek; 2008 - 2009) during the spring season (April 1 – May 14) across the South Peace region of northeastern British Columbia.

In August 2009, an Oil and Gas stimulus package was established by the provincial government to boost the economy, make the oil and gas industry more competitive, and attract new investors (Proulx 2010). Included in the stimulus package was a \$50 million allotment to invest in the development of affiliated infrastructure (i.e., roads and pipelines). During 2009, there were new applications granted for 71 well sites, 63 pipelines, and 5 seismic lines located within 100 km of Tumbler Ridge (Proulx 2010).

Two open-pit coal mines that specialize in the extraction of metallurgical (coking) coal are found within the core winter range of the Quintette caribou herd. The Wolverine mine has extracted approximately 2 million tons of coal annually since beginning production in 2005. A proposed expansion would include the EB and Herman mines (2013) and is in the early stages of development. The Trend mine began extracting coal in December of 2005 and is estimated to produce up to 2 million tons of coal annually through 2015. The Roman mine (2013), an expansion project adjacent to Trend, would be located just to the south of the existing facility and would more than double annual production of coal between the two facilities. In addition, Teck Resources began a feasibility study in the fall of 2010 for the reopening of the Quintette coal mine, a mine that has been dormant since 2000. If approved, the Quintette mine would be in full operation by 2013, producing up to 3 million tons of coal per year. As of January of 2011, excavation processes had already begun in alpine areas that provide core winter habitat for populations of caribou in the Quintette herd (B. Culling, *personal communication*).

The development of wind energy is increasing across the South Peace region. As of February 2010, tenures in the form of Investigative Use Permits (IUPs) were granted for most ridgelines and mountain tops within an 85-km radius of Tumbler Ridge. Seven wind

projects, totalling more than \$3 billion worth of investment, are currently approved or undergoing approval processes for initial phases of construction that would begin as early as 2012 (Finevara Wind Energy Inc., Capital Power Corp.). Although facilities related to wind extraction were not included in my analyses, the ridgeline locations and associated road networks required for the construction of wind turbines can include habitat for caribou and should be recognized when considering the cumulative effects of future developments.

Large-scale forest harvesting has occurred in this region since the early 1970s (B. Pate, *personal communication*). In 2010, the provincial government awarded Tumbler Ridge a Community Forest Agreement. This 25-year agreement allows for an annual harvest of 20,000 m<sup>3</sup> of timber. Initial stages of planning are also underway to construct a manufacturing facility for wood pellets. Once built, 600,000 m<sup>3</sup> of wood biomass will be required annually to supply this facility (Proulx 2010). Across the South Peace region, forestry companies operate at 100% capacity during the winter (Nov. 15 ~ April 7, West Fraser Timber Co., *personal communication*).

Cumulative impacts related to activities associated with human development result in negative consequences for populations of wildlife (Johnson et al. 2005, Wärnbäck and Hilding-Rydevik 2009, Johnson and St-Laurent 2011). Large-scale exploration and development of natural resources can lead to compounding instabilities for populations of caribou: displacement from portions of their range, increased movement and vigilance, and altered predator-prey dynamics (Bradshaw et al. 1997, Nellemann and Cameron 1998, Cameron et al. 2005, Faille et al. 2010, Latham et al. 2011a). Furthermore, these relationships are complex and may be confounded by ecological sinks, non-linear responses to certain feature types and time-lag effects.

Chapter 2: Effects of Anthropogenic Landscape Change on Wolf (*Canis lupis*) and Woodland Caribou (*Rangifer tarandus caribou*) Distribution

## Introduction

Understanding the distribution of organisms is fundamental to conservation. Where the dynamics between predators and their prey are altered by industrial development, a better understanding of the changing distribution of populations through space and time can provide guidance for recovery and conservation efforts (Johnson and St-Laurent 2011). In general, predators orient themselves to areas where there are greater densities of prey, whereas prey avoid areas with increased predation risk while attempting to meet nutritional requirements (Sih 1984, Lima and Dill 1990, Rettie and Messier 2000). Industrial development can influence that relationship. Loss of contiguous habitat, disturbance, and the generation of linear corridors can alter the density and distribution of both species. For example, the alteration of habitats resulting from human developments can change the quantity and quality of vegetation and force prey to concentrate in space facilitating predation (Dzus 2001, Schlaepfer et al. 2002). Also increasing rates of predation, linear corridors can seasonally increase the movement potential of predators that interact with low-density prey populations (Bergerud et al. 1984, Jalkotzy et al. 1997, James and Stuart-Smith 2000, McKenzie 2006, Latham et al. 2011c).

Changing patterns of land use over the past 100 years have altered the relationships among wolves, woodland caribou and other prey species. Wolves, a generalist species, now serve as a primary predator of caribou (Bergerud and Elliot 1986, Seip 1992). Regenerating forests resulting from human developments favour higher densities of moose, elk, and deer. This alteration in landscape composition facilitates a broader distribution of wolves and increasing opportunities to use caribou as an alternate prey species (Fuller and Keith 1981, James et al. 2004, Johnson et al. 2004a, Wittmer et al. 2007, DeCesare et al. 2010).

Contributing to this dynamic, large-scale resource exploration and extraction can result in a variety of linear features that occur as narrow paths of early-successional vegetation communities. These features can increase the vagility of wolves and provide greater access into the habitats of caribou otherwise isolated by topography or vegetation (James and Stuart-Smith 2000, McCutchen 2007, Rinaldi 2010, Latham et al. 2011c).

Variation in resource selection by caribou within seasons and across spatial scale may be a behavioural strategy to decrease predictability to predators (Gustine et al. 2006b). Rettie and Messier (2000) discussed the behavioural and distributional implications of predation and hypothesised that caribou should respond to the most important limiting factor at the scale of the landscape and to less important factors at progressively smaller spatial scales. In the case of caribou populations limited by predators (Bergerud and Elliot 1986, Seip 1991, Wittmer et al. 2005, Latham et al. 2011b), this would involve selecting large areas with a relatively lower risk of predation. Past research across BC and western Alberta has shown that woodland caribou demonstrate variable distribution strategies across seasons and years. For example, caribou of the same population will winter on high, windswept alpine ridges, while others will winter in lower-elevation pine-lichen forests (Cichowski 1993, Terry and Wood 1999, Johnson et al. 2004a, Jones et al. 2007). Johnson et al. (2002b) suggested that at the patch scale forage was a more important factor than predation risk. Gustine et al. (2006b) also found that only at larger spatial scales did caribou significantly increase their distance from wolves.

Similar to caribou, wolves have the ability to adapt to local conditions including spatial and temporal variation in prey availability (Mladenoff et al. 1999, Paquet and Carbyn 2003, Latham et al. 2011a). Wolf distribution does, however, depend on landscape

conditions characterized by low densities of humans and active roads. For example, Mladenoff et al. (1995) reported that areas occupied by wolves in the Northern Great Lakes region had a much lower density of roads when compared to areas not used by wolves. Packs selected forested habitats dominated by conifers on public land relative to areas with a higher density of agricultural development (Mladenoff et al. 1995). In Italy, Corsi et al. (1999) found wolves to be absent in areas supporting higher human and road densities and greater levels of cultivation. Consistent with previous studies, Whittington et al. (2005) also found that wolves in Alberta avoided areas of high road and trail density, but selected lowuse roads and trails as travel corridors.

Despite the vast number of studies linking wolf occurrence with road density and level of human use, there is still a need to better understand the behaviour and distribution of wolves in areas where cumulative anthropogenic disturbances might influence predator-prey dynamics (Nitschke 2008, Houle et al. 2010). Many studies of wolf movement have occurred in landscapes exposed to higher densities of and longer-term use by humans. Although a correlation exists between wolf occurrence and a low probability of encountering humans, this relationship may not hold true where industrial footprints are large and human densities remain low. Also, past studies that have considered wolf interactions with industrial development have considered only a few disturbance types, but not the cumulative effects of multiple types (but see Lesmerises et al. 2012). Considering the co-occurrence of caribou and wolves, there is uncertainty about the ability of caribou to adapt to predation risk in the context of landscape change that includes altered successional dynamics and an increase in the prevalence of linear corridors. There are unexplored relationships between cumulative industrial developments and the interacting responses of wolves and caribou.

My principal research goal was to better understand the distribution and interactions of wolves and caribou across a landscape with high levels of industrial development. I first developed resource selection functions (RSFs) to determine the seasonal distribution and habitat selection of two herds of northern woodland caribou. Then, I used count models to investigate not only selection, but also the frequency of wolf occurrence relative to disturbance features and caribou habitat. Detailed investigations of both caribou and wolf habitat ecology serve as a foundation for increasing our knowledge of the spatial and temporal relationships of these two species. Such insights may also apply to other species influenced by increasing human disturbances and apparent competition (Robinson et al. 2002, Kristan and Boarman 2003, Baldi et al. 2004, Bryant and Page 2005, Gibson et al. 2006). Understanding the spatial complexities of co-occurring populations can aid in conservation planning for the long-term persistence of threatened species.

### Methods

## Study Animals

#### Woodland Caribou

A total of 27 caribou within two herds (Bearhole/Redwillow (BHRW) = 5, Quintette = 22) were captured between February 2003 and March 2009 by net-gunning from a helicopter. Caribou were fitted with either Televilt (n = 4; Televilt, TVP Positioning AB, Bandygatan 2, SE-71134 Lindesberg, Sweden, Model: GPS-VHF remote download) or ATS (n = 21; Advanced Telemetry System, 470 First Ave. N., Box 398, Isanti, Minnesota, USA, Model: GPS Remote-Release Collar) GPS collars equipped with VHF transmitters and remote-release devices. Televilt GPS collars were programmed to take fixes every four hours and locations were downloaded remotely. All four Televilt GPS collars failed to function as programmed and, therefore, each dataset was incomplete; animals were recaptured and refitted with either a VHF (n = 1) or ATS GPS collar (n = 3). ATS collars were programmed to take location fixes every 20 hours up until 2005; collars programmed after April 2005 acquired fixes between two and six times daily. In addition, two female caribou were captured in the study area in 2007 and collared with Lotek ARGOS GPS collars (F900 and F901 of the BHRW herd; Lotek Inc., Newmarket, Ontario, Canada). Data acquired from each GPS collar were examined and screened for erroneous locations using a combination of methods (Appendix B; Moen et al. 1997, D'Eon et al. 2002, D'Eon and Delparte 2005).

Wolves

Between March 2007 and March 2010, a total of 31 wolves from five packs (Lower Sukunka, Upper Sukunka, Onion Creek, Upper Murray, and Chain Lakes) were captured using a tranquilizer dart (Pneu-Dart, Inc. 15223 Route 87 Highway, Williamsport, Pennsylvania USA, Model: 196 Projector) or net gun deployed from a helicopter. Each wolf was fitted with either a remotely downloadable GPS (n = 16, Lotek Inc., Newmarket, Ontario, Canada, model: GPS 4400S) or VHF (n = 15, Lotek) collar. GPS collars were equipped with VHF transmitters, as well as remote-release devices. Collars were programmed to take a location fix every three hours (n = 14; two collars were programmed for high-frequency intervals and collected a location every 20 min) and were remotely downloaded from a fixed-wing aircraft approximately bimonthly during routine tracking flights. Of the 31 collared wolves, data from 16 were specific to the study area and used for analysis. Similar to caribou, wolf data were screened and examined for erroneous locations (Appendix B).

## **Defining Seasons**

Drawing on variation in biology, snow conditions and movement patterns, Sopuck (1985) and Jones et al. (2007) identified biological seasons for four herds of caribou found adjacent to, or within my study area. I used this information to define four primary seasons June 14), summer/fall (June 15 – October 31), and winter (November 1 – March 31). Also, I used past research (Mech 1970, Fuller 1989, Ballard et al. 1991, Kreeger 2003, Mech and Boitani 2003, Packard 2003) to develop three biological seasons to model the response of wolves to their surroundings: non-winter (April 16 – October 14), early winter (October 15 – January 31) and late winter (February 1 -April 15). Non-winter months include the time when wolves become responsible for the raising and rearing of pups and therefore, centralize around dens or homesites (Mech 1970, Ballard et al. 1991). By mid-October, pups are approximately six-months old and have grown large enough to travel and keep up with the nomadic pack as they transition towards the winter months (Packard 2003). In North America, breeding season occurs between late January and early April, depending on latitude; this marks the transition into late winter (Kreeger 2003). Late winter extends until the wolves begin localizing around a den site between the months of March and May (Fuller 1989, Mech and Boitani 2003).

#### Distribution of Caribou: Resource Selection Functions

I used resource selection functions (RSFs) to quantify the spatial relationships between GPS-collared caribou and a number of variables that were hypothesized to influence caribou distribution. An RSF is any mathematical function that provides an estimate of resource use that is proportional to the true probability of use (Manly et al. 2002). Coefficients from RSFs represent selection for or avoidance of a resource (i.e., habitat or industrial features). Selection is assumed when an animal uses a resource out of proportion to the availability of that resource across some defined area (e.g., home range), or the distance to a disturbance feature is less for animal observations relative to a comparison set of random locations. I used GIS to apply RSF coefficients from the top-ranked models to the corresponding spatial data and produced maps representing the relative value (poor- to high-quality) of habitat, by season, across the range of the Quintette and BHRW caribou herds.

I used a conditional fixed-effects logistic regression to develop the RSFs (Compton et al. 2002, Manly et al. 2002). Instead of pooling used and available locations, a fixed-effects logistic regression considers the difference between each used location and the set of associated random locations. Pairing of used and random locations in space and time provides a more precise definition of resource availability relative to the seasonal and annual differences in the distribution of a monitored animal (Johnson et al. 2004b). RSFs estimated from this style of matched regression were appropriate for my study as caribou have large home ranges compared to their relocation intervals (Arthur et al. 1996, Compton et al. 2002, Duchesne et al. 2010). All regression analyses were conducted using STATA (version 9.2, StataCorp. 2007).

RSFs constructed using conditional logistic regression were dependent on a restricted spatial domain, representing a specific distance an animal could have travelled during a time period, for identifying resource availability. I used the programming interval between GPS locations to define that spatial domain. For this calculation, I centered a circular buffer on the preceding collar location for each individual study animal (Johnson et al. 2005). This circle had a radius equivalent to the 95<sup>th</sup> percentile movement distance for a period of 24
hours. Five comparison locations were then randomly selected from within this spatial and temporal buffer, defined as the availability radius.

Similar to Johnson et al. (2005), I assumed that caribou would not respond to a disturbance feature at excessively large distances. Thus, I used the conditional regression to statistically remove the responses of individual caribou locations that exceeded a set distance threshold to individual disturbance features. The threshold was exceeded when the nearest disturbance feature of a specific type (e.g., coal mine) was found outside the availability radius for that caribou location. This approach allowed me to model a matched sample of caribou and random locations based on the effects of habitat, while statistically removing effects of an ecologically implausible 'disturbance' (Johnson et al. 2005).

Caribou were monitored independently throughout the study, but I pooled GPS locations by herd for each season. Pooling locations forfeited my ability to detect variation in resource use among individuals. However, pooling locations allowed for a sufficient sample of relocations to build sets of complex seasonal models.

# Distribution of Wolves: Count Models

I used a statistical model based on counts to relate the number of wolf locations within a habitat selection unit (HSU) to covariates that represented environmental or industrial features that might explain the seasonal distribution of wolves. Count models contained two parts; similar to RSFs, the binary portion of the count model represented the probability of occurrence of wolves, while the count portion represented the relative frequency of use in areas occupied by wolves (Nielsen et al. 2005, Sawyer et al. 2006). Therefore, this technique had greater power, relative to the RSFs for caribou, to describe the differential use of resources by wolves (Nielsen et al. 2005). Where possible, I used zeroinflated count models to quantify the binary and count portions of the wolf location data. I used wolf behaviour (i.e., predation) to identify a square sampling unit, the HSU, to model the relative frequency of wolf locations relative to vegetation, selection value of caribou habitat as determined from the RSF analysis, and disturbance attributes. Each HSU was large enough to capture variation in wolf occurrence, as recorded using GPS collars (Sawyer et al. 2006).

I defined the spatial extent of the HSU as the average area occupied by wolves after killing and consuming what was assumed to be a large prey item (e.g., moose, deer, caribou; Figures 5, 6; Appendix C). During three summers (2008 - 2010), we investigated wolf kill sites identified from clusters of GPS collar locations distributed throughout each pack territory. Each cluster represented a grouping of GPS collar locations defined as two or more consecutive locations within 200 m of one another. To minimize search effort of non-kill sites (e.g., bed sites, etc.), we investigated clusters containing  $\geq$  four location fixes (four fixes = 12 hours of time) only. The area of use (AOU; ha) by collared wolves at each identified kill site was calculated as the minimum convex polygon (100% MCPs) of locations that occurred within a one-week time period surrounding the assumed date of kill (Figure 5). For each pack territory, the area of a HSU was calculated as the mean of all AOUs for collared wolves of that pack (e.g., Figure 6; Appendix C). Kills were identified for each collared wolf ( $\geq$  3 per pack) and throughout each pack territory (Appendix C).

Depending on the distribution of data, count models were premised on the Poisson or negative binomial distribution (Pielou 1969). I used a likelihood ratio test to check for overdispersion and determine if a Poisson (PRM) or negative binomial (NBRM) model was most appropriate.



Figure 5. Minimum convex polygons (100% MCP) representing the area of use (AOU) associated with each of 10 kill sites for members of the Chain Lakes wolf pack (2008 – 2010) in the South Peace region of northeastern British Columbia.



Figure 6. A grid map of habitat selection units (HSUs) developed from the average area of use (AOU) for collared members of the Chain Lakes wolf pack in the South Peace region of northeastern British Columbia. Sizes of HSU cells were determined as the average wolf(s) area of use (AOU) affiliated with kill sites identified throughout the territory.

Both the PRM and NBRM can under-estimate the occurrence of zero counts. Therefore, I used a Vuong Test (Vuong 1989) to determine if zero-inflated versions of each model (ZIP or ZINB) were appropriate. Because data collected from GPS collars were correlated in space and time, I used the robust option in Stata to adjust standard errors (SE) for an auto-correlated error structure.

### Resource and Human Disturbance Variables

Drawing from past research on wildlife-development interactions and observations of the study area, I identified a number of resource and human disturbance variables for modeling the responses of caribou and wolves to their environments (Table 1). For each seasonal RSF for caribou, I examined two categorical and multiple continuous variables: forest cover type (categorical), seral stage of forest (categorical), solar insolation, and distance to and density of disturbance features. Human disturbance variables were grouped by industry type as well as their ability to influence caribou and wolf behaviour across the landscape: roads, linear features (roads, seismic lines and pipelines combined), forestry (roads and cutblocks), open-pit operations for coal mining, oil and natural gas exploration and extraction (mine/oil/gas; non-linear open-pit coal mine footprints, well and facility pads  $\geq 1$  ha), and cumulative effects from development features (linear features, forestry, and mine/oil/gas combined).

I identified six variables that may be important predictors of seasonal wolf distribution. For each season, I analyzed count models that contained combinations of forest cover type (categorical), seral stage of forest (categorical), selection value of caribou habitat in pixel cells determined from the RSF analysis, and distance to and density of disturbance features. Table 1. Description of variables used to model habitat selection for both caribou and wolves

Variable	Description
Alpine	high elevation with few or no trees with primary cover being rock, snow, herbs,
	shrubs, bryoids and terrestrial lichens
Blk Spruce	black spruce (Picea mariana)
Fir	subalpine fir (Abies lasiocarpa)
HBS	herbs (forbs, graminoids), bryoids and shrubs
Other	specific to herd and season; combination of variables listed with too few
	occurrences to model
Pine	lodgepole pine (Pinus contorta) and whitebark pine (P. albicaulis)
Spruce	other spruce varieties: Picea spp., Engelmann (P. engelmannii), white (P. glauca),
	hybrid (P. engelmannii x glauca)
Tamarack	tamarack (Larix laricina)
Tree -	other non-listed broadleaf trees: aspen (Populus tremuloides), cottonwood (P.
Broadleaf	balsamifera) and birch (Betula papyrifera)
Tree - Other	other non-listed conifers, Douglas-fir (Pseudotsuga menziesii)
Upland Nveg	upland areas dominated by talus, rock, snow, tailing ponds, or no additional data
	for land cover
Water	lake, reservoir, river, stream or a non-spruce or tamarack dominated wetland
	(caribou only)
No Age Data	no data available to determine seral age of forest
Young	forest age $0 \le 40$ yrs
Growing	forest age $41 \le 80$ yrs
Mature	forest age $81 \le 120$ yrs
Old	forest age $\geq 121$ yrs
RSF_BHRW	RSF values for caribou in the Bearhole/Redwillow (BHRW) herd
RSF_Q	RSF values for caribou in the Quintette herd
Solar	measure of incoming solar radiation on a surface $(W/m^2)$
Insolation	
Road	distance to road (km)
Seismic Line	distance to seismic line (km)
Pipeline	distance to pipeline (km)
SeisPipln	distance to seismic line and/or pipeline combined (movement models only; km)
Cutblock	distance to forestry cutblock (km)
Mine	distance to coal mine footprint (km)
Oil and	distance to non-linear oil and gas well pad or facility pad $\geq 1$ hectare in size (km)
Natural Gas	
Water	distance to water (wolves only; km)

across the South Peace region of northeastern British Columbia.

I also tested the importance of water (proximity) as an additional predictor of wolf distribution.

Habitat variables – Forest cover type and seral stage were estimated using the provincial Vegetation Resource Inventory (VRI; BC Ministry of Forests and Range 2007a, b). I used existing knowledge of caribou ecology to consolidate categories of forest cover from the VRI into 11 new classes, based on the leading commercial or brush species (Table 1). Similar to forest cover, I categorized seral stage into five age classes based on regimes of fire disturbance for dominant species in each BEC zone and past research pertaining to habitat selection and behaviour of woodland caribou (Medinger and Pojar 1991, Table 1). Across my study area, VRI data were incomplete for a portion of alpine-type habitats. Therefore, I classified age in these 'no age data' habitats as late-succession forests (i.e., old). Categorical variables for forest cover and age class were modeled with deviation coding (Menard 2002). This method of coding takes individual variables and compares their deviations to the grand mean across all categories.

Solar insolation – Solar insolation (SI) represented the amount of radiation striking a surface. I used solar insolation in this study as a proxy of slope and aspect and therefore, as a potential indicator of forage availability and snow conditions for caribou. Snow melt and growth of vegetation can occur more rapidly in areas with increased radiation. In addition, alpine areas that experience higher levels of solar radiation could be indicative of windblown ridgelines that are often ideal habitats for northern woodland caribou in winter. I used a digital elevation model (DEM 25m x 25m; BC Land and Resource Data Warehouse 2007) to calculate seasonal averages of SI in watts per square meter ( $W/m^2$ ) across the South Peace region for each year caribou locations were collected (2003 – 2009). When mapping RSFs, I

used SI values from the most recent year (2009). I chose not to include elevation as a topographical variable; elevation can often correlate with habitats classified as alpine which further complicates results and model interpretation.

Disturbance features – I used databases from government and industry to identify the location of roads and forestry cutblocks (BC Land and Resource Data Warehouse 2007; West Fraser Timber Company). I did not classify roads by use or status. During the period of monitoring for caribou and wolves, the Wolverine and Trend coal mines were fully operational and spatial data were acquired directly from their parent corporations (Western Coal and Peace River Coal Ltd.). This variable representing mines was applied to caribou (Quintette herd) and wolves (Upper Sukunka, Upper Murray, and Onion Creek) that occurred within the vicinity of active coal mines. Lastly, I used the Oil and Gas Commission of BC's public database, complete through 2009, to identify the spatial locations of seismic lines, pipelines, well sites and other developed areas related to the exploration and development of oil and natural gas reserves across the South Peace (http://www.ogc.gov.bc.ca/GIS.asp, 2009).

I calculated the distance (km) from caribou and wolf locations to human disturbance features as well as the density of disturbance features (total area of features/unit area; linear features = ha/km, non-linear features = ha/km<sup>2</sup>) at each animal location using IDRISI (V 15.0, The Andes Edition; Eastman 2006). I used a standard moving-window algorithm to calculate the density of disturbance features. I fit RSF models to three sizes of moving windows (0.56 ha, 1.56 ha and 3.06 ha) and used Akaike's Information Criterion for small sample sizes (AIC<sub>c</sub>) and Akaike weights (AIC<sub>w</sub>; see *Model Selection and Validation* below

for more information) to identify the best-fitting moving window size for the analysis of habitat selection by caribou.

Modeling nonlinear responses – I used a Gaussian function to model the nonlinear responses (if applicable) of caribou or wolves to disturbance features. For each seasonal model, I used Akaike weights (*w*) to determine if a linear or Gaussian term was most appropriate. Where I observed a nonlinear relationship, I determined a threshold value using the point of inflection for each disturbance type or class. Values indicating disturbance thresholds for caribou need to be interpreted cautiously, as these thresholds may be unique to the South Peace study area, study animals, and/or my chosen method of analyses (e.g., logistic regression, size of availability radius, etc.). A variety of analytical tools are available to researchers to aid in the definition of an ecological threshold (e.g., Nielsen et al. 2009, Leblond et al. 2011), but there remains uncertainty surrounding the ability to correctly identify these points of change (Ficetola and Denoël 2009).

<u>Distribution of caribou habitat</u> – I multiplied coefficients from the most parsimonious RSF models by the corresponding GIS data layer to generate seasonal maps illustrating the most strongly selected habitats by collared caribou from the BHRW and Quintette herds. I used these maps to model the response of wolves to habitats of different value to caribou across the South Peace region.

Random point generation for count models – When constructing the count models for wolf location data, I systematically generated random points for each pack territory (e.g., Figure 7). I then extracted values for each point and took the median value across each HSU to quantify habitat class, RSF value of caribou habitat, and distance to or density of disturbance feature.



Figure 7. Individual habitat selection units (HSUs) for the Chain Lakes wolf pack. Random points were systematically generated for extracting habitat variables, selection value of caribou habitat and disturbance attributes across each territory for wolf packs in the South Peace region of northeastern British Columbia.

## Model Selection and Interpretation

I used Akaike's Information Criterion for small sample sizes (AIC<sub>c</sub>) and Akaike weights (AIC<sub>\*</sub>) to identify the most parsimonious model from a suite of ecologically plausible candidate models for both caribou and wolves (Anderson et al. 2000). I also used the delta ( $\Delta$ ) AIC<sub>c</sub> as a measure to compare each candidate to the top-ranked model (i.e., the model with the lowest AIC<sub>c</sub>; Burnham and Anderson 2002). I reported coefficients ( $\beta$ ) from the most parsimonious model and used 95% confidence intervals to illustrate the precision of each covariate. For covariates that fell close to or overlapped with 0, selection or avoidance of habitat or disturbance features could not be determined. I used tolerance scores to assess collinearity among variables (Menard 2002). Where tolerance scores were less than the threshold value of 0.2, I used bivariate correlation and visual inspection of standard errors to determine if there was a large effect on model inference. Where collinearity occurred between disturbance variables, I preferentially retained linear features to better understand how these disturbances might influence the distribution of caribou and wolves.

# Model Validation

I used k-fold cross validation to assess the capability of the most parsimonious RSF model to predict resource selection by caribou (Boyce et al. 2002). Here, I determined if there was a Spearman rank correlation ( $r_s$ ) between the predicted RSF values and the frequency of occurrence of animal locations (Boyce et al. 2002). I also examined the classification accuracy of top-ranked models by using the more conservative receiver operating characteristic (ROC) curve. Models demonstrating an area under the ROC curve (AUC) > 0.7 are thought to perform well, whereas a score of 1 represents perfect discrimination between used and available locations (Hosmer and Lemeshow 2000). I

generated independent k-fold and AUC scores by withholding approximately 20% of the animal locations from the model-building process.

For the count models for wolves, I randomly partitioned wolf locations into training (80%) and testing (20%) groups. Using the withheld data, I determined if there was a relationship between the observed probabilities of counts and the predicted probabilities of counts (prcounts.ado: Long and Freese 2006). As a second measure of model fit and prediction, I calculated the unstandardized residuals. Perfect prediction occurred when the mean residuals for a count class equaled zero, whereas positive values indicated under-prediction and negative values indicated over-prediction.

# Results

I used a total of 38,116 GPS collar locations from members of the Bearhole/Redwillow (BHRW: 12,297 locations) and Quintette (25,819 locations) caribou herds to develop 19 seasonal resource-selection models (Table 2). For all four seasons, the most parsimonious models for both BHRW and Quintette caribou were also the most complex in each candidate set and contained variables for all habitat and human-caused disturbances (Table 3). The predictive ability of the cumulative effects (CE) model for the BHRW herd ranged from a mean  $r_s$ = 0.820 in calving to  $r_s$ = 0.981 in winter (AUC = 0.737 and 0.725, respectively).

The most parsimonious model for BHRW in summer/fall demonstrated poor predictive ability using k-fold cross validation, but the more conservative ROC (AUC = 0.726) implied an acceptable level of discrimination. Table 2. Statistical models representing hypothesized resource selection strategies of northern woodland caribou and wolves monitored from 2003 – 2009 in the South Peace region of northeastern British Columbia. Variables for solar insolation, distance and density of human disturbances were modeled as either a linear or Gaussian (squared) term depending on best fit for each season.

Model name	Covariates included in model
Forest Cover	Forest cover type (alpine, black spruce, fir, HBS, pine,
	spruce, tamarack, broadleaf trees, other trees, upland non-
	vegetated, and water)
Forest Age	Forest age class $(0-4)$
Solar Insolation	Solar insolation (W/m <sup>2</sup> )
Landscape	Forest Cover + Forest Age + Solar Insolation
Road Distance (Dist; km)	Landscape + Dist to Road
Road Density (Dens; ha/km <sup>2</sup> )	Landscape + Road Dens
Road Dist and Dens	Landscape + Dist to Road + Road Dens
Linear Feature (LF) Dist	Landscape + Dist to LF (road, seismic line and/or pipeline)
Linear Feature (LF) Dens	Landscape + LF Dens
Linear Feature (LF) Dist and	Landscape + Dist to LF + LF Dens
Dens	-
Forestry (FOR) Dist	Landscape + Dist to Cutblock + Dist to Roads
Forestry (FOR) Dens	Landscape + Cutblock Dens + Road Dens
Forestry (FOR) Dist and Dens	Landscape + Dist to Cutblock + Dist to Roads + Cutblock
	Dens + Road Dens
Mine, Oil, and/or Natural Gas (MOG) Dist	Landscape + Dist to MOG + Dist to LF
Mine, Oil, and/or Natural Gas (MOG) Dens	Landscape + MOG Dens + LF Dens
Mine, Oil, and/or Natural Gas (MOG) Dist and Dens	Landscape + Dist to MOG + Dist to LF+ MOG Dens + LF Dens
Cumulative Effects (CE) Dist	Landscape + Dist to LF + Dist to Cutblock + Dist to MOG
Cumulative Effects (CE) Dens	Landscape + LF Dens + Cutblock Dens + MOG Dens
Cumulative Effects (CE) Dist and Dens	Landscape + Dist to LF + LF Dens + Dist to Cutblock + For Dens + Dist to MOG + MOG Dens

Table 3. Number of parameters (k), Akaike's Information Criterion values (AIC<sub>c</sub>), AIC<sub>c</sub> weights (AIC<sub>w</sub>), and  $\Delta$  AIC<sub>c</sub> values presented for two top-ranked seasonal resource selection models for members of the Bearhole/Redwillow (BHRW) and Quintette caribou herds monitored from 2003 – 2009 across the South Peace region of northeastern British Columbia. Sample size of caribou locations is presented in parentheses. Model covariates are given in Table 2.

BHRW	Spring (n = 3,401)			Calving (n = 2,200)				Sum/Fall (n = 8,669)				Winter (n = 11,625)				
Model Covariates	k	AIC <sub>c</sub>	ΔΑΙΟ	AIC <sub>w</sub>	k	AIC <sub>c</sub>	ΔΑΙϹ	AIC <sub>w</sub>	k	AIC <sub>c</sub>	ΔΑΙΟ	AIC <sub>w</sub>	k	AIC <sub>c</sub>	ΔΑΙΟ	AIC <sub>w</sub>
CE Dist <sup>b</sup>	26	3137.2	4.6	0.09	25	1854.6	3.5	0.15	27	7402.6	48.2	<0.001	32	10065.1	65.4	<0.001
CE Dist + CE	30	3132.5	0.0	0.91	27	1851.1	0.0	0.85	31	7354.4	0.0	1.00	34	9999.7	0.0	1.00
Dens <sup>b.c</sup>																
Quintette		Spring	(n = 9,7	91)		Calving	(n = 5,80	68)	Sum/Fall (n = 22,458)				Winter (n = 28,368)			
Model Covariates	k	AIC <sub>c</sub>	ΔAIC	AIC <sub>w</sub>	k	AIC <sub>c</sub>	ΔΑΙϹ	AIC <sub>w</sub>	k	AIC <sub>c</sub>	ΔΑΙϹ	AIC <sub>w</sub>	k	AIC <sub>c</sub>	ΔΑΙϹ	AIC <sub>w</sub>
CE Dist <sup>b</sup>	34	5466.2	10.6	<0.001	35	4102.0	6.3	0.04	30	15933.3	30.1	<0.001	34	19949.3	275.8	<0.001
CE Dist <sup>b</sup> CE Dist <sup>b</sup> + CE	34 37	5466.2 5455.5	10.6 0.0	<0.001 1.00	35 38	4102.0 4095.8	6.3 0.0	0.04 0.96	30 33	15933.3 15903.2	30.1 0.0	<0.001 1.00	34 39	19949.3 19673.6	275.8 0.0	<0.001 1.00

<sup>a</sup>Gaussian (squared) term was most parsimonious in at least one seasonal candidate model

<sup>b</sup>Linear term was most parsimonious in at least one seasonal candidate model

For Quintette caribou, models containing covariates for cumulative effects also predicted well from a mean  $r_s = 0.893$  in summer/fall to a mean  $r_s = 0.984$  in spring (AUC = 0.815 and 0.866). Models excluding disturbance features failed to enter into the final top-model set for each season. Collared caribou demonstrated clear differences in the use of forest cover, forest age, solar insolation, and disturbance features across the South Peace study area.

### Resource Selection by Season for Caribou

Differences in selection for forest cover and age were evident between the two caribou herds for each season (Figures 8, 9). In general, the BHRW herd selected for lowelevation habitats across the boreal forest dominated by black spruce (all four seasons) and tamarack. Caribou that overwintered in the boreal forest selected older pine-leading stands in addition to black spruce and tamarack. A proportion of the BHRW herd was observed migrating to higher elevations during the calving and summer/fall seasons and selected subalpine fir and alpine habitats, in addition to habitats dominated by herbs, bryoids, and shrubs (Figures 8, 9; Appendix A). Quintette caribou remained at high-elevations and selected alpine, subalpine fir, spruce and pine-leading habitats of late-succession throughout the year. Caribou in both the BHRW and Quintette herds selected for areas with greater levels of solar insolation (SI) across each of the four seasons. Seasonal co-occurrence of caribou and wolves was greatest near forestry cutblocks and in areas with increased densities of disturbance features, as both species were observed selecting for these disturbance types. However, these interactions varied for both the BHRW and Quintette herds of caribou according to differences in topography and industrial development found across the boreal or mountainous landscape.



Figure 8. The percentage (%) of used and available locations occurring within each class of forest cover during the spring and calving seasons for caribou in the Bearhole/Redwillow (BHRW) and Quintette herds. Model covariates for forest cover are described in Table 1. An asterisk (\*) indicates a forest cover class with greater than 5% use by caribou.



Figure 9. The percentage (%) of used and available locations occurring with each class of forest cover during the summer/fall and winter seasons for caribou in the Bearhole/Redwillow (BHRW) and Quintette herds. Model covariates for forest cover are described in Table 1. An asterisk (\*) indicates a forest cover class with greater than 5% use by caribou.

Spring. Some members of the BHRW caribou herd occupied the boreal forest prior to calving and selected habitats dominated by black spruce of a moderate age during spring (41 - 120 years; Figure 10). These habitats contained 30% of all locations for the BHRW herd during the spring season (Figure 8). Caribou in the BHRW herd avoided alpine habitats as well as forests classified as old. In contrast, Quintette caribou remained at higher elevations during spring, selected alpine and subalpine habitats and avoided forests dominated by black spruce, tamarack, broadleaf and other mixed-conifer species. Alpine habitats contained 74.2% of all locations for the Quintette caribou during the spring season (Figure 8). The mean solar incidence was similar for caribou in both herds during this period (BHRW: 1030.9 ± 331.4 W/m<sup>2</sup>; Quintette: 1029.7 ± 120.3).

The BHRW and Quintette herds demonstrated a nonlinear avoidance response to road and pipeline features during spring (Figure 10, Table 4). BHRW caribou selected against roads to an unknown distance, whereas Quintette caribou showed an avoidance response up to 3.5 km (Table 4; e.g., Figures 11, 12). Pipelines were avoided up to 2.5 and 20 km by BHRW and Quintette caribou, respectively. Caribou in the BHRW herd selected for areas that were adjacent to cutblocks. Quintette caribou, in contrast, avoided individual cutblocks, but demonstrated a higher relative probability of occurrence within areas with increased densities of forestry features (cutblocks and roads). During spring, Quintette caribou selected for areas that were closer than random to coal mines.

*Calving*. Similar to spring, BHRW remained in the low-elevation boreal forest to calve and continued their selection for habitats dominated by black spruce. Caribou in the Quintette herd remained at high elevations to calve in alpine-dominated landscapes (Figure 13).





Figure 10. Coefficients for the parameters in the most parsimonious resource-selection models for Bearhole/Redwillow (A; n = 3,401) and Quintette (B; n = 9,791) caribou herds during the spring season. An asterisk (\*) indicates a Gaussian term and variable descriptions are given in Table 1.

Table 4. Results of seasonal resource selection function models and the affiliated nonlinear avoidance distances (Dist; km) and densities (Dens; ha/km<sup>2</sup>) calculated using Gaussian covariates for caribou across the South Peace region of northeastern British Columbia (Appendix E).

BHRW	Spring	Calving	Sum/Fall	Winter
Road Dist	linear	4.5	linear	11
Seismic Dist	0.6	linear	2.25	3
Pipeline Dist	2.5	linear	2	linear
Cutblock Dist	linear	6	linear	20
Oil/Gas Dist	21	10.5	7	4.5
Forestry Dens	24	linear	56	linear
Quintette	Spring	Calving	Sum/Fall	Winter
Road Dist	3.5	3.5	4.5	3.5
Seismic Dist	6	3.5	2.5	1.5
Pipeline Dist	20	5.5	3.5	2
Cutblock Dist	3	20	3.5	4.5
Oil/Gas Dist	0.6	15	1	0.9
Mine Dist	linear	5	4.5	linear
Forestry Dens	linear	44	linear	28

\*Values may be unique to the South Peace study area, study animals, and/or my chosen method of analyses (e.g., logistic regression, size of availability radius, etc.; Ficetola and Denoël 2009).



Figure 11. Likelihood of occurrence of monitored caribou in the Quintette herd during the calving season relative to the density of forestry features (cutblocks and roads) found across the South Peace region of northeastern British Columbia (2003 - 2009). Habitat covariates were held at their mean values, while caribou occurrence was allowed to vary with density of disturbance features.



Figure 12. Likelihood of occurrence of monitored caribou in the Quintette herd during the winter season relative to forestry cutblocks found across the South Peace region of northeastern British Columbia (2003 - 2009). Habitat covariates were held at their mean values, while caribou occurrence was allowed to vary with distance from disturbance features.





Figure 13. Coefficients for the parameters in the most parsimonious resource-selection models for Bearhole/Redwillow (A; n = 2,200) and Quintette (B; n = 5,868) caribou herds during the calving season. An asterisk (\*) indicates a Gaussian term and variable descriptions are given in Table 1.

The use of cover types and patch age for both herds was more variable during the calving season. Some members of the BHRW herd calved at higher elevations in subalpine fir habitat, while others selected tamarack and black spruce-leading stands in the low-elevation boreal forests. Subalpine fir, tamarack and black spruce habitats contained 51% of all calving locations for BHRW caribou (Figure 13). Caribou in the BHRW herd avoided forests of early-successional ages. Quintette caribou selected older patches of pine and spruce in addition to alpine habitats during calving (containing 86.7% of GPS collar locations; Figure 8), but avoided areas dominated by water, herbs, bryoids, shrubs, and forests classified up to 120 years of age. Solar incidence during calving ranged from a mean of 1036.7 W/m<sup>2</sup> ( $\pm$  103.1) to 1068.0 W/m<sup>2</sup> ( $\pm$  133.1) for the BHRW and Quintette herds, respectively.

The probability of finding caribou near roads remained low for herds residing in boreal and alpine habitats during calving (Figure 13). Oil and gas facilities were avoided by BHRW caribou up to a distance of 10.5 km and caribou in the Quintette herd demonstrated nonlinear avoidance responses to seismic lines. Coefficients suggested that cutblocks and coal mines had a negative influence on the distribution of caribou during calving. Location data also suggested that caribou from each herd had a larger relative probability of occurrence in the vicinity of some disturbance features. During calving, Quintette caribou were found in habitats closer than random to oil and gas features. The BHRW demonstrated selection of habitats located near seismic lines, pipelines and forestry cutblocks. Caribou from the Quintette herd also demonstrated a tolerance of forestry disturbances up to a density of 44 ha/km<sup>2</sup> (Figure 11, Table 4), after which an avoidance response was observed. Summer/Fall. During the summer/fall season, individuals within the BHRW herd remained divided between high- and low-elevation habitats while raising their calves (Figure 9). BHRW caribou inhabiting mountainous terrain selected herb, bryoid, and shrub communities, although use and availability of these habitat types were extremely low across their seasonal range (Figure 9, Figure 14). Caribou in the BHRW herd that remained in the low-elevation boreal forest continued to select black spruce and tamarack-leading stands during the summer and fall months. Alpine habitats and forests dominated by spruce (non-*P. mariana*) were avoided by BHRW caribou (Figure 14). Similar to the calving season, Quintette caribou demonstrated strong selection for alpine, pine and spruce-leading habitats, where 79.9% of all summer/fall locations occurred (Figure 9). Forests dominated by broadleaf and other mixed conifers were avoided by caribou in the Quintette herd. Caribou in the BHRW herd were located in habitats with increased levels of solar insolation (x =  $1038.3 \pm 109.7 \text{ W/m}^2$ ), whereas locations for Quintette caribou were exposed to relatively less solar insolation during the summer/fall season (x =  $1022.8 \pm 143.7 \text{ W/m}^2$ ).

Avoidance of anthropogenic disturbances was more prominent during the summer and fall months (Figure 14). BHRW demonstrated an avoidance to roads up to an unknown distance, whereas Quintette caribou avoided roads up to a distance of 4.5 km (Table 4). In addition, coal mines were avoided throughout the summer and fall and both BHRW and Quintette caribou avoided features related to oil and gas extraction. Quintette and BHRW caribou avoided seismic lines to a distance of 2.5 and 2.25 km, respectively. Avoidance responses towards pipelines were also comparable between herds during these post-calving months. As the density of linear features increased, the relative probability of caribou occurrence decreased.



Figure 14. Coefficients for the parameters in the most parsimonious resource-selection models for Bearhole/Redwillow (A; n = 8,669) and Quintette (B; n = 22,458) caribou herds during the summer/fall season. An asterisk (\*) indicates a Gaussian term and variable descriptions are given in Table 1.

Forestry cutblocks were avoided by caribou in the Quintette herd to a distance of 3.5 km. For BHRW, negative coefficients suggested an avoidance of habitats where the density of forestry features exceeded 56 ha/km<sup>2</sup>. Quintette caribou also avoided habitats with increased densities of mines and oil and gas features, but the top-ranked model produced coefficients that suggested selection of habitats near forestry cutblocks.

*Winter*. BHRW and Quintette caribou demonstrated variation in resource selection during winter (Figure 15). Animals in both herds demonstrated selection for alpine, subalpine fir and pine-dominated landscapes of older age classes, although habitats used by caribou in the two herds differed considerably (Figures 8, 9). During the winter months, 66.3% of Quintette locations occurred in the alpine while only 0.2% of the BHRW locations occurred in the alpine. Likewise, 58.7% of locations for caribou in the BHRW herd and 8.9% of locations for the Quintette herd were located in pine-leading forests (Figure 9). Members of the BHRW herd overwintering in the boreal forest selected habitats dominated by pine, black spruce, tamarack and other species of spruce. Both herds avoided mixed conifer, broadleaf, upland areas without vegetation, and water-dominated habitats. During winter, caribou in the BHRW herd were located in habitats with less solar incidence (x =  $1029.7 \pm 62.1 \text{ W/m}^2$ ) as compared to caribou in the Quintette herd (x =  $1082.4 \pm 113.8 \text{ W/m}^2$ ).

During winter, industrial activities influenced the habitat selection of the Quintette and BHRW herds (Figure 15). Quintette caribou avoided areas of their seasonal range where cutblock (and associated road) densities exceeded 28 ha/km<sup>2</sup> in addition to habitats located within close proximity to roads and cutblocks (Figure 12, Table 4).



Figure 15. Coefficients for the parameters in the most parsimonious resource-selection models for Bearhole/Redwillow (A; n = 11,625) and Quintette (B; n = 28,368) caribou herds during the winter season. An asterisk (\*) indicates a Gaussian term and variable descriptions are given in Table 1.

Landscape features related to oil and gas exploration and extraction were avoided by caribou wintering in high-elevation mountainous habitats. Caribou of the BHRW herd also demonstrated avoidance of roads, cutblocks, oil and natural gas features. Quintette caribou however, were observed closer than their random locations to coal mines during winter.

## Count Models for Wolves

I used 24,075 GPS collar locations for Upper Sukunka (US; n = 6,783), Upper Murray (UM; n = 6,478), Onion Creek (OC; n = 4,624) and Chain Lakes (CL; n = 6,190) to generate statistical count models. Seventy-three kill sites (US, n = 20; UM, n = 15; OC, n = 117; CL, n = 21; Figure 16) served as the foundation for determining the average wolf area of use (AOU) and size of the habitat selection unit (HSU) for each pack (Appendix C). Habitat Selection Units ranged in size from 6.6 ha for the Upper Sukunka pack to 155.4 ha for the Upper Murray pack of wolves (Appendix C). The Vuong test suggested that count data were fitted better to zero-inflated regression models (ZINB) for all packs across seasons (Vuong  $4.31 \le z \le 9.08$ , p < 0.001). I was unable to maximize the log likelihood values for five seasonal models using the preferred ZINB. For each of these five seasons, I chose to use the more simplistic NBRM. Tolerance scores for continuous variables were low for some packs and variables. With a primary study focus on linear features, I excluded cutblocks and nonlinear features linked to oil and natural gas from candidate models for the Upper Sukunka and Chain Lakes packs. For the Onion Creek pack, distance to mine was highly correlated with distance to oil and gas features; I retained the distance to mine variable as the Onion Creek territory was less influenced by features associated with oil and gas development.



Figure 16. Prey selection (%) by GPS collared wolves as identified through the investigation of location clusters (2008 - 2010; n = 73 kills) across the South Peace region of northeastern British Columbia.

Based on AIC<sub>c</sub>, a combination of landscape attributes, selection value of caribou habitat and human disturbances was best able to model the seasonal occurrence and relative frequency of habitat use by wolves across the South Peace region (Table 5). For all three seasons, the most parsimonious models for both the Onion Creek and Chain Lakes packs were also the most complex in each candidate set and contained variables for landscape, caribou habitat and anthropogenic disturbances. During late winter, the second-ranked model for the Upper Sukunka pack was comparable to the top-ranked model ( $\Delta AIC_c = 1.0$ ). I observed similar model selection uncertainty for the two top-ranked models for the Upper Murray pack during winter ( $\Delta AIC_c = 1.9$ ). The predictive ability of seasonal count models was generally good for HSUs across the study area (Figure 17).

Table 5. Number of parameters (k), Akaike's Information Criterion values (AIC<sub>c</sub>), AIC<sub>c</sub> weights (AIC<sub>w</sub>), and  $\Delta$  AIC<sub>c</sub> values for competing seasonal count models for wolves. Models were developed (using ZINB or NBRM) for each of four wolf packs monitored from 2008 – 2010 across the South Peace region of northeastern British Columbia. Sample size used to define habitat selection units (HSUs) is presented in parentheses for each pack. Model covariates are given in Table 2 and the full set of candidate models can be found in Appendix E.

Upper Sukunka (n = 33,599)	Non-Winter <sup>NBRM</sup>					Early	Winter <sup>ZIN</sup>	3	Late Winter <sup>NBRM</sup>				
Model Covariates	k	AIC <sub>c</sub>	ΔΑΙΟ	AIC <sub>w</sub>	k	AIC	$C_c  \Delta AIC$	AIC <sub>w</sub>	k	AIC <sub>c</sub>	ΔAIC	AIC <sub>w</sub>	
MOG Dist <sup>a</sup>	22	2 9636.6	44.4	<0.001	23	3 5087	7.1 37.1	<0.001	22	6116.9	0	0.45	
MOG Dist + MOG Dens <sup>a</sup>	23	3 9629.1	36.9	< 0.001	25	5 5084	.8 34.9	<0.001	23	6118.3	1.4	0.22	
CE Dist <sup>a</sup>	19	9 9598.8	6.6	0.04	26	5 5073	3.1 23.2	< 0.001	23	6117.8	0.9	0.27	
CE Dist + CE Dens <sup>a</sup>	2	9592.2	0	0.96	32	2 5049	0.9 0	1	25	6120.6	3.7	0.07	
Upper Murray (n = 35,959)	Non-Winter <sup>NBRM</sup>				Early Winter <sup>NBRM</sup>					Late Winter <sup>ZINB</sup>			
Model Covariates	k	AIC <sub>c</sub>	ΔΑΙΟ	AIC <sub>w</sub>	k	AIC <sub>c</sub>	ΔΑΙϹ	AIC <sub>w</sub>	k	AIC <sub>c</sub>	ΔΑΙϹ	AIC <sub>w</sub>	
MOG Dist	16	11027.1	39.2	< 0.001	15	4417.2	59.9	< 0.001	14	5816	132.3	<0.001	
MOG Dist + MOG Dens	18	11029.8	41.9	< 0.001	18	4357.2	0	0.72	15	5778.8	95.1	<0.001	
CE Dist <sup>a</sup>	20	11026.9	39	< 0.001	15	4417.2	59.9	< 0.001	16	5789.3	105.6	< 0.001	
CE Dist + CE Dens <sup>a</sup>	27	10987.9	0	1	17	4359.1	1.9	0.28	18	5683.6	0	1	
Onion Creek (n = 10,493)		Non-Wi	nter <sup>ZINB</sup>		Early Winter <sup>ZINB</sup>				Late Winter <sup>ZINB</sup>				
Model Covariates	k	AIC <sub>c</sub>	ΔΑΙΟ	AIC	k	AIC <sub>c</sub>	ΔΑΙϹ	AIC <sub>w</sub>	k	AIC <sub>c</sub>	ΔΑΙϹ	AICw	
CE Dist + CE Dens	20	6722.1	0	1	25	3079.1	0	1	23	3675.6	0	1	
Chain Lakes (n = 3,389)		Non-Wi	nter <sup>ZINB</sup>			Early	Winter <sup>NBR</sup>	M	Late Winter <sup>ZINB</sup>				
Model Covariates	k	AIC <sub>c</sub>	ΔΑΙΟ	AIC <sub>w</sub>	k	AIC <sub>c</sub>	ΔΑΙϹ	AIC <sub>w</sub>	k	AIC <sub>c</sub>	ΔΑΙϹ	AIC	
CE Dist + CE Dens	18	4014.2	0	1	22	7174.7	0	1	18	3252.2	0	1	

<sup>a</sup>Gaussian (squared) term was most parsimonious in at least one seasonal candidate model



Figure 17. Differences in the observed (withheld data) and predicted probability of counts of wolf locations within habitat selection units (HSUs) for the Upper Sukunka (A), Upper Murray (B), Onion Creek (C) and Chain Lakes (D) packs residing in the South Peace region of northeastern British Columbia. Predicted data were generated from the most parsimonious zero-inflated (ZINB) or negative binomial regression model (NBRM; Table 5). A value of zero indicated perfect prediction, whereas positive values indicated under-prediction and negative values indicated over-prediction.

Inspection of residuals indicated the probability of models to predict occurrences of wolves across the landscape was relatively poor for zero and low frequencies, but improved as wolf locations increased within habitat selection units.

# Occurrence and frequency of wolf locations across the South Peace

Seasonal variation in the selection and use of forest cover, caribou habitat, and disturbance features was observed for each study pack of wolves. Wolves residing in mountainous regions occurred in pine-dominated forests throughout the year. Habitats dominated by broadleaf or mixed-conifer trees, water, and non-linear features were also important indicators of wolf occurrence. Linear features were avoided by boreal and mountainous wolves during each of the three seasons. In general, wolves were infrequently located in habitats valued as high quality for BHRW or Quintette caribou.

*Non-winter*. During the non-winter season, Onion Creek wolves occurred in pinedominated habitats and wolves in both the Onion Creek and Chain Lakes packs avoided mature and late-successional forests (81 – 120, and > 120 years) dominated by broadleaf species (Table 6; Appendix D). ZINB models showed that processes influencing the presence or absence of wolves on a landscape were different from those affecting the frequency of use. Three packs with territories in the mountainous regions (Upper Sukunka, Upper Murray, and Onion Creek) showed higher frequencies of locations in HSUs containing upland or spruce habitats. Wolves in the Chain Lakes pack were commonly located in the lower elevation boreal areas with aspen, cottonwood and birch of unknown ages. Habitats dominated by water bodies were frequently selected by all packs. Wolves rarely used latesuccessional forests containing pine and other mixed-conifer species.

Table 6. Seasonal selection (S) and avoidance (A) of habitat features by wolves across the South Peace region of northeastern British Columbia. Presence or absence (binary) and the frequency of habitat use (count) were determined using  $\beta$  coefficients from count models. Models were developed for the Upper Sukunka (US; n = 33,599), Upper Murray (UM; n = 35,959), Onion Creek (OC; n = 10,493) and Chain Lakes (CL; n = 3,389) packs. Model covariates are given in Table 1 and Table 2.

	Non-winter (S)		<u>Early w</u>	vinter (S)	Late wir	nter (S)	Non-w	inter (A)	Early wi	nter (A)	Late winter (A)	
Variable	Binary	Count	Binary	Count	Binary	Count	Binary	Count	Binary	Count	Binary	Count
Alpine						US						
Black spruce										CL		
No VRI		UM		UM	UM							
Other		UM,US		CL	OC,UM							US
Pine	OC		OC	OC		UM		UM		CL		
Spruce		OC									UM	US
Tamarack												
Tree broadleaf		CL		CL		US	oc		US	US		
Tree other			US					UM,US		OC		UM
No age								UM,US				
YG (0-80 yrs)		OC		CL		OC						
YGM (0-120 yrs)		US				US				UM		
Young												
Growing		UM										
Mature							CL				UM	UM
Old	CL				CL,UM			UM		CL		OC,US
Water <sup>a,b</sup>		CL,OC,UM,US		UM,CL		US			US,OC		OC,UM	
RSF_BHRW		UM	OC			UM				CL		CL,OC
RSF_Quintette							ос	UM	US		UM	

<sup>a</sup> Covariate measuring distance (km) to a feature; selection is therefore represented by a  $-\beta$  coefficient and avoidance is represented by a  $+\beta$  coefficient

<sup>b</sup> Either a Gaussian (squared) or linear term was used in the top model

Upper Murray, Onion Creek and Chain Lakes wolves avoided higher quality habitats for Quintette caribou during the non-winter months. Only wolves from the Upper Murray pack frequented habitats selected by the BHRW caribou herd (Table 6).

Members of the boreal Chain Lakes pack were present in HSUs with few roads and few locations occurred in areas with high densities of linear features. Members were observed in HSUs near forestry cutblocks, but the total number of locations was not strongly related to such features. Wolves in the Onion Creek and Upper Sukunka packs avoided seismic lines, pipelines, and coal mines (Onion Creek only; Table 7, Appendix D). Although habitats near roads were selected by wolves in the Upper Murray pack, non-linear features were more informative in describing wolf distribution between mid-April and mid-October. Only Upper Sukunka and Upper Murray wolves frequented areas near coal mines and oil and gas facilities; however, as the density of these features increased, the frequency of wolf locations decreased.

*Early winter*. Similar to non-winter, wolves in the Onion Creek pack occurred in HSUs where pine was the predominant species. Upper Sukunka wolves were present in habitats of primarily mixed conifer. Habitats dominated by broadleaf trees were avoided by wolves in the Upper Sukunka pack, but were frequently used by members of the Chain Lakes pack in the boreal forest and the Upper Murray pack residing in the mountains (Appendix D). Higher frequencies of wolf locations occurred in early-successional forests classified as pine (Onion Creek), upland and habitats dominated by herbs, bryoids, and shrubs (Chain Lakes and Upper Murray; Table 6).

The frequency of wolf locations was not related to habitats strongly selected by caribou.

Table 7. Seasonal selection (S) and avoidance (A) of disturbance features by wolves across the South Peace region of northeastern British Columbia. Presence or absence (binary) and the frequency of habitat use (count) were determined using  $\beta$  coefficients from count models. Models were developed for the Upper Sukunka (US; n = 33,599), Upper Murray (UM; n = 35,959), Onion Creek (OC; n = 10,493) and Chain Lakes (CL; n = 3,389) packs. Model covariates are given in Table 1 and Table 2.

	Non-winter (S)		vinter (S) Early winter (S)		Late winter (S)		Non-winter (A)		Early winter (A)		Late winter (A)	
Variable	Binary	Count	Binary	Count	Binary	Count	Binary	Count	Binary	Count	Binary	Count
Road <sup>a,b</sup>		UM					CL	CL	US	US	UM	
SeisPipln <sup>a.b</sup>							ос	OC,US	US	UM	OC,UM	OC
Ctblk <sup>a,b</sup>	CL		US	US						CL		OC
OG <sup>a.b</sup>		US	US	US		US						
Mine <sup>a.b</sup>		UM	US,OC	UM			ос	OC,US			OC	OC,US
MOG_Dens <sup>b</sup>								CL,UM				
FOR_Dens <sup>b</sup>		CL,OC,UM				UM			US	UM,US	UM	
LF_Dens <sup>b</sup>	CL				UM			UM		UM,CL	OC	CL, OC

<sup>a</sup> Covariate measuring distance (km) to a feature; selection is therefore represented by a -β coefficient and avoidance is represented by a +β coefficient

<sup>b</sup> Either a Gaussian (squared) or linear term was used in the top model

Forests of late succession ( $\geq$  121 years of age) and HSUs classified as black spruce or pine-leading contained few locations of wolves across the territory of the Chain Lakes pack. In addition, quality habitat for caribou in the BHRW herd was avoided by most wolves in the boreal forest. Only members of the Onion Creek pack occurred, but were not frequently located in HSUs containing high-value habitat for caribou in the BHRW herd (Table 6). Areas containing cutblock, oil, gas, and coal mine features supported high frequencies of wolf locations during early winter for both the Upper Sukunka and Onion Creek packs. Conversely, boreal wolves were uncommon in HSUs close to cutblock features or with a high density of linear features or cutblocks (Table 7).

*Late Winter*. Between February and mid-April, the presence of wolves was best described by a variety of forest cover types. Upper Murray wolves used mountainous habitats classified as upland and alpine, as well as communities dominated by herbs, bryoids, shrubs, water (ice) or broadleaf trees. Wolves in the Onion Creek pack occurred in HSUs where mixed conifers prevailed. As in other seasons, wolves in the Upper Sukunka and Upper Murray packs frequented forests dominated by aspen, cottonwood, birch, and pine between 0 and 120 years of age. Both Upper Murray and Chain Lakes wolves did occur, although not frequently, in late-successional forests during late winter (> 120 years). Wolves in the Upper Murray pack were absent from mature (81 – 120 years) forests dominated by white, Engelmann, or hybrid spruce. In addition, HSUs with communities of herbs, bryoids, shrubs or upland areas, all contained low frequencies of wolf locations. Throughout late winter, both Upper Murray and Onion Creek wolves also demonstrated an avoidance of habitats containing water features (Table 6).
Although Upper Sukunka wolves rarely had the opportunity to overlap populations of woodland caribou, they demonstrated increased frequencies of use of alpine habitats during late winter. In contrast, and consistent with the early winter, Onion Creek and Chain Lakes wolves did not frequently occur in habitats selected by caribou in the boreal forest. Upper Murray wolves also demonstrated an avoidance of habitats used by the Quintette caribou herd during late winter (Table 6).

Anthropogenic disturbances continued to influence the distribution of wolves across the study area throughout the late-winter months (Table 7). Wolves in the Upper Sukunka and Upper Murray packs frequented HSUs near oil and gas features as well as habitats with greater densities of cutblocks. Avoidance of disturbance features was more apparent in late winter for wolves in both the boreal forest and in the mountains. Packs occurring in mountainous portions of the study area were absent or rarely occurred in areas near linear features (Upper Murray and Onion Creek), coal mines (Upper Sukunka and Onion Creek), and areas with high densities of cutblocks and roads (Upper Murray). In addition, locations of wolves from both the Chain Lakes and Onion Creek packs were uncommon or absent from habitats with relatively high densities of linear features.

# Discussion

This study supports the general conclusions of others that the cumulative effects of industrial development have strong influences on the patterns of habitat selection and distribution for both wolves and woodland caribou in mountainous and boreal ecosystems (Dyer et al. 2001, James et al. 2004, Vors et al. 2007, Nitschke 2008, Houle et al. 2010). However, my results suggest that regionally-specific information and knowledge of the

processes of predator-prey interactions are essential for understanding the ecological impacts of those cumulate effects. This is especially the case for woodland caribou, a threatened species that is influenced directly and indirectly by disturbance, habitat modification and altered predator-prey dynamics.

I used an innovative combination of field and statistical methods to understand the seasonal distribution of wolves relative to caribou habitat and industrial development. The application of count models to HSUs allowed me to develop statistical relationships that represented the frequency of habitat use, not simply habitat selection. The number of wolf locations in an HSU may be associated with predatory behaviour, such as hunting and prey handling, or the size of pack territories. In addition, the inclusion of the RSF variable that quantified the selection value of habitats for monitored caribou herds, provided a more holistic description of habitats related to the distribution of caribou. Resource selection functions represented not only vegetation that would serve as forage for caribou, but also human disturbances that influence the distribution of each herd.

#### Habitat Selection by Caribou and Wolves

My study of the BHRW and Quintette herds provided a unique opportunity to observe differences in behaviours between populations of caribou that winter in low-elevation boreal and high-elevation alpine habitats, respectively. Few studies have looked at behaviourally distinct populations of caribou as they respond to direct threats from industrial encroachment and predation by wolves. Caribou of the BHRW herd demonstrated selection for mature and late-successional forests dominated by black spruce (all four seasons), tamarack, and to a lesser extent, subalpine fir, alpine and communities of herbs, bryoids, and shrubs. Caribou

that overwintered in the boreal forest selected black spruce, tamarack, and older pine-leading stands. Although a small proportion of the BHRW herd was observed selecting highelevation habitats during winter, GPS collar locations were rare in alpine habitats. Quintette caribou selected alpine, subalpine fir, spruce and pine-leading habitats of late-succession during winter. Similar results were documented for caribou in the Quintette herd by Sopuck (1985) and Jones et al. (2007).

Across all seasons, caribou in both herds were observed avoiding early-successional habitats dominated by aspen, cottonwood, birch, and mixed conifers. These avoidance behaviours may be a result of the increased abundance of other ungulates and associated predators typically found in these forest types. As documented for other populations of both northern (Cichowski 1993, Johnson et al. 2002b) and boreal ecotypes (Saher and Schmiegelow 2004, Culling et al. 2006, Neufeld 2006, Courbin et al. 2009), my results suggest that high-risk habitats are avoided by caribou from the Quintette and BHRW herds.

Like caribou, wolves residing in mountainous regions demonstrated selection for pine-dominated forests throughout the year. Unlike caribou, wolves frequented habitats of early seral ages. During all three seasons, habitats dominated by broadleaf or mixed-conifer trees and water were important indicators of wolf, but not caribou occurrence. In addition, wolves favoured habitats dominated by herbs, bryoids, and shrubs during the winter, whereas caribou in both the BHRW and Quintette herds avoided these habitats. Upper Murray and Onion Creek wolves demonstrated some selection of habitats used by BHRW caribou.

Caribou in both the BHRW and Quintette herds were at a relatively low risk of predation during late winter, even though the use of subalpine (e.g., subalpine fir, upland and herbs, bryoids, and shrub-dominated habitats often in 'other' category; Appendix D) and

alpine habitats by wolves generally increased during this season. In contrast to Latham (2009), who reported increased levels of overlap between caribou and wolves during winter in the low-elevation forests of western Alberta, black spruce and tamarack forests were rarely selected by either of the two packs of wolves I monitored. Furthermore, the Chain Lakes and Onion Creek packs avoided habitats classified as high quality for BHRW caribou during winter. These findings are supported by observations of prev remains at kill sites where caribou accounted for 1.3% of identified wolf kills in the South Peace region (Figure 16; Appendix C). I lack information delineating the habitats of other prey species, but my results are comparable with past studies suggesting wolf populations are typically supported by prey other than caribou (i.e., moose, deer, elk, beaver, other small mammals and birds; Figure 16; Bergerud et al. 1984, James et al. 2004, Gustine et al. 2006b, DeCesare et al. 2010, Latham et al. 2011a, Milakovic and Parker 2011, Steenweg 2011). Although my data suggest wolves are not using habitat patches selected by caribou, the level of spatial separation remains greater for the Quintette herd than the BHRW herd because wolves have increased opportunities, with relatively low costs of movement, to use caribou habitat across the boreal forest.

Solar insolation correlated with the distribution of caribou. However, interpreting the mechanism by which this variable influenced caribou was challenging. Levels of solar insolation were generally less for BHRW under the cover of the boreal forest than for Quintette caribou residing in exposed alpine and subalpine habitats. In future studies, a topographic variable representing windblown ridgelines in alpine habitats, in addition to solar incidence, could further our understanding of caribou distribution.

Habitat selection studies can suggest that certain resources or habitat types are important simply as a product of the availability of those types. For example, I observed selection for alpine habitats by a relatively few caribou of the BHRW herd – this relationship was the product of the low availability of the habitat not a high level of use. To clarify such relationships, I determined the seasonal availability and use of each forest cover type (e.g., Figures 8, 9; Appendix D). Special consideration should be given to habitat types that are commonly used and selected.

#### Behavioural Responses of Wolves and Caribou to Industrial Disturbances

Wolves in all four packs demonstrated avoidance of linear features during each of the three seasons. Also, I modeled a low frequency of wolf occurrence in habitats with high densities of roads, seismic lines and/or pipelines. These findings parallel similar studies of wolves in industrial landscapes (Thurber et al. 1994, Whittington et al. 2005, Houle et al. 2010). Such avoidance responses are likely due to direct and indirect risks associated with exposure to areas used by humans (i.e., mortalities from increased access for hunting, trapping, and vehicular collisions; Fuller 1989, Mladenoff et al. 1995, Callaghan 2002, Hebblewhite and Merrill 2008, Person et al. 2008). Because only one pack (Upper Murray) was observed frequently using habitats near roads during the non-winter season, my results suggest that cumulative road densities across the majority of the study area may have surpassed levels acceptable for travel by wolves (~0.25 km/km<sup>2</sup> – 0.6 km/km<sup>2</sup>; Mech et al. 1988, Fuller 1989, Merrill 2000, Person 2008).

Caribou demonstrated a strong avoidance of linear features during all four seasons, although roads were the only feature consistently avoided each season. Similar to Nellemann

et al. (2001), Dyer et al. (2002) and Latham (2009), roads were avoided (but up to a greater distance of 3.5 km) by both BHRW and Quintette caribou most significantly during the winter months. Winter is the busiest season for activities related to the exploration and development of petroleum reserves and forestry operations and could explain the observed avoidance by caribou. Although I used conditional regressions to statistically remove the responses of individual caribou locations to disturbance features that occurred at large distances, nonlinear avoidance thresholds still occurred at large distances not currently reported in the literature (Table 4). Future studies could consider exploring alternative statistical methods that are not constrained by a Gaussian function, such as I used, and should also consider analysing caribou behaviour in the presence of individual disturbances at multiple scales.

Unlike avoidance of roads, caribou in the BHRW herd demonstrated selection for specific habitats near seismic lines and pipelines during calving and winter. These linear features vary in intensity of disturbance and age, and although I did not measure such factors, they may explain seasonal tolerance by BHRW caribou. Close proximity to these features may also suggest that caribou have not yet reached a threshold level of intolerance. Also, caribou may demonstrate long-term fidelity to seasonal habitats that become adjacent to early-successional habitats or industrial developments. Persistent use of such sites may increase the risk of predation for caribou and their calves, thus, serving as ecological traps (Schlaepfer et al. 2002, Faille et al. 2010). While past studies suggest predation risk for caribou increases near linear features, results from the count models for wolves suggest that risk is less severe. Wolves generally avoided roads, seismic lines and pipelines, as well as habitats that supported greater densities of linear features. Contrary to other studies (James

and Stuart-Smith 2000, Latham et al. 2011c), my results suggest that in this area, the current density of linear features may not result in a direct increase in predation risk for caribou.

High densities of linear features also influenced the distribution of caribou across a larger regional area. During calving, summer and fall, caribou avoided areas of their range with high densities of linear features. Like Polfus et al. (2011) and Curatolo and Murphy's (1986) study, my results suggests that high levels of human use near roads indirectly results in functional habitat loss for caribou across the South Peace region.

Wolves in boreal and mountainous habitats occurred in areas closer to, and with higher densities of cutblocks during the non-winter season. Wolves may be advantageously selecting these habitats for increased hunting opportunities of moose and deer. Wolves may also frequent these habitats because they are suitable for denning or homesites. The use of cutblocks by wolves was less consistent during early and late winter. The Upper Murray pack frequently selected habitats closer to and with greater densities of cutblocks in early winter. Unlike early winter, all four packs avoided cutblocks during the late-winter months the time of year when forestry, oil, and gas industries are most active and when deep snow begins to restrict moose from foraging in cutblocks (D. Heard, personal communication). Similarly, Houle et al. (2009) found that wolf occurrence decreased as cutblock density increased in Quebec. Wolves in the South Peace may be responding to the cumulative influence of roads and cutblocks at both a home range and regional scale (inter-pack; Houle et al. 2010). Also, there is often little browse for moose in newly harvested areas (Nielsen et al. 2005). The infrequent occurrence of wolves could indicate a relatively large proportion of recent cutblocks, and their associated roads, in some territories as opposed to those with older regenerating cutblocks containing more suitable habitat for moose (Courtois et al. 1998).

Caribou in both boreal and mountainous habitats responded differently to cutblocks than to linear features. BHRW caribou selected habitats within close proximity to individual cutblocks during spring and calving, but avoided areas with high densities of cutblocks during the summer, fall, and winter seasons. Quintette caribou also avoided habitats with higher densities of cutblocks during winter. Similar to wolves, caribou from both herds were found within areas of their ranges containing high densities of cutblocks during calving. These results, though counterintuitive, further support my hypotheses that female caribou may select for particular habitat characteristics regardless of human disturbance or predation risk (i.e., fidelity; Rettie and Messier 2001, Wittmer et al. 2006, Faille et al. 2010).

There are a number of plausible explanations for the observed distribution of caribou near cutblocks. Behaviours associated with the learned use of distinct calving sites may take precedence over the risks associated with spending increased amounts of time in early seral forests. Similar to Hins et al. (2009), caribou across the region might also select remnant strips of old-growth forest often found adjacent to cutblocks. Thus, I may have observed a pattern of selection associated with juxtaposition, not composition of habitats. Alternatively, or in combination, caribou may be demonstrating seasonal tolerances towards regenerating cutblocks as there can be a time lag of 20 years between the initial phases of forestry extraction and avoidance of those areas (Nielsen et al. 2005, Vors et al. 2007). In total, my results suggest the possibility of maladaptive sinks for populations of caribou across the South Peace region. These negative fitness outcomes may be subject to a lag effect, being realised only after moose and associated predators adjust their distribution to emerging habitats (Nielsen et al. 2005).

Features associated with the development of oil and gas deposits also influenced behaviours of wolves and caribou across the study area. The Chain Lakes and Upper Murray packs avoided areas of their range with a high density of oil or gas features during the nonwinter seasons. In contrast, wolves in the Sukunka Valley demonstrated a greater frequency of use of habitats within close proximity to oil or gas features. These patterns of selection suggest that levels of human activity associated with oil and gas development vary across the territories of collared wolves, or some wolves have developed strategies to accommodate disturbance stimuli (Hebblewhite and Merrill 2008). Caribou were located further than random from well pads and other oil and gas sites during calving, summer/fall, and winter, but demonstrated the greatest avoidance during calving (BHRW) and summer/fall. My results are similar to studies on Arctic caribou herds where the indirect losses of higherquality habitat were most apparent during post-calving seasons (Cameron et al. 2005, Johnson et al. 2005). During the non-winter months, co-occurrence of wolves and caribou near non-linear features associated with oil and gas development was rare.

The Upper Murray and Onion Creek packs of wolves occupied mountainous territories adjacent to, but were infrequently located near coal mines. Two packs of wolves (Upper Sukunka and Onion Creek) usually avoided mines during the non-winter and latewinter seasons. As wolves focus on the rearing of pups, the high levels of human activity and vehicular traffic associated with mine sites might deter them from frequenting those areas (Lesmerises et al. 2012). During winter, wolves may naturally avoid industrial features, such as mines, if they continue to hunt primary prey in the valley bottoms. Coal mines occurred only within the range of Quintette caribou (Sopuck 1985). These caribou avoided mines up to a distance of 5 km during calving and throughout the summer and fall

months, but selected habitats near mines during spring and winter. Elongated ridges in alpine wintering habitats are of high value to Quintette caribou. Again, caribou may trade-off the learned use of high-quality habitat (i.e., fidelity) with a tolerance of human activities and disturbance.

## Cumulative Effects of Resource Extraction and Development on Wolves and Caribou

The cumulative effects of anthropogenic activities are now recognized as one of the most pressing problems facing the conservation and management of wildlife (Vistnes and Nellemann 2001, Johnson et al. 2005, Vors et al. 2007, Johnson and St-Laurent 2011, Krausman and Harris 2011). Habitat alterations from large-scale forestry, oil, natural gas, and mineral exploration, have resulted in dramatic transformations of the South Peace region and continue to threaten the ecological integrity of the landscape (Nitschke 2008). Avoidance of habitats with high densities of linear (i.e., roads, seismic lines and/or pipelines) or non-linear disturbance features (i.e., cutblocks, coal mines, oil and gas facilities) strongly suggests that industrial activities have reduced the quality and quantity of contiguous habitat for caribou across this region. Human-caused disturbance in combination with altered vegetation communities result in compounding instabilities for populations of caribou: increased movement and vigilance, displacement from portions of the range and altered predator-prey dynamics (Bradshaw et al. 1997, Nellemann and Cameron 1998, Cameron et al. 2005, Faille et al. 2010, Latham et al. 2011a). Furthermore, these relationships are complex and may be confounded by ecological sinks and lag effects.

Habitat and movement analyses, in addition to field investigations of wolf kill sites from my study area suggest that co-occurrence between caribou and wolves is rare. In

general, wolf packs rarely selected habitats that were ranked as high quality for either herd of caribou. Similar to caribou, wolves avoided habitats with high densities of linear and nonlinear features. Wolves also avoided roads, seismic lines, and/or pipelines, but selected habitats within close proximity to non-linear features (i.e., cutblock, oil or gas footprints) during some seasons, where a presence of ungulates, other than caribou, was likely. However, if caribou continue to demonstrate seasonal fidelity to developments that support early-successional habitats or predator movement, risks of encountering their primary predators increase. Furthermore, although caribou kills from wolves were infrequently identified during field investigations across the South Peace region, slight increases in the rate of adult mortality from predation can have significant impacts on the stability of small herds of caribou (Wittmer et al. 2005, Gustine et al. 2006a, Latham et al. 2011b).

A challenge for resource managers is to balance the demand for expanding coal mines, oil and gas reserves, and wind-farms with caribou conservation. New projects are being proposed and constructed across caribou winter range throughout the South Peace region. The continued rate of development and resulting loss of contiguous habitat across this area will likely push already small populations of caribou further into decline (Seip and Jones 2011). Caribou inhabiting the low-elevation boreal habitats may be demonstrating a maladaptive strategy in the context of multiple disturbance regimes on the landscape. Specifically, encounters between caribou and wolves are most likely to occur in areas closer to and with higher densities of cutblocks, as both species were observed selecting these features during the non-winter season. As my results suggest, however, interactions among predators, caribou and land-use development are not easily predicted or temporally static. Further monitoring of caribou and wolves is necessary in the context of a changing and

interacting landscape to understand when distribution strategies of these species begin to be affected and to minimize changes that permanently alter the ability of landscapes to support populations of caribou. Chapter 3: Movement Ecology of Wolves in an Industrialized Landscape

## Introduction

Throughout Canada, agriculture and industrial activities provide economic development, but are also responsible for habitat change, fragmentation, altered community dynamics, and ultimately, a reduction in biodiversity (Bradshaw et al. 1997, Dyer et al. 2001, Schneider et al. 2003, Festa-Bianchet et al. 2011). Since the early 1990s, the Peace River and Moberly regions of northeastern British Columbia have undergone rapid land-use change as a result of large-scale commercial forestry, energy, and mineral development (Nitschke 2008). Woodland caribou are now of considerable conservation concern across that region. Throughout much of boreal Canada, habitat alteration and disturbance resulting from human developments are responsible for declining herds, a loss of connectivity of contiguous habitat and increasing predation through apparent competition (Vors and Boyce 2009, Festa-Bianchet et al. 2011).

Activities related to large-scale resource exploration and extraction serve as a catalyst for creating efficient travel corridors for wolves, a primary predator of caribou in the boreal forest. Roads, seismic lines, pipelines, and other linear features (e.g., power lines) can provide greater mobility for wolves as well as access to habitats that would otherwise be isolated by topography or snow. Following human developments, early seral forests become more abundant and support regenerating habitats that favour higher densities of ungulate species, such as moose, elk, and deer. This change in landscape composition increases the distribution of wolves and the likelihood of interactions with caribou (Fuller and Keith 1981, James et al. 2004, Johnson et al. 2004a, Wittmer et al. 2007, DeCesare et al. 2010).

Movement parameters describing animal paths can provide an index of animal behaviour relative to variation in resource availability (e.g., Ferguson et al. 1998, Johnson et

al. 2002b, Nams and Bourgeois 2004, Whittington et al. 2005). Behaviours associated with movement can increase our understanding of how wolves hunt prey and use landscapes altered by human developments. Wolf movements can be categorized as dispersal, movements within territories, and prey searching (Mech 1974). To minimize the energetic costs of movement or maximize encounter rates, wolves travel roads, trails or other linear features that have little human use (Mech 1970, Thurber et al. 1994, Paquet and Carbyn 2003, Wittington et al. 2005). In the valley bottoms of Jasper, Alberta, Whittington et al. (2005) studied the spatial responses of wolves to roads and trails. Using snow tracking to identify movement paths, they found that wolves avoided areas with high densities of trails and roads. Consistent with other studies, wolves selected areas near low-use trails and roadways (Whittington et al. 2005). McCutchen (2007), also working in Alberta, looked at wolf use of linear corridors and how these features may be contributing to declining caribou populations. Based on simulation models, she found that the use of linear corridors by wolves did not contribute to increased rates of predation on caribou. Caribou predation was most influenced by an increase in the total number of wolves on the landscape (McCutchen 2007).

Past research has suggested wolves move more efficiently through habitats within close proximity to linear features with low human use (Thurber et al. 1994, James and Stuart-Smith 2000, Whittington et al. 2005, Rinaldi 2010), but researchers have not yet looked at the variation in movement behaviour across multiple seasonal and temporal scales in direct relation to populations of caribou. Studying movement parameters at both fine and coarse scales can increase our knowledge of factors that may influence seasonal predation rates on caribou and how the movements of wolves are influenced by human-caused changes on the

landscape. Furthermore, understanding the relationship between carnivore movements and landscape composition may have applications to other predator-prey systems influenced by human developments (Kinley and Apps 2001, Robinson et al. 2002, Bryant and Page 2005, Gibson 2006, Cooley et al. 2008).

In this chapter, I quantified variation in wolf movement and used these measures as an index of wolf behaviour in relation to the distribution of woodland caribou and industrial features. I accounted for factors such as cover type and distance to water, that may also influence seasonal movement rates and the sinuosity of movement paths by wolves. Based on past research and results from Chapter 2, I predicted that movements of wolves would differ seasonally and according to the condition of the landscape. As winter progressed, wolf movements would be less sinuous and movement rates would decrease due to the additional energy expenditure required to travel through deep snow as well as the increased availability of vulnerable prey across the landscape. Alternatively, during the non-winter months wolf travel would be more efficient and movement rates would increase as a variety of prey species and ages (i.e., neonates, rodents, birds, etc.) become available. Sinuosity of paths would vary depending on the seasonal availability of prey and increase in habitats across the study area where wolves spend more time searching and hunting.

I expected wolves to travel at increased rates and in a more linear direction in alpine habitats where fewer vegetative barriers, changes in topography, and increased snow hardness reduce the energetic costs of movement. As tree cover thickens, wolves would move more slowly and sinuously. Movement rates and time spent searching and hunting throughout non-conifer habitats would increase due to the availability of browse preferred by

moose, deer and elk. Likewise, searching and hunting behaviours would increase for wolves in seasonal areas supporting populations of caribou.

If wolves in the South Peace region behave similarly to other populations across North America, I would expect less sinuous movements across areas of the landscape influenced by human developments. Non-linear features with low human use would aid behaviours of hunting and prey searching, and linear features would facilitate linear travel and movement across pack territories. As wolves travel close to, or across early-successional forests and where habitat for primary prey is plentiful, I would expect greater sinuosity of movement paths as searching and hunting behaviours increase. Finally, I expected wolf movement to differ between daily (fine-scale use) and weekly (course-scale use) spatial scales. At the daily scale, short-term movements by wolves would indicate behaviours associated with hunting and searching. Alternatively, I expected weekly movements, which facilitate patrol and defense of territories, to result in greater use of caribou habitat as wolves had increased opportunities to use features in mountainous and boreal habitats (e.g., alpine, established game trails) during large-scale movements.

#### Methods

## Study Area and Wolf Telemetry

Located on the eastern slopes of the Rocky Mountains in northern British Columbia, the South Peace study area is approximately 12,000 km<sup>2</sup> (Figure 1, Chapter 1). Tumbler Ridge is located near the center of the area, which then extends northwest towards the town of Mackenzie, northeast towards Dawson Creek and south along the Alberta border. Four Biogeoclimatic Ecosystem Classification zones characterize the study area: Boreal White and Black Spruce (BWBS), Sub-Boreal Spruce (SBS), Engelmann Spruce – Subalpine Fir (ESSF), and Alpine Tundra (AT; Meidinger and Pojar 1991). Large-scale commercial forestry, natural gas, oil, mineral, and most recently, wind developments exist throughout the region (Sopuck 1985, Nitschke 2008). The cumulative effects resulting from these industrial developments have produced forested landscapes that are progressively younger and increasingly fragmented (see Chapter 2 for a more comprehensive description of the study area).

Between 2008 and 2010, 16 wolves were captured and fitted with GPS collars (Lotek Inc., Newmarket, Ontario, Canada, model: GPS 4400S). Collars were programmed to take a location fix every three hours (n = 14; two collars were programmed for high-frequency intervals and collected locations every 20 minutes) and were remotely downloaded from a fixed-wing aircraft approximately bimonthly during routine tracking flights. Data were examined for erroneous locations using the number of satellites required to obtain locations (2D or 3D) and visual inspection (Appendix B).

## **Defining Seasons**

I used past research to develop two biological seasons to model the movement of wolves: non-winter (April 16 – October 14) and winter (October 15 – April 15). Non-winter months included the time when wolves are responsible for the rearing and raising of pups and therefore, centralize around dens, rendezvous or homesites (Mech 1970, Ballard et al. 1991). By mid-October, pups are approximately six months old and have grown large enough to travel with the nomadic pack as they transition towards the winter months (Packard 2003). Winter extends through the breeding season until the wolves begin localizing around den sites between March and May (Mech and Boitani 2003).

## Movement Paths, Rates, and Sinuosity

I created movement paths using consecutive GPS collar locations recorded over daily and weekly intervals. These paths allowed me to compare the relationship between movement rate or path sinuosity and land cover, caribou habitat and disturbance variables. Paths generated from 24-hour relocation intervals allowed me to identify fine-scale behaviours and provided results that were comparable to past studies of wolf movement (Fritts and Mech 1981, Jędrzejewski et al. 2001, Walton et al. 2001, Whittington et al. 2005). Wolves patrol territories in cyclic patterns approximately every week (Jędrzejewski et al. 2001); therefore, I analysed movement patterns over a longer 7-day period.

I assumed a straight-line distance between consecutive GPS locations when inferring movement paths. I used Julian dates from the GPS collars to define the temporal extent of each 24-hour (i.e., Julian calendar date = 1, 2, 3, etc.) and 7-day path segment (i.e., Julian calendar dates 1 - 7, 8 - 14, 15 - 21, etc.). Movement paths were considered incomplete if the number of acquired locations was less than 50% of the total number of expected GPS fixes for each temporally constrained interval. I pooled movement paths across individual wolves; pooled movement paths provided sufficient sample size for statistical analysis. I calculated movement rate as the total distance travelled (km) by individual wolves for each daily and weekly interval. I calculated the sinuosity of each path as the total distance of all line segments divided by the net displacement (i.e., distance between the start and end locations of each path).

I used polygonal buffers around each movement path to quantify the characteristics of the landscape traversed by collared wolves. I used high-frequency location data (relocation interval = 20 minutes) to determine an appropriate buffer for each daily and weekly

movement path. I used the same buffer size for daily and weekly paths; a series of daily movements served as the foundation for calculating weekly movement paths. I grouped high-frequency locations into 24-hour intervals and applied 100% MCPs around each temporally constrained group of locations to represent the total area (km<sup>2</sup>) available to each of the collared wolves. The width of all buffers was determined and calculated as the median distance (km) across each daily MCP polygon.

#### Resource and Human Disturbance Variables

I drew from past research on wildlife-development interactions and observations of the study area to identify a number of variables that I hypothesized would influence the movement behaviours of wolves (Table 1, Chapter 2). I examined five classes of variables within each buffered polygon: forest cover, caribou habitat, distance to water, and distance to and density of disturbance features.

Habitat Variables. – Forest cover was estimated using the provincial Vegetation Resource Inventory (VRI; BC Ministry of Forests and Range, 2007a, b). I consolidated the vegetation types into four super-classes: alpine, conifer, deciduous, and mixed-other forests (Table 8). Each class was converted into a binary raster layer so the average value (%) could be extracted for each daily and weekly movement polygon. I also tested the seasonal importance of water (proximity) as an additional predictor of wolf movement across the landscape. Water features included lakes, rivers, creeks/streams, and reservoirs.

Values from the spatial resource selection function (RSF) analyses (Chapter 2) for Bearhole/Redwillow (BHRW) and Quintette caribou were extracted for each season. Nonwinter represented the median value for caribou habitat modeled during the spring, calving, and summer/fall, whereas winter was used in its original context.

Variable	Description
Alpine	high elevation with few or no trees with primary cover being rock, snow, herbs, shrubs, bryoids and terrestrial
	lichens
Conifer	includes black spruce (Picea mariana), tamarack (Larix laricina), subalpine fir (Abies lasiocarpa), lodgepole pine
	(Pinus contorta) and whitebark pine (P. albicaulis), other spruce varieties: Picea spp., Engelmann (P.
	engelmannii), white (P. glauca), hybrid (P. engelmannii x glauca),
Deciduous	includes aspen (Populus tremuloides), cottonwood (P. balsamifera), birch (Betula papyrifera)
(Decid)	
Mixed-Other	includes Douglas-fir (Pseudotsuga menziesii), upland areas dominated by talus, rock, snow, tailing ponds, herbs
	(forbs, graminoids), bryoids and shrubs
Water	distance to water (km)
BHRW	RSF values for caribou in the Bearhole/Redwillow herd
Quintette (Q)	RSF values for caribou in the Quintette herd
Road	distance to road (km)
SeisPipln	distance to seismic line and/or pipeline combined (km)
Cutblock (Ctblks)	distance to forestry cutblock (km)
Mine	distance to coal mine footprint (km)
Oil and Gas (OG)	distance to non-linear oil and gas well pad or facility pad $\geq 1$ hectare in size (km)
LF Dens	density (ha/km) of linear features on the landscape (roads, seismic lines, and pipelines)
NLF Dens	density (ha/km <sup>2</sup> ) of non-linear features on the landscape (cutblocks, mine, oil, and gas facilities)

Table 8. Description of variables used to model movement of wolves across the South Peace region of northeastern British Columbia.

There was no overlap in the range of the Lower and Upper Sukunka wolf packs and the BHRW caribou herd; thus, I did not apply RSF values to those movement paths. Similarly, because wolves in the Chain Lakes pack do not have opportunities to overlap with caribou in the Quintette herd, the caribou habitat variable was excluded from those seasonal movement models.

*Disturbance Features*. – I used databases from government and industry to identify the location of disturbance features across the South Peace region (BC Land and Resource Data Warehouse 2007, Oil and Gas Commission of BC 2009, West Fraser Timber Company Ltd., Western Coal, Inc., Peace River Coal Ltd.). Following methods from Chapter 2, I used the most parsimonious moving window (1.56 hectares), identified during the RSF analysis to calculate the density of industrial features (linear: ha/km; non-linear: ha/km<sup>2</sup>). I combined spatial data for forestry (cutblocks) and mine/oil/gas to create a variable representing the density of non-linear features (ha/km<sup>2</sup>). GIS calculations for distance and density were computed using IDRISI (The Andes Edition; Eastman 2006). I used Hawth's Tools and GME (Spatial Ecology LLC 2009) in ArcGIS 9.3 (2009; ESRI, Redlands, CA) to create and develop daily and weekly movement paths for wolves, as well as to attribute habitat, caribou RSF and disturbance values to movement paths.

## Modeling Movement of Wolves

I used mixed effects generalized linear models to statistically relate movement distance and sinuosity to landscape variables recorded within the area (km<sup>2</sup>) buffered around each 24-hour or 7-day movement interval. Pooling movement paths for wolves from all packs resulted in a nested sampling design. Adding a random effect accounted for additional variation that may have occurred among individuals or packs (Gillies et al. 2006,

Hebblewhite and Merrill 2008). I conducted a sensitivity analysis to determine if additional variation was best described using a random effect for individual wolf, pack, or wolf and pack. Each model contained a random effect for "pack".

I used linear regression to model movement rate. I used a square root transformation to normalize those data. Because of extremely non-normal data, I transformed the sinuosity measures into binary categories and applied logistic regression. I used the median value across each seasonal dataset to classify paths as high (1) or low (0) sinuosity.

I built a suite of 18 ecologically plausible candidate models to determine the influence of habitat and disturbance variables on wolf movement (Table 9). Variables for distance (km) and density (total area of features/unit area; linear features = ha/km, non-linear features = ha/km<sup>2</sup>) were modeled as linear and as 2-term Gaussian functions (distance to road + distance to road squared) for each season. I used tolerance scores (> 0.2) and visual inspection of bivariate correlation matrices to assess excessive multicollinearity. Where collinearity occurred between disturbance variables, I preferentially removed non-linear features to retain the oftentimes more abundant linear features.

I used the AIC<sub>c</sub> ( $\Delta$ ) difference to select the most parsimonious fixed effects linear or logistic regression model for each season (Burnham and Anderson 2002). If competing models were present, I considered the model with the smallest  $\Delta$  AIC<sub>c</sub> to be the most parsimonious. I applied the random effect to the most parsimonious model and reran the analysis to generate model coefficients. I then used the coefficient of determination ( $R^2$ ) to assess predictive fit for linear regression models. I partitioned wolf movement paths into training (80%) and testing (20%) groups.

Table 9. Candidate models to examine the movement of wolves monitored between 2008 - 2010 across the South Peace region of northeastern British Columbia. Each model (except Land cover) was fit as either a linear or Gaussian (\*squared) term depending on best fit for each movement parameter and season. Distance was measured in kilometers (km) and density was measured in hectares/unit area (linear features = ha/km and non-linear features = ha/km<sup>2</sup>).

Model Group	Model Name	Model Variables				
Habitat	Land cover	% land cover (alpine, conifer, deciduous, mixed-species)				
	Caribou/Water (CarWat)	Caribou RSF + water distance (Dist)				
	Caribou/Water (CarWat)*	Caribou RSF + water $(Dist)^2$				
	Landscape*	% land cover + Caribou RSF + water $(Dist)^2$				
Linear Features (LF)	Road Distance (Dist)	Landscape + Road Dist				
	Road Distance (Dist)*	Landscape + Road Dist <sup>2</sup>				
	LF (roads, seismic lines and/or pipelines) Distance (Dist)	Landscape + LF Dist				
	LF Distance (Dist)*	Landscape + LF $Dist^2$				
	LF Density (LF Dens)	Landscape + LF Dens				
	LF Density (LF Dens)*	Landscape + LF Dens <sup>2</sup>				
	LF Total (LF CE)	Landscape + LF Dist + LF Dens				
	LF Total (LF CE)*	Landscape + LF Dist <sup>2</sup> + LF Dens <sup>2</sup>				
Cumulative Effects (CE)	CE Distance (CE Dist)	Landscape + LF Dist + Non-Linear Feature (NLF) Dist				
	CE Distance (CE Dist)*	Landscape + LF Dist <sup>2</sup> + NLF Dist <sup>2</sup>				
	CE Density (CE Dens)	Landscape + LF Dens + NLF Dens				
	CE Density (CE Dens)*	Landscape + LF Dens <sup>2</sup> + NLF Dens <sup>2</sup>				
	CE Total (CE)	Landscape + LF Dist + LF Dens+ NLF Dist + NLF Dens				
	CE Total (CE)*	Landscape + LF Dist <sup>2</sup> + LF Dens <sup>2</sup> + NLF Dist <sup>2</sup> + NLF Dens <sup>2</sup>				

Using the withheld data, I assessed residuals to determine if there was a relationship between the observed values and the predicted movement rates. I also evaluated fit for the top-ranked logistic regression (sinuosity) model by calculating the area under the receiver operating characteristic curve (ROC; Hosmer and Lemeshow 2000).

# Results

I used a total of 25,254 GPS locations collected from wolves to develop 3,749 daily and 493 weekly movement paths. Two wolves of the Chain Lakes pack provided an additional 8,493 high-frequency locations (n = 168 daily MCPs). The daily area used by these wolves had a median width of 4.44 km; I used these data to identify the area of use around each daily and weekly movement path. In general, I observed variation between annual and seasonal movement rates and path sinuosity when movements were pooled for collared wolves across the South Peace study area (Figure 18). As predicted, movement rates of wolves were highest during the non-winter season. However, seasonal variation in movement was greater than variation in the use or proximity to linear and non-linear features, suggesting that other factors also influenced the movement dynamics of wolves (Figure 19).

For each season, the most parsimonious models for daily and weekly movement rates were also the most complex and contained variables for all habitat cover types and humancaused disturbances (Table 10). Models with a random effect for pack performed best across all seasonal movement rate and sinuosity models. One model (daily movement rate during the winter season) was an exception and performed better with a random effect for individual wolf. More than 30% of the variation in movement rate was explained by the weekly (nonwinter  $R^2 = 0.3429$ , winter  $R^2 = 0.5012$ ) regression models.



Figure 18. Mean monthly (±SE) movement rates (km/day) and sinuosity for wolf movement paths sampled daily across the South Peace region of northeastern British Columbia. Movement paths were pooled for wolves by year (A, B) as well as across all years (C; 2008 – 2010).



Figure 19. Mean ( $\pm$ SE) monthly (2008 – 2010) movement rates (A, B) and sinuosity (C, D) for daily (km/day) and weekly (km/week) sampling periods as they relate to densities of linear (ha/km) and non-linear features (ha/km<sup>2</sup>) across the South Peace region of northeastern British Columbia.

Table 10. Number of parameters (k), Akaike's Information Criterion  $(AIC_c)$  and  $AIC_c$  weights  $(AIC_w)$  for linear regression models describing seasonal daily and weekly movement rates of wolves. Models were developed for wolves monitored between 2008 and 2010 across the South Peace region of northeastern British Columbia. Model covariates are given in Table 9 and sample size of seasonal movement paths is indicated in parentheses.

	Daily								Weekly					
		Non-Winter $(n = 1599)$			Winter $(n = 1403)$			Non-Winter $(n = 212)$			Winter $(n = 186)$			
Model	k	AIC <sub>c</sub>	ΔΑΙΟ	AIC <sub>w</sub>	AIC <sub>c</sub>	ΔΑΙΟ	AIC <sub>w</sub>	AIC <sub>c</sub>	ΔAIC	AIC <sub>w</sub>	AIC <sub>c</sub>	ΔΑΙΟ	AICw	
Land cover	5	5172.64	97.49	< 0.001	4333.39	226.19	< 0.001	327.47	21.50	< 0.001	349.33	81.57	<0.001	
CarWat	4	5220.72	145.57	< 0.001	4334.25	227.05	< 0.001	349.14	43.17	< 0.001	349.41	81.65	<0.001	
CarWat*	5	5209.19	134.04	< 0.001	4305.40	198.19	< 0.001	347.59	41.62	<0.001	350.59	82.83	< 0.001	
Landscape*	9	5166.58	91.43	< 0.001	4302.65	195.45	< 0.001	330.23	24.26	<0.001	342.88	75.11	< 0.001	
Road Dist	9	5177.73	102.58	< 0.001	4329.89	222.68	< 0.001	331.47	25.50	<0.001	346.86	79.10	<0.001	
Road Dist*	11	5165.58	90.43	< 0.001	4278.91	171.71	< 0.001	331.67	25.70	<0.001	342.34	74.58	<0.001	
LF Dist	10	5179.74	104.59	< 0.001	4331.52	224.31	< 0.001	333.55	27.58	< 0.001	344.81	77.05	<0.001	
LF Dist*	13	5162.24	87.09	< 0.001	4274.96	167.75	< 0.001	323.62	17.65	<0.001	335.45	67.69	<0.001	
LF Dens	9	5180.51	105.36	< 0.001	4329.65	222.45	< 0.001	331.24	25.27	<0.001	345.45	77.69	<0.001	
LF Dens*	11	5165.81	90.66	< 0.001	4276.23	169.03	<0.001	328.12	22.15	<0.001	316.67	48.90	< 0.001	
LF CE	11	5181.76	106.61	< 0.001	4333.38	226.18	< 0.001	334.89	28.92	<0.001	346.91	79.15	<0.001	
LF CE*	15	5157.87	82.72	<0.001	4204.44	97.24	< 0.001	316.03	10.06	0.01	293.83	26.07	<0.001	
CE Dist	12	5154.54	79.39	< 0.001	4330.62	223.42	<0.001	329.24	23.27	< 0.001	345.00	77.24	<0.001	
CE Dist*	17	5131.77	56.62	< 0.001	4249.40	142.20	<0.001	316.38	10.41	0.01	338.90	71.13	<0.001	
CE Dens	10	5164.93	89.78	<0.001	4331.52	224.32	< 0.001	332.10	26.13	<0.001	346.01	78.25	<0.001	
CE Dens*	13	5130.10	54.95	<0.001	4260.68	153.48	<0.001	320.37	14.40	<0.001	320.36	52.60	< 0.001	
CE	14	5154.84	79.69	<0.001	4329.71	222.50	<0.001	333.65	27.68	<0.001	327.71	59.95	<0.001	
CE*	21	5075.15	0.00	1.00	4107.20	0.00	1.00	305.97	0.00	0.99	267.76	0.00	1.00	

\*Gaussian (squared) term

When modeling daily movement rates, less than 20% of the overall variation was explained (non-winter  $R^2 = 0.117$ , winter  $R^2 = 0.1746$ ) by variables representing habitat and disturbance features. Inspection of residuals indicated the ability of models to predict daily and weekly movement rates for wolves was generally good as values were evenly dispersed around zero.

Similar to movement rate, the most parsimonious daily logistic regression models for sinuosity were also the most complex in each candidate set (Table 11) and received strong support (AIC<sub>w</sub> > 0.95 for both seasons). Area under the curve (AUC) scores indicated poor predictive performance for the best-ranked seasonal models (non-winter AUC = 0.55, winter AUC = 0.62). Results from the weekly sinuosity models indicated multiple candidate models had reasonable support compared to the top-ranked model (Table 11). Models were not averaged due to the complexity of the random effect. During the non-winter season, the most parsimonious model for weekly sinuosity included covariates for forest cover, distance to water, caribou habitat and distance to linear features. The top model for weekly sinuosity during winter was similar to non-winter, but included covariates for linear feature density (in addition to distance) across the landscape. Model fit was generally poor for weekly sinuosity models during the non-winter season (AUC = 0.64), but improved during winter (AUC = 0.75).

## Cumulative Effects of Industrial Disturbances on Seasonal Wolf Movements

*Non-Winter.* – Daily movement rates for wolves decreased as they traveled closer to water features and cutblocks (Figure 20). However, the large confidence interval surrounding the coefficient for cutblocks suggested considerable variation in response by wolves.

Table 11. Number of parameters (k), Akaike's Information Criterion (AIC<sub>c</sub>) and AIC<sub>c</sub> weights (AIC<sub>w</sub>) for logistic regression models describing seasonal daily and weekly sinuosity of wolf movements. Models were developed for wolves monitored between 2008 and 2010 across the South Peace region of northeastern British Columbia. Model covariates are given in Table 9 and sample size of seasonal movement paths is indicated in parentheses.

	Daily							Weekly					
		Non-Winter $(n = 1599)$			Winter $(n = 1403)$			Non-Winter $(n = 212)$			Winter $(n = 186)$		
Model	<u>k</u>	AIC <sub>c</sub>	ΔΑΙΟ	AIC <sub>w</sub>	AIC <sub>c</sub>	ΔAIC	AICw	AIC <sub>c</sub>	ΔAIC	AIC <sub>w</sub>	AIC <sub>c</sub>	ΔΑΙΟ	AIC
Land cover	5	2220.91	8.88	0.01	1950.97	30.61	<0.001	300.58	3.75	0.05	250.70	10.21	< 0.001
CarWat	4	2222.94	10.91	<0.001	1951.25	30.89	<0.001	299.26	2.43	0.10	263.77	23.28	<0.001
CarWat*	5	2221.59	9.56	0.01	1951.54	31.18	<0.001	301.16	4.34	0.04	264.82	24.33	< 0.001
Landscape*	9	2223.52	11.49	< 0.001	1954.94	34.57	<0.001	305.04	8.22	0.01	240.68	0.19	0.24
Road Dist	9	2226.88	14.85	< 0.001	1954.96	34.60	<0.001	304.95	8.12	0.01	243.46	2.97	0.06
Road Dist*	11	2217.98	5.96	0.04	1955.19	34.83	<0.001	309.25	12.43	<0.001	244.43	3.94	0.04
LF Dist	10	2227.13	15.11	<0.001	1954.94	34.58	< 0.001	297.92	1.09	0.20	244.14	3.65	0.04
LF Dist*	13	2221.83	9.81	0.01	1956.63	36.26	< 0.001	304.52	7.69	0.01	246.54	6.05	0.01
LF Dens	9	2226.70	14.68	< 0.001	1957.07	36.71	<0.001	303.62	6.80	0.01	244.18	3.69	0.04
LF Dens*	11	2225.78	13.75	< 0.001	1953.28	32.92	< 0.001	307.80	10.98	<0.001	242.31	1.82	0.11
LF CE	11	2228.67	16.64	<0.001	1956.66	36.30	<0.001	300.08	3.25	0.07	244.36	3.87	0.04
LF CE*	15	2223.77	11.74	<0.001	1956.09	35.72	<0.001	305.96	9.14	<0.001	246.77	6.28	0.01
CE Dist	12	2225.98	13.95	<0.001	1951.49	31.13	<0.001	296.82	0.00	0.35	247.18	6.69	0.01
CE Dist*	17	2224.52	12.50	<0.001	1933.46	13.10	<0.001	304.09	7.27	0.01	250.94	10.45	<0.001
CE Dens	10	2223.79	11.76	<0.001	1957.02	36.66	<0.001	300.67	3.85	0.05	242.17	1.68	0.12
CE Dens*	13	2218.63	6.60	0.03	1951.75	31.39	<0.001	307.12	10.30	< 0.001	240.49	0.00	0.27
CE	14	2227.79	15.76	< 0.001	1955.33	34.97	<0.001	299.51	2.69	0.09	248.48	7.99	< 0.001
CE*	21	2212.03	0.00	0.88	1920.36	0.00	1.00	310.40	13.57	<0.001	252.27	11.78	<0.001

\*Gaussian (squared) term.



Figure 20. Coefficients for the parameters in the most parsimonious mixed-effects models for daily (A; n = 1,599) and weekly (B; n = 212) movement rates during the non-winter season for wolves in the South Peace region of northeastern British Columbia. An asterisk (\*) indicates a Gaussian term and model variables are given in Table 8.

Higher daily and weekly movement rates were associated with high densities of non-linear features (oil and gas well sites, facility stations, coal mines). Weekly movement rates decreased slightly near coal mines, but increased in alpine habitats. Roads were the only linear feature wolves responded to during the non-winter months; movement rates decreased as wolves travelled within close proximity to roads at the weekly scale.

During the non-winter season, movement paths became increasingly linear as wolves travelled near deciduous habitats and areas with higher densities of non-linear features (Figure 21). In addition, linear movements increased slightly near roads and coal mines as wolves traversed across the landscape. Sinuosity of weekly movement paths increased near conifer forests, mixed-species forests and cutblocks. At the daily scale, I observed a slight increase in sinuous movements in habitats of high quality for the BHRW and Quintette caribou herds. Similarly, sinuosity of weekly paths increased slightly in BHRW, but not Quintette habitat.

*Winter.* – Daily movement patterns of wolves during the winter season were influenced more by forest cover, caribou habitat and disturbance features than during nonwinter (Figures 21, 22). Daily movement rates decreased in habitats dominated by conifer forests; weekly movement rates increased in mixed-species forests. Movement rates decreased as wolves approached water features and cutblocks (Figure 22). Although to a lesser extent, movement rates of wolves also decreased near roads, seismic lines, pipelines, and mines during winter. However, as densities of linear and non-linear disturbance features increased across the landscape, wolves increased daily and weekly movement rates. Daily movement rates also increased in habitats important to BHRW caribou.



Figure 21. Coefficients for the parameters in the most parsimonious mixed-effects models for daily (A; n = 1,599) and weekly (B; n = 212) sinuosity during the non-winter season for wolves in the South Peace region of northeastern British Columbia. An asterisk (\*) indicates a Gaussian term and model variables are given in Table 8.



Figure 22. Coefficients for the parameters in the most parsimonious mixed-effects models for daily (A; n = 1,403) and weekly (B; n = 186) movement rates during the winter season for wolves in the South Peace region of northeastern British Columbia. An asterisk (\*) indicates a Gaussian term and model variables are given in Table 8.

Sinuosity of daily and weekly paths decreased in habitats dominated by deciduous forest (Figure 23). Conifer forests facilitated increased daily sinuosity, but decreased sinuosity of weekly movement paths. Wolves demonstrated linear travel in alpine habitats at the scale of a week, but not the day. During winter, the sinuosity of wolf movements increased slightly in habitats of high quality for Quintette caribou. Wolves demonstrated increased linear travel where the density of non-linear features was high and in habitats valued as important to BHRW caribou. As wolves traveled close to coal mines, I observed a slight relative increase in sinuous movements.



Figure 23. Coefficients for the parameters in the most parsimonious mixed-effects models for daily (A; n = 1,403) and weekly (B; n = 186) sinuosity during the winter season for wolves in the South Peace region of northeastern British Columbia. An asterisk (\*) indicates a Gaussian term and model variables are given in Table 8.
## Discussion

I used two parameters of movement as an index of wolf behaviour across forested boreal and mountainous environments occupied by woodland caribou. Considering the large range of factors that influence animal movement and the broad spatiotemporal scales of analysis I developed, the majority of explanatory models had strong statistical relationships. My results indicated that the cumulative effects from industrial disturbances had an influence on the movement behaviour of wolves in both environments. Past studies of wolf movement have not quantified compounding effects from multiple sources of human disturbances (e.g., forestry and oil/gas extraction), determined how these behaviours change across spatiotemporal scales, or examined how wolves move across areas supporting populations of caribou (but see Kuzyk et al. 2004, Neufeld 2006, Houle et al. 2010, Latham et al. 2011c). Following my predictions, the influence of habitat and development features on movement varied across season and scale (Table 12).

At the weekly scale, my results indicated that movement rates were generally higher for wolves across the South Peace region during the non-winter months (Figure 19). If wolf packs across the study area successfully reproduced throughout the duration of this study, increased movement rates (up to 2 km/hr) could result from wolves rapidly travelling back to dens or homesites after feeding bouts (Mech 1994). However, as responsibilities associated with pup care are dependent on an individual's pack status and because I pooled movement rates, behavioural interpretation remains challenging without investigating the direct ecological determinants of path characteristics (e.g., behaviour, activity type or association with a den or homesite).

Table 12. The predicted and observed variation ( $\uparrow$  = increased,  $\downarrow$  = decreased) in movement using movement rate and path sinuosity as indices of wolf behaviour across the South Peace region of northeastern British Columbia. If observed movements were scale- or season-dependent, results are indicated in parentheses (seasonal: NW = non-winter, W = winter; scale: daily or weekly).

		Movement Index			
		Movement Rate		Path Sinuosity	
Factor	Hypothesized Movement Response of Wolves	Predicted	Observed	Predicted	Observed
Season/Scale					
Non-winter	Movement rates increase in response to reproduction and greater availability of prey. Sinuosity of movements decrease concurrent with less human disturbance.	ſ	ſ	Ţ	Not statistically influential
Winter	Movement rates and sinuosity decrease in response to greater snow accumulation and availability of vulnerable prey.	Ļ	Ļ	Ļ	Not statistically influential
Daily Movements	Movement rates decrease and sinuosity increase as short-term movements are associated with hunting and searching of prey.	Ļ	Ļ	Î	Î
Weekly Movements	Movement rates increase and sinuosity decrease as long-term movements are associated with territory use and patrol.	ţ	ſ	Ļ	Ļ
Habitat Class					
Alpine	Movement rates increase and sinuosity decrease in response to reduced travel resistance.	1	↑ (weekly)	Ļ	↓ (weekly)
Forest cover type: conifer	Movement rates decrease and sinuosity increase in response to greater prey availability and selection of habitats for den/homesites.	Ļ	NW: Not statistically influential, W: $\downarrow$ (daily)	¢	<b>NW: ↑, W: ↑</b>
Forest cover type: mixed-species	Movement rates decrease and sinuosity increase in response to greater prey availability and selection of habitats for den/homesites.	Ţ	NW: Not statistically influential, W: ↑ (weekly)	Î	NW: ↑, W: ↑ (weekly)
Forest cover type: deciduous	Movement rates decrease and sinuosity increase in response to greater prey availability and selection of habitats for den/homesites.	Ļ	NW: Not statistically influential	1	NW:↓(weekly), W:↓

Table 12. Continued.

***************************************		Movement Index			
		Movement Rate		Path Sinuosity	
Factor	Hypothesized Movement Response of Wolves	Predicted	Observed	Predicted	Observed
Caribou Habitat					
RSF Caribou - BHRW (Ch.2)	Movement rates decrease and sinuosity increase in response to greater availability of caribou as prey.	Ļ	NW: Not statistically influential, W: ↑	1	NW: ↑, W: ↓ (daily)
RSF Caribou - Quintette ( Ch.2)	Movement rates decrease and sinuosity increase in response to greater availability of caribou as prey.	Ļ	Not statistically influential	1	† (slight)
Human Disturbances	_				
Linear feature - Proximity	Movement rates increase and sinuosity decrease in response to reduced travel resistance. Linear features facilitate rapid travel by wolves.	Î	NW:↓(roads, weekly), W:↓(daily)	Ţ	NW:↓(roads, weekly), W: Not statistically influential
Non-linear feature - Proximity	Movement rates decrease and sinuosity increase in response to greater prey availability.	Ţ	NW: ↓ (cutblocks, daily; mines, weekly), W: ↓ (daily)	Î	NW: ↑ (cutblocks, daily), ↓ (mines, weekly), W: ↓ (mines, daily)
Linear feature - Density	Movement rates increase and sinuosity decrease in response to reduced travel resistance and low human- use.	Î	NW: Not statistically influential, W: ↑	Ļ	Not statistically influential
Non-linear feature - Density	Movement rates decrease and sinuosity increase in response to greater prey availability.	Ļ	1	1	$\downarrow$ (daily)

At the scale of weekly movements, wolves traveled through alpine habitats at greater speeds, but only during the non-winter months (Table 12). Alpine habitats did not affect movement rates in winter, but resulted in more linear travel as wolves traversed the landscape. Past studies found that wolves avoided conifer forests during winter (Kunkel and Pletscher 2001, Houle et al. 2010, Milakovic et al. 2011). In partial support to this, my results suggest that conifer forests facilitated linear, or direct travel through these forests as wolves traversed the landscape during winter. Linear travel has been shown to aid in the maintenance of territories and facilitate the element of surprise during hunting bouts (Mech et al. 1998). Dissimilar to the abovementioned studies, however, slow and sinuous daily movements in conifer habitats indicated that wolves also demonstrated behaviours associated with brief hunting bouts.

Unlike conifer and mixed-species forests, deciduous habitats facilitated linear movements during both seasons. Hebblewhite et al. (2009) and Laurian et al. (2008) reported that populations of moose, deer, and wolves were better supported in post-harvested forests where deciduous species prevailed. My results did not detect increases in sinuosity or variations in the rate of movement at either daily or weekly scales across such habitats. Linear travel by wolves through deciduous forests during winter might suggest ungulates seasonally shift habitat use, or that wolves, by remaining unpredictable, avoid creating localized reductions in prey (Mech and Boitani 2003, Jędrzejewski et al 2001, Fortin et al. 2005). The adoption of linear movements by wolves in deciduous forests could also be in response to environmental cues or interactions with the structure of the landscape which I did not assess during this study. Furthermore, sinuous movements associated with hunting may become detectable only at finer observational scales (Morales et al. 2010).

Water features influenced movement parameters at both spatiotemporal scales (Table 12). Throughout the year, wolves traveled more slowly near water, but this response was statistically significant for daily models only. Lowland or riparian habitats provide wolves with increased opportunities to hunt moose, deer, and beaver and are also important in the selection of natal dens and homesites (Mech 1970, Packard 2003, Latham 2009). As important as lakes, rivers, or creeks may be for prey searching and hunting, water features did not facilitate direct travel in winter, as weekly movement paths were increasingly sinuous.

Habitats important to caribou did not influence the movement rates of collared wolves during the non-winter season, although sinuosity increased slightly at both scales during this period. Spatial separation between BHRW caribou and wolves may occur in the boreal forest as wolves were observed travelling more rapidly in habitats classified as black spruce, tamarack, or other peatland-type complexes – habitats that may also become seasonally void of non-caribou prey (i.e., moose; James et al. 2004, Chapter 2). However, if populations of caribou remain small and isolated, even an opportunistic kill in these habitat types will influence the decline of small remnant populations (Kinley and Apps 2001, Festa-Bianchet et al. 2006, McLellan et al. 2010).

In contrast to movements in habitats used by caribou in the BHRW herd, the sinuosity of movement paths for wolves increased slightly in habitats used by Quintette caribou (Table 12). A covariate representing density of primary prey, which is unavailable across the South Peace region, would further our understanding of predation behaviour by wolves in caribou habitat as well as how movements through particular habitats influence other inter-specific interactions. My study provides supportive evidence (i.e., prey selection, count and

movement analyses) that encounters between caribou and wolves resulting from increased use of disturbance features is less significant to population declines than the potential number and variety of alternate prey available to wolves across the landscape (McCutchen 2007, Latham 2011a, b, Tremblay-Gendron 2012).

Industrial disturbances influenced the movement behaviour of wolves at both spatiotemporal scales throughout the year. Practices related to forestry, natural gas, oil, and coal extraction all rely on an affiliated network of roads for site access. During the nonwinter months, wolves decreased weekly travel rates and sinuous movements near roads. Levels of human activity drop during the non-winter months, thus allowing low-risk opportunities for wolves to travel along road corridors for short intervals of time.

During winter, close proximity of wolves to roads may have been associated with searching and hunting for prey (Table 12). Moose select habitats near roads to forage not only on abundant vegetation and accumulating mineral deposits, but also to travel across seasonal ranges (Fraser and Thomas 1984, Child et al. 1991, Rea 2003, Laurian et al. 2008). If roads were simply used by wolves to increase travel efficiency, I would expect an increase in movement rates and linear travel. My data do not support this hypothesis as increased linear movements were observed only at larger spatial scales during non-winter, when human activity related to industrial activities is less. Therefore, I suspect that road corridors are more important for hunting than increased travel efficiency.

The cumulative effects of roads and other linear features had the greatest influence on wolf movements at the daily scale during winter. Daily movement rates decreased near seismic lines and pipelines (in addition to roads) until these features became abundant across the landscape, at which point rates increased. In conjunction with decreasing rates, the

cumulative densities of roads, seismic lines and pipelines did not result in more linear travel for wolves at either the daily or weekly scale. Slower movement rates during winter suggest that wolves hunt along these corridors, but that behaviour is restricted to the linear corridor, at least for the scales of movement that I observed.

Contrary to movements near individual linear features, wolves travelled quickly through habitats with high densities of linear features (Table 12). This suggests that there may be a landscape effect, where wolves can exploit individual features within their range for hunting, but high densities of features, and associated human disturbance, result in the avoidance of such areas. Similar avoidance responses of high densities of linear features were noted for wolves studied in Alberta and Quebec (James 1999, Whittington et al. 2005, Hebblewhite and Merrill 2008, Houle et al. 2010).

Non-linear industrial features affected movement parameters of wolves more consistently than linear features at both scales. Movement rates decreased each season near forestry cutblocks and coal mines, but increased at both scales once the density of features increased (Table 12). The initial phases of exploration or construction associated with forest harvesting and oil and natural gas extraction result in high levels of disturbance to wildlife (Bradshaw et al. 1997). Well sites and other oil and gas facilities differ from cutblocks in that human presence occurs throughout the year once initial developments are complete. Across the South Peace region, activity at such sites peaks between September and December; increased rates and linear movements near oil and gas extraction facilities during winter suggest wolves move rapidly through these areas in response to higher levels of human activity (Houle et al. 2010, Energy and Resources Conservation Board 2011). For this study, I did not classify the age of disturbance features, or the level of human activity

associated with each disturbance type. However, such data could contribute to our understanding of the movement behaviours of wolves relative to prey availability and wolf tolerance for human presence.

In conclusion, habitat features had a strong influence on the movement parameters of wolves when considering broad spatiotemporal scales. Disturbance features facilitated behaviours associated with hunting and searching more during winter. In addition, wolves generally increased linear movements in winter when territory patrol intensifies during the breeding season. As suggested by Mech et al. (1998), linear travel may also facilitate the element of surprise during hunting. Wolves decreased movement rates when close to disturbance features, suggesting that hunting behaviours are associated with those sites. Increased movement rates and linear travel through habitats containing high densities of disturbance features suggest wolves avoid spending time in high-risk areas associated with human presence. Due to the complexity of cumulative effects from activities associated with resource exploration and extraction, I was unable to detect obvious correlations between wolf movement and increased predation risk for caribou. However, patterns of wolf movement (i.e., increased sinuosity and decreased movement rates) indicate caribou are most vulnerable to predation when in close proximity to disturbance features (Table 12).

Recorded movements provide researchers with an opportunity to better understand population dynamics as they relate to finer-scale animal behaviours (Turchin 1998). However, it is important to consider the scale of data collection, sample size and accuracy of locations when interpreting behavioural patterns from animal movement paths. My results provide some novel insights on the responses of wolves to landscape heterogeneity, but only

across a small range of behavioural scales and with limited inference to the mechanisms influencing movement.

Quantifying movements of wolves across two spatial scales furthers our understanding of wolf distribution in habitats supporting populations of caribou within a matrix of industrial developments. Daily movements of collared animals provide evidence that wolf behaviour is driven by a combination of seasonal life cycle stages, environmental factors, prey availability and human disturbances (Peters and Mech 1975, Bibikov et al. 1985, Jędrzejewski et al. 2001). Weekly movements corroborate that wolf behaviour is associated with territory maintenance and patrol (Mech et al. 1998, Jędrzejewski et al. 2001). In conjunction with past studies, my results demonstrate that movement behaviours of an apex predator are seasonally influenced by complex relationships that occur at multiple spatiotemporal scales (Johnson et al. 2002a, Morales and Ellner 2002). Chapter 4: General Research Summary

Woodland caribou are a species of increasing conservation concern. Habitat alteration, disturbance and predation have resulted in population declines across much of their distribution (Vors and Boyce 2009, Festa-Bianchet et al. 2011). Activities related to large-scale resource exploration and extraction displace caribou from areas of their range and result in early seral habitats. This change in landscape structure increases the accessibility of caribou habitat, influences movement efficiency of predators, and supports a broader distribution and density of predators that use caribou as a secondary or alternate prey species (Fuller and Keith 1981, James et al. 2004, Johnson et al. 2004a, Wittmer et al. 2007, DeCesare et al. 2010).

My study was conducted at a regional-scale and was designed to quantify the impacts of a variety of human-disturbance features on wolf and caribou interactions across a rapidly developing landscape in northeastern British Columbia. Because caribou herds within the study area winter in different habitats (Figures 2, 3; Appendix A), I quantified seasonal variations in wolf distribution in the context of herd-specific distribution strategies. To address these objectives, I used animal locations collected with global positioning system (GPS) collars, field data and information theoretic model comparisons to develop seasonal resource selection functions (RSFs) for caribou, count models of habitat occupancy by wolves and movement parameters that served as indices of wolf behaviour.

In Chapter 2, I used RSFs to quantify the spatial relationships between two herds of collared northern woodland caribou and a number of variables that were hypothesized to influence their distribution. I then used a count model to relate the number of wolf locations within a habitat selection unit (HSU) to covariates that represented environmental or industrial features that might explain the seasonal distribution of wolves. Count models

contained two parts; similar to RSFs, the binary portion of the count model represented the probability of occurrence of wolves, while the count portion represented the relative frequency of use in areas occupied by wolves (Nielsen et al. 2005, Sawyer et al. 2006). Therefore, this technique had greater power, relative to the RSFs for caribou, to describe the differential use of resources by wolves (Nielsen et al. 2005).

Habitat selection for both the Bearhole/Redwillow (BHRW) and Quintette herds of caribou were best described using a combination of forest cover, forest age, solar insolation, and distance to and density of disturbance features for all four seasons (spring, calving, summer/fall, and winter). BHRW caribou selected for mature and late-successional forests dominated by black spruce, tamarack and subalpine fir; these caribou expanded their use of the winter range to include pine forests of late succession. Caribou in both herds were at relatively low risk of increased predation by wolves during winter (Table 13). Black spruce and tamarack forests were rarely selected by either of the two overlapping packs of wolves. Furthermore, the Chain Lakes and Onion Creek packs avoided habitats classified as high quality for BHRW caribou throughout the winter months. Quintette caribou consistently selected alpine, subalpine, spruce and pine-leading habitats year round; wolves demonstrated avoidance behaviours of habitats selected by caribou in the Quintette herd during all three seasons (non-winter, early winter and late winter).

The frequency of occurrence of wolves across their seasonal range was best described using a combination of forest class, forest age, caribou habitat, and cumulative effects from anthropogenic disturbances.

Table 13. Hypothetical risk of wolves encountering caribou across the South Peace region of northeastern British Columbia. Level of risk (low, low-moderate, moderate or high) is based on the results from the resource selection functions (RSFs) for caribou, and count and movement models for wolves that quantified the distribution and movement ecology of GPS-collared animals.

Habitat/Disturbance Type	Risk of Encounter	Supporting Analysis	Comments
Alpine	Low	RSF, Count, Movement	Wolves generally avoided and increased linear movements across alpine habitats.
Conifer	Moderate	RSF, Movement	Wolves selected for early seral forests.
Pine	Moderate	RSF, Count	Wolves selected for early seral forests.
Deciduous	Low	RSF	Caribou avoided deciduous habitats.
Mixed-species	Low	RSF	Caribou avoided mixed-species habitats.
Black spruce/ tamarack/peatland	Low	Count, Movement	Wolves avoided these lowland habitats.
Water	Low	RSF, Count	Caribou avoided habitats near lakes, rivers or creeks.
Caribou habitat - RSF values for BHRW	Low-Moderate	RSF, Count, Movement	Wolves selected early seral, subalpine fir, pine, and conifer forests (seasonal). Wolves avoided black spruce/tamarack/peatland in addition to BHRW RSF habitats during winter.
Caribou habitat - RSF values for Quintette	Low-Moderate	RSF, Count, Movement	Wolves avoided Quintette RSF habitats throughout the year. Wolves increased sinuous movements in subalpine fir, pine and conifer habitats.

## Table 13. Continued.

Habitat/Disturbance Type	Risk of Encounter	Supporting Analysis	Comments
Roads	Low	RSF, Count, Movement	Both caribou and wolves avoided roads. However, decreased movement rates suggest habitats near roads can have some encounter risk to caribou.
Seismic lines	Low - Moderate	RSF, Count, Movement	BHRW selected habitats near seismic lines during calving and winter. Wolves avoided and were infrequently located near these habitats throughout the year. However, slight decreases in movement rates suggest moderate encounter risk to caribou during winter.
Pipelines	Low - Moderate	RSF, Count, Movement	BHRW selected habitats near pipelines during calving and winter. Wolves avoided and were infrequently located near these features throughout the year. However, slight decreases in movement rates suggest moderate encounter risk to caribou during winter.
Cutblocks	High (NW), Moderate (W)	RSF, Count, Movement	BHRW selected habitats near cutblocks during spring and calving. Wolves reduced use of cutblocks during winter.
Mine/Oil/Gas features (MOG)	Low - Moderate	RSF, Count, Movement	Quintette selected habitats near MOG features during spring and winter. Caribou and wolf co-occurrence is most likely during the late-winter months.
High densities of linear features	Low - Moderate	RSF, Count, Movement	BHRW selected habitats near linear features during calving and summer/fall and are therefore, at moderate encounter risk as Chain Lakes wolves were observed infrequently selecting these habitats during the non-winter months. Wolves generally increased movement rates across these habitats.

Similar to caribou, wolves residing in mountainous regions selected for pine-dominated forests throughout the year, but unlike caribou, wolves frequented habitats of early succession. Broadleaf forests, mixed-species forests, water, and shrub habitats were important indicators of wolf occurrence, but not of caribou occurrence. Two packs of wolves residing in mountainous portions of the study area demonstrated selection of habitats used by boreal caribou. However, these wolves were often found distant to the known range of the BHRW caribou during winter (Table 13; Appendix A).

During all four seasons, caribou demonstrated a strong avoidance of linear features that can serve as travel corridors or habitat for predators and other ungulate species. Also, linear features were the most likely places for human activity, possibly displacing caribou from adjacent habitats. Roads were avoided most strongly during the winter months by both herds and were the only features consistently avoided by caribou each season (up to distances between 3.5 and 11 km). Similarly, high densities of linear features influenced the seasonal distribution of caribou. Winter is the busiest season for activities related to petroleum and forestry exploration and development and could explain the strong avoidance of roads, seismic lines, and pipelines.

Caribou in the BHRW herd did select habitats within close proximity to and with increased densities of linear features (seismic lines and pipelines) during calving, summer/fall and winter. Selection of habitats near linear sites suggests that caribou can tolerate some levels of disturbance. Alternatively, the high level of industrial activity across the range of the BHRW may offer few intact habitats distant from linear features. Caribou may also show long-term fidelity to habitats that are degraded, but now act as an ecological sink relative to disturbance or occurrence of predators (Schlaepher et al. 2002, Faille et al.

2010). Similar to caribou, wolves in all four packs demonstrated avoidance of linear features during each of the three seasons. Furthermore, I modeled a low frequency of wolf occurrence in habitats with high densities of roads, seismic lines and/or pipelines. Avoidance behaviours are likely due to the direct and indirect risks associated with exposure to areas used by humans (i.e., mortalities from increased access for hunting, trapping, and vehicular collisions) and my results suggest that cumulative densities of these features across the majority of the study area high (Mech et al. 1988, Fuller 1989, Mladenoff et al. 1995, Callaghan 2002, Person 2008).

Non-linear disturbances across the landscape also influenced the distribution and occurrence of wolves and caribou (Table 13). Caribou in the boreal forest responded differently to cutblocks than did caribou in the mountains. BHRW caribou selected habitats near individual cutblocks during spring, calving, and winter, but were more sensitive to increased densities of cutblocks during the summer/fall and winter seasons. Quintette caribou also avoided habitats with higher densities of cutblocks during winter, but selected these habitats most strongly during calving. These results indicate that calving sites occur adjacent to early-successional forests and that selection of particular habitat characteristics may take precedence over the risks associated with spending increased amounts of time near early seral forests (Faille et al. 2010). Also, both herds of caribou may be demonstrating some seasonal tolerance to regenerating cutblocks; there can be a time lag of 20 years between the initial cut and the regeneration of high-quality habitats for moose that can result in the eventual extirpation of caribou from those areas (Nielsen et al. 2005, Vors et al. 2007). Similar to caribou, wolves in the boreal and mountainous portions of the study area occurred in habitats closer to, and with higher densities of cutblocks (and roads) during the non-winter

season (Table 13). Wolves presumably selected those habitats for increased hunting opportunities of moose and deer (Laurian et al. 2008, Hebblewhite et al. 2009) or because they were suitable for denning or homesites.

Caribou were located more distant than random from features associated with the development of oil and gas deposits during calving, summer/fall, and winter, but demonstrated the greatest avoidance during calving (BHRW) and summer/fall. Wolves in the Chain Lakes pack did not frequent areas with relatively high densities of oil or gas features during the non-winter season. For wolves in the boreal forest, there was no strong pattern of selection or avoidance of these features. Caribou of the Quintette herd avoided coal mines up to a distance of 5 km during calving and throughout the summer and fall months, but selected habitats near mines during spring and winter. Elongated ridges in the alpine are of high value to Quintette caribou during winter, thus, selection of areas near mines may be explained by the use of these important winter habitats. Two packs of wolves that occupied territories adjacent to mine sites were infrequently located in habitats close to mine footprints.

My field investigations and statistical results suggest that co-occurrence between caribou and wolves is rare (Tables 12, 13), but due to the small size and isolation of caribou herds, any amount of adult or neonate mortality from predation could have severe impacts on herd stability and recruitment (Wittmer et al. 2005, Courbin et al. 2009). Wolves residing in mountainous and boreal habitats appear to be supported by other prey species (i.e., moose, deer, elk, beaver, small mammals and birds; Figure 16; Bergerud et al. 1984, James et al. 2004, Gustine et al. 2006b, DeCesare et al. 2010, Gillingham et al. 2010, Milakovic and Parker 2011, Steenweg 2011). Similar to McCutchen (2007) and Latham et al. (2011a) in

Alberta, my results suggest that encounters between caribou and wolves resulting from increased use of disturbance features by wolves is less significant to population declines than the potential number and variety of alternate prey to support high densities of multiple predators (McCutchen 2007, Latham 2011a, b). In summary, my results from the analysis of caribou and wolf distribution revealed that:

- During winter, caribou are at relatively low risk of encountering wolves (Table 13). Caribou selected black spruce, tamarack, alpine, subalpine and pine-leading habitats of late succession. Wolves also selected subalpine and pine-leading habitats, but of early succession. Wolves avoided high-quality habitats for Quintette caribou throughout the year. Caribou are likely at greatest risk of encountering wolves in forests dominated by subalpine species, spruce, and pine.
- Linear features, as well as habitats with high densities of linear features, were avoided by both caribou and wolves across all seasons. Wolves also demonstrated low frequencies of occurrence where densities of linear features were high. BHRW caribou did select areas where seismic lines and pipelines occurred during calving, summer/fall, and winter.
- Cutblocks influenced the distribution of both caribou and wolves. Both species
  seasonally selected habitats close to cutblocks, as well as habitats with higher
  densities of cutblocks. However, during summer/fall and winter, BHRW caribou
  avoided habitats with increased densities of cutblocks. Similarly, Quintette
  caribou avoided habitats with a high density of cutblocks during winter.
- Non-linear features associated with mine/oil/gas development were generally avoided by both caribou and wolves. Caribou avoided these features most during

the calving and summer/fall season (coal mines, Quintette caribou only). Alternatively, Quintette caribou were found within close proximity to mine features during the spring and winter months. Wolves were infrequently located in habitats near coal mines or where densities of non-linear features were high.

In Chapter 3, I quantified seasonal variation in wolf movement. I examined 1) how human changes to the landscape affected the speed at which wolves moved and 2) the sinuosity of movement paths in the context of the inferred distribution of caribou (Chapter 2). For each season, the rate and sinuosity of wolf movements were best explained using the full suite of habitat and human disturbance variables. This result was consistent across daily and weekly periods, although the weekly period demonstrated better model fit.

Alpine habitats did not affect travel rates in winter, but resulted in more linear movements for wolves. Wolf travel was more sinuous in conifer and mixed-species forests during non-winter, but linear through conifer forests during winter and deciduous habitats during both seasons at the scale of weekly movements. On the contrary, daily movement paths were more sinuous throughout conifer habitats during winter. Water features did not facilitate linear travel as weekly movement paths were sinuous. At the daily scale, movement rates decreased near lakes, rivers, or creeks and suggested that habitats near water features provided wolves with increased hunting opportunities.

The occurrence of habitats I assessed as important to caribou did not influence the movement rates of collared wolves during the non-winter season. Spatial separation between BHRW caribou and wolves may occur in the boreal forest as wolves were observed travelling more rapidly in habitats classified as black spruce, tamarack, or other peatland-type complexes and where the presence of other prey may be minimal (e.g., moose; James et al.

2004, Chapter 2). However, spatial separation between wolves and caribou may occur at finer scales than analyzed here (i.e., patch scale) and will likely vary between boreal and mountainous habitats. In contrast to caribou in the BHRW herd, the sinuosity of movement paths for wolves increased in habitats used by Quintette caribou.

Industrial disturbances influenced movement behaviours of wolves throughout the year (Table 12). Paralleling the distribution patterns of wolves (Chapter 2), non-linear features affected movement parameters more than linear features did at both the fine and coarse scale. Daily movement rates decreased near forestry cutblocks, coal mines, and oil and gas facilities, but increased where those features were relatively dense across the study area. In addition to decreases in daily travel rates, movement was sinuous and suggested wolves spent time hunting and searching near these habitats. As densities of non-linear features increased across the study area, wolves avoided these areas associated with human presence. In summary, my results from the analysis of wolf movement revealed that:

- In general, movement rates of wolves were higher during the non-winter months.
   However, seasonal variation in movement was greater than variation in the use or proximity to linear and non-linear features, suggesting that other factors also influenced the movement dynamics of wolves (Figure 19).
- Habitat and disturbance features better explained wolf movements during the weekly as compared to the daily temporal scale.
- Linear movements generally increased during winter and paralleled past studies that suggested linear travel was associated with the maintenance of territories.

- Wolves decreased movement rates, but not sinuosity within close proximity to disturbance features, thus implying behaviours near such features were more closely associated with searching and hunting.
- Wolves increased movement rates and linear travel through areas with higher densities of linear and non-linear industrial features; this response suggested that wolves avoided spending time in high-risk areas associated with human activities.

Due to the complex set of interacting habitat variables, range of prey types and variety of activities associated with resource exploration and extraction, I was unable to detect obvious correlations between wolf movement and increased opportunities to encounter caribou (Table 13). However, patterns of wolf movement and distribution (Chapter 2) indicated that caribou may be most vulnerable to wolf encounters when in close proximity to cutblocks. Future studies of the cumulative effects of development on the distribution of wolf and caribou populations should include interactions associated with the ecology of moose, deer, elk and other predators including bears, wolverines and cougars. In addition, it is unclear how caribou behaviour might be influenced by short- and long-range wolf movements as well as wolf presence across overlapping habitats. Quantifying current and future levels of direct and indirect habitat loss resulting from industrial developments would also provide additional support to managers focusing on the long-term conservation of woodland caribou.

Activities associated with forestry, oil, natural gas, and mineral exploration and development have resulted in dramatic transformations of the South Peace region and continue to threaten the ecological integrity of these landscapes (Nitschke 2008). Reductions in the quantity and quality of contiguous habitats can result in compounding instabilities for populations of caribou: a reduction in the availability of habitat, altered predator-prey dynamics and increased movement rates that can lead to reductions in body mass and reproductive success (Bradshaw et al. 1997, Nellemann and Cameron 1998, Cameron et al. 2005, Faille et al. 2010). Due to the complex interactions between the cumulative effects of disturbance and the distribution of caribou, I may not have captured all the dynamics (e.g., ecological sinks, time lags, etc.) responsible for influencing selection or avoidance behaviours. In a region where wolf territories overlap caribou range, I was unable to corroborate (i.e., through the investigation of kill sites, count or movement models) that wolves select, or frequently use habitats of high value to caribou. However, it remains unclear how distributions of caribou respond to variations in wolf movement or the increased presence of wolves across portions of their home range. Furthermore, I did not assess vital rates or population change across caribou herds, the ultimate measures of cumulative impacts. Recent (2008) population inventory data has shown, however, that the BHRW herd is in decline while the Quintette population of caribou is increasing (Seip and Jones 2011).

Quantifying the distribution of caribou and the frequency of habitat use and movement by wolves increased our understanding of predator-prey dynamics across a changing landscape. My study, based on habitat selection, movement ecology, and behaviours linked to predation, indicates that disturbance effects from anthropogenic developments occur at multiple scales (i.e., patch scale and valley scale) for both caribou and wolves. My results indicate there is relatively little spatial overlap among the two species with this overlap being greatest in the boreal forest, where wolves have increased opportunities to adjust behaviours to increase their use of high-quality habitat for caribou. Caribou inhabiting the low-elevation boreal habitats may be demonstrating a maladaptive

strategy in the context of multiple disturbance regimes on the landscape. Specifically, encounters between caribou and wolves are most likely to occur in areas closer to and with higher densities of cutblocks, as both species were observed selecting these features during the non-winter season. As my results suggest, however, interactions among predators, caribou and land-use development are not easily predicted or temporally static. As the density and types of industrial disturbances increase across the boreal forest, predators and other ungulates will become more widespread and predation risk for caribou will increase with the reduction of available refugia.

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Appendix A. Figure 1. Distribution of Bearhole/Redwillow caribou (BHRW; 2007 - 2009) and three packs of wolves (Chain lakes, Onion Creek, and Upper Murray; 2008 - 2009) during the spring season (April 1 – May 14) across the South Peace region of northeastern British Columbia.



Appendix A. Figure 2. Distribution of Bearhole/Redwillow caribou (BHRW; 2007 – 2009) and three packs of wolves (Chain lakes, Onion Creek, and Upper Murray; 2008 – 2009) during the calving season (May 15 – June 14) across the South Peace region of northeastern British Columbia.



Appendix A. Figure 3. Distribution of Bearhole/Redwillow caribou (BHRW; 2007 – 2009) and three packs of wolves (Chain lakes, Onion Creek, and Upper Murray; 2008 – 2009) during the summer/fall season (June 15 – October 31) across the South Peace region of northeastern British Columbia.


Appendix A. Figure 4. Distribution of Bearhole/Redwillow caribou (BHRW; 2007 – 2009) and three packs of wolves (Chain lakes, Onion Creek, and Upper Murray; 2008 – 2009) during the winter season (November 1 – Mar 31) across the South Peace region of northeastern British Columbia.



Appendix A. Figure 5. Distribution of Quintette caribou (2003 – 2009) and three packs of wolves (Upper Sukunka, Upper Murray and Onion Creek; 2008 – 2009) during the spring season (April 1 – May 14) across the South Peace region of northeastern British Columbia.



Appendix A. Figure 6. Distribution of Quintette caribou (2003 - 2009) and three packs of wolves (Upper Sukunka, Upper Murray and Onion Creek; 2008 - 2009) during the calving season (May 15 – June 14) across the South Peace region of northeastern British Columbia.



Appendix A. Figure 7. Distribution of Quintette caribou (2003 – 2009) and three packs of wolves (Upper Sukunka, Upper Murray and Onion Creek; 2008 – 2009) during the summer/fall season (June 15 – October 31) across the South Peace region of northeastern British Columbia.



Appendix A. Figure 8. Distribution of Quintette caribou (2003 – 2009) and three packs of wolves (Upper Sukunka, Upper Murray and Onion Creek; 2008 – 2009) during the winter season (November 1 – March 31) across the South Peace region of northeastern British Columbia.

Appendix B. Table 1. GPS collar fix and success rate (based on 24-hour period) for woodland caribou in the South Peace region of northeastern British Columbia.

			Total	Fix	Attempted	Acquired	Fix	Rec	20	% 2D	30	% 3D
Caribou	Dates o	of Collar	Days	Rate	Fixes	Fixes	Rate	Altitude	Fixes <sup>b</sup>	Fixes <sup>b</sup>	Fixes <sup>b</sup>	Fixes <sup>b</sup>
Quintette ATS									<u></u>			
car012Aª	12/11/2003	4/17/2005	493	1	575	474	0.8241	Yes	33	7.16	428	92.84
car031ª	12/11/2003	4/17/2005	493	1	575	550	0.9562	Yes	48	8. <del>9</del> 2	490	91.08
car040ª	4/4/2005	10/25/2006	569	1, 2	569, 1138	670	1.18, 0.59	Yes	66	10.28	576	89.72
car041ª	4/4/2005	1/30/2006	303	1, 2	303, 606	303	1, 0.50	Yes	61	21.63	221	78.37
car042ª	4/4/2005	7/20/2006	472	1, 2	472, 944	561	1.19, 0.59	Yes	22	3.99	529	96.01
car045	12/22/2005	4/4/2007	468	5	2340	1600	0.6838	Yes	44	2.77	1545	97.23
car046	12/22/2005	12/3/2006	346	3	1038	462	0.4451	Yes	56	12.33	398	87.67
car057	1/30/2007	1/16/2009	717	4	2868	2830	0.9868	Yes	157	5.61	2644	94.39
car059	1/30/2007	10/31/2008	640	4	2560	1989	0.777	Yes	706	37.57	1173	62.43
car068	4/4/2007	3/14/2009	710	4	2840	2530	0.8908	Yes	449	18.91	1925	81.09
car069	4/4/2007	1/3/2009	640	4	2560	2093	0.8176	Yes	673	34.32	1288	65.68
car070	4/4/2007	3/7/2009	703	4	2812	2688	0.9559	Yes	252	9.63	2365	90.37
car071	4/5/2007	1/2/2009	638	4	2552	2243	0.8789	Yes	253	11.72	1906	88.28
car072	4/5/2007	5/29/2007	54	4	216	141	0.6528	Yes	56	45.53	67	54.47
car074	4/5/2007	2/25/2009	692	4	2768	2442	0.8822	Yes	725	31.12	1605	68.88
car075	4/5/2007	3/14/2009	709	4	2836	2630	0.9274	Yes	328	12.81	2233	87.19
car105	1/10/2009	7/31/2009	202	4	808	680	0.8416	Yes	27	4.01	646	95.9 <del>9</del>
car112	1/24/2009	12/21/2009	331	4	1324	662	0.5	Yes	20	5.05	376	94.95

<sup>a</sup> Quintette collars initially fixed at 20hr (1-2/day) intervals, and then at 12 hours intervals.

<sup>b</sup> premised on data already screened for erroneous locations.

Appendix	Β.	Table	1.	Continued	
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							Fix					
			Total	Fix	Attempted	Acquired	Success	Rec	2D	% 2D	3D	% 3D
Caribou	Dates o	of Collar	Days	Rate	Fixes	Fixes	Rate	Altitude	Fixes <sup>b</sup>	Fixes <sup>b</sup>	Fixes <sup>b</sup>	Fixes <sup>b</sup>
Bearhole	Start	End										
car054	12/20/2006	10/19/2007	303	3	909	734	0.8075	Yes	68	9.26	666	90.74
car055	12/20/2006	8/3/2007	226	3	678	592	0.8732	Yes	24	4.05	56 <b>8</b>	95.95
car077	12/18/2007	12/17/2009	730	3	2190	1652	0.7543	Yes	352	21.32	1299	78.68
car078	1/8/2008	5/14/2009	492	3	1476	1130	0.7656	Yes	158	14.21	954	85.79
Redwillow												
F900	12/21/2006	1/26/2009	767	6	4602	4325	0.9398	Yes	791	18.57	3468	81.43
F901	1/30/2007	1/26/2009	727	6	4362	4008	0.9188	Yes	665	16.79	3296	83.21
Quintette												
τν												
car012	2/12/2003	4/7/2003	54	6	324	321	0.9907	No	104	32.4	217	67.6
car013	2/12/2003	3/19/2003	35	6	210	98	0.4667	No	30	30.61	68	69.39
car014	2/12/2003	7/26/2003	164	6	984	886	0.9004	No	257	29.01	629	70.99
car015	2/12/2003	3/16/2003	32	6	192	174	0.9063	No	21	12.07	153	87.93

<sup>a</sup> Quintette collars initially fixed at 20hr (1-2/day) intervals, and then at 12 hours intervals.

<sup>b</sup> premised on data already screened for erroneous locations.

Appendix B. Table 2. Category classes of GPS collar locations developed to determine erroneous locations for caribou. All but 2.99% of 3D and 16.4% of 2D fixes were used in statistical analyses.

GPS					% of	Loc Class
Location	2D	PDOP	Elevation		all	Removed?
Category	Filter	Filter	Filter	Frequency	Locs	(Y/N)
0	0	N/A	N/A	40,506	81.72	Y
1	1	1	1	4,152	8.38	Y
2	1	1	2	1,302	2.63	Y
3	1	1	3	629	1.27	Y
4	1	2	1	185	0.37	Y
5	1	2	2	50	0.1	Y
6	1	2	3	46	0.09	Y
7	1	3	1	121	0.24	Y
8	1	3	2	38	0.08	Y
9	1	3	3	28	0.06	Y
10	1	4	1	83	0.17	Y
11	1	4	2	22	0.04	Y
12	1	5	1	96	0.19	Y
13	1	5	2	34	0.07	Y
14	1	4	3	9	0.02	Y
15	1	4	4	5	0.01	N
16	1	4	5	21	0.04	Ν
17	1	5	3	24	0.05	Ν
18	1	5	4	12	0.02	Ν
19	1	5	5	37	0.07	Ν
20	1	3	4	19	0.04	Ν
21	1	3	5	30	0.06	Ν
22	1	2	4	23	0.05	Ν
23	1	2	5	48	0.1	Ν
24	1	1	4	371	0.75	Ν
25	1	1	5	894	1.8	N
26	1	1	0	775	1.56	Y
27	1	2	0	7	0.01	Ν

Appendix B. Table 3. GPS collar fix and success rate (based on 24-hour period) for wolves in the South Peace region of northeastern British Columbia. Due to the improved precision of GPS collars, wolf locations were checked using GIS and dates of collar deployment. Twodimensional fixes (2D) accounted for 0.04 - 17.19% of all downloaded locations. Recorded altitude was used to ensure elevation was recorded from the GPS collar. The Chain Lakes pack had a number of locations that occurred beyond the BC/Alberta boarder and were thus discarded from analyses.

							Fix			%		%
			Total	Fix Rate	Attempted	Acquired	Success	Recorded	3D	3D	2D	2D
Pack	Dates	of Collar	Days	(per 24h)	Fixes	Fixes	Rate	Altitude	Fixes	Fixes	Fixes	Fixes
Lower Sukunka	Start	End										
W008a <sup>a,b</sup>	1/7/08	1/31/08	25	1	25	24	0.96	1	23	99.96	1	0.04
W008b	2/1/08	1/14/09	348	8	2760	2384	0.86	1	2070	99.86	290	0.14
Upper Sukunka												
W010a <sup>b</sup>	1/22/08	1/31/08	9	1	9	7	0.78	1	5	0.60	2	0.40
W010b	2/1/08	10/27/08	269	8	2152	1712	0.80	1	1485	0.85	229	0.15
W027	2/17/09	4/11/10	418	8	3344	2754	0.82	1	2356	85.55	398	14.45
W029	3/14/09	3/20/10	371	8	2968	2310	0.78	1	1906	82.51	404	17.49
Upper Murray												
W015	2/3/08	1/14/09	346	8	2768	2384	0.86	1	2073	86.95	311	13.05
W019	2/4/08	3/8/08	33	8	264	232	0.88	1	207	89.22	25	10.78
W022	2/10/09	2/5/10	360	8	2880	2325	0.81	1	1999	85.98	326	14.02
W023	2/10/09	9/27/09	229	8	1832	1537	0.84	1	1346	87.57	191	12.43

<sup>a</sup> These data were excluded from analyses as they occurred beyond the range of monitored caribou

<sup>b</sup> GPS collar locations separated into two classes (a,b) due to a programming changes in their GPS collars

Appendix	В.	Table	: 3.	Continued.	
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							Fix					%	
			Total	Fix Rate	Attempted	Acquired	Success	Recorded	3D	% 3D	2D	2D	BC
Pack	Dates of	of Collar	Days	(per 24h)	Fixes	Fixes	Rate	Altitude	Fixes	Fixes	Fixes	Fixes	Total <sup>a</sup>
Onion Creek	Start	End											
W020	2/5/08	11/17/08	286	8	2288	1950	0.85	1	1697	87.03	253	12.97	
W025	2/16/09	4/11/09	54	8	432	411	0.95	1	375	91.24	36	8.76	
W026	2/16/09	2/5/10	354	8	2832	2263	0.80	1	1874	82.81	389	17.19	
Chain Lakes													
W016	2/3/08	4/15/09	437	8	3496	3173	0.91	1	2824	91.30	269.00	8.70	3093
W024	2/10/09	11/3/09	266	8	2128	1614	0.76	1	1269	87.22	186.00	12.78	1455
W028	3/14/09	2/5/10	328	8	2624	2521	0.96	1	1414	86.11	228.00	13.89	1642
W030	12/3/09	3/19/10	106	72	7632	7462	0.98	1	3609	95.88	155.00	4.12	3764
W031	2/11/10	6/2/10	111	72	7992	7442	0.93	1	4516	95.50	213.00	4.50	4729

<sup>a</sup> Analyses were based on wolf locations occurring in British Columbia only; locations for Chain Lakes that occurred in Alberta were discarded.

Kill ID	Kill #	Species	Age Class	Sex	Pack	Wolf	Date
1	08-001	Moose	Adult	Unknown	Chain Lakes	W016	2/9/2008
2	08-002	Moose	Adult	Unknown	Chain Lakes	W016	2/18/2008
3	08-003	Unknown	Adult	Unknown	Chain Lakes	W016	4/20/2008
4	08-004	Elk	Unknown	Unknown	Onion Creek	W020	4/15/2008
5	08-005	Moose	Adult	Unknown	Upper Murray	W019	2/20/2008
6	08-006	Moose	Adult	Unknown	Upper Murray	W015	4/22/2008
7	08-007	Moose	Adult	Unknown	Upper Sukunka	W010	3/16/2008
8	08-008	Moose	Unknown	Unknown	Upper Murray	W015	5/8/2008
9	08-009	Moose	Adult	Unknown	Upper Murray	W015	5/17/2008
10	08-010	Moose	Adult	Female	Onion Creek	W020	7/31/2008
11	08-011	Moose	Adult	Female	Chain Lakes	W016	8/22/2008
12	08-012	Moose	Adult	Unknown	Chain Lakes	W016	8/13/2008
13	09-001	Deer	Adult	Unknown	Onion Creek	W025	2/23/2009
14	09-002	Elk	Adult	Unknown	Onion Creek	W025	3/21/2009
15	09-003	Moose	Unknown	Unknown	Onion Creek	W026	2/24/2009
16	09-004	Deer	Adult	Unknown	Onion Creek	W026	3/12/2009
17	09-005	Deer	Adult	Unknown	Onion Creek	W025	3/15/2009
18	09-006	Deer	Adult	Unknown	Onion Creek	W025	4/6/2009
19	09-007	Deer	Adult	Unknown	Onion Creek	W026	4/6/2009
20	09-008	Moose	Adult	Unknown	Onion Creek	W026	2/22/2009
21	09-009	Unknown	Unknown	Unknown	Upper Sukunka	W027	9/23/2009
22	09-010	Moose	Adult	Unknown	Onion Creek	W025	3/12/2009
23	09-011	Elk	Adult	Male	Onion Creek	W026	3/19/2009
24	09-012	Moose	Unknown	Unknown	Upper Sukunka	W029	3/24/2009
25	09-013	Unknown	Adult	Unknown	Upper Sukunka	W027	3/22/2009

Appendix C. Table 1. Kill sites identified using clusters of GPS locations and site investigations for wolves in the South Peace region of northeastern British Columbia. Field investigations were completed over three years (5/2008 - 9/2010); a total of 73 kill sites were used to analyze wolf area of use (AOU).

Kill ID	Kill #	Species	Age Class	Sex	Pack	Wolf	Date
26	09-014	Deer	Adult	Unknown	Upper Sukunka	W029	4/12/2009
27	09-015	Deer	Adult	Unknown	Upper Sukunka	W029	4/12/2009
28	09-016	Unknown	Unknown	Unknown	Upper Sukunka	W027	4/6/2009
29	09-017	Moose	Adult	Unknown	Chain Lakes	W016	2/1/2009
30	09-018	Moose	Adult	Unknown	Chain Lakes	W028	3/15/2009
31	09-019	Moose	Calf	Unknown	Chain Lakes	W028	3/16/2009
32	09-020	Moose	Adult	Unknown	Chain Lakes	W016	2/3/2009
33	09-021	Moose	Adult	Unknown	Upper Murray	W022	5/21/2009
34	09-022	Moose	Adult	Unknown	Onion Creek	W026	6/3/2009
35	09-023	Unknown	Calf	Unknown	Onion Creek	W026	6/8/2009
36	09-024	Muskrat	Adult	Unknown	Upper Murray	W022	5/27/2009
37	09-025	Moose	Adult	Unknown	Upper Murray	W022	5/27/2009
38	09-026	Mt. Goat	Adult	Unknown	Upper Sukunka	W029	5/6/2009
39	09-027	Moose	Calf	Unknown	Onion Creek	W026	6/5/2009
40	09-028	Moose	Adult	Female	Onion Creek	W026	6/5/2009
41	09-029	Caribou	Adult	Unknown	Upper Murray	W022	5/19/2009
42	09-030	Moose	Adult	Unknown	Onion Creek	W026	5/27/2009
43	09-031	Moose	Yearling	Unknown	Upper Sukunka	W027	3/19/2009
44	09-032	Moose	Adult	Unknown	Upper Sukunka	W027	6/3/2009
45	09-033	Moose	Adult	Unknown	Chain Lakes	W024	5/13/2009
46	09-034	Moose	Adult	Male	Chain Lakes	W028	5/10/2009
47	09-035	Moose	Yearling	Unknown	Chain Lakes	W028	4/18/2009
48	09-036	Moose	Adult	Female	Chain Lakes	W028	3/29/2009
49	09-037	Moose	Adult	Female	Chain Lakes	W024	3/22/2009
50	09-038	Moose	Adult	Female	Chain Lakes	W028	7/11/2009

Appendix C. Table 1. Continued.

## Appendix C. Table 1. Continued.

Kill ID	Kill #	Species	Age Class	Sex	Pack	Wolf	Date
51	09-039	Unknown	Calf	Unknown	Upper Murray	W023	6/30/2009
52	09-040	Unknown	Unknown	Unknown	Upper Murray	W023	7/5/2009
53	09-041	Mt. Goat	Unknown	Unknown	Upper Murray	W023	7/17/2009
54	09-042	Unknown	Unknown	Unknown	Upper Murray	W022	6/15/2009
55	09-043	Unknown	Unknown	Unknown	Upper Murray	W022	6/30/2009
56	09-044	Moose	Adult	Unknown	Upper Sukunka	W029	8/19/2009
57	09-045	Moose	Adult	Unknown	Upper Sukunka	W029	8/11/2009
58	09-046	Moose	Adult	Female	Chain Lakes	W024	8/9/2009
59	09-047	Moose	Adult	Unknown	Chain Lakes	W024	8/1/2009
60	09-048	Moose	Yearling	Unknown	Upper Sukunka	W027	9/25/2009
61	09-049	Moose	Unknown	Unknown	Upper Murray	W023	8/28/2009
62	09-050	Moose	Adult	Male	Upper Murray	W023	9/22/2009
63	10-001	Deer	Unknown	Unknown	Upper Sukunka	W029	3/15/2010
64	10-002	Deer	Adult	Unknown	Upper Sukunka	W029	2/26/2010
65	10-003	Deer	Adult	Unknown	Upper Sukunka	W029	2/26/2010
66	10-004	Deer	Adult	Male	Upper Sukunka	W029	3/4/2010
67	10-005	Deer	Unknown	Unknown	Upper Sukunka	W029	2/19/2010
68	10-006	Moose	Adult	Female	Chain Lakes	W031	3/17/2010
69	10-007	Deer	Adult	Unknown	Chain Lakes	W028	1/4/2010
70	10-008	Moose	Adult	Male	Chain Lakes	W028	12/31/2009
71	10-009	Deer	Adult	Unknown	Chain Lakes	W028	2/8/2010
72	10-010	Moose	Calf	Unknown	Upper Sukunka	W027	3/13/2010
73	10-011	Moose	Adult	Unknown	Upper Sukunka	W027	2/13/2010

Appendix C. Table 2. Area of use (AOU) calculated using 100% MCPs that surrounded kill sites for each wolf across the South Peace region of northeastern British Columbia. Kill sites were identified through the investigation of location clusters over three summers (2008 – 2010).

					<b>W</b>		
		AOU	AOU	AOU		# Pts	
Wolf ID	Sex	(m²)	<u>(km²)</u>	(per 100 Ha)	AOU (ha)	in Cluster	Wolf Pack
		0001(1		06.5		24	
W016	Male	930161	0.93	86.5	93.02	34	Chain Lakes
W024	Male	996167	1.00	99.2	99.62	26	Chain Lakes
W028	Female	804663	0.80	64.7	80.47	18	Chain Lakes
W030 <sup>a</sup>	Male	3500262	3.50	1225.2	350.03	5	Chain Lakes
W031 <sup>a</sup>	Female	3500262	3.50	1225.2	350.03	5	Chain Lakes
W020	Male	64809	0.06	0.4	6.48	23	Onion Creek
W025	Male	95208	0.12	1.4	11.90	17	Onion Creek
W026	Male	69866	0.09	0.8	8.89	14	Onion Creek
W015	Male	4672523	4.67	2183.2	467.25	15	Upper Murray
W019	Female	205363	0.21	4.2	20.54	23	Upper Murray
W022	Female	276753	0.33	11.0	33.21	12.2	Upper Murray
W023	Female	1007388.8	1.0	101.5	100.7	14	Upper Murray
W010	Female	62194	0.06	0.4	6.22	22	Upper Sukunka
W027	Male	95526.4	0.1	0.9	9.6	13.9	Upper Sukunka
W029	Female	41226.0	0.04	0.2	4.1	14	Upper Sukunka

<sup>a</sup> W030 and W031 were fitted with high-frequency collars programed to collect locations every 20 mins; data were therefore, excluded from AOU calculations to maintain consistancy across all packs.



Appendix C. Figure 1. Average area of use (AOU; ha) by pack identified through the investigation of wolf kill sites over three summers (2008 - 2010) across the South Peace region of northeastern British Columbia.



Appendix D. Figure 1. Coefficients from count model describing frequency of occurrence of wolf locations within habitat selection units (HSUs; n = 3,389) relative to environmental and disturbance covariates during the non-winter season (April 16 – Oct 14) from wolves collared in the Chain Lakes pack. An asterick (\*) indicates a Guassian (squared) term was used in the model.



Appendix D. Figure 2. Coefficients from binary model describing the presense or absense of wolves within HSUs relative to environmental and disturbance covariates during the non-winter season from wolves collared in the Chain Lakes pack.



Appendix D. Figure 3. Coefficients from count model describing frequency of occurrence of wolf locations within HSUs during the early winter season (Oct 15 - Jan 31) from wolves collared in the Chain Lakes pack.



Appendix D. Figure 4. Coefficients from count model describing frequency of occurrence of wolf locations within HSUs during the late winter season (Feb 1 - April 15) from wolves collared in the Chain Lakes pack.



Appendix D. Figure 5. Coefficients from binary model describing the presense or absense of wolves within HSUs during the late winter season from wolves collared in the Chain Lakes pack.



Appendix D. Figure 6. Coefficients from count model describing frequency of occurrence of wolf locations within HSUs (n = 10,493) during the non-winter season from wolves collared in the Onion Creek pack.



Appendix D. Figure 7. Coefficients from binary model describing the presense or absense of wolves within HSUs during the non-winter season from wolves collared in the Onion Creek pack.



Appendix D. Figure 8. Coefficients from count model describing frequency of occurrence of wolf locations within HSUs during the early winter season from wolves collared in the Onion Creek pack.



Appendix D. Figure 9. Coefficients from binary model describing the presense or absense of wolves within HSUs during the early winter season from wolves collared in the Onion Creek pack.



Appendix D. Figure 10. Coefficients from count model describing frequency of occurrence of wolf locations within HSUs during the late winter season from wolves collared in the Onion Creek pack.



Appendix D. Figure 11. Coefficients from binary model describing the presense or absense of wolves within HSUs during the late winter season from wolves collared in the Onion Creek pack.



Appendix D. Figure 12. Coefficients from count model describing frequency of occurrence of wolf locations within HSUs (n = 35,959) during the non-winter season from wolves collared in the Upper Murray pack.



Appendix D. Figure 13. Coefficients from count model describing frequency of occurrence of wolf locations within HSUs during the early winter season from wolves collared in the Upper Murray pack.



Appendix D. Figure 14. Coefficients from count model describing frequency of occurrence of wolf locations within HSUs during the late winter season from wolves collared in the Upper Murray pack.



Appendix D. Figure 15. Coefficients from binary model describing the presense or absense of wolves within HSUs during the late winter season from wolves collared in the Upper Murray pack.



Appendix D. Figure 16. Coefficients from count model describing frequency of occurrence of wolf locations within HSUs (n = 33,599) during the non-winter season from wolves collared in the Upper Sukunka pack.



Appendix D. Figure 17. Coefficients from count model describing frequency of occurrence of wolf locations within HSUs during the early winter season from wolves collared in the Upper Sukunka pack.



Appendix D. Figure 18. Coefficients from binary model describing the presense or absense of wolves within HSUs during the early winter season from wolves collared in the Upper Sukunka pack.



Appendix D. Figure 19. Coefficients from count model describing frequency of occurrence of wolf locations within HSUs during the late winter season from wolves collared in the Upper Sukunka pack.

EARLY WINTER					LATE	WINTER		NON- WINTER				
		Frequent				Frequent				Frequent		
Variables	Use	Use	Availability	Variables	Use	Use	Availability	Variables	Use	Use	Availability	
Upper Sukunka				Upper Sukunka				Upper Sukunka				
Alpine	32.54	28.00	35.86	Alpine	30.80	25.00	35.91	Alpine	26.62	17.02	36.06	
Other	32.72	52.00	20.79	Other	33.43	50.00	29.56	Other	41.22	59.57	22.82	
Tree Broadleaf	14.44	12.00	2.19	Pine	9.94	3.57	12.23	Tree Other	32.16	23.40	41.12	
Tree Other	20.29	8.00	41.16	Spruce	12.29	14.29	20.15	Upper Murray				
Upper Murray				Tree Broadleaf	13.54	7.14	2.15	No VRI	15.01	8.82	18.72	
No VRI	48.55	67.86	18.37	Upper Murray				Other	13.20	5.88	32.33	
Other	12.30	14.29	32.29	No VRI	15.01	8.82	18.72	Pine	28.57	32.35	12.51	
Spruce	15.21	7.14	18.33	Other	13.20	5.88	32.33	Spruce	31.46	44.12	18.14	
Tree Other	23.94	10.71	31.01	Pine	28.57	32.35	12.51	Tree Other	11.75	8.82	18.31	
Onion Creek				Spruce	31.46	44.12	18.14	Onion Creek				
Alpine	8.94	5.26	9.95	Tree Other	11.75	8.82	18.31	Alpine	8.94	5.26	9.95	
Other	13.13	10.53	12.23	Onion Creek				Other	13.13	10.53	12.23	
Pine	22.91	21.05	28.28	Alpine	5.64	8.00	10.07	Pine	22.91	21.05	28.28	
Spruce	24.86	52.63	22.17	Other	20.32	24.00	35.89	Spruce	24.86	52.63	22.17	
Tree Broadleaf	18.99	10.53	3.93	Pine	33.63	16.00	27.94	Tree Broadleaf	18.99	10.53	3.93	
Tree Other	11.17	0.00	23.45	Spruce	21.44	36.00	22.27	Tree Other	11.17	0.00	23.45	
Chain Lakes				Tree Broadleaf	18.96	16.00	3.83	Chain Lakes				
Alpine	0.21	0.00	0.50	Chain Lakes				Alpine	0.20	0.00	0.47	
Black Spruce	17.95	14.94	18.52	Alpine	0.26	0.00	0.45	Black Spruce	15.22	14.29	18.82	
Subalpine Fir	0.11	0.00	1.06	Black Spruce	20.04	14.29	18.24	HBS	0.40	0.00	1.12	
HBS	0.53	0.00	1.17	Subalpine Fir	0.26	0.00	0.91	No VRI	1.78	0.00	2.95	
No VRI	1.38	0.00	3.22	HBS	1.05	0.00	1.03	Pine	39.33	23.81	47.23	
Pine	43.45	31.17	47.13	No VRI	0.00	0.00	3.35	Spruce	7.31	12.70	8.81	
Spruce	7.31	9.74	9.10	Pine	40.40	37.14	47.00	Tamarack	7.11	9.52	3.18	
Tamarack	4.91	6.49	3.28	Spruce	7.12	11.43	8.86	Tree Broadleaf	25.30	36.51	15.17	
Tree Broadleaf	21.26	34.42	15.03	Tamarack	4.22	0.00	3.61	Tree Other	2.77	1.59	1.55	
Tree Other	2.35	2.60	0.27	Tree Broadleaf	23.47	31.43	15.71	Upland NonVeg	0.20	0.00	0.38	
Upland NonVeg	0.11	0.00	0.42	Tree Other	3.16	5.71	0.49	Water	0.40	1.59	0.32	
Water	0.43	0.65	0.30	Water	0.00	0.00	0.36					

Appendix D. Table 1. The percent (%) of total habitat used, frequently used, or available across the range of wolves based on the occurrence of Habitat Selection Units (HSUs) dominated by a land cover type. Use includes Habitat Selection Units (HSUs) with  $\geq 1$  wolf location, whereas *Frequent Use* includes HSUs with  $\geq 10$  wolf locations. Model variables are described in Table 1.

Appendix E. Table 1. Number of parameters (k), Akaike's Information Criterion values (AIC<sub>c</sub>), and AIC<sub>c</sub> weights (w) for seasonal resource selection models for the Bearhole/Redwillow (BHRW) caribou herd monitored from 2006 – 2009 across the South Peace region of northeastern British Columbia. Sample size of caribou locations is represented in parentheses.

	Spring (n = 3,401)					Calving (n = 2,200)				ummer/H	fall (n = 8)	3,669)	Winter (n = 11,625)			
Model Covariates	k	AIC <sub>c</sub>	ΔΑΙϹ	AIC <sub>w</sub>	k	AIC	ΔΑΙϹ	AIC <sub>w</sub>	k	AIC <sub>c</sub>	ΔAIC	AIC	k	AIC <sub>c</sub>	ΔΑΙϹ	AIC <sub>w</sub>
Forest cover	9	3550.2	417.7	< 0.001	8	2205.4	354.4	< 0.001	10	8063.0	708.6	< 0.001	11	12018.2	2018.4	< 0.001
Forest age	5	3596.8	464.3	< 0.001	5	2319.9	468.8	< 0.001	5	9189.7	1835.3	< 0.001	5	12339.0	2339.3	<0.001
Solar insolation <sup>b,c</sup>	1	3583.9	451.4	< 0.001	1	2253.1	402.1	< 0.001	1	9008.3	1653.9	<0.001	3	12353.9	2354.2	< 0.001
Landscape	15	3519.2	386.7	< 0.001	14	2127.1	276.1	< 0.001	16	7801.1	446.7	<0.001	19	11856.8	1857.1	<0.001
Road Dist <sup>b</sup>	18	3514.3	381.8	< 0.001	17	2103.9	252.8	< 0.001	19	7795.9	441.5	< 0.001	22	11696.1	1696.3	< 0.001
Road Dens	16	3519.5	387.0	< 0.001	15	2123.8	272.7	<0.001	17	7743.8	389.4	< 0.001	20	11739.0	1739.3	< 0.001
Road Dist <sup>b.c</sup> + Road																
Dens	19	3515.2	382.7	< 0.001	18	2099.6	248.6	<0.001	20	7740.0	385.6	<0.001	23	11645.4	1645.7	< 0.001
LF Dist <sup>b</sup>	24	3210.2	77.7	< 0.001	23	1961.7	110.6	< 0.001	25	7448.8	94.5	< 0.001	28	10817.6	817.9	< 0.001
LF Dens	16	3518.8	386.3	< 0.001	15	2128.8	277.7	<0.001	17	7724.0	369.6	< 0.001	20	11849.8	1850.0	< 0.001
LF Dist <sup><i>b.c</i></sup> + LF Dens	25	3211.9	79.4	< 0.001	24	1963.0	111.9	<0.001	26	7420.4	66.0	< 0.001	29	10819.6	819.9	< 0.001
FOR Dist <sup>b.c</sup>	21	3447.0	314.5	< 0.001	16	2079.1	228.1	< 0.001	22	7789.4	435.0	< 0.001	25	11489.5	1489.7	< 0.001
FOR Dens	17	3521.2	388.7	< 0.001	16	2103.9	252.9	< 0.001	18	7723.6	369.2	< 0.001	21	11851.8	1852.1	<0.001
FOR Dist <sup>b.c</sup> + FOR																
Dens	23	3450.1	317.6	< 0.001	18	2065.9	214.8	<0.001	24	7717.0	362.6	< 0.001	27	11421.4	1421.7	< 0.001
MOG Dist <sup>a</sup> , <sup>b</sup>	27	3210.4	77. <b>9</b>	< 0.001	26	1921.3	70.3	< 0.001	28	7429.3	75.0	< 0.001	31	10247.2	247.5	< 0.001
MOG Dens <sup>a</sup>	-	-	-	-	-	-	-	-	17	7724.0	369.6	<0.001	-	-	-	-
MOG Dist <sup>a</sup> , <sup>b,c</sup> +																
MOG Dens <sup>a</sup>	28	3212.2	<b>79</b> .7	< 0.001	27	1922.9	71.9	< 0.001	29	7401.9	47.5	<0.001	32	10249.1	249.4	< 0.001
CE Dist <sup>b</sup>	26	3137.2	4.6	0.09	25	1854.6	3.5	0.15	27	7402.6	48.2	< 0.001	32	10065.1	65.4	< 0.001
CE Dens	19	3522.9	390.4	<0.001	16	2107.6	256.6	<0.001	20	7693.3	338.9	<0.001	21	11851.8	1852.1	<0.001
CE Dist <sup>b.c</sup> + CE Dens	30	3132.5	0.0	0.91	27	1851.1	0.0	0.85	31	7354.4	0.0	1.00	34	9999.7	0.0	1.00

<sup>a</sup>MOG may or may not have been included due to seasonal proximity (distance) from herd

<sup>b</sup>Gaussian (squared) term was most parsimonious in at least one seasonal candidate model

<sup>c</sup>Linear term was most parsimonious in at least one seasonal candidate model

Appendix E. Table 2. Number of parameters (k), Akaike's Information Criterion values (AIC<sub>c</sub>), and AIC<sub>c</sub> weights (w) for seasonal resource selection models for the Quintette caribou herd monitored from 2003 - 2009 across the South Peace region of northeastern British Columbia. Sample size of caribou locations is in parentheses.

	Spring (n = 9,791)					Calving (n = 5,868)				Summer/F	all (n = 22	2,458)	Winter (n = 28,368)			
Model Covariates	k	AIC <sub>c</sub>	ΔΑΙϹ	AIC	k	AIC <sub>c</sub>	ΔΑΙϹ	AICw	<i>k</i>	AIC <sub>c</sub>	ΔΑΙΟ	AIC	k	AIC <sub>c</sub>	ΔΑΙΟ	AIC <sub>w</sub>
Forest cover	8	7490.9	2035.3	< 0.001	9	4939.8	844.0	< 0.001	9	19032.4	3129.3	< 0.001	10	24357.5	4684.0	< 0.001
Forest age	5	8277.3	2821.8	< 0.001	5	5159.1	1063.4	< 0.001	5	20116.6	4213.4	<0.001	5	26493.5	6819.9	<0.001
Solar insolation <sup>b,c</sup>	3	8274.9	2819.3	< 0.001	3	5101.2	1005.4	< 0.001	1	21442.4	5539.2	< 0.001	3	25082.7	5409.2	< 0.001
Landscape	16	6415.0	959.5	< 0.001	17	4411.0	315.2	< 0.001	15	18393.7	2490.5	<0.001	18	22322.4	2648.9	<0.001
Road Dist <sup>b</sup>	19	5763.9	308.3	< 0.001	19	4370.0	274.2	< 0.001	18	16984.3	1081.2	< 0.001	21	21227.9	1554.4	< 0.001
Road Dens	17	6351.2	895.7	< 0.001	18	4369.2	273.4	< 0.001	16	18145.5	2242.4	<0.001	19	22068.9	2395.4	< 0.001
Road Dist <sup><math>b</math></sup> + Road Dens	20	5764.8	309.2	< 0.001	20	4330.9	235.2	< 0.001	19	16966.6	1063.4	< 0.001	22	21197.5	1524.0	< 0.001
LF Dist <sup>b</sup>	25	5744.6	289.1	< 0.001	26	4288.3	192.6	<0.001	24	16737.4	834.2	<0.001	27	20969.4	1295.9	< 0.001
LF Dens	17	6413.6	958.1	< 0.001	17	4396.5	300.8	< 0.001	16	18345.4	2442.2	< 0.001	19	22281.9	2608.3	< 0.001
LF Dist <sup><math>b</math></sup> + LF Dens	26	5746.5	291.0	< 0.001	27	4285.4	189.6	<0.001	25	16725.5	822.4	<0.001	28	20968.7	1295.1	< 0.001
FOR Dist <sup>b</sup>	22	5671.5	216.0	< 0.001	24	4276.0	180.2	<0.001	21	16939.2	1036.1	<0.001	24	21086.0	1412.4	<0.001
FOR Dens	18	5663.5	207.9	< 0.001	19	4359.6	263.8	< 0.001	17	18140.1	2237.0	< 0.001	20	22064.9	2391.3	< 0.001
FOR Dist <sup>b</sup> + FOR Dens	24	5651.3	195.8	< 0.001	26	4265.1	169.3	<0.001	23	16844.7	941.6	<0.001	26	20765.9	1092.3	< 0.001
$MOG Dist^{a,b}$	31	5520.7	65.1	< 0.001	32	4175.2	79.5	< 0.001	30	15979.6	76.4	<0.001	31	20109.2	435.7	< 0.001
MOG Dens <sup>a</sup>	18	6353.6	898.0	< 0.001	19	4397.4	301.6	< 0.001	17	18299.9	2396.7	<0.001	20	22239.8	2566.2	<0.001
$MOG Dist^{a, b} + MOG$																
Dens <sup>a</sup>	33	5522.0	66.4	< 0.001	34	4172.5	76.8	<0.001	32	15968.0	64.9	<0.001	33	20103.0	429.4	<0.001
CE Dist <sup>b</sup>	34	5466.2	10.6	<0.001	35	4102.0	6.3	0.04	30	15933.3	30.1	< 0.001	34	19949.3	275.8	<0.001
CE Dens	19	6322.1	866.6	<0.001	20	4386.9	291.2	< 0.001	18	18301.0	2397.8	<0.001	23	22166.5	2492.9	<0.001
CE $Dist^b$ + CE Dens	37	5455.5	0.0	1.00	38	4095.8	0.0	0.96	33	15903.2	0.0	1.00	39	19673.6	0.0	1.00

<sup>a</sup>MOG may or may not have been included due to seasonal proximity (distant) from herd

<sup>b</sup>Gaussian (squared) term was most parsimonious in at least one seasonal candidate model

'Linear term was most parsimonious in at least one seasonal candidate model

Appendix E. Table 3. Number of parameters $(k)$ , Akaike's Informatic	on Criterion values (AIC <sub>c</sub> ), and AIC <sub>c</sub> weights (w) for seasonal
count models for wolf packs monitored between 2008 – 2010 across t	he South Peace region of northeastern British Columbia.

Upper	Sukunka (n = 33,599)		Non-V	Winter <sup>nbru</sup>			Early	Winter <sup>zi</sup>	ab		Late Winter <sup>abrm</sup>				
Model #	Model Covariates	k	AICc	ΔΑΙΟ	AIC	k	AICc	ΔΑΙΟ	AIC <sub>w</sub>	k	AIC <sub>c</sub>	∆AIC	AIC		
1	Forest cover	3	10824.8	1232.6	<0.001	4	6146.5	1096.6	<0.001	5	7565.3	1448.5	<0.001		
2	Forest age	3	10882.1	1289.8	< 0.001	3	6316.9	1267.0	< 0.001	3	7556.3	1439.4	< 0.001		
3	Water Dist <sup>a</sup>	3	10810.1	1217.9	< 0.001	3	6208.0	1158.1	< 0.001	3	7496.5	1379.7	< 0.001		
4	Caribou	1	10898.4	1306.1	< 0.001	1	6291.4	1241.4	< 0.001	1	7552.9	1436.1	<0.001		
5	Landscape	10	10642.1	1049.9	< 0.001	11	5975.5	925.5	< 0.001	12	7322.5	1205.7	<0.001		
6	LF Dist <sup>a</sup>	16	10529.5	937.3	<0.001	17	5867.9	818.0	<0.001	18	7170.0	1053.2	<0.001		
7	LF Dist + LF Dens <sup>a</sup>	17	10516.4	924.2	< 0.001	18	5867.3	817.3	<0.001	19	7168.0	1051.1	<0.001		
8	FOR Dist <sup>a</sup>	16	10508.7	916.5	<0.001	17	5862.1	812.2	<0.001	16	7190.2	1073.3	<0.001		
9	FOR Dist + FOR Dens <sup>a</sup>	15	10529.1	936.9	< 0.001	18	5860.3	810.4	< 0.001	17	7192.2	1075.3	<0.001		
10	MOG Dist <sup>a</sup>	22	9636.6	44.4	<0.001	23	5087.1	37.1	<0.001	22	6116.9	0.0	0.45		
10		23	9629.1	36.9	< 0.001	25	5084.8	34.9	< 0.001	23	6118.3	1.4	0.22		
11	MOG Dist + MOG Dens"														
12	CE Dist <sup>a</sup>	19	9598.8	6.6	0.04	26	5073.1	23.2	< 0.001	23	6117.8	0.9	0.27		
13	CE Dist + CE Dens <sup>a</sup>	21	9592.2	0.0	0.96	32	5049.9	0.0	1.00	25	6120.6	3.7	0.07		

<sup>a</sup>Gaussian (squared) term was most parsimonious in seasonal candidate model

Upper	Murray (n = 35,959)		Non-V	Vinter <sup>abri</sup>	18		Early	Winter	rm	Late Winter <sup>zinb</sup>				
Model					_									
#	Model Covariates	<i>k</i>	AIC <sub>c</sub>	ΔΑΙΟ		k	AIC <sub>c</sub>	ΔΑΙΟ	AICw	<u>k</u>		ΔΑΙΟ	AIC <sub>w</sub>	
1	Forest cover	5	11682.2	694.3	< 0.001	4	5130.2	773.0	< 0.001	5	6224.2	540.6	< 0.001	
2	Forest age	5	11699.1	711.2	< 0.001	3	5177.4	820.2	< 0.001	4	6364.4	680.8	< 0.001	
3	Water Dist	1	11550.6	562.7	< 0.001	1	5264.5	907.3	< 0.001	1	6262.5	578.8	< 0.001	
4	Caribou	2	11718.9	731.0	< 0.001	2	5252.1	894.9	< 0.001	2	6233.8	550.1	< 0.001	
5	Landscape	13	11516.4	528.5	< 0.001	10	5061.3	704.1	< 0.001	12	6066.4	382.8	< 0.001	
	-													
6	LF Dist <sup>a</sup>	19	11312.2	324.4	< 0.001	12	4826.5	469.3	< 0.001	18	5789.1	105.4	< 0.001	
7	LF Dist + LF Dens <sup>a</sup>	22	11289.2	301.4	< 0.001	13	4824.1	466.9	< 0.001	19	5737.4	53.8	< 0.001	
8	FOR Dist <sup>a</sup>	16	11521.4	533.5	<0.001	11	5043.9	686.7	< 0.001	15	5982.2	298.6	< 0.001	
9	FOR Dist + FOR Dens <sup><math>a</math></sup>	19	11515.4	527.6	< 0.001	14	5036.2	679.0	< 0.001	18	5978.9	295.3	< 0.001	
10	MOG Dist	16	11027.1	39.2	< 0.001	15	4417.2	59.9	< 0.001	14	5816.0	132.3	< 0.001	
11	MOG Dist + MOG Dens	18	11029.8	41.9	< 0.001	18	4357.2	0.0	0.72	15	5778.8	95.1	< 0.001	
12	CE Dist <sup>a</sup>	20	11026.9	39.0	<0.001	15	4417.2	59.9	<0.001	16	5789.3	105.6	<0.001	
13	CE Dist + CE Dens <sup>a</sup>	27	10987.9	0.0	1.00	17	4359.1	1.9	0.28	18	5683.6	0.0	1.00	

Appendix E. Table 3. Continued.

<sup>o</sup>Gaussian (squared) term was most parsimonious in seasonal candidate model

Onion	Creek (n = 10,493)		Non	-Winter <sup>zial</sup>	b		Early	Winter	nb	Late Winter <sup>zinb</sup>				
Model #	Model Covariates	k	AICc	ΔΑΙC	AICw	k		ΔΑΙϹ	AIC	k	AIC <sub>c</sub>	ΔΑΙϹ	AIC	
1	Forest cover	6	7139.0	416.9	<0.001	6	3565.0	485.9	<0.001	5	4339.3	663.7	<0.001	
2	Forest age	3	7136.2	414.1	< 0.001	3	3659.9	580.9	< 0.001	3	4423.6	748.0	< 0.001	
3	Water Dist <sup>a</sup>	3	7030.8	308.7	< 0.001	3	3563.9	484.9	< 0.001	3	4321.1	645.5	< 0.001	
4	Caribou	2	7150.9	428.8	< 0.001	2	3513.5	434.4	< 0.001	2	4357.5	681.9	< 0.001	
5	Landscape	14	6942.3	220.2	< 0.001	14	3364.5	285.4	< 0.001	13	4153.7	478.1	< 0.001	
6	LF Dist <sup>a</sup>	20	6873.8	151.7	<0.001	16	3326.9	247.8	<0.001	19	3975.5	299.8	<0.001	
/	LF Dist + LF Dens	21	68/2.8	150.7	<0.001	1/	3314.0	235.5	<0.001	20	3968.8	293.2	<0.001	
8	FOR Dist <sup>a</sup>	15	6930.0	6891.9	<0.001	17	3345.7	266.7	<0.001	19	4042.1	366.5	< 0.001	
9	FOR Dist + FOR Dens <sup>a</sup>	16	6925.8	6887.7	< 0.001	18	3338.8	259.7	< 0.001	20	4018.7	343.1	< 0.001	
10	MOG Dist	17	6731.6	147.0	<0.001	23	3092.9	13.8	<0.001	20	3694.7	19.1	<0.001	
11	MOG Dist + MOG Dens	19	6727.0	142.5	< 0.001	24	3093.4	14.3	< 0.001	21	3692.9	17.3	<0.001	
12	CE Dist	17	6731.6	9.4	<0.001	23	3092.9	13.8	<0.001	17	3711.1	35.4	<0.001	
13	CE Dist + CE Dens	20	6722.1	0.0	1.00	25	3079.1	0.0	1.00	23	3675.6	0.0	1.00	

Appendix E. Table 3. Continued.

<sup>a</sup>Gaussian (squared) term was most parsimonious in seasonal candidate model

Chain Lakes (n = 3,389)			Non-	Winter <sup>zit</sup>	ab	Early Winter <sup>ubrm</sup>					Late Winter <sup>zieb</sup>				
Model #	Model Covariates	k	AIC <sub>c</sub>	ΔΑΙϹ	AIC	k	AIC <sub>c</sub>	ΔΑΙΟ	AIC <sub>w</sub>	k	AIC <sub>c</sub>	ΔΑΙϹ	AIC <sub>w</sub>		
1	Forest cover	4	4422.9	408.7	<0.001	6	7414.5	239.9	<0.001	4	3412.9	160.7	<0.001		
2	Forest age	3	4368.2	354.0	< 0.001	3	7394.8	220.1	<0.001	3	3394.0	141.8	< 0.001		
3	Water Dist <sup>a</sup>	3	4329.2	315.0	< 0.001	3	7357.8	183.2	<0.001	3	3392.0	139.8	< 0.001		
4	Caribou	1	4365.9	351.7	< 0.001	1	7390.5	215.8	< 0.001	1	3373.9	121.7	< 0.001		
5	Landscape	11	4140.0	125.7	< 0.001	13	7263.0	88.4	<0.001	11	3320.5	68.3	<0.001		
6	LF Dist <sup>a</sup>	13	4095.2	81.0	<0.001	15	7212.5	37.8	<0.001	17	3295.7	43.5	<0.001		
7	LF Dist + LF Dens	14	4055.4	41.2	<0.001	16	7189.9	15.2	<0.001	18	3270.8	18.7	<0.001		
8	FOR Dist <sup>a</sup>	17	4061.2	46.9	<0.001	19	7206.8	32.1	<0.001	13	3289.0	36.8	<0.001		
9	FOR Dist + FOR Dens <sup>a</sup>	18	4044.7	30.5	<0.001	20	7203.9	29.2	<0.001	14	3280.2	28.1	< 0.001		
10	MOG Dist	14	4083.7	69.4	<0.001	22	7212.9	38.2	<0.001	14	3297.6	45.4	< 0.001		
11	MOG Dist + MOG Dens	18	4067.7	53.4	<0.001	24	7189.2	14.5	<0.001	16	3278.4	26.3	<0.001		
12	CE Dist	15	4041.9	27.7	<0.001	19	7199.6	24.9	<0.001	15	3278.5	26.3	<0.001		
13	CE Dist + CE Dens	18	4014.2	0.0	1.00	22	7174.7	0.0	1.00	18	3252.2	0.0	1.00		

Appendix E. Table 3. Continued.

<sup>a</sup>Gaussian (squared) term was most parsimonious in seasonal candidate model