

Influence of Disturbance and Potential Predator Effects on the Persistence of Boreal
Woodland Caribou (*Rangifer tarandus caribou*) in Manitoba

by

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ABSTRACT

The Western Canadian population of boreal caribou (*Rangifer tarandus caribou*) is of special concern and is listed as “threatened” under the Canadian Species at Risk Act (SARA). In Canada, National and Provincial boreal caribou range-based management plans are guided by the application of non-disturbance thresholds that require 65% of a given range to be maintained in a non-disturbed state to achieve a 35% chance of persistence. In this research, I compared Lambda rates (λ) that were estimated and compared among disturbance regimes on 5 boreal caribou evaluation ranges in northwestern Manitoba and a control area in eastern Manitoba. Evaluation ranges were determined using telemetry, resulting in updated ranges, where a minimum of 20 female caribou were monitored in each range during 2011 through 2012. Fine scale disturbance was also investigated using fuzzy classification to determine disturbance across core, peripheral and overlapping ranges. Estimated lambda was at or below 1 for populations studied but confidence intervals overlapped 1. Regressions of λ against percentage of landscape disturbance for natural and anthropogenic sources, and the total were not significant. Analysis of disturbance in non-overlapping and overlapping portions of the fuzzy ranges indicated higher levels of disturbance in overlap areas with increased disturbance near the outer isopleths. A Linear Discriminant Analysis (LDA) indicated that the areas shared between adjacent ranges have consistently higher percentage of disturbance than non-overlapping areas. Although all ranges had disturbance that was less than the threshold specified by current recovery strategies, the spatial pattern of disturbance within ranges may have important implications in population and metapopulation dynamics.

Predation by wolves (*Canis lupis*) is the most frequently referenced contributing factor to negative growth rates in boreal caribou populations. To examine wolves as a main mortality source, I conducted an assessment of grey wolf and boreal caribou habitat selection and interaction during calving and the calf-rearing period. In examining calving and calf loss, aerial surveys and step analysis indicated very high rates of neonatal mortality in the first weeks of life, while adult female survival is comparable to other boreal ranges where populations are stable. Based on the resource selection models developed, there is significant separation in habitat selection between wolves and caribou over the period of high mortality. The results indicate that boreal caribou calf mortality in the area studied is not easily explained by wolf predation. Trail camera and aerial reconnaissance identified substantial black bear presence in the calving areas. Mortality of boreal caribou neonates by black bears requires further investigation.

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1.0 INTRODUCTION

Woodland Caribou, including boreal and southern and northern mountain ecotypes, are formally legislated as ‘threatened’ under the Canadian *Species at Risk Act* (SARA), and under similar legislation for all provincial and territorial jurisdictions in western Canada (Environment Canada 2012). Provinces and territories are obligated by legislation to the conservation and recovery of populations at self-sustaining levels throughout their current range (Environment Canada 2012). In Manitoba, woodland caribou are protected under the Manitoba Endangered Species and Ecosystems Act (MESEA 2015).

The woodland caribou of Manitoba consists of two major ecotypes that include both the forest-dwelling and the coastal or forest-tundra (migratory) animals (COSEWIC 2002). The coastal or forest-tundra ecotype is genetically inseparable from forest-dwelling animals but, unlike sedentary forest animals, they select individual isolated calving sites (spacing out), they migrate across a taiga/tundra transition zone and calve in congregations (Bergerud 1996). Forest-tundra post-calving behaviour in coastal tundra habitats along Hudson Bay are social characteristics more commonly associated with barren-ground caribou (Thompson and Abraham 1994). The highest known threat to the wellbeing of woodland caribou is anthropogenic disturbance within or near ranges that alter the habitat to such an extent such that resident animals are vulnerable to higher levels of predation, principally by wolves and black bears (Neufeld 2006, NCASI 2004). The appreciation of cause and effect relationships surrounding this imbalance compounds by the complexity of multi-predator and multi-prey environments that are, to a large extent, driven by the nature of the range and the extent of the anthropogenic disturbance (Latham and Boutin 2011).

Boreal woodland caribou persist at low densities and prefer large tracts of intact mature coniferous forests and wetland bogs that present an obstacle to the approval of the major industrial projects given the lack of proven mitigation measures and restoration practices. Mitigation measures including predator culling (Hayes et al. 2003, Hervieux et al. 2014), fertility control (Hayes 2013), seismic line blocking (Neufeld 2006), diversionary feeding (Gullage et al. 2012), maternity enclosures (Smith and Pittaway 2008, Chisana Caribou Recovery Team 2010, Boutin and Merrill 2016), translocations (Leech 2015, Hayek et al. 2016) and interspecific prey density balancing (Gillingham et al. 2008, Steenweg 2011, Klaczek and Heard 2016) have provided varying results.

Additional knowledge on the cause and effect relationships arising from anthropogenic disturbance, and its role in affecting the sustainability of woodland caribou populations will assist resource managers and developer's adaptive management and resource planning. In the context of Manitoba, this objective requires a clear understanding of the ecology of boreal woodland caribou and the identification of critical gaps in knowledge that increase the risk associated with the approval of proposed industrial projects.

Objectives

The objectives of this thesis are;

- Delineate evaluation ranges using current telemetry data to assess disturbance thresholds relative to industrial development
- Assess calf recruitment and adult female survival within the evaluation ranges
- Examine total disturbance including anthropogenic and natural
- Compare Lambda (λ) rates between and among evaluation ranges to determine effects of disturbance on rates of survival and calf recruitment

- Examine predator and prey interactions through the development of Resource Selection Models
- Evaluate possible explanations for calf and female mortality by predators (bears and wolves)

1.1 General Biology of Woodland Caribou

Rangifer sp. originated in Beringia some 1.6 million years ago, after which a protracted process of repeated cycles of glacial advances and retreats ultimately culminated in a degree of geographical and distinguishable behavioural separations into northern and southern populations (Weckworth et al. 2012). Festa-Bianchet et al. (2011) describe the current organization of both woodland and arctic caribou into various ecotypes across their broad distribution. Arctic caribou, represented by Alaskan (*R. t. granti*) and Canadian tundra subspecies (*R. t. groenlandicus*), are profoundly migratory with cows undertaking significant annual spring group movements to well-defined calving grounds. Woodland caribou are forest specialists, are distributed across the extent of the boreal forest and western mountain ranges of Canada. Limited zones of range overlap that exist along the whole interface between tundra and boreal animals facilitate a small degree of genetic mixing between the subspecies. Bergerud (1996) suggested that caribou be classified as either migratory or sedentary based on their calving strategy. Animals that tended to disperse from their small bands of winter conspecifics and ‘space-out’ across landscapes to individual calving sites in early spring represented sedentary animals, typical of most boreal and southern mountain woodland caribou. Parturient cows that maintain fidelity with other calving females, and mostly ‘space away’ as a group from predators, are classed as migratory caribou. These may include small groups inhabiting high-altitude mountain plateaus above the treeline (Bergerud and Elliott 1986).

Woodland caribou are a foraging specialist in that their diet, unlike other boreal ungulates, utilize a variety of terrestrial vegetation (*Cladina* spp., *Cladonia* spp., *Stereocaulon* spp.) (DesMeules and Heyland 1969). They also use arboreal plant species such as *Byroria* spp., *Alectoria* spp., and lichens (Cumming and Beange 1987). Lichens are resilient post-disturbance re-colonizers of suitable habitats (Goward 1999, Johansson 2006). Nival conditions or snow adherence influences caribou foraging behaviour (Stardom 1975); they tend to prefer semi-open and open bogs during fall and early winter, but often select mature coniferous uplands containing rock ridges with jack pine as winter progresses (Darby and Pruitt 1984). During early winter, when snow conditions are favourable for travel, caribou feed intensively on arboreal lichens. When nival conditions result in thicker, harder snow pack, bogs can limit caribou utilization of arboreal lichens (Stardom 1975, Darby and Pruitt 1984, Schaefer and Pruitt 1991) at which time terrestrial lichens associated with jack pine dominated rock ridges become more important (Stardom 1977). Stardom (1977) suggested a snow depth threshold of approximately 65 cm, was sufficient to initiate the shift to terrestrial lichens, but Brown and Theberge (1990) observed that caribou were capable of locating forage under various snow-covered terrain conditions exceeding this threshold. Woodland caribou will undertake energetic trade-offs to select lichen rich areas, rather than lichen-poor habitats with less snow (Schaefer 1990).

All woodland caribou, with exception of the migratory populations of northern Labrador and Newfoundland that have periodically exhibited dramatic cyclical expansions and contractions in population growth rates, present a rather consistent profile of population dynamics across all ranges in Canada, regardless of ecotype. The

Environment Canada (2012) science review update provides an excellent overview of general caribou biology. Adult females (2.5 years of age) generally have high pregnancy rates (>90%) and only carry a single foetus. Calving dates, while somewhat variable regionally, are synchronous (\pm 30 days) within any region. High rates of early calf mortality within the first six weeks of birth are common resulting at the beginning of fall recruitment rates that rarely exceed 30 calves/100 cows. Most stable populations of woodland caribou demonstrate high adult survival (>86%), while populations in decline tend to exhibit a combination of lower adult survival and low annual recruitment (<20 calves/100 cows). Most woodland caribou populations in Canada are stable except for Alberta and British Columbia for which the majority present decade-long negative growth rates (Hervieux et al. 2013, Johnson et al. 2015). Boreal woodland caribou populations in this Study area are “acceptable” (Manitoba Boreal Woodland Caribou Management Committee 2015).

1.2 Seasonal Habitat Preferences

In northwest Manitoba, the Kississing and Naosap Reed woodland caribou populations were shown to select mature coniferous stands and avoid disturbance across multiple scales (Lander 2006). Caribou inhabiting the Naosap Reed range were associated with arboreal lichens, spruce trees, and large diameter trees, and negatively associated with trembling aspen and higher deadfall density (Metsaranta and Mallory 2007). Members of the Wabowden and Gormley populations used large open and treed peatland complexes during both winter and summer (Brown et al. 2000). Similarly, Rettie and Messier (1998) demonstrated that the Smoothstone-Wapaweka caribou population north of Prince Albert National Park in Saskatchewan preferred open and treed peatlands,

lowland black spruce and upland black spruce/pine stands. Animals in the Weyakwin Lake area of Saskatchewan selected jack pine, white spruce stands, upland and lowland black spruce, and open peatland and avoided burned areas (Rettie and Messier 2000).

1.3 Calving Habitat

Boreal woodland caribou shift behaviour with the onset of calving to isolated calving sites as a predator avoidance strategy (Bergerud and Elliot 1986). The National Recovery Strategy for boreal populations in Canada (Environment Canada 2012) identifies a wide range of calving habitat types ranging from muskegs, marshes, proximity to water, open coniferous forests, tussock tundra, low shrub, riparian, recent burned areas, and south and west aspects of hills as critical. There are relatively few studies that characterize calving sites of boreal woodland caribou at the stand level with the peatland or Canadian Shield boreal forest habitats common to most caribou in Manitoba. DeMars (2015) identified calving sites for some adult females inhabiting peatland complexes in northeastern British Columbia. He reported that females shifted from a winter association with lichen-rich bogs to landscapes with a higher proportion of open poor fens that supported an abundance of emergent vegetation and shrubs for calving. Based on the Latham et al. (2011*a*, 2013) assessments that fens held higher predation risk than bogs, they hypothesized that females may be entertaining a higher predation risk to access higher quality forage. He also noted that parturient cows tended to avoid uplands, lakeshores, and anthropogenic disturbance, behaviours he surmised to represent a predator avoidance strategy. At a coarser scale, animals in the Wabowden area of west central Manitoba, selected lowland black spruce, peatlands with forested islands and treed muskeg for calving habitat, while avoiding other conifer species and deciduous

cover (Hirai 1998). In the Naosap Reed area of Manitoba, caribou were observed using islands during calving (Shoesmith and Storey 1977). In the Smoothstone-Wapaweka region of Saskatchewan, both peatlands and black spruce-dominated stands were selected for calving and rearing (Rettie and Messier 1998). Northwestern Ontario caribou preferred treed bogs/peatlands with forested Islands as well as islands and lakeshores, while avoiding deciduous forest, shrub-rich fens and wetlands (Armstrong et al. 2000, Hillis et al. 1998).

1.4 Post-calving Habitat

Cows with calves tend to maintain their pattern of isolation, preferring to remain rather sedentary and spaced out until mid- to late- summer. Calving area selection was observed at a landscape scale in in both the Smoothstone-Wapawekka in Saskatchewan and in the Kississing-Naosap range in west-central Manitoba (Dyke and Manseau 2011). An association with wooded lakeshores, upland conifer-spruce, and treed muskeg was observed for animals within the Naosap range in Manitoba (Malasiuk 1999, Metsaranta and Mallory 2007), while Reed Lake range animals exploited islands, lakeshores, and sparsely treed rock areas during summer (Shoesmith and Storey 1977). For the Kississing, Naosap and Reed populations Lander (2006) reported caribou preference for sites with greater arboreal lichen cover during summer. In northwestern Ontario, high use of islands and large contiguous patches of dense mature coniferous forests and treed peatlands were contrasted by an avoidance of recent burns, shrub-rich fens, and dense deciduous forest or shrub during summer (Hillis et al. 1998, Armstrong et al. 2000, Pearce and Eccles 2004).

1.5 Rutting Habitat

The use of muskegs that harbor ground lichen and sedges, mixed bush areas, and sparsely vegetated regenerating burns have all been reported (Environment Canada 2012). In northwestern Ontario, caribou used dense conifer, sparse conifer, and mixed forests while avoiding recent burns, shrub-rich fens, and dense deciduous forest and shrub areas (Hillis et al. 1998).

1.6 Winter Habitat

During late winter and early spring, caribou associate with habitats supporting abundant terrestrial and arboreal lichens, even when Api (snow) conditions are more favourable in habitats with less lichen abundance (Schaefer 1990, 1996, Dyke and Manseau 2011). On the Naosap range, Manitoba, caribou selected lichen-rich mature upland spruce and pine stands and treed muskeg and avoided deciduous forests (Malasiuk 1999, Metsaranta and Mallory 2007). On the Kississing range, Manitoba, O'Brien et al. (2006) observed a winter preference for jack pine dominated forests while Lander (2006) reported that Kississing, Naosap and Reed range animals preferred areas with greater visibility distanced from the forest edge. In northwestern Ontario, large contiguous patches of dense mature conifer forest, sparse coniferous forest, mixed forest and treed bogs were all selected while recent burns, shrub-rich fens, and dense deciduous forest or shrub were avoided (Hillis et al. 1998, Armstrong et al. 2000, Pearce and Eccles 2004).

1.7 Biophysical Environment

The project study area is located in parts of three ecozones; Taiga Shield, Southern Arctic and Boreal Shield. The Taiga Shield Ecozone contains rolling upland hills, lowland bog and fen peatlands, rocky outcrops, and glacial till forming eskers and kettle

lakes. Stands of jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), and tamarack (*Larix laricina*) cover the southern portion of this ecozone and transition to the treeless Southern Arctic Ecozone in the north. White spruce, balsam poplar, and paper birch are found along protected areas lining waterways (Smith et al. 1998). The Boreal Shield Ecozone that overlays most of north-central and eastern Manitoba is typified by metamorphic gneiss bedrock, typically thin, cool, acidic, soils with low nutrient availability, oxygen-poor organic wetlands (Smith et al. 1998), numerous lakes and waterways. Dominant vegetation cover includes white (*Picea glauca*), black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), and tamarack (*Larix laricina*) with broadleaf species becoming more prevalent in the south, such as white birch (*Betula papyifera*), trembling aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*) becoming more abundant towards the south (Zoladeski et al. 1995). The Boreal Plains Ecozone that extends from the south Interlake to the north Interlake and west to the Saskatchewan border is a composite of nearly level to gently rolling plains consisting of hummocky and kettled to gently undulating morainal till deposits and level to depressional glaciolacustrine sediments. Productive mixed coniferous and hardwood forests are associated with industrial forest management and well-drained areas with suitable soils suitable for agricultural uses (Smith et al. 1998).

Mammals common to all ecozones, include moose (*Alces alces*), grey wolves (*Canis lupus*), woodland caribou, black bears (*Ursus americanus*), mink, fisher (*Martes pennati*), marten (*Martes americana*), weasel (*Martes nivalis*), lynx (*Lynx canadensis*), red fox (*Vulpes vulpes*) and snowshoe hares (*Lepus americanus*).

1.8 Industrial Development

Industrial activities in the study area during the time of this study include forestry, mining and hydro-electric transmission. Tolko Industries Ltd., was the largest leaseholder of a management area (>8.5 million hectares) that overlaid parts of the Churchill River Upland, Hayes River Upland, and Mid-Boreal Lowlands Ecoregions. Potential impacts of industrial activities within the Study Area include clearing, construction, operational noise, underground blasting, waste disposal, and increased public access to previously remote areas (Weir et al. 2007).

1.9 Home Range Estimation

Advances in remote GPS telemetry systems has dramatically improved the analytical opportunities in mapping of population range and habitat use, identify core habitats and determine animal response to habitat change and disturbance. The following provides an overview of methods utilized throughout the thesis.

1.10 Minimum Convex Polygon (MCP)

Home ranges delineated as the area bounded by the smallest polygons formed by joining the outside geo-referenced observation points, commonly referred to as the minimum convex polygon (MCP) (Burt 1943). The application of the MCP method often consists of the removal of a small percentage of extreme observations situated farthest from the concentration of observations to eliminate extraordinary movements that appear to be outside the range of normal activities (Calenge 2011). However, the inclusion of unused areas between the outermost locations still tends to overestimate home range (Katajisto and Moilanen 2006).

1.11 Kernel Density Estimation (KDE)

Worton (1989), suggested the Kernel Density Estimator (KDE) for home range estimation provides a representative biological area of habitat use as observations are weighted relative to their proximity of all other observations. He proposed the application KDE, as a surrogate for the amount of time spent by the animal at that location. The utilization distribution (UD) explains spatial variability in wildlife intensity by both individuals and populations. This information can be particularly revealing where subpopulation range exploitation results in either higher or lower intensities of use than expected (Smith and Dobson 1994, Seaman and Powell 1996).

A discussion of the advantages and disadvantages respecting the use of telemetry data for home range analyses is summarized by Walter et al. (2011). Investigators face a trade-off between the frequency of location data and duration of the study which is a function of the battery life of Global Positioning System (GPS) collars. Highly compressed observations inherent in telemetry studies usually result in overweighting of the importance of some observations (Otis and White 1999). The usual case is for correlation to be positive and to weaken with increasing distance between the points (Lennon 2000). Similarly, truncation or rounding of satellite positional data may result in observations closer numerically than actually occurs in nature leading to the same effect (Walter et al. 2011).

The width of each kernel is called the smoothing parameter (h), window width, or bandwidth. The smoothing parameter must be specified and can have a dramatic effect on the resulting estimate. Harris et al. (1990) noted that relatively minor changes in the smoothing parameter value had a large effect on overall range size and suggested the

approach may be more suited to the analysis of range use than the estimation of home-range size. Two methods used extensively for home-range analyses include ‘least squares cross-validation’ (LSCVh) and a method that determines the optimal h (hopt). The latter tends to ‘over-smooth’ multimodal data (Worton 1995). Rodgers and Kie (2010) noted that problems of over-smoothing of multi-modal distribution data could be managed using the LSCVh and ‘bias crossed validation’ requiring a minimum of 1000 data. Rodgers and Kie (2010) cautioned that the use of subsampling to satisfy this requirement results in underestimations of some important habitats. LSCVh has other drawbacks, including high variability (Park and Marron 1990, Jones et al. 2006), a tendency to under-smooth data (Sain et al. 1994), and multiple local minima in the LSCVh function (Sain et al. 1994).

1.12 Core Area Determination

Core area analysis is a logical extension of KDE. They are defined by Vander Wal and Rogers (2012) as areas within home ranges within which an animal spends a preponderance of time. Schindler et al. (2006) described the sequential treatment of GPS animal location for woodland caribou in eastern Manitoba to determine core areas. First, location data were normalized to reduce the effects of autocorrelation by setting a fixed observation rate, and then pooling and stratifying the data by season. Next, monthly and seasonal adaptive kernels are calculated for each animal and populations pooled using Rodgers and Carr’s (1998) ‘Home Range Extension’ (HRE) function in Arc GIS. Monthly seasonal polygons are amalgamated and mapped to create seasonal utilization distribution (UD) isopleths. The 70% isopleths represented the home range core areas (Schindler et al. 2006).

1.13 Defining Caribou Range

Population home ranges are the functional unit for the identification of distinct populations and for the measure of overall disturbance and identification of appropriate management strategies to comply with the National Recovery Strategy. An animal's home range is the area traversed by the individual in its normal activities of food gathering, mating and caring for young (Burt 1943). Caribou population is a defined area of occupation distinguished spatially from other groups where population dynamics are driven by local demographic factors opposed to intragroup mixing (Esler et al. 2006). Hastings (1993) suggested that gains or losses due to immigration or emigration should not exceed 10%, while Dey et al. (2006), using a simulation modeling approach, made a case that subpopulations behave as one larger population once migration rates reach 20%. Although the question is fundamental to understanding population processes, this topic has received limited attention (Waples and Gaggiotti 2006).

Woodland caribou populations across Canada range from 30 to >2,000 animals within ranges that vary from less than 1,000 km² to more than 50,000 square kilometres (Environment Canada 2008, Callaghan et al. 2010). Environment Canada (2011) suggest that a minimum of 300 animals occupying ranges of at least 10,000 to 15,000 km² is a requisite for self-sustaining populations, although this conclusion is debatable based on findings of McLoughlin et al. (2016) suggesting greater stability for some boreal shield populations in northern Saskatchewan. Also, the application of comparative population metrics such as recruitment to small populations occupying limited ranges introduces substantially higher uncertainty related to small population sampling errors. The idea of range and range use are dynamic concepts and delineation requires regular assessment

and updating (Racey and Arsenault 2007). Thus, while a range may be defined as the geographic area within which there is a high probability of occupancy by individuals of a local population, Lewis and Mahoney (2014) demonstrated fluidity among memberships and range definitions for caribou in Newfoundland.

The National Boreal Caribou Recovery Strategy (2012) recognizes three types of boreal caribou ranges, categorized by the degree of certainty in the delineated boundaries for 51 boreal ranges across Canada. Of these, almost half (45%) fall into categories of either low or medium certainty of boundary integrities. The Strategy states that changes to range boundaries are expected as procedures for range demarcation are standardized across Canada. Advancements in GPS collar technology, combined with the availability of highly specialized GIS and applied statistical analysis packages, allows for habitat, feature, and movement pattern analysis (Boyce et al. 2012). In the case of a highly social species like woodland caribou, there may be an added dimension of whether or not disturbance may influence the way in conspecifics within social groups spatially relate to other groups, is of particular significance to managers' efforts to appreciate whether or not there are consequences of habitat fragmentation to the demarcation of discrete ranges (McLoughlin et al. 2004, Banks et al. 2007).

The recovery strategy for caribou in Manitoba has identified a total of twelve distinct ranges based on 100 percent minimum convex polygons using year round collar data, incidental observations, faecal collection survey data, and aerial track survey data from the past 10 years (Manitoba Boreal Woodland Caribou Management Committee 2015). Three additional ranges were tentatively mapped but it was suggested they would require more evaluation to determine whether or not they were distinct from adjacent

ranges. There exists substantial overlap in the boundaries of five ranges identified in northwestern Manitoba, including Naosap/Reed, Wheadon, Wapisu/Wimapedi, Wabowden and Harding (Manitoba Boreal Woodland Caribou Management Committee 2015).

1.14 Fuzzy Cluster Analysis in Refinement of Range Delineation

For multiple local populations within a continuous habitat, cluster analysis of movements can be useful to define group membership (Taylor et al. 2001). Schaefer and Wilson (2002) applied fuzzy classification to the Geroge River caribou in Quebec to determine group membership and fractional membership within the larger herd to better understand range occupation. Fuzzy classification resulted in the assignment of individual animals to one of four subpopulations to clarify the underpinnings of differential rates of recruitment and mortality for each. Satellite collar data for barren-ground caribou (*Rangifer tarandus groenlandicus*) were used to quantify differences in habitat use of sub-populations in the Northwest Territories using fuzzy clustering (Nagy et al. 2011). In northwest Ontario, fuzzy cluster analysis provided an understanding of demographic structure in an industrial landscape, and identified 6 separate woodland caribou units with strong membership structure (Shuter and Rodgers 2012).

McLoughlin et al. (2002) used cluster analysis of movement data for grizzly bears, and suggested that annual exchange rates of 3.4-13% for females and 7-35% for males was sufficient to be considered one continuous (open) population. Conversely, Bethke et al. (1996) concluded from their analysis of polar bears (*Ursus maritimus*) in the western Canadian Arctic, that three populations identified in their study were relatively closed with little immigration or emigration of radio-collared females among populations that

overlapped for part of the year. They tested for the presence of spatial clusters of animals based on movement data, then applied a home range estimator to identify the geographic range of populations for conservation purposes.

1.15 Habitat Utilization - Resource Selection Functions

Wildlife research and management are disciplines that are largely dedicated to an appreciation of how animals use and exploit their environment to satisfy life requirements of food, water and cover in the face of changing conditions, and interrelationships with conspecifics, interspecific competitors and predators (Manly et al. 2002). Wildlife habitat is where animals live and have resources and conditions that promote occupancy by a species (Morrison et al. 2006). The usage of a resource is defined as that quantity of the resource that is utilized by an animal or population in a fixed period in which the availability of a resource is the quantity accessible to the animal or population during that same period (Manly et al. 2002). The likelihood that a resource will be selected defines the preference for a particular resource relative to all other available resources (Johnson 1980).

RSFs can be applied at various scales including the geographic home range of a population, seasonal ranges or calving sites by parturient caribou females and predators (DeMars 2015). Telemetry data also allow for measurements of distances from anthropogenic features to determine if animals select or avoid such features for travel (Latham et al. 2011*b*). The datasets supporting RSF analyses obtained from telemetry systems involve large numbers of individual observations from a few animals (GPS transmitters), a small number of observations for a small or large number of animals (VHF transmitters), or a large number of individual observations (GPS) from a large

number of animals. Hebblewhite and Haydon (2010) surveyed 30 habitat and movement related studies that showed mean sample sizes for GPS studies of 18.1 (range 4 - 82) collared animals compared to 58.7 (range 14 - 188) for VHF-based research. They also indicated that 10 studies used a combination of GPS and VHF collars. When estimating animal survival only, and budgets are constrained, much larger sample sizes are affordable using VHF collars (Latham et al. 2015).

Spatial autocorrelation is inherent to all telemetry data, given that each new location is, to a varying degree, dependent on the time between previous observations; the closer the time, the higher the probability of it being correlated with the previous location (Boyce et al. 2002, Koper and Manseau 2012). Spatial autocorrelation violates the premise respecting the independence of residuals, the effect of which is to both inflate the degrees of freedom, and therefore the test statistic that may result in a Type I error (Boyce et al. 2002, 2010, Pollitt et al. 2012). Some methods have been used to reduce the effect of autocorrelation, including the elimination of data points, to more evenly distribute spatial observations across time (Swihart and Slade 1985). Other evaluations of the effects of autocorrelation suggest that such destructive subsampling is neither productive nor warranted (de Solla et al. 1999, Boyce et al. 2002). De Solla et al. (1999) failed to demonstrate that rarefying data reduced autocorrelation among observations of snapping turtles (*Chelydra serpentina*) or antler flies (*Protopiophila litigate*). Boyce et al. (2002) noted that rarefaction procedures removed some habitats critical to an animal's fitness and suggested that the use of variance inflators that do not alter model coefficients provide a robust mathematical solution where autocorrelation may be a concern related to the scale of the project.

Wildlife species use habitats at a variety of scales and selection of calving sites may be shaped by the preference and availability of forage resources, water, avoidance of insects, or combinations of some or all factors (Bergerud and Elliot 1986, Vors and Boyce 2009, Hornseth and Rempel 2015).

Some of the earliest work, incorporating methodologies similar to RSFs included that of James (1999), who mapped caribou locations for 109 collared animals between 1991-1997. He separated these into three seasons; winter (November - February), spring (March - June) and fall (July - October) and distinguished two general vegetation communities including bog/fen and well-drained sites. Latham (2011*b*), working in the same peatland complexes as James (1999), refined the biophysical dataset to include covariates and evaluation parameters were tested using regression analyses and compared using Akaike's information criterion (AIC) and found that bears selected similar habitat to caribou during the calving period.

Another caribou habitat suitability study was undertaken in east central Ontario by Brown et al. (2006) with an objective to develop a spatially explicit predictive model of habitat suitability for woodland caribou. They applied three different management simulations on habitat across a 120-year planning horizon using Patchworks (Spatial Planning Systems Copyright © 2004 - 2009). Telemetry-based GPS locations for 58 collared animals were plotted on a modified provincial forest resource inventory supplemented with Landsat inventory data into habitat and anthropogenic disturbance classes. These included shrub-rich treed muskeg, mature black spruce, intermediate aged black spruce, mixed conifer, deciduous forest, primary roads, cutovers, and mean preferred patch size. Mean RSF scores within 100 km² sampling hexagons provided an

index for comparisons among management strategies and planning periods. Results of RSF modeling illustrated that areas of mature and intermediate black spruce provided the best proxy for caribou habitat, and an avoidance of deciduous and mixed-wood stands.

McCarthy et al. (2011) used total disturbance, barrens, coniferous forest, deciduous forest and mixed-wood forest in their linear modeling. Using AIC, they selected the top model that illustrated caribou avoidance of disturbance and mixed wood stands during calving. DeMars (2015) used habitat and anthropogenic parameters to explain the selection of habitats by caribou cows, black bears and wolves during the caribou calving season in Northern BC and found similar habitat selection for bears and calving females. MacNearney et al. (2016) applied RSF approaches, including step analysis, in the assessment of oil and gas development on calving site selection. They analyzed data from 69 radio-collared woodland caribou cows for two boreal ranges along the BC and Alberta borders (Little Smoky, Chinchaga). Land cover parameters included various forest cover types, wetlands, and shrublands. Human disturbance parameters measured were seismic lines, roads, pipelines and well sites. Results of step analysis indicated that 23 of 58 calves died within the first four weeks life of calving. Calving sites for the Chinchaga range were predominantly treed wetland and shrub habitats, while those of the Little Smoky range were mostly moderate and dense canopy conifer (MacNearney et al. 2016).

For southern mountain populations, Wittmer (2004) considered the proportions of non-forested and forested habitats by age class (one-40 years of age and >40 years of age), distributions of patch sizes, edge densities, mean nearest neighbor patch-age (0-40 and 40-100-year-old stands), and winter snow accumulation. Hornseth and Rempel (2016), used GPS telemetry data from woodland caribou within the Boreal Shield region

in Northern Ontario to assess seasonal resource selection evaluation at five spatial scales. They compressed twenty-seven forest inventory classes into seven land cover parameters and found that the strongest selection patterns were at the scale of 10,000 hectares and that global models with common variables worked using range specific coefficients.

The addition of RSFs for predators sharing ranges with caribou further provides the opportunity to infer potential spatial and temporal overlaps that could potentially lead to higher rates of predation based on the probabilities of sharing habitats during critical seasons (Latham et al. 2011c, Lewis and Mahoney 2014, DeMars 2015). Boyce et al. (2002) noted that if an RSF can reliably predict the location of organisms, then it is a good model, and the stronger the statistical inference respecting observations, or the more robust the application of the model at predicting habitat use or occupation in other areas, the better.

1.16 Range Disturbance and Effect on Woodland Caribou

The National Scientific Review for the Identification of Critical Habitat for Boreal Caribou (Environment Canada 2011) documented that the combination of natural and anthropogenic disturbances explained 61% of the variation in mean recruitment rates (ratio of calves/adult female) for 24 boreal caribou populations across Canada.

Anthropogenic disturbance is the cumulative effects of all human-caused changes within landscapes including roads, trails and ROWs common to all industrial intrusions, and the landscape fragmentation linked to stand-level commercial forestry operations (Environment Canada 2011).

The rapid economic growth throughout North America in the 1960s created high demands for construction lumber and newsprint and fueled the expansion of the Canadian

forest industry (Paillé 2014). Forest harvest levels have trended sharply lower in all provinces from peak harvest levels of the 1980s to mid- 2000s (National Forestry Database 2017). Conversely, forest harvest trends in Alberta have increased inclusive of 2014. Sustained yield forestry in the 1960s targeted the harvest and renewal of old-aged stands first to maintain a constant distance of wood haul to mill locations (Udell 2003). In the early 1990s, economic, environmental, social and cultural factors were being integrated into forest planning approval processes. Forest management models tended to promote intensive post-harvest silvicultural treatments of coniferous stands including site preparation, planting, and tending to minimize harvest cycle (Udell 2003).

In Manitoba, commercial forestry has occurred throughout ecoregions supporting woodland caribou with peak forest harvest being 24,600 hectares in 1979 (National Forestry Database). Between 2011 and 2014 that estimate ranged from 7,500 to 10,600 hectares with the total cumulative area 1975-2014 exceeding 550,000 hectares. The aggregate area impacted by fire over the same time frame exceeded 12.8 million hectares averaging over 320,000 ha's/year, but the 2016 publication of Kansas et al. (2016) for northern Saskatchewan suggested that LANDSAT fire mapping over-estimated the area burned by >30% owing to the extent of non-burned residuals. McLoughlin et al. (2016) also noted that stable northern Saskatchewan woodland caribou populations balanced low annual recruitment rates (<20 calves/100 cows) with high adult female survival (>92%) and very high adult female pregnancy rates (>94%). The creation of resource development access in proximity to caribou range can also result in higher mortality from unregulated hunting and increased predation (Apps et al. 2013).

Courtois et al. (2007) and Beauchesne (2012) observed that caribou in proximity to fragmented ranges in Quebec tended to initially increase their home ranges in search of alternate foraging areas. They found that caribou reduced areas of use to smaller core where there was a higher risk of predation. Regeneration of stands harvested in proximity to caribou ranges results in a flush of woody browse regrowth that is favourable for moose and deer, both interspecific competitors to woodland caribou (Thompson et al. 2003).

Much of the evidence respecting the nature of impacts of linear corridors has come from studies on ranges in Alberta and British Columbia that have documented extensive linear feature (roads, pipelines, transmission corridors, seismic lines) developments in support of oil and gas exploration projects. Some early research tracked movements of VHF radio-collared wolves, the results of which indicated that linear features, particularly seismic lines, functioned as travel corridors for wolves (James 1999, James and Stuart-Smith 2000). Conversely, Kuzyk (2002), Neufeld (2006), and Latham (2009) found that caribou predation was not statistically closer to linear features. Neufeld analyzed movement data (30 minutes to 1-hour intervals) for 13 wolves in 5 packs 2002-2005 in the Little Smoky area of Alberta and showed that wolves had a strong attraction to seismic lines, as did moose, bears and coyotes, but that wolves did not strongly select areas frequented by caribou. However, a rework of the wolf movement data from Alberta using a refined step selection analysis (Thurfjell et al. 2014), did reveal evidence that wolves selected seismic lines during the snow-free season leading to some inference respecting the possibility of encounters between caribou and wolves (Latham et al. 2011*b*). Dickie et al. (2016) analyzed 5 minute interval movement patterns of 20

wolves in 6 packs in the summers of 2013 and 2014 and 11 wolves in the winter of 2014 in east central Alberta and west central Saskatchewan. They found that wolves selected for some linear features in some seasons, and travelled faster and covered more territory than in the forest. In winter, wolves were two to 8 times more likely to select for roads, railways, and transmission corridors.

Revegetation of low impact meandering seismic lines (<4 m width), represents a challenge compared to wider disturbance corridors such as roads and permanent transmission lines (Bayne et al. 2011). The relatively narrow width of many seismic disturbances limit the penetration of sunlight to cleared areas, thereby retarding natural regeneration, a problem particularly evident for wet fens within which regeneration failures were evident on some lines for up to 50 years (Bayne et al. 2011, van Rensen et al. 2015). James (1999) determined an association of caribou with fens and bogs in peatland complexes and presented evidence that wolf movement associated with linear corridors was 2.8X faster than extensive forest travel.

The National Recovery Strategy (Environment Canada 2012) measures disturbance by the area bounded by a 500 m buffer around all anthropogenic linear and polygon features, plus the area of natural disturbance for natural fire areas ≤ 40 years age to arrive at a total area of range disturbance and assigns a maximum disturbance target of 35% for a 60% probability of sustaining a resident population with a minimum membership of 300 animals. Obvious persistent disturbance features such as seismic lines that fail to regenerate, plus roads, transmission lines and pipeline corridors are essentially permanent anthropogenic features, all of which contribute to the overall calculation of individual

range disturbance as defined by the National Recovery Strategy (Environment Canada 2012).

1.17 Determining Lambda (λ) Rates

Measures of population abundance predict changes in the size of populations and their distribution as the suitability of habitat changes. The prediction of population response to change is not always possible, however, even when there is a sound understanding of the mechanisms underlying cause and effect relationships (Krebs 2015). Given the importance of woodland caribou from an industry constraints perspective, the role of anthropogenic and natural disturbance on population response requires an understanding of population growth. Currently, population estimates include predictive sampling designs to determine time-referenced changes to the total population size or estimates of variations in population metrics for adult female survival and recruitment through subsampling (Hatter and Bergerud 1991, McLoughlin et al. 2003).

Ungulate population surveys can be problematic should wide confidence limits of population estimates introduce uncontrolled management decision risks (Carr et al. 2010). Several sources of visibility biases are also inherent to aerial survey-based population estimates of large mammals. These include effects of season and weather conditions, aircraft type, number, skill, and experience of observers (Lubow and Ransom 2016). Availability biases, which refer to the probability of animal detection, is harder to correct without increasing the intensity of survey effort (Laake et al. 2008). Bergerud and Elliot (1986) found variation in seasonal and annual estimates of caribou population size and recruitment rates as a response to wolf culling treatments. Alternative approaches to

determining rates of population change include intensive stratified, random block surveys using modified Gasaway survey methods for caribou (Heard et al. 2008).

Environment Canada (2012) has established a minimum 20-year target of a stable λ (the likelihood of the population remaining stable or increasing over 20 years) based on indicators of population trends and disturbance level within a boreal caribou range. Total range disturbance that exceeds 35% is believed to introduce substantial uncertainty as to whether populations can be sustained (Environment Canada 2012). However, the specific statistical approaches used to estimate λ , are not specified. Hervieux et al. (2013) estimated the empirical means of adult female survival rates for 13 woodland caribou populations in Alberta. Annual survival rate estimates utilized datasets obtained by field checking the mortality status of radio-collared adult females several times/year. Recruitment rates were obtained from aerial observations of the number of calves observed/adult female from groups located by telemetry locations. Rates of population growth (λ) ranged from 0.883 (Little Smokey) to 1.07 (A La Peche).

The use of λ as a surrogate metric of population growth provides context of the relationships to range disturbance resulting in apparent competition and population stress (James 1999, Latham 2009, Hervieux et al. 2013, Johnson et al. 2015, McLoughlin et al. 2016). Numerous studies have estimated global adult survival rates from telemetry monitoring of radio-collared adult females, ranging from 75%-95% adult survival in any one year, and annual recruitment rates varying from 10 to 30 calves/100 cows (Edmonds 1988, Seip 1992, Stuart-Smith et al. 1997, McLoughlin et al. 2003, 2005, 2016, Latham 2009, ASRD 2010, Hervieux et al. 2013, Lewis and Mahoney 2014, Hayek et al. 2016).

Calf recruitment and adult female survival are critical determinants of population growth rates of woodland caribou populations (DeCesare et al. 2012). Tracking of collared female caribou during spring and summer to determine survival rates of calves has resulted in evidence that the majority of calf mortality occurs in the early weeks of life as a result of predation (Franzmann et al. 1980, Hauge et al. 1981, Osborne et al. 1991, Stuart-Smith et al. 1997, Patterson et al. 2013). Seip (1992) conducted summer calf counts from collared females in southern British Columbia to determine calf survival through the summer months into fall and found that calf survival was dependent upon wolf occupancy with no survivorship of calves when wolves were present.

1.18 Apparent Competition

The National Recovery Strategy considers anthropogenic disturbance accounting for most of the decline in boreal caribou populations and set a 65% non-disturbance target for ranges. Much of the data and information used for the 2008 national scientific review of woodland caribou (Environment Canada 2008) were extracted from research of populations associated with zones of concentration of historical anthropogenic developments in Alberta and BC. Many of these populations have exhibited multi-decadal population decline coincident with landscape-level habitat changes that have shifted the predator-prey dynamic in favour of the predator (Hervieux et al. 2013, Johnson et al. 2015). The federal, provincial and territorial governments' caribou recovery strategies developed in the first decade of the 2000s all embraced the idea of apparent competition as an important potential agent of caribou population declines (Environment Canada 2012). The main issues identified through threat assessments

targeted the effect of anthropogenic landscape disturbances as drivers of boreal woodland caribou population declines mediated through wolf predation (Thomas 1995, James and Stuart-Smith 2000, Dyer et al. 2001, Courbin et al. 2009).

The direction and focus of much of the woodland caribou research over the past 25 years has emerged from the theory of ‘apparent competition’ (Holt 1977). This theory was adopted by Bergerud and Elliot (1986) to explain wolf, moose, and mountain caribou population dynamics in northwestern British Columbia in the late 1970’s and early 1980’s. A critical conclusion was that predation on young calves was the chief mortality factor, and, in those ranges where moose biomass increased, a higher incidental loss of caribou neonates followed. Bergerud and Elliot (1986) identified both wolves and bears as potential predators, but in the ecosystems in which they worked, wolves were identified as the main predator.

Predators are known to be the primary limiting factor for woodland caribou (Seip 1992, Rettie and Messier 2000, Johnson et al. 2001). Predators such as grey wolf (*Canis lupus*) are associated with more evenly distributed and higher density larger prey species such as moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) (Messier 1985, 1991, Bergerud and Elliott 1998, Zager and Beecham 2006, Bergerud 2007). Moose and deer are typically associated with disturbed forests through anthropogenic activities such as timber harvest and natural disturbance events, including fire and insect infestation (Peek et al. 1976, Rempel et al. 1997, Fisher and Wilkinson 2005). Predation by wolves (Dyer et al. 2001, 2002, Wittmer et al. 2005b, 2007) and black bears (Boutin 1992, Ballard 1994) are also known to be a factor in limiting ungulate populations through predation of calves.

Habitat alteration from human development including forestry and hydro transmission development results in increased forage for early seral species due to the lush and succulent growth from tree removal. This benefits primary prey species such as deer, moose, hare and rodents, thus increasing the biomass availability for top predators such as wolves and bears (Peek et al. 1976, Monthey 1984, Clarke et al. 2007, Zwolak 2009). Boreal caribou habitat typically has low prey densities due to lack of young seral forest (Cumming and Beange 1987, Seip 1992). Linear development and the types of anthropogenic activities associated with linear features may lead to a cumulative effect response that could influence λ through habitat alteration, and changes to predator-prey relationships leading to a decline in local or regional caribou populations (Dyer et al. 2001, McLoughlin et al. 2003). These effects include the possibility of changing the natural distribution of primary prey such that it coincides with boreal woodland caribou habitat, resulting in increased incidental interactions with predators seeking primary prey (moose) (James et al. 2004). This potential for increased incidental predation on boreal caribou can lead to decreased λ , with the primary cause being predation (Schaefer 2003, Vors et al. 2007).

Wolves, as the common predator of all of these ungulates, benefit from access to additional meat biomass that may ultimately lead to higher densities of wolves and the potential for other incidental predation upon woodland caribou (Wittmer et al. 2005*b*, Latham 2009, Boutin et al. 2012). Holt (1977) described “apparent competition” when two or more prey species are sought by a common predator whose population is increasing, resulting in higher mortality rates on the secondary prey. Apparent competition has been identified as the primary cause of caribou population declines in

Alberta and British Columbia (Wittmer et al. 2007, DeCesare et al. 2010, Serrouya et al. 2011, Boutin et al. 2012, Hervieux et al. 2013).

1.19 Predation of Caribou Calves

The vulnerability of woodland caribou to high early calf predation mortality was also observed in Newfoundland in the late 1950's (Bergerud 1971). Bergerud's research was initiated to isolate the causes of depressed populations, despite the extirpation of wolves from the Island in 1911 and substantial protection of caribou from hunting since 1924 (Bergerud 1971). Field observations on the calving grounds revealed predation by Canada lynx (*Lynx canadensis*) as the probable source of the low rates of calf survival. An experimental culling of lynx from calving grounds resulted in higher calf survival (Bergerud 1971). He also noted the presence of black bears on the calving grounds, but failed to find evidence that bears were depredating calves at that time. He documented that females migrated in groups to high open plateaus for calving, an anti-predator vigilance strategy he called 'spacing away' (Bergerud 1978, Bergerud and Elliot 1986). He postulated that the addition of moose as a food source ultimately resulted in higher populations of wolves and therefore was additive to incidental depredation of caribou calves, a relationship consistent with the theory of apparent competition (Holt 1977).

Each of the ecotypes of woodland caribou exhibit somewhat different adaptive survival strategies (Festa-Bianchet et al. 2011). Southern mountain caribou in British Columbia and Alberta "space out" during calving to avoid cougars, wolves, black bears and grizzly bears, and interspecific competitors that may include elk and deer in addition to moose (Seip 1992, Wittmer 2004, Stotyn et al. 2007). Boreal animals present a mix of strategies depending on their range associations. Parturient cows find separation from

moose and wolves in extensive peatlands and rugged forest areas (McLoughlin et al. 2005, Latham et al. 2011a). Migratory populations of insular Newfoundland and northern Quebec space away in groups during calving (Lewis and Mahoney 2014). Historically, moose have been the primary interspecific competitor to caribou in Alberta, but in recent years, a northward expansion of white-tailed deer has redefined the dynamics of the predator-prey complex that includes wolves, black bears, and coyotes (Latham et al. 2011d). For boreal caribou inhabiting Shield ranges in Saskatchewan, Manitoba, Ontario, and Quebec, the predator-prey dynamic is one of moose, wolves and black bears (Rettie and Messier 2000, Dupont 2014). However, in northern Quebec and Newfoundland, boreal forest caribou groups migrate to common calving grounds.

Woodland caribou are vulnerable to increases in adult mortality accompanied by a high incidence of predation-related calf mortality (Environment Canada 2011, Hayek et al. 2016). Gustine et al. (2006), and Parker and Gustine (2007) documented wolverines (*Gulo gulo*), wolves, grizzly bears, and golden eagles (*Aquila chrysaetos*) to all be active predators of calves. Tracking the fate of 25 newborns equipped with mortality sensor collars each year showed that 55% and 75% of the calves survived to the end of summer over a two year period. Pinard et al. (2012) placed VHF radio collars on 64 calves whose fate was tracked from mid-May to the end of August in each year from 2004-2006, resulting in an estimated fall recruitment rate of approximately 46 calves/100 cows. Of the 36 calves that died, 61% were due to predation (95% bears, 5% wolves) in the first two weeks of life and 23% of the calves were believed to have died from natural causes with the remaining 16% undetermined.

In Newfoundland, boreal forest caribou, ‘space away’ to calve; moose are their only interspecific competitor, while bears and coyotes are the principal predators of calves (Lewis and Mahoney 2014). During one growth phase in Newfoundland (1979-1997), mean calf survival to 6 months of age was estimated slightly above 60%, but during the decline that started post-1996, less than 10% of the calves survived annually. In the period 2003-2012, in which survival has averaged above 30%, predation accounted for 70% of all known calf mortalities; this estimate was 20% higher during the decline phase (Lewis and Mahoney 2014). Black bears were responsible for more than half of all predator-related mortality followed by coyotes, lynx, and bald eagles. The incidence of black bear and lynx predation was higher during the growth phase, although coyotes were not well established at that time (Lewis and Mahoney 2014).

Bears have long been identified as major predators of moose, elk, and deer calves across all ranges occupied by bears in North America (Ballard et al. 1981, Stewart et al. 1985, Nolan and Barrett 1985, Mahoney et al. 1990, Zager and Beecham 2006). In northeastern Minnesota, both wolves and bears were reported to share in the predation of white-tailed deer fawns (Kunkel and Mech 1994). Black bears, in the absence of wolves were also viewed as an important predator of caribou calves in Newfoundland in the late 1980’s (Mahoney et al. 1990, Mahoney and Virgil 2003).

There exists a roughly 20-year senescence (1985–2005) of quality published reports on general ecology, population dynamics, or the effects of landscape anthropogenic disturbance on boreal black bear populations for most of the woodland caribou ranges in Canada. In Newfoundland black bears accounted for mostly half of the predator-related

mortality of calves (Blake 2006, Bastille-Rousseau et al. 2015). In Quebec, 95% of predator-related calf mortality was attributed to bears (Dussault et al. 2012).

Edmonds (1988) tracked 24 radio-collared southern mountain and boreal range adult caribou in west central Alberta in the 1980's and reported high rates of calving success, but fall recruitment estimates of only 14.5% calves led to the idea that significant early calf mortality was attributable to wolves. The fate of radio-collared caribou and wolves in southeastern BC resulted in variable May-June calf mortality rates ranging from 35%-65% in which wolves were suggested to be the likely primary source of mortality (Seip 1992). Stuart-Smith et al. (1997) confirmed 88% adult survival, but low (<10%) annual recruitment rates based on the fate of 65 adult females that were radio-collared between 1991-1994. Wolf predation was determined to be the cause for 9 of 16 adult female mortalities.

Latham et al. (2011a) identified that up to 1/3 of radio-collared black bears associated with upland mixed wood forest communities in east central Alberta undertook spring forays into peatlands used by calving caribou, and recommended the inclusion of bears in future predation studies. In eastern Canada, the role of black bears and/or coyotes as the major sources of early neonate mortality have been reported (Dussault et al. 2012, Pinard et al. 2012, Lewis and Mahoney 2014, Mahoney et al. 2016, Leblond et al. 2016, Bastille-Rousseau et al. 2016).

There is limited direct biological evidence linking wolves to the mortality of boreal caribou calves across Canada. One calf mortality study in Quebec tracked the fate of 64 cow/calf pairs (2004-2007) from which 40 calves died in the first weeks of life. Of these, 21 calf mortalities were attributed to black bears and one by wolves (Pinard et al. 2012).

The authors believed that the caribou calving site selection provided separation from wolves but not black bears, an observation also shared by DeMars (2015). Adult female boreal caribou have been reported vulnerable to predation by wolves from April through August following the loss of calves (McLoughlin et al. 2003, Latham 2009). Gustine et al. (2006) monitored the fates of 25 radio collared neonates in each of 2002 and 2003, 19 of which died in the first 8 weeks of life. All but two were attributed to predation with 9 killed by wolves.

1.20 Wolves

The biological record and argument favouring wolves as the primary predator of any ungulate they share ranges with, is compelling given that wolves, unlike bears, are an obligate carnivore whose wellbeing and survival is intimately linked to their capacity to capture and consume other animals (Theberge and Theberge 2004, Latham et al. 2011*b*). Wolf predation is considered to be primarily compensatory, partly compensatory, or potentially additive where anthropogenic hunting of prey and extrinsic environmental factors such as climate are introduced (Jedrzejewski et al. 2002, Gazzola et al. 2007, Wilmers et al. 2007). Rates of woodland caribou decline in Alberta and British Columbia have been associated with apparent competition, brought on by anthropogenic landscape-scale disturbance (Seip 1992, James et al. 2004, McLoughlin et al. 2005, Latham 2009, Boutin et al. 2012, Hervieux et al. 2014, Johnson et al. 2015, Klazek and Heard 2016).

Wolves are highly territorial social carnivores, typically organized into family units (packs) of 3-15 animals that can be maintained for several years through the aggressive protection of their territories from competing packs (Murray 2003). A pack usually

includes at least a breeding pair and usually some collection of offspring and family; if healthy, the pair is expected to produce pups every year. Packard (2003) provides a detailed description of the reproductive and rearing cycle in wild wolves. Wolves breed in late winter and have a gestation period of approximately 60 days, with pups being born in May, coinciding with the flush of herbivore availability. The pups are raised at den sites, and are functionally immobile for the first 4-5 weeks of life, and mostly dependent on mother's milk for nutrition (Packard 2003). Other pack members, particularly the breeding male, providing food to the den site either by carrying meat or regurgitative provisioning (average 1.25 kg), providing sustenance to both the mother and the pups (Mech et al. 1999). Once the pups are a month old and out of the den, the mother can begin making short hunting forays near the den site, while other pack members ensure the security of the pups (Packard 2003). By 3-4 months of age, pups are sufficiently mobile to follow the family unit, but may maintain an association with the pack for 9-36 months, after which, they disperse in search of mates and the formation of new social groups including the establishment of new territories (Packard 2003, Mech and Boitani 2007). During the denning season, the pups are the social centre of the unit, from which members radiate out to hunt, and return to the den site once they have food that they may regurgitate to share with the denning female and/or her pups (Packard 2003). Once the pups can accompany the breeding female, the pack enters a rather nomadic phase that can last up to 6 months (Alfredéén 2006, Mech and Boitani 2007).

Mech and Boitani (2007) describe the pack as a 'dispersal pump' that convert prey into the offspring across the landscape with dispersal triggered by the onset of the breeding season, or in the spring before denning. Wolves are active colonizers, and new

social units try to carve out territories away from existing packs (Mech and Boitani 2007). Wolves defend their territories using scent marks (particularly on the edge of their range) and howling at rendezvous sites to advertise their presence (Murray 2003, Llaneza et al. 2014). Once a wolf pair successfully establishes a territory, they actively resist losing that territory, and at times may engage in direct attacks on competitors in defence of the territory (Mech and Boitani 2007). Wolves are known to move along the easiest travel routes including trails, shorelines, frozen waterways and roads to both hunt and to mark their territory (Latham et al. 2011*b*).

Wolves have shown substantial plasticity in a diet that includes all herbivorous mammals essentially within their ranges, avifauna and in some locales and even fish (Forbes and Theberge 1996, Spaulding et al. 1998, Upton 2004, Darimont et al. 2008). Wolves prey mainly on moose, deer, elk, and caribou or in some combination and beavers also comprise a significant source of nutrition for short periods during the snow-free months (Latham et al. 2011*b*). Wolf packs are also known to specialize in their preference for ungulate prey species; prey preferences are not immutable (Forbes and Theberge 1996, Upton 2004, Latham et al. 2011*b*). Woodland caribou are generally referenced as a secondary or opportunistic source of food for wolves (Bergerud and Elliot 1986, Seip 1992, James and Stuart-Smith 2000, Hayes et al. 2003, Wittmer 2004, Upton 2004, McLoughlin et al. 2003, 2005, Gustine et al. 2006, Stotyn et al. 2007, Latham 2009, DeMars 2015, Leblond et al. 2016). Wolves also select lowland areas as denning sites near watercourses and in proximity to upland stands, providing access to diverse and abundant foraging opportunities (Latham et al. 2011*b*).

The data defining the fates of >220 radio-collared boreal range adult females monitored from 2012-2015 in NE BC showed wolves to be the principal cause of death for 65% of 77 animals that had died, 70% of which occurred in late winter-early spring, covering the period of calving site selection to the end of the calving season (Culling and Culling 2015). However, the recent assessment of woodland caribou populations for boreal shield populations in Northern Saskatchewan does not implicate wolves as important agents of either adult or neonatal mortality (McLoughlin et al. 2016).

Wolves are believed to be indirect beneficiaries from shifts in vegetation community structure that favour interspecific competitors, thereby improving hunting success and the opportunity to increase their populations (Latham et al. 2011*d*). Latham et al. (2011*d*) documented the doubling of the wolf population to >11 animals/1000 km² between 1995 and 2005 for two highly disturbed boreal ranges in northeastern Alberta, coincident with sharp declines in woodland caribou populations. The increase in the wolf population was linked to a coincidental increase in white-tailed deer populations over the same period, and substantial evidence that wolves successfully exploited this new-found food resource (Latham 2009). Neufeld (2006) showed a high incidence of use of cut-blocks and cutlines by moose, and a disproportionately high use of conventional seismic lines by wolves, bears, and coyotes. The contribution of linear corridors to increases in direct mortality of caribou from wolves remains somewhat uncertain (Apps et al. 2013, Kittle et al. 2015, Dickie et al. 2016).

1.21 Black Bears

Black bears historically have occupied all forested regions of North America (Hall 1981) and are currently common in all regions in Canada. Black bears, although

omnivorous, belong to the Order Carnivora (Kurten and Anderson 1980). There are few empirical population estimates for bears in North America, and even less information regarding their responses to natural or anthropogenic forest structural disturbances, and, what information is available, is largely dated by at least 25 years. The best published data for both brown and black bear populations in western Canada was drawn from survey data obtained more than 15 years ago, on a 9,500 km² range in east central BC (Mowat et al. 2002, 2005). Mowat et al. (2002, 2005) estimated 270 black bears/1000 km² (CI 173 – 428) within a highly developed industrial spruce, pine, aspen, and subalpine fir forest landscape. They also estimated 100 black bears/1000 km² (CI 55 – 210) for a high elevation, less developed subalpine ecosystem. Best population estimates for black bears in the fragmented Charlevoix boreal range of southern QC derived from 1989 mark-recapture data, resulted in estimates of approximately 220 bears/1000 km². The current bear population is now believed to be much higher based on hunter and trapper harvest successes in recent years (Jolicoeur 2004). In east-central Alberta, population data were compiled in 1968-1975 within a small 218 km² study area. Averages of >360 bears/1000 km² in 1968-71 and increased to >800 animals/1000 km² by 1973, following the removal of 23 adult males, and subsequently settled back to <630 animals/1000 km² by 1975 (Kemp 1976, Young and Ruff 1982). The last major management planning document for black bears in AB (Gunson 1993) suggested average province-wide densities for suitable ranges of approximately 200 bears/1000 km²; Gunson (1993) also opined that industrial forestry and petroleum, and oil and gas exploration activities, leading to earlier succession-aged forest structures, favoured the growth of black bear populations.

Black bears are a versatile omnivore and consume a wide variety of plant, insect and animal foods (Graber and White 1983, Benson and Chamberlain 2006, Munro et al. 2006). They feed at both the upper and lower strata of the food chain and have adapted to a primary diet of vegetation; they prefer small food items that are low in cellulose, high in nutrients and available for only part of the year (Bull et al. 2001, Iverson et al. 2001). Nutritional needs differ among cohorts with larger male bears requiring more protein due to body size (Rogers 1987). Diets vary among geographic region and season influenced by the available food sources of forest communities in which they reside (Pelton 2003, McDonald and Fuller 2005). Both adult and neonate ungulates are also consumed and can form an important part of their diet (Pelton 2003, Zager and Beecham 2006). In the autumn, black bears preferentially seek foods that are high in carbohydrates and fats, and low in fibre that contribute to the accumulation of fat stores for hibernation (Elowe and Dodge 1989). Although fruit is considered to be a preferred food of bears, they consume a mixed diet even when fruit is abundant. Such variation, independent of availability, has also been documented for brown bears that continue to supplement readily available meat diets with a very high proportion of berries (Robbins et al. 2007). For black bears, a lack of quality primary foods, can be compensated for by searching and consuming alternative food resources such as animal matter, agricultural products, and food from anthropogenic sources (Fuller and Sievert 2001). They may also shift diets where land use and/or human activities alter the availability of food (Landers et al. 1979, Maehr and Brady 1984, Hellgien and Vaughan 1988, Boileau et al. 1994, Bull et al. 2001).

Nutritional and physiological needs change with factors such as season, sex, and age, and reproductive status also influences diet (Bacon and Burghardt 1983). Larger

bears tend to consume more meat, when available, relative to smaller bears (Robbins et al. 2007). The nutritional condition affects litter sizes, breeding intervals, and survival rates of cubs (Rogers 1976, Lindzey et al. 1986, Elowe and Dodge 1989). Reproductive rates in bears are nutritionally regulated and density-dependent, and as such, intra-specific competition contributes to the nutritional condition of females (Bunnell and Tait 1981, Wathen 1983, Elowe 1984). When high-quality food is available, populations may increase relatively rapidly (Lindzey et al. 1986). Quality diets also can promote earlier reproductive maturation and the production of larger litters at shorter intervals (Rogers 1987). Increased mass gains and fecundity in black bears can also be enhanced by high-protein diets that include ungulates (Tate and Pelton 1983, McLean and Pelton 1990, Hilderbrand et al. 1999, Beckmann and Berger 2003). Milk is the primary food of cubs, which are determined by the pre-denning condition of the sow (Elowe and Dodge 1989). Bears illustrate extensive frugivory and gain most of their weight on nuts and berries eaten after mid-July (Noyce and Coy 1990). However, caribou calves may be an important source of protein for breeding viability and lactation in some grizzly bear populations (Young and McCabe 1997). Ungulate availability is not typically limiting to bear habitat carrying capacity where other food sources are available, especially when anthropogenic inputs are available (Graber and White 1980).

Bayne et al. (2011) and Tigner et al. (2014), reported a strong selection of seismic lines by black bears, and concluded that seismic lines seemed to act as movement routes for black bears, but cautioned that more research was required to establish links of this behaviour to calf depredation. Bears in lowlands were only found in association with seismic lines (Bayne et al. 2011). Neufeld (2006) captured 25 black bear and 22 grizzly

bear images, respectively, compared to only 16 wolf images from trail cameras situated on seismic clearings on a range in west central Alberta. Mosnier et al. (2008) reported high bear use of roads as travel corridors and sources of forage resources, and portrayed bears to be in constant pursuit of food resources, beginning with high use of graminoids during spring green up. He cautioned that forest disturbance and regeneration in proximity to caribou calving habitats could attract more bears in search of preferred forage resources. Latham et al. (2011a) observed that up to one-third of radio-collared bears moved from upland to peatland habitats during the caribou calving season within one east-central Alberta range, and suggested possible additive source of neonate mortality. Bastille-Rousseau et al. (2011) further noted that the features with the highest vegetation biomass attractive to bears in the spring included roadsides and bogs, followed by shrublands and regenerating clear-cuts.

Lindzey et al. (1986) tracked the population dynamics of a small island (21 km²) black bear population in Washington State from the termination of extensive logging in the late 1960s through to the early 1980s as the forest matured. They observed a noticeable increase in both the size of the adult (>1 year age) population (>1.6 bears/km²), and productivity (average litter size of adult females of 1.83) in 1974-1975, followed by a population decline after 1978, accompanied by a collapse in recruitment (0 cubs/11 adult females) by 1982. ASRDa (2008) estimates black bear populations at 100 animals/1000 km² in proximity to caribou ranges in Alberta despite the aggressive quadrupling of forest harvesting (>87,000 ha's 2014) since 1975 (National Forestry Database 2014), much of which is in proximity to caribou ranges.

1.22 Consideration of the Contribution of Species' Foraging Strategies to the Predator-Prey Relationship

Feeding strategies of animals are the direct result of specific evolutionary adaptations that permit species to exploit their environments to reproduce and survive (Stephens and Krebs 1986). All foragers face choices as to where and how to acquire the necessary energy to meet both their short- and long-term life cycle requirements. General foraging decisions of animals can be related to a number of functions including security, reproductive habitat needs, territoriality, cannibalism, and competition from other foragers or predators (Giraldeau and Caraco 2000). In North America, ungulates, including woodland caribou, face threats from wolves, black bears, grizzly bears, coyotes, lynx, cougars, wolverines, and eagles (Bergerud 1971, Edmonds 1988, James and Stuart-Smith 2000, Gustine et al. 2006, Latham 2009, Boutin et al. 2012, Mahoney et al. 2016). All are opportunistic predators of caribou calves; wolves, cougars, and grizzly bears are also effective predators of adults, with wolves and cougars preying on caribou year round (Wittmer et al. 2005*b*). All other predators, excluding bears, are obligate carnivores with a functional reliance on meat consumption for survival. The dynamics defining the relationships both between and among prey and predators are shaped by variety of adaptations and survival mechanisms. Kleptoparasitism, or prey stealing by interspecific competitors and can force the victims of such behaviour to increase hunting effort to survive resulting in an increase in mortality rates of some prey species (Elbroch et al. 2015).

Wolf density is dependent on the seasonal availability and density of all prey species they may exploit (Mech et al. 1999, Loveless 2010). Wolves being social predators, benefit from group hunting when forage resources are highly abundant

(Zimmermann et al. 2014). Wolf family units continually adjust their hunting to the distribution and availability of prey resources in an effort to maximize food rewards relative to energy expended. This is a foraging strategy that can result in short to long-term prey switching that can confound density-dependent theories of predator-prey ratios (Garrot et al. 2007, Gower et al. 2008, Latham 2009, Zimmermann et al. 2015). Boreal woodland caribou persist by selecting habitat niches in which they exist as an exclusive ungulate widely spaced in very low densities (Latham et al. 2011a). This foraging strategy enforces a subtle separation from wolves whose wellbeing is governed by access to more abundant prey associated with upland deciduous forest communities (Leblond et al. 2016). Calving and whelping in the May-June period, however, provide some degree of temporal and spatial overlap between caribou and wolves. (DeMars 2015). Wolf foraging strategies dictate the selection of rather different components of the wetland at this time of year (Latham 2009, DeMars 2015). The high energetic demands of lactation to support calves highlight an attraction for early season 'green up' of rich herbaceous vegetation (*Carex spp.*, *Equisetum spp.*), poor fens to caribou (DeMars 2015). Denning wolves prefer riparian areas associated with creeks, streams, rivers, and lakes as they provide access to habitats for small game and beavers which separate them from unproductive lowland complexes used by caribou during the calving period (Latham 2009, DeMars 2015). Wolf hunting activities are concentrated in proximity to den sites during this time, thereby limiting the opportunity for wolves to interact with caribou calves (Mech et al. 1999, Packard 2003).

Black bears, as hibernators, must secure high energy inputs during the snow-free months to store sufficient resources to support their energy demands when they emerge

from hibernation. Their metabolic rate remains somewhat suppressed for up to 3 weeks following emergence from the den (Tøien et al. 2012). Noyce and Garshelis (1998) weighed black bears pre- and post-winter denning in Minnesota and reported that bears tended to maintain late winter body weights into early spring. Barteau et al. (2012) evaluated body conditions for 139 euthanized problem bears in the NWT between 1998-2009 and observed high variability in body condition, but that all bears were in the poorest condition in the month following spring emergence from dens. Black bears must respond to seasonal variability of food sources, taking advantage of plant phenology and occasional sources of high protein, resulting in frequent movements from one food-rich patch to another (Bastille-Rousseau et al. 2011).

Potential for bear-caribou interaction relates to the foraging patterns of bears that are closely linked to the seasonal growth cycle of plants starting with ‘green up’ of grasses and sedges in early spring (Powell et al. 1997). Grizzly bears have been well documented to follow altitudinal gradients of vegetation green-up, a particularly visible trait in mountain ranges. Bears sought out those slopes and aspects conducive to early vegetation flushes including horsetails (*Equisetum sp.*) and grasses, sedges and rushes (Raine and Kansas 1990). The seasonal pulses and periodic concentrations of food availability requires that bears adopt foraging strategies consistent with food availability, and security from other bears (sows with cubs and yearlings).

Given that caribou calves are distributed in widely spaced patches, they are not a primary food source for black bears, and, for the most part, black bears are believed to be incidental predators of calves (Bastille and Rousseau et al. 2011, 2016). The simultaneous selection of spring foraging resources by both black bears and parturient caribou cows,

introduces a dynamic to their relationship that may increase the probability of interactions between bears and caribou (Pinard et al. 2012, DeMars 2015, Bastille-Rousseau et al. 2016, Leblond et al. 2016). In the case of a predation event, the feeding patch, in this instance, is the calf being consumed by a single forager (Recer and Caraco 1989).

Vickery (1991) categorized three general types of food searching behaviours: 1) producers, 2) scroungers and 3) opportunists. Black bears could be classified into all three categories, depending on demographics. Producers search for food, and usually prevent other producers from using the resource; excepting kinship sharing may occur if the patch or reward surpasses the individual's own consumption ability (Giraldeau and Caraco 2000). Scroungers capitalize on the successful efforts of producers and opportunists within food patches or events through stealthy or aggressive scavenging (Giraldeau and Caraco 2000). Opportunists foraging strategies integrate traits of producers and scroungers, but are less efficient than a specialized forager. Giraldeau and Caraco (2000) discussed the mutual dependence (payoffs and penalties) for various foraging strategies. Cooperation and non-cooperation is both conditional and non-conditional based on predation hazard and survival probabilities. Producer-scrounger tactics are a factor in assessing an individual's foraging behaviour within a group (Flynn and Giraldeau 2001). These independent factors set social foraging theory apart from traditional foraging theory as these dynamics affect economic return for effort in game theory (Giraldeau and Caraco 2000).

In some animal populations, all individuals may adopt the same strategy phenotype. Such a strategy is said to be an evolutionary stable strategy (or ESS) if that strategy cannot be replaced, or invaded by any other strategy through natural selection. A Nash

equilibrium (NE), is a set of strategies in game theory, one for each individual, such that no individual has an incentive to unilaterally change its action (Giraldeau and Caraco 2000). Individuals are in equilibrium if a change in strategies by any one of them would lead that individual benefiting less than if it remained with its current strategy. ESS and NE results when individuals (players) establish a set of foraging strategies, such that no one individual can improve its benefit by changing strategy as long as the other individuals continues using their NE Strategies (Giraldeau and Caraco 2000). The ideal free distribution model (IFD), assumes that: resources are distributed in discrete patches, all animals equally compete, all animals have a complete understanding of the spatial distribution of resources and available energy, they are free to move between patches at no energy cost, the quality of the patch does not change over time and, all have an equal opportunity to reproduce (Fretwell and Lucas 1970). This leads to resource matching, where the forager distribution matches potential resources; if depletion of energy does not occur, then all foragers have access and will utilize the most profitable patches (Morris 1994). Any modifications, such as individuals moving to other patches, are disadvantageous because departure from the equilibrium condition leads to unequal competition for resources (Packard 1978). At larger scales, continuous inputs of one particular resource and the immediate consumption of that resource is invalid as the density of animals may depend upon other measures of resource availability (Morris 1994).

An alternative model, the Ideal Despotic Distribution (IDD), suggests that subordinate animals are dominated by mature animals such that all animals do not have the same access to all resources, and therefore do not share equal reproductive successes

(Messier et al. 1990). The concept of NE is problematic when considering black bears as individuals with the capacity to cause unequal competition, including the overuse and underuse of patches (Kennedy and Gray 1993). Black bears are highly territorial at times (i.e., competition for mates, finite food), and dominant individuals may exclude subordinates from utilizing the best foraging opportunities, thereby forcing them to crowd into sub-optimal habitats (Berec et al. 2006). Beckmann and Berger (2003) observed that bears in the western Great Basin Desert and in the Lake Tahoe basin conformed to an IDD based on findings that urban-interface areas (urban bears) had higher densities, smaller home ranges and higher reproductive capacity than their wildland conspecifics.

NE theory also applies to predator/prey dynamics, with the assumption that animals behave ideally and maximize their fitness benefits (Fretwell and Lucas 1970, Kacelink et al. 1992). The Fretwell and Lucas (1970) model assumes that predators freely distribute themselves among the available patches, and that the predators in each patch have equal energy rewards. The model has been expanded to include other factors such as interference, differences in ability to compete for resources (Parker and Sutherland 1986, Morris 1994), adjustment to predator behaviour through learning (Bernstein et al. 1988, Mazur and Seher 2008), and resource dynamics (Lessells 1995). Models must also take into consideration other key factors in predator/prey dynamics, such as the mortality rate of the prey (Krivan 1997). The elements of foraging models (optimality models) include three main component assumptions: 1) decision, 2) currency, and 3) constraint (Stephens and Krebs 1986); essentially the forager must decide which prey to consume, the amount of time searching patches, and the time spent in a patch looking for that particular prey. Other assumptions of these foraging models include factors such as foraging behaviour

that requires vigilance for security of the individual and its offspring. Furthermore, currency or pay off assumptions are forager choice principles which maximize intake while minimizing effort, and residence time versus economic gains represent complicated trade-offs for the forager in deciding when to leave or stay in the patch (Giraldeau and Caraco 2000). As such, a 'time-minimizing forager' would maximize the size of the energy reward for the least amount of effort. Constraint variables would be those that limit the forager in its hunting or foraging behaviour (Stephens and Krebs 1986). These include both intrinsic and extrinsic variables (Giraldeau and Caraco 2000). Natural constraints for black bears could relate to an individual forager's size, speed or mobility relative to its prey that may affect chase time and effort in a variety of cover types while extrinsic constraints may be related to the existence and availability of high-quality habitats such as escape habitat allowing the prey (i.e., caribou) to readily flee from danger or attack (Giraldeau and Caraco 2000).

As calving boreal woodland caribou tend to 'space out' throughout calving areas, each calving female would represent a different patch. A black bear encounter with a female caribou and calf could be followed by a similar search and successful predation event as a patch related foraging behaviour which has been observed by Bastille-Rousseau et al. (2011). Black bear predation on neonate ungulates, persistence on behalf of the foraging black bear is likely to result in a successful event (Zager and Beecham 2006). This may represent 'learned' behaviour, thereby increasing the probability of reinforcing future encounters (Mazur and Seher 2007). Therefore, it is likely that search and behaviours as described by Stephens and Krebs (1986) could be applied in a potential foraging model for black bears, with the variable being encounters with caribou calves

and a conditioned response to attack. A more important variable for black bears would relate to the amount of search time to allocate to unsuccessful encounters before moving to the next patch. The problem for the forager is that food (calf) is found in a patch and travel time is necessary between patches. Decisions must be made by the forager to move on to the next patch making the best use of reward for effort (Charnov 1976).

Decisions respecting occupancy time of patches are dependent on the opportunistic omnivorous nature of bears, thereby reducing the consequences of patch-prey (search or eat) decisions, facilitating greater search time and enhancing the persistence capabilities of bears in search of neonate caribou. Ten of 12 radio-tracked bears moved selectively between patches offering high vegetation biomass, while significantly limiting the time spent in poor patch transition areas (Bastille-Rousseau et al. 2011). Due to the innate opportunistic foraging behaviour of bears, a flattening or reduction in the assumed negative correlation of gain as a function of residence time in a patch as described in Stephens and Krebs (1986) would be expected. Charnov's (1976) marginal-value theorem that states choice of foraging time in patches to achieve a marginal or average rate of energy gain, may provide more opportunities for encounters. This may apply to bear foraging behaviour as their encounters with caribou calves would increase through expanded searching area. In natural communities, the richer habitats are often the most dangerous owing to a higher predation rate (Werner et al. 1983). DeMars (2015) illustrated that bear foraging behaviour results in similar habitat selection for woodland caribou during the calving period, which would contribute to calf mortality. Similarly, Bastille-Rousseau et al. (2011, 2016) found that bears frequently moved among similar bog and fen habitats to caribou and expected higher rates of encounters between the two.

1.23 Vigilance

Prey vigilance to the presence of the predators reinforced by negative non-lethal interactions is referred to as the “ecology of fear” (Brown et al. 1999). Apparent competition, in which caribou, as the secondary prey, become an incidental target of wolf predation in situations where moose expand in proximity to caribou ranges as a result of natural or anthropogenic disturbances favouring primary prey (Boutin et al. 2012). But as shown by Cressman and Garay (2007), parturient female caribou do not have a high sense of vigilance to the presence of bears, and selection of habitats providing separation from wolves, do not simultaneously provide protection from bears during a short calving season (Leblond et al. 2016). Vigilance to predators is a learned behaviour reinforced by memorable negative encounters with predators in which the prey survived, therefore able to develop a sensitization to the visual, auditory and olfactory cues indicating the presence of the predator (Brown et al. 1999, Berger 2008).

Berger (2008) tested the progressive response of male and female moose to the odors and sounds of wolves, both before and after 5 years following the re-introduction of wolves to Yellowstone. He observed little reaction to these stimuli by either males, or cows with calves prior to the re-establishment of wolves. However, the awareness response of cows with calves increased year over year following the re-introduction. He suggested that fear was learned, and when not negatively reinforced, ungulates seem to forget over time. Boreal caribou are widely dispersed across their calving grounds, and the few very short-term negative experiences with a somewhat silent and opportunistic predator that they may encounter but a few short weeks/year, may be insufficient to drive a high flight response at times their calves are rather sedentary.

1.24 Management and recovery planning

Recovery planning includes the identification of the nature and extent of disturbances, planning and mitigation of anthropogenic disturbances that may be additive to natural and anthropogenic disturbances that already exist on the landscape. The uncertainties regarding the complexity of ecosystem processes partnered with the long-term risk profiles presented by persistent downside population trends, is further exacerbated by the absence of proven and/or acceptable mitigation measures to stabilize or reverse these trends. As a result, the National Recovery Strategy provided a framework that prioritized the identification, conservation and management of sufficient critical habitat to support minimum viable populations of caribou, and for the recovery the most threatened populations (Environment Canada 2012).

1.25 References

- Apps CD, McLellan BN, Kinley TA, Serrouya R, Seip DR, Wittmer HU. 2013. Spatial factors related to mortality and population decline of endangered mountain caribou. *J Wildl Manage.* 77: 1409-1419.
- Armstrong TR, Racey GD, Bookey N. 2000. Landscape-level considerations in the management of forest-dwelling woodland (*Rangifer tarandus caribou*) in northwestern Ontario. *Rangifer.* 12: 187-189.
- ASRDa (Alberta Sustainable Resource Development). 2008. Athabasca Caribou Landscape Management Options Report 1: Current Situation Assessment, Athabasca Landscape Team.
- ASRDb (Alberta Sustainable Resource Development). 2010. Status of Woodland Caribou in Alberta. Alberta Wildlife Status Report. Report No.: 30.
- Bacon ES, Burghardt GM. 1983. Food preference testing of captive black bears. *Bears: their biology and management.* 5: 102-105. doi:10.2307/3872525
- Ballard WB, Spraker TH, Taylor KP. 1981. Causes of neonatal moose calf mortality in south central Alaska. *J Wildl Manage* [Internet]. 45(2): 335-342. Available from: <http://www.jstor.org.proxy2.lib.umanitoba.ca/stable/pdf/3807916.pdf> doi:10.2307/3807916
- Ballard WB. 1994. Effects of black bear predation on caribou - a review. *Alces.* 30: 25-35.
- Banks SC, Piggot M, Stow A, Taylor AC. 2007. Sex and sociality in a disconnected world: a review of the impacts of habitat fragmentation on animal social interactions. *Can J Zool.* 85(10): 1065-1079.
- Barteau TM, Larder NC, Cluff HD, Leone EH. 2012. Body condition and growth dynamics of American black bears in northern Canada. *Ursus.* 23(1): 12-20.
- Bastille-Rousseau G, Fortin D, Dussault C, Courtois R, Ouellet JP. 2011. Foraging strategies by omnivores: are black bears actively searching for ungulate neonates or are they simply opportunistic predators? *Ecography.* 34(4): 588-596. doi: 10.1111/j.1600-0587.2010.06517.x
- Bastille-Rousseau G, Potts JR, Schaefer JA, Lewis MA, Ellington EH, Rayl ND, Mahoney SP, Murray DL. 2015. Unveiling trade-offs in resource selection of migratory caribou using a mechanistic movement model of availability. *Ecography.* 38(10): 1049-1059. doi: 10.1111/Ecog.01305
- Bastille-Rousseau G, Rayl ND, Ellington EH, Schaefer JA, Michael JL, Peers, Mumma MA, Mahoney SP, Murray DL. 2016. Temporal variation in habitat use, co-occurrence, and risk among generalist predators and a shared prey. *Can J Zool.* 94(3): 191-198. dx.doi.org/10.1139/cjz-2015-0127

- Bayne Dr. E, Lankau H, Tigner J. 2011. Ecologically-based criteria to assess the impact and recovery of seismic lines: The importance of width, regeneration, and seismic density. Report No.: 192. Edmonton, AB. 98 p.
- Beauchesne D. 2012. Influence of disturbances on the movements of female woodland caribou (*Rangifer tarandus caribou*) across multiple spatiotemporal scales [dissertation]. Concordia University. Montreal, Quebec.
- Beckmann JP, Berger J. 2003. Using black bears to test ideal-free distribution models experimentally. *J Mammal.* 84(2): 594-606. doi: 10.1644/1545-1542(2003)084<0594:UBBTI>2.0.CO;2
- Benson JF, Chamberlain MJ. 2006. Food habits of Louisiana black bears (*Ursus americanus luteolus*) in two subpopulations of the Tensas River Basin. *The American midland naturalist.* 156(1): 118-127. Available from: [https://doi.org/10.1674/0003-0031\(2006\)156\[118:FHOLBB\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2006)156[118:FHOLBB]2.0.CO;2)
- Berec L, Angulo E, Courchamp F. 2006. Multiple allee effects and population management. *Trends in Ecology and Evolution.* 22(4): 185-191. doi:10.1016/j.tree.2006.12.002
- Bergerud AT. 1971. The population dynamics of Newfoundland caribou. *Wildlife monographs.* 25: 3-55.
- Bergerud AT. 1974. Decline of caribou in North America following settlement. *J Wildl Manage.* 38(4): 757-770. Available from: <http://www.jstor.org/stable/3800042>
- Bergerud T. 1978. The status and management of caribou in British Columbia. *Sustainable Resource Management and Water, Land and Air Protection, Govt. of BC.* Victoria. 162 p.
- Bergerud AT, Elliott JP. 1986. Dynamics of caribou and wolves in northern British Columbia. *Can J Zool.* 64(7): 1515-1529.
- Bergerud AT. 1996. Evolving perspectives on caribou population dynamics, have we got it right yet?. *Rangifer.* 16(4): 95-116.
- Bergerud AT, Elliott JP. 1998. Wolf predation in a multiple-ungulate system in northern British Columbia. *Can J Zool.* 76(8): 1551-1569.
- Bergerud AT. 2007. The need for the management of wolves - an open letter. *Rangifer.* 27(4): 39-50.
- Bernstein C, Kacelnik A, Krebs JR. 1988. Individual decisions and the distribution of predators in a patchy environment. *J Anim Ecol.* 57: 1007-1026.
- Bethke R, Taylor M, Amstrup S, Messier F. 1996. Population delineation of polar bears using satellite collar data. *Ecol Appl.* 6(1): 311-317.
- Blake J. 2006. Coyotes in insular Newfoundland: current knowledge and management of the islands newest mammalian predator. Department of Environment and Conservation Wildlife Division, Government of Newfoundland and

- Labrador, Canada. 11. Available from:
www.env.gov.nl.ca/env/publications/wildlife/51f40a0ed01.pdf
- Boileau F, Crete M, Huot J. 1994. Food habits of the black bear (*Ursus americanus*) and habitat use in Gaspésie Park, Eastern Quebec. *Canadian Field-Naturalist*. 108(2): 162-169.
- Boutin S. 1992. Predation and moose population dynamics: A critique. *J Wildl Manage*. 56(1): 116-127.
- Boutin S, Boyce MS, Hebblewhite M. 2012. Why are caribou declining in the oil sands? Peer-reviewed letter. *Wildlife Biology Faculty Publications*. The Ecological Society of America. Paper 22.
- Boutin S, Merrill E. 2016. A review of population-based management of Southern Mountain caribou in BC. Department of Biological Sciences, University of Alberta, Edmonton, Alberta. Submitted to Columbia Mountains Institute, March 2016.
- Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA. 2002. Evaluating resource selection functions. *Ecol Modell*. 157(2): 281-300.
- Boyce MS, Pitt J, Northrup JM, Morehouse AT, Knopff KH, Cristescu B, Stenhouse GB. 2010. Temporal autocorrelation functions for movement rates from global positioning system radiotelemetry data. *Philos Trans R Soc Lond B Biol Sci*. 365(1550): 2213-2219. doi:10.1098/rstb. 2010.0080
- Boyce MS, Baxter PWJ, Possingham HP. 2012. Managing moose harvests by the seat of your pants. *Theor Popul Biol*. 82(4): 340-347. Available from:
<https://doi.org/10.1016/j.tpb.2012.03.002>
- Brodeur V, Ouellet JP, Courtois R, Fortin D. 2008. Habitat selection by black bears in an intensely logged boreal forest. *Can J Zool*. 86(11): 1307-1316.
- Brown WK, Theberge JB. 1990. The effect of extreme snow cover on feeding-site selection by woodland caribou. *J Wildl Manage*. 54(1): 161-168.
- Brown JS, Laundré JW, Gurung M. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *J Mammal*. 80(2): 385-399.
- Brown KG, Elliott C, Messier F. 2000. Seasonal distribution and population parameters of woodland caribou in central Manitoba: implications for forestry practices. *Rangifer*. 20(5): 85-94.
- Brown WK, Rettie WJ, Wynes B, Morton K. 2000. Wetland habitat selection by woodland caribou as characterized using the Alberta wetland inventory. *Rangifer*. 12: 153-157. Available from: <http://www.cabdirect.org/abstracts/20013018835.html>
- Brown GS, Rettie WJ, Mallory FF. 2006. Application of a variance decomposition method to compare satellite and aerial inventory data: a tool for evaluating wildlife-habitat relationships. *J Appl Ecol*. 43(1): 173-184. Available from:
<https://doi.org/10.1111/j.1365-2664.2005.01124.x>

- Bull EL, Torgersen TR, Wertz TL. 2001. The importance of vegetation, insects, and neonate ungulates in black bear diet in northeastern Oregon. *Northwest Science*. 75(3): 244-253.
- Bunnell FL, Tait DEN. 1981. Population dynamics of bears - implications. *Dynamics of large mammal populations*. John Wiley and Sons, New York, New York, USA. p. 75-98.
- Burt WH. 1943. Territoriality and home range concepts as applied to mammals. *J Mammal*. 24(3): 346-352.
- Calenge C. 2011. Analysis of animal movements in R: the adehabitatLT Package. R Found. Stat. Comput. Vienna.
- Callaghan C, Viric S, Duffe J. 2010. Woodland caribou, boreal population, trends in Canada. *Canadian Biodiversity: Ecosystem Status and Trends 2010, Technical Thematic Report No. 11*. Canadian Councils of Resource Ministers. Ottawa, ON. iv + 36 p. Available from: <http://www.biodivcanada.ca/default.asp?lang=En&n=137E1147-0>
- Carr NL, Rodgers AR, Kingston SR, Hettinga PN, Thompson LN, Renton JL, Wilson PJ. 2010. Comparative woodland caribou population surveys in Slate Islands Provincial Park, Ontario. 13th North American Caribou Workshop Winnipeg, Manitoba, Canada 25–28. October, 2010.
- Charnov EL. 1976. Optimal foraging, the marginal value theorem. *Theor Popul Biol* [Internet]. 9(2): 129-136. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/1273796>
- Chisana Caribou Recovery Team. 2010. Recovery of the Chisana caribou herd in the Alaska/Yukon Borderlands: captive-rearing trials. *Yukon Fish and Wildlife report*. TR-10-02. 29 p.
- Clarke DJ, Pearce KA, White JG. 2007. Powerline corridors: degraded ecosystems or wildlife havens? *Wildl Res*. 33(8): 615-626. Available from: <http://www.publish.csiro.au/?paper=WR05085>
- COSEWIC. 2002. Assessment and update status report on the woodland caribou (*Rangifer tarandus caribou*) in Canada.
- Courbin N, Fortin D, Dussault C, Courtois R. 2009. Landscape management for woodland caribou: the protection of forest blocks influences wolf-caribou co-occurrence. *Landsc Ecol*. 24(10): 1375-1388. Available from: <https://doi.org/10.1007/s10980-009-9389-x>
- Courtois R, Ouellet JP, Breton L, Gingras A, Dussault C. 2007. Effects of forest disturbance on density, space use, and mortality of woodland caribou. *Ecoscience*. 14(4): 491-498. Available from: [https://doi.org/10.2980/1195-6860\(2007\)14\[491:EOFDOD\]2.0.CO;2](https://doi.org/10.2980/1195-6860(2007)14[491:EOFDOD]2.0.CO;2)
- Culling DE, Culling BA. 2015. BC boreal caribou implementation plan: 2014-2015 field activities progress report. Prepared for SCEK, Victoria, BC. 28pp + appendices.

- Cumming HG, Beange DB. 1987. Dispersion and movements of woodland caribou near Lake Nipigon, Ontario. *J Wildl Manage.* 51: 69-79.
- Darby WR, Pruitt WO. 1984. Habitat use, movements and grouping behaviour of woodland caribou (*Rangifer tarandus caribou*) in southeastern Manitoba. *The Canadian Field-Naturalist.* 98(2): 184-190. Available from: <http://www.csa.com/partners/viewrecord.php?requester=gs&collection=ENV&recid=821126>
- Darimont CT, Paquet PC, Reimchen TE. 2008. Spawning salmon disrupt tight trophic coupling between wolves and ungulate prey in coastal British Columbia. *BMC Ecology.* 8(1): 14.
- DeCesare NJ, Whittington J, Hebblewhite M, Robinson H, Bradley M, Neufeld LM, Musiani M. 2010. The role of translocation in recovery of woodland caribou populations. *Conserv Biol.* 25(2): 365-373. Available from: <https://doi.org/10.1111/j.1523-1739.2010.01609.x>
- DeCesare NJ, Hebblewhite M, Bradley M, Hervieux D, Smith K, Hervieux D, Neufeld LM. 2012. Estimating ungulate recruitment and growth rates using age ratios. *J Wildl Manage.* 76(1): 144-153. doi: 10.1002/jwmg.244
- De Solla S, Bonduriansk R, Brooks RJ. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. *J Anim Ecol.* 68(2): 221-234.
- DeMars CA. 2015. Calving behavior of boreal caribou in a multi-predator, multi-use landscape [dissertation]. Department of Biological Sciences, University of Alberta. 215 p.
- DesMeules P, Heyland J. 1969. Contribution to the study of the food habits of caribou. Part 1-Lichen preferences. *The Canadian Field-Naturalist.* 96: 317-331.
- Dey S, Dabholkar S, Joshi A. 2006. The effect of migration on metapopulation stability is qualitatively unaffected by demographic and spatial heterogeneity. *J Theor Biol.* 238(1): 78-84. Available from: <https://doi.org/10.1016/j.jtbi.2005.05.013>
- Dickie M, Serrouya R, McNay RS, Boutin S. 2016. Faster and farther: wolf movement on linear features and implications for hunting behaviour. *J Appl Ecol.* Available from: <https://doi.org/10.1111/1365-2664.12732>
- Dupont DLJ. 2014. Calving ground habitat selection of boreal woodland caribou (*Rangifer tarandus caribou*) in the Owl-Flintstone range [dissertation]. University of Manitoba, Winnipeg, MB.
- Dussault C, Pinard V, Ouellet JP, Courtois R, Fortin D. 2012. Avoidance of roads and selection for recent cutovers by threatened caribou: fitness-rewarding or maladaptive behaviour?. *Proc Roy Soc B.* 279: 4481-4488.
- Dyer SJ, Neill JPO, Wasel SM, Boutin S. 2001. Avoidance of industrial development by woodland caribou. *J Wildl Manage.* 65(3): 531-542.

- Dyer SJ, O'Neill JP, Wasel SM, Boutin S. 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. *Can J Zool.* 80(5): 839-845. Available from: <https://doi.org/10.1139/Z02-060>
- Dyke C, Manseau M. 2011. Characterization of woodland caribou (*Rangifer tarandus caribou*) calving habitat in the boreal plains and boreal shield ecozones of Manitoba and Saskatchewan. *Rangifer Special Issue.* 31(2): 151.
- Edmonds EJ. 1988. Population status, distribution, and movements of woodland caribou in west central Alberta. *Can J Zool.* 66(4): 817-826.
- Elbroch LM, Lendrum PE, Allen ML, Wittmer HU. 2015. Nowhere to hide: pumas, black bears, and competition refuges. *Behav Ecol.* 26(1): 247-254. doi:10.1093/beheco/aru189
- Elowe KD. 1984. Home range, movements, and habitat preferences of black bear (*Ursus americanus*) in western Massachusetts [master's thesis]. University of Massachusetts, Amherst. 112 pp.
- Elowe KD, Dodge WE. 1989. Factors affecting black bear reproductive success and cub survival. *J Wildl Manage.* 53(4): 962-968.
- Environment Canada. 2011. Scientific assessment to inform the identification of critical habitat for woodland caribou (*Rangifer tarandus caribou*), Boreal Population, in Canada: 2011 update. Ottawa, Ontario, Canada. 102 pp. plus appendices.
- Environment Canada. 2012. Recovery strategy for the woodland caribou (*Rangifer tarandus caribou*), boreal population, in Canada. Update. <https://doi.org/10.2307/3796292>
- Esler D, Iverson SA, Rizzolo DJ. 2006. Genetic and demographic criteria for defining population units for conservation: the value of clear messages. *The Condor.* 108(2): 480-483.
- Festa-Bianchet M, Ray JC, Boutin S, Côté SD, Gunn A. 2011. Conservation of caribou (*Rangifer tarandus caribou*) in Canada: an uncertain future. *Can J Zool.* 89(5): 419-434.
- Fisher JT, Wilkinson L. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Review.* 35(1): 51-81. Available from: <https://doi.org/10.1111/j.1365-2907.2005.00053.x>
- Flynn RE, Giraldeau LA. 2001. Producer-scrounger games in a spatially explicit world: tactic use influences flock geometry of spice finches. *Ethology.* 107(3): 249-257. Available from: <https://doi.org/10.1046/j.1439-0310.2001.00657.x>
- Franzmann AW, Schwartz CC, Peterson RO. 1980. Moose calf mortality in summer on the Kenai Peninsula, Alaska. *J Wildl Manage.* 44(3): 764-768. Available from: <https://doi.org/10.2307/3808038>

- Fretwell SD, Lucas HL. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* 19: 16-36.
- Forbes GL, Theberge JB. 1996. Response by wolves to prey variation in central Ontario. *Can J Zool.* 74(8): 1511-1520.
- Fuller TK, Sievert PR. 2001. Carnivore demography and the consequences of changes in prey availability. Cambridge University Press and the Zoological Society of London. Cambridge, London, United Kingdom.
- Gazzola A, Avanzinelli E, Bertelli I, Tolosano A, Bertotto P, Musso R, Apollonio M. 2007. The role of the wolf in shaping a multi-species ungulate community in the Italian western Alps. *Ital J Zool.* 74(3): 297-307.
- Giraldeau L, Caraco T. 2000. Social foraging theory. Princeton University Press. Princeton, NJ, USA.
- Gower CN, Garrott RA, White PJ, Watson FG, Cornish SS, Becker MS. 2008. Spatial responses of elk to wolf predation risk: using the landscape to balance multiple demands. In: Garrott RA, White PJ, and Watson FG, editors. Large mammal ecology in Central Yellowstone: a synthesis of 16 years of integrated field studies. Elsevier, Academic Press.
- Gillingham MP, Steenweg RW, Heard DC. 2008. Parsnip caribou recovery trial – report on activities during 2007-08. Peace/Williston Fish and Wildlife Compensation Program Report No. 321. 10 p.
- Goward T. 1999. Fire, terrestrial lichens, and the Itcha-Ilgachuz caribou. Proceedings of a conference on the biology and management of species and habitats at risk. Kamloops, BC. 2: 665-669.
- Graber DM, White M. 1983. Black bear food habits in Yosemite National Park. *Bears: Their biology and management.* 5: 1-10.
- Gullage S, Soulliere CE, Mahoney SP, Morgan K, Porter T. 2012. Diversionary feeding of black bear and coyote in a caribou calving area in eastern Newfoundland. National Fish and Wildlife Conservation Congress. Ottawa, Ontario. 1 p.
- Gunson JR. 1993. Management plan for black bears in Alberta. Wildlife Management Planning. Environmental Protection and Fish and Wildlife Services. Edmonton, Alta. Ser. No. 10.
- Gustine DD, Parker KL, Lay RJ, Gillingham MP, Heard DC. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife monographs.* 165: 1-32.
- Hall ER. 1981. *The Mammals of North America.* 2nd Edition. John Wiley and Sons, New York.
- Hastings A. 1993. Complex interactions between dispersal and dynamics: lessons from coupled logistic equations. *Ecology.* 74(5): 1362-1372.

- Harris S, Cresswell WJ, Forde PG, Trehwella WJ, Woollard T, Wray S. 1990. Home-range analysis using radio-tracking data – a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review*. 20(2-3): 97-123.
- Hatter IW, Bergerud WA. 1991. Moose recruitment, adult mortality, and rate of change. *Alces*. 27: 65-73.
- Hauge TM, Keith LB. 1981. Dynamics of moose populations in northeastern Alberta. *J Wildl Manage*. 45: 573-597.
- Hayek T, Lloyd N, Stanley-Price MR, Saxena A, Moehrenschrager A. 2016. An exploration of conservation breeding and translocation tools to improve the conservation status of boreal caribou populations in western Canada: pre-workshop document. Centre for Conservation Research. Calgary Zoological Society. Calgary, Alberta, Canada.
- Hayes RD, Farnell R, Ward RM, Carey J, Dehn M, Kuzyk GW, O'Donoghue M. 2003. Experimental reduction of wolves in the Yukon: ungulate responses and management implications. *J Wildl Manage*. 67(3): 1-35.
- Hayes B. 2013. Quesnel Highland wolf sterilization pilot assessment 2012: an independent evaluation of the response of mountain caribou. Prepared for Ministry of Forests, Lands and Natural Resource Operations. Prince George, British Columbia, Canada.
- Heard DC, Walker AB, Ayotte JB, Watts GS. 2008. Using GIS to modify a stratified random block survey design for moose. *Alces*. 44: 111-116.
- Hebblewhite M, Haydon DT. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philos Trans R Soc Lond B Biol Sci*. 365(1550): 2303-2312. doi:10.1098/rstb.2010.0087
- Hervieux D, Hebblewhite M, DeCesare NJ, Russell M, Smith K, Robertson S, Boutin S. 2013. Widespread declines in woodland caribou (*Rangifer tarandus caribou*) continue in Alberta. *Can J Zool*. 91(12): 872-882. doi:10.1139/cjz-2013-0123
- Hervieux D, Hebblewhite M, Stepnisky D, Bacon M, Boutin S. 2014. Managing wolves (*Canis lupus*) to recover threatened woodland caribou (*Rangifer tarandus caribou*) in Alberta. *Can J Zool*. 92(12): 1029-1037. dx.doi.org/10.1139/cjz-2014-0142
- Hilderbrand GV, Schwartz CC, Robbins CT, Jacoby ME, Hanley TA, Arthur SM, Servheen C. 1999. Importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Can J Zool*. 77(1): 132-138.
- Hillis TL, Mallory FF, Dalton WJ, Smiegielski AJ. 1998. Preliminary analysis of habitat utilization by woodland caribou in northwestern Ontario using satellite telemetry. *Rangifer*. 18(5): 195-202.

- Hirai T. 1998. An evaluation of woodland caribou (*Rangifer tarandus caribou*) calving habitat in the Wabowden area, Manitoba [master's thesis]. University of Manitoba. Winnipeg, Manitoba, Canada.
- Holt RD. 1977. Predation, apparent competition, and the structure of prey communities. *Theor Popul Biol.* 12(2): 197-229.
- Hornseth ML, Rempel RS. 2015. Seasonal resource selection of woodland caribou (*Rangifer tarandus caribou*) across a gradient of anthropogenic disturbance. *Can J Zool.* 94(2): 79-93. Available from: <https://doi.org/10.1139/cjz-2015-0101>
- Iverson SJ, McDonald Jr. JE, Smith LK. 2001. Changes in the diet of free-ranging black bears in years of contrasting food availability revealed through milk fatty acids. *Can J Zool.* 79(12): 2268-2279. Available from: <https://doi.org/10.1139/cjz-79-12-2268>
- James ARC. 1999. Effects of industrial development on the predator-prey relationship between wolves and caribou in northeastern Alberta [dissertation]. University of Alberta. Edmonton, Alberta, Canada.
- James ARC, Stuart-Smith AK. 2000. Distribution of caribou and wolves in relation to linear corridors. *J Wildl Manage.* 64(1): 154-159.
- James ARC, Boutin S, Hebert DM, Rippin AB. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. *J Wildl Manage.* 68(4): 799-809. Available from: [http://www.bioone.org/doi/abs/10.2193/0022-541X\(2004\)068\[0799:SSOCFM\]2.0.CO;2](http://www.bioone.org/doi/abs/10.2193/0022-541X(2004)068[0799:SSOCFM]2.0.CO;2)
- Jędrzejewski W, Schmidt K, Theuerkauf J, Jędrzejewska B, Selva N, Zub K, Szymura L. 2002. Kill rates and predation by wolves on ungulate populations in Białowieża Primeval Forest (Poland). *Ecology.* 83(5): 1341-1356. Available from <http://www.jstor.org/stable/pdf/3071948.pdf>
- Johansson P. 2006. Effects of habitat conditions and disturbance on lichen diversity: studies on lichen communities in nemoral, boreal and grassland ecosystems [doctoral thesis]. Swedish University of Agricultural Sciences. Uppsala, Sweden.
- Johnson DH. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology.* 61(1): 65-71.
- Johnson CJ, Parker KL, Heard DC. 2001. Foraging across a variable landscape: behavioural decisions made by woodland caribou at multiple spatial scales. *Oecologia.* 127(4): 590-602. Available from: <https://doi.org/10.1007/s004420000573>
- Johnson CJ, Ehlers LP, Seip DR. 2015. Witnessing extinction - Cumulative impacts across landscapes and the future loss of an evolutionarily significant unit of woodland caribou in Canada. *Biol Conserv.* 186: 176-186.
- Jolicoeur H. 2004. Estimation de la densité d'ours noirs dans différents types de végétation à l'aide de traceurs radioactifs. Période 1984–1994. Direction du

- développement de la faune. Ministère des Ressources naturelles et de la Faune. Québec, Canada. 44 p.
- Jones DOB, Hudson IR, Bett BJ. 2006. Effects of physical disturbance on the cold-water megafaunal communities of the Faroe-Shetland Channel. *Mar Ecol Prog Ser.* 319: 43-54.
- Kansas J, Vargas J, Skatter HG, Balicki B, McCullum K. 2016. Using landsat imagery to backcast fire and post-fire residuals in the Boreal Shield of Saskatchewan: implications for woodland caribou management. *Int J Wildland Fire.* 25: 597-607.
- Katajisto J, Moilanen A. 2006. Kernel-based home range method for data with irregular sampling intervals. *Ecol Modell.* 194(4): 405-413.
- Kemp GA. 1976. The dynamics and regulation of black bear (*Ursus americanus*) populations in northern Alberta. *Bears: Their biology and management.* 191-197 p.
- Kennedy M, Gray RD. 1993. Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the ideal free distribution. *OIKOS.* 68: 158-166.
- Kittle AM, Anderson M, Avgar T, Baker JA, Brown GS, Hagens J, Iwachewski E, Moffatt S, Mosser A, Patterson BP, et al. 2015. Wolves adapt territory size, not pack size to local habitat quality. *J Anim Ecol.* 84(5): 1177-1186.
- Klaczek M, Heard D. 2016. Assessing the wolf numerical response to a moose reduction experiment in central British Columbia. Abstract of poster: presented at 50th Moose Conference and Workshop, Brandon, Manitoba, Sept. 6-10, 2016.
- Koper N, Manseau M. 2012. A guide to developing resource selection functions from telemetry data using generalized estimating equations and generalized linear mixed models. *Rangifer.* 32(2): 195-204.
- Krebs CJ. 2015. One hundred years of population ecology: Successes, failures and the road ahead. *Integr Zool.* 10(3): 233-240.
- Krivan V. 1997. Dynamic ideal free distribution: effects of optimal patch choice on predator-prey dynamics. *The American Naturalist.* 149(1): 164-178.
- Kunkel KE, Mech LD. 1994. Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. *Can J Zool.* 72(9): 1557-1565.
- Kurten B, Anderson E. 1980. Pleistocene mammals of North America. Columbia University Press. New York, New York. ISBN 0-231-51696-7.
- Kuzyk GW. 2002. Wolf distribution and movements on caribou ranges in west-central Alberta [master's thesis]. University of Alberta. Edmonton, Alberta, Canada.
- Laake J, Dawson MJ, Hone J. 2008. Visibility bias in aerial survey: mark-recapture, line-transect or both? *Wildlife Research.* 35(4): 299-309.

- Lander CA. 2006. Distribution and movements of woodland caribou on disturbed landscapes in west-central Manitoba: implications for forestry [dissertation]. University of Manitoba. Winnipeg, Manitoba, Canada.
- Landers JL, Hamilton RJ, Johnson AS, Marchinton RL. 1979. Foods and habitat of black bears in southeastern North Carolina. *J Wildl Manage.* 43(1): 143-153.
- Latham ADM. 2009. Wolf ecology and caribou-primary prey-wolf spatial relationships in low productivity peatland complexes in northeastern Alberta [dissertation]. University of Alberta. Edmonton, Alberta, Canada.
- Latham ADM, Boutin S. 2011. Caribou, primary prey and wolf spatial relationships in northeastern Alberta. *Rangifer Special Issue.* 31(2): 155.
- Latham ADM, Latham MC, Boyce MS. 2011a. Habitat selection and spatial relationships of black bears (*Ursus americanus*) with woodland caribou (*Rangifer tarandus caribou*) in northeastern Alberta. *Can J Zool.* 89(4): 267-277.
- Latham ADM, Latham MC, Boyce MS, Boutin S. 2011b. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecol Appl.* 21(8): 2854-2865.
- Latham ADM, Latham MC, Boyce MS, Boutin S. 2011c. The role of predation in woodland caribou population declines in northeastern Alberta – coyotes. Report prepared for the Alberta Upstream Petroleum Research Fund. Petroleum Technology Alliance of Canada. 54 p.
- Latham ADM, Latham MC, Knopff KH, Hebblewhite M, Boutin S. 2011d. Wolves, white-tailed deer, and beaver: implications of seasonal prey switching for woodland caribou declines. *Ecography.* 36(12): 1276-1290.
- Latham ADM, Latham MC, Knopff KH, Hebblewhite M, Boutin S. 2013. Wolves, white-tailed deer, and beaver: implications of seasonal prey switching for woodland caribou declines. *Ecography.* 36(12): 1276-1290. <https://doi.org/10.1111/j.1600-0587.2013.00035.x>
- Latham ADM, Latham MC, Anderson DP, Cruz J, Herries D, Hebblewhite M. 2015. The GPS craze: six questions to address before deciding to deploy GPS technology on wildlife. *N Z J Ecol.* 39(1): 143-152.
- Leblond M, Dussault C, Ouellet JP, St-Laurent MH. 2016. Caribou avoiding wolves face increased predation by bears – caught between Scylla and Charybdis. *J Appl Ecol.* 53(4): 1078-1087.
- Leech H. 2015. Seasonal habitat selection by resident and translocated caribou in relation to cougar predation risk [dissertation]. Department of Geography, University of Victoria. Victoria, British Columbia, Canada. 149 p.
- Lennon JJ. 2000. Red-shifts and red herrings in geographical ecology. *Ecography.* 23: 101-113.

- Lessells CM. 1995. Putting resource dynamics into continuous input ideal free distribution models. *Anim Behav.* 49(2): 487-494.
- Lewis KP, Mahoney SP. 2014. Caribou survival, fate, and cause of mortality in Newfoundland: a summary and analysis of the patterns and causes of caribou survival and mortality in Newfoundland during a period of rapid population decline (2003-2012). Technical Bulletin No. 009, Sustainable Development and Strategic Science. Government of Newfoundland and Labrador. St. John's, NL.
- Lindzey FG, Barber KR, Peters RD, Meslow EC. 1986. Responses of a black bear population to a changing environment. *Bears: their Biology and Management.* 6: 57-63.
- Loveless K. 2010. Foraging strategies of eastern wolves in relation to migratory prey and hybridization [master's thesis]. Trent University. Peterborough, Ontario, Canada.
- Lubow BC, Ransom JI. 2016. Practical bias correction in aerial surveys of large mammals: validation of hybrid double-observer with sightability method against known abundance of feral horse (*Equus caballus*) populations. *PLoS one.* 11(5): e0154902. doi:10.1371/journal.pone.0154902
- MacNearney D, Pigeon K, Finnegan L. 2016. Behaviour and calving success of boreal caribou in relation to oil and gas development. Final report prepared for the Petroleum Technology Alliance Canada. Alberta Upstream Petroleum Research Fund (15-ERPC-06) and British Columbia Oil and Gas Research and Innovation Society (2016-15), April 2016. Pp vii + 42.
- Mahoney SP, Abbott H, Russell LH, Porter BR. 1990. Woodland caribou calf mortality in insular Newfoundland. In: Transactions of the 19th international union of game biologists congress. Trondheim. 19: 592-599.
- Mahoney SP, Virgl JA. 2003. Habitat selection and demography of a nonmigratory woodland caribou population in Newfoundland. *Can J Zool.* 81(2): 321-334. Available from <http://article.pubs.nrc-cnrc.gc.ca/ppv/RPViewDoc?issn=1480->
- Mahoney SP, Lewis KP, Weir JN, Morrison SF, Luther GJ, Schaefer JA, Pouliot D, Latifovic R. 2016. Woodland caribou calf mortality in Newfoundland: insights into the role of climate, predation and population density over three decades of study. *Popul Ecol.* 58(1): 91-103. Available from: <https://doi.org/10.1007/s10144-015-0525-y>
- Malasiuk JA. 1999. Aboriginal land use patterns in the boreal forest of north-central Manitoba: applications for archaeology [master's thesis]. University of Manitoba. Winnipeg, Manitoba, Canada.
- Manitoba Boreal Woodland Caribou Management Committee. 2015. Conserving a Boreal Icon, Manitoba's Boreal Woodland Caribou Recovery Strategy. Manitoba Conservation and Water Stewardship. Winnipeg, Manitoba. 30 p.

- Manly BFL, McDonald L, Thomas D, McDonald TL, Erickson WP. 2002. Resource selection by animals: statistical design and analysis for field studies. *J Anim Ecol.* January 2002, DOI: 10.2307/5247
- Mazur R, Seher V. 2008. Socially learned foraging behavior in wild black bears (*Ursus americanus*). *Anim Behav.* 75(4): 1503-1508.
- McCarthy SC, Weladji RB, Doucet C, Saunders P. 2011. Woodland caribou calf recruitment in relation to calving/post-calving landscape composition. *Rangifer.* 31(1): 35-47.
- McDonald JEJ, Fuller TK. 2005. Effects of spring acorn availability on black bear diet, milk composition, and cub survival. *J Mammal.* 86(5): 1022-1028. Available from: [https://doi.org/10.1644/1545-1542\(2005\)86\[1022:EOSAAO\]2.0.CO;2](https://doi.org/10.1644/1545-1542(2005)86[1022:EOSAAO]2.0.CO;2)
- McLean PK, Pelton MR. 1990. Some demographic comparisons of wild and panhandler bears in the Smoky Mountains. *Int Conf Bear Res and Manage.* 8: 105-112.
- McLoughlin PD, Cluff HD, Gau RJ, Mulders R, Case RL, Messier F. 2002. Population delineation of barren-ground grizzly bears in the central Canadian Arctic. *Wildlife Society Bulletin.* 30(3): 728-737.
- McLoughlin PD, Dzus EH, Wynes B, Boutin S. 2003. Declines in population of woodland caribou. *J Wildl Manage.* 67(4): 755-761. Available from: <http://www.jstor.org/stable/3802682>
- McLoughlin PD, Paetkau D, Duda M, Boutin S. 2004. Genetic diversity and relatedness of boreal caribou populations in western Canada. *Biol Conserv.* 118(5): 593-598.
- McLoughlin PD, Dunford JS, Boutin S. 2005. Relating predation mortality to broad-scale habitat selection. *J Anim Ecol.* 74(4): 701-707.
- McLoughlin PD, Stewart K, Superbie C, Perry T, Tomchuk T, Greuel R, Singh K, Truchon-Savard A, Henkelman J, Johnstone JF. 2016. Population dynamics and critical habitat of woodland caribou in the Saskatchewan Boreal Shield. Interim Project Report 2013–2016. Department of Biology. University of Saskatchewan. Saskatoon, Saskatchewan, Canada. 162 p.
- Mech LD, Wolf PC, Packard JM. 1999. Regurgitative food transfer among wild wolves. *Can J Zool.* 77(8): 1192-1195.
- Mech LD, Boitani L. 2007. *Wolves: behavior, ecology and conservation.* University of Chicago Press.
- Messier F. 1985. Social organization, spatial distribution, and population density of wolves in relation to moose density. *Can J Zool.* 63(5): 1068-1077.
- Messier F, Desaulniers DM, Goff AK, Nault R, Patenaude R, Crete M. 1990. Caribou pregnancy diagnosis from immunoreactive progestins and estrogens excreted in feces. *J Wildl Manage.* 54(2): 279-283. Available from: <http://www.jstor.org/stable/3809042>

- Messier F. 1991. The significance of limiting regulating factors on the demography of moose and white-tailed deer. *J Anim Ecol.* 60(2): 377-393.
- Metsaranta JM, Mallory FF. 2007. Ecology and habitat selection of a woodland caribou population in west-central Manitoba, Canada. *Northeastern Naturalist.* 14(4): 571-588. Available from: [https://doi.org/10.1656/1092-6194\(2007\)14\[571:EAHSOA\]2.0.CO;2](https://doi.org/10.1656/1092-6194(2007)14[571:EAHSOA]2.0.CO;2)
- Monthey RW. 1984. Effects of timber harvesting on ungulates in northern Maine. *J Wildl Manage.* 48(1): 279-285. Available from: <http://www.jstor.org/stable/3808489>
- Morris DW. 1994. Habitat matching: alternatives and implications to populations and communities. *Evol Ecol.* 8(4): 387-406.
- Morrison ML, Marcot BG, Mannan RW. 2006. *Wildlife habitat relationships: concepts and applications (third edition)*. Island Press, Washington, Covelo, London.
- Mosnier A, Ouellet JP, Courtois R. 2008. Black bear adaptation to low productivity in the boreal forest. *Ecoscience.* 15(4): 485-497. Available from: <https://doi.org/10.2980/15-4-3100>
- Mowat G, Poole KG, Seip DR, Heard DC, Smith R, Paetkau DW. 2002. Grizzly (*Ursus arctos*) and black bear (*Ursus americanus*) densities in interior British Columbia. Final Report for Canadian Forest Products, Chetwynd, BC, and BC Ministry of Water, Lands and Air. Prince George, BC.
- Mowat G, Heard DC, Seip DR, Poole KG, Stenhouse G, Paetkau DW. 2005. Grizzly (*Ursus arctos*) and black bear (*Ursus americanus*) densities in the interior mountains of North America. *Wildl Biol.* 11(1): 31-48.
- Munro RHM, Nielsen SE, Price MH, Stenhouse GB, Boyce MS. 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. *J Mammal.* 87(6): 1112-1121. Available from: <https://doi.org/10.1644/05-MAMM-A-410R3.1>
- Murray JD. 2003. Wolf territoriality, wolf-deer interaction and survival. in: *mathematical biology ii: spatial models and biomedical applications*. Springer - Verlag, New York, Berlin, Heidelberg. ISBN 0-387-95228-4
- Nagy JA, Johnson DL, Larter NC, Campbell MW, Derocher AE, Kelly A, Dumond M, Allaire D, Croft B. 2011. Subpopulation structure of caribou (*Rangifer tarandus L.*) in arctic and subarctic Canada. *Ecol Appl.* 21(6): 2334-2348. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/21939065>
- National Council for Air and Stream Improvement Inc (NCASI). 2004. *Ecological interactions among caribou, moose, and wolves: literature review*. Review literature and arts of the Americas. 1
- Neufeld LM. 2006. *Spatial dynamics of wolves and woodland caribou in an industrial forest landscape in west-central Alberta [dissertation]*. University of Alberta. Edmonton, Alberta, Canada. Available from: http://www.carnivoreconservation.org/files/thesis/neufeld_2006_msc.pdf

- Nolan JW, Barrett MW. 1985. A preliminary study of moose calf mortality in northeastern Alberta. Alberta Environmental Centre, Vegreville.
- Noyce KV, Coy PL. 1990. Abundance and productivity of bear food species in different forest types of northcentral Minnesota. *Bears: their biology and management*. 8: 169-181.
- Noyce KV, Garshelis DL. 1998. Spring weight changes in black bears in northcentral Minnesota: the negative foraging period revisited. *Ursus*. 10: 521-531. Available from: <http://www.jstor.org/stable/pdf/3873164.pdf>
- O'Brien D, Manseau M, Fall A, Fortin MJ. 2006. Testing the importance of spatial configuration of winter habitat for woodland caribou: an application of graph theory. *Biol Conserv*. 130(1): 70-83. Available from: <https://doi.org/10.1016/j.biocon.2005.12.014>
- Osborne TO, Paragi TF, Bodkin JL, Loranger AJ, Johnson WN. 1991. Extent, cause, and timing of moose calf mortality in western interior Alaska. *Alces*. 27: 24-30.
- Otis DL, White GC. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. *J Wildl Manage*. 63: 1039-1044.
- Packard J. 2003. Wolf behavior: reproductive, social, and intelligent. In: Mech LD, Boitani L, editors. *Wolves: behavior, ecology, and conservation*. University of Chicago Press.
- Paillé G. 2014. History of Forestry in Canada. FPInnovations.
- Park BU, Marron JS. 1990. Comparison of data-driven bandwidth selectors. *J Amer Statist Assoc*. 85(409): 66-72.
- Parker GA, Sutherland WJ. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. *Anim Behav*. 34(4): 1222-1242.
- Parker KL, Gustine DD. 2007. Winter habitat selection and calving strategies of woodland caribou in the Besa-Prophet. Part 1 of an ecosystem approach to habitat capability modelling and cumulative effects management. Final Report submitted to the Muskwa-Kechika Advisory Board. Fort St John, British Columbia. 52 p.
- Patterson BR, Benson JF, Middel KR, Mills KJ, Silver A, Obbard ME. 2013. Moose calf mortality in central Ontario, Canada. *J Wildl Manage*. 77(4): 832-841. Available from: <http://doi.wiley.com/10.1002/jwmg.516>
- Paquet PC. 1991. Winter spatial relationships of wolves and coyotes in Riding Mountain National Park, Manitoba. *J Mammal*. 72(2): 397-401. Available from: <http://www.jstor.org/stable/1382113>
- Pearce J, Eccles G. 2004. Characterizing forest-dwelling woodland caribou distribution in Ontario, Canada. Canadian Forest Service. Sault Ste Marie, Ontario.
- Peek JM, Urich DL, Mackie RJ. 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. *Wildlife Monographs*. 48: 3-65.

- Pelton MR. 2003. Black bear (*Ursus americanus*). In Feldhamer GA, Thompson BC, Chapman JA, editors. Wild mammals of North America: biology, management, and conservation. The Johns Hopkins University Press. Baltimore, Maryland, USA. 547–555 p.
- Pinard V, Dussault C, Ouellet JP, Fortin D, Courtois R. 2012. Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. *J Wildl Manage.* 76(1): 189-199. Available from: <https://doi.org/10.1002/jwmg.217>
- Pollitt LC, Reece SE, Mideo N, Nussey DH, Colegrave N. 2012. The problem of auto-correlation in parasitology. *PLoS Pathog.* 8(4): e1002590. doi:10.1371/journal.ppat.1002590
- Powell RA, Zimmerman JW, Seaman DE. 1997. Ecology and behaviour of North American black bears: home ranges, habitat and social organization. Springer Science and Business Media. Chapman and Hall, London, UK. 4.
- Racey GD, Arsenault AA. 2007. In search of a critical habitat concept for woodland caribou, boreal population. *Rangifer.* 27(4): 29-37.
- Raine RM, Kansas JL. 1990. Black bear seasonal food habits and distribution by elevation in Banff National Park, Alberta. *Bears: Their biology and management.* 8: 297-304.
- Recer GM, Caraco T. 1989. Sequential-encounter prey choice and effects of spatial resource variability. *J Theor Biol.* 139(2): 239-249.
- Rempel RS, Elkie PC, Rodgers AR, Gluck MJ. 1997. Timber-management and natural-disturbance effects on moose habitat evaluation. *J Wildl Manage.* 61(2): 517-524.
- Rettie WJ, Messier F. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. *Can J Zool.* 76(2): 251-259. Available from: <https://doi.org/10.1139/cjz-76-2-251>
- Rettie WJ, Messier F. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography.* 23(4): 466-478. Available from: <https://doi.org/10.1034/j.1600-0587.2000.230409.x>
- Robbins CT, Fortin JK, Rode KD, Farley SD, Shipley LA, Felicetti LA. 2007. Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. *Oikos.* 116(10): 1675-1682. Available from: <https://doi.org/10.1111/j.2007.0030-1299.16140.x>
- Rodgers AR, Kie JG. 2010. HRT: Home Range Tools for ArcGIS ®, version 1.1. Available from: <http://flash.lakeheadu.ca/~arodgers/hre/HRT%20Users%20Manual%20Draft%20August%2010%202011.pdf>
- Rodgers AR, Carr AP. 1998. HRE: the home range extension for ArcView. Centre for Northern Forest Ecosystem Research. Ontario Ministry of Natural Resources. Thunder Bay, Ontario, Canada.

- Rogers LL. 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. *Trans North Am Wildl and Nat Resour Conf.* 41(43): 1-438.
- Rogers LL. 1987. Effects of food supply and kinship on social behavior, movements, and population dynamics of black bears in northeastern Minnesota. *Wildlife Monograph.* 97: 3-72.
- Sain SR, Baggerly KA, Scott DW. 1994. Cross-validation of multivariate densities. *J Am Stat Assoc.* 89(427): 807-817.
- Schaefer JA. 1990. Canopy, snow and lichens on woodland caribou range in southeastern Manitoba. No. Research Report No. 20.
- Schaefer JA, Pruitt WO. 1991. Fire and woodland caribou in southeastern Manitoba. *Wildlife Monographs.* 116: 3-39. Available from: <http://www.jstor.org/stable/pdf/3830581.pdf?acceptTC=true>
- Schaefer JA. 1996. Canopy, snow, and lichens on woodland caribou range in southeastern Manitoba. *Rangifer.* 16(4): 239-244.
- Schaefer JA, Wilson CC. 2002. The fuzzy structure of populations. *Can J Zool.* 80(12): 2235-2241. Available from: <http://doi.org/10.1139/Z02-184>
- Schaefer JA. 2003. Long-term range recession and the persistence of caribou in the Taiga. *Conserv Biol.* 17(5): 1435-1439. Available from: <https://doi.org/10.1046/j.1523-1739.2003.02288.x>
- Schindler DW. 2006. Home range and core area determination, habitat use and sensory effects of all weather access on boreal woodland caribou (*Rangifer tarandus caribou*) in eastern Manitoba [master's thesis]. University of Manitoba. Winnipeg, Manitoba, Canada. 165 p.
- Schindler DW, Walker DD, Davis T, Westwood R. 2007. Determining effects of an all weather logging road on winter woodland caribou habitat use in southeastern Manitoba. *Rangifer.* 27(17): 23-27. Available from: <http://septentrio.uit.no/index.php/rangifer/article/view/346/337>
- Seaman DE, Powell RA. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology.* 77(7): 2075-2085.
- Seip DR. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Can J Zool.* 70(8): 1494-1503. Available from: <https://doi.org/10.1139/z92-206>
- Serrouya R, McLellan BN, Boutin S, Seip DR, Nielsen SE. 2011. Developing a population target for an overabundant ungulate for ecosystem restoration. *J Appl Ecol.* 48(4): 935-942. Available from: <https://doi.org/10.1111/j.1365-2664.2011.01998.x>

- Shoosmith MW, Storey DR. 1977. Movements and associated behaviour of woodland caribou in central Manitoba. Manitoba Department of Renewable Resources and Transportation Services. Research Manuscript No. 77-15. 74 p.
- Shuter JL, Rodgers AR. 2012. Delineating demographic units of woodland caribou (*Rangifer tarandus caribou*) in Ontario: cautions and insights. *Rangifer*. 32(2): 159-182. Available from:
<http://septentrio.uit.no/index.php/rangifer/article/viewFile/2267/2108>
- Smith AT, Dobson FS. 1994. A technique for evaluation of spatial data using asymmetrical weighted overlap values. *Anim Behav*. 48(6): 1285-1292.
- Smith RE, Veldhuis H, Mills GF, Eilers RG, Fraser WR, Lelyk GW. 1998. Terrestrial eozones, ecoregions and eodistricts of Manitoba: An ecological stratification of Manitoba's natural landscapes. No. Technical Bulletin 9E. Research Branch: Agriculture and Agri-Food Canada. Brandon Research Centre. Brandon, Manitoba, Canada.
- Smith KG, Pittaway L. 2008. Little smoky woodland caribou calf survival enhancement project. The 12th North American Caribou Workshop. Happy Valley/Goose Bay, Labrador, Canada. 4-6 November, 2008.
- Spaulding RL, Krausman PR, Ballard WB. 1998. Summer diet of gray wolves (*Canis lupus*) in northwestern Alaska. *Canadian Field-Naturalist*. 112(2): 262-266.
- Stardom R. 1975. Woodland caribou and snow conditions in southeast Manitoba. In: Luick JR, Lent PC, Klein DR, and White RG, editors. Proceedings of the first international reindeer/caribou symposium. Fairbanks: University of Alaska. 324-334 p.
- Stardom RRP. 1977. Winter ecology of woodland caribou, *Rangifer tarandus caribou*, and some aspects of the winter ecology of moose, *Alces alces andersoni*, and whitetail deer, *Odocoileus virginianus dacotensis* (mammalia: cervidae) in southeastern Manitoba [master's thesis]. University of Manitoba. Winnipeg, Manitoba, Canada.
- Steenweg RW. 2011. Interactions of wolves, mountain caribou, and an increased moose-hunting quota - primary-prey management as an approach to caribou recovery [master's thesis]. University of Northern British Columbia. Prince George, British Columbia, Canada.
- Stephens DW, Krebs JR. 1986. Foraging Theory. Princeton University Press. Princeton, New Jersey, USA.
- Stewart RR, Kowal EH, Beaulieu R, Rock TW. 1985. The impact of black bear removal on moose calf survival in east central Saskatchewan. *Alces*. 21: 403-418.
- Stotyn SA, McLellan BN, Serrouya R. 2007. Mortality sources and spatial partitioning among mountain caribou, moose, and wolves in the north Columbia Mountains, British Columbia. Columbia Basin Fish and Wildlife Compensation Program. Nelson, British Columbia.

- Stuart-Smith AK, Bradshaw CJA, Boutin S, Hebert DM, Rippin AB. 1997. Woodland caribou relative to landscape patterns in northeastern Alberta. *J Wildl Manage.* 61(3): 622-633. Available from: <http://www.jstor.org/stable/3802170>
- Swihart RK, Slade NA. 1985. Testing for independence of observations in animal movements. *Ecology.* 66(4): 1176-1184.
- Tate J, Pelton MR. 1983. Human-bear interactions in Great Smoky Mountains National Park. *International conference of bear research and management.* 5: 312-321.
- Taylor MK, Akeagok S, Andriashek D, Barbour W, Born EW, Calvert W, Cluff HD, Ferguson S, Laake J, Rosing-Asvid A, et al. 2001. Delineating Canadian and Greenland polar bear (*Ursus maritimus*) populations by cluster analysis of movements. *Can J Zool.* 79(4): 690-709.
- Theberge JB, Theberge MT. 2004. The wolves of Algonquin Park: A 12 year ecological study. Department of Geography. Publication No. 56. University of Waterloo. Waterloo, Ontario.
- Thomas D. 1995. A review of wolf-caribou relationships and conservation implications in Canada. In: Carbyn LN, Fritts SH, Seip DR, editors. *Ecology and conservation of wolves in a changing world.* Canadian Circumpolar Institute, Occasional Publication No. 35. Edmonton, Alberta, Canada. 261-273 p.
- Thompson JE, Abraham KF. 1994. Range, seasonal distribution and populations dynamics of the pen island caribou herd of southern Hudson Bay. OMNR unpublished final report. Moosonee, Ontario.
- Thompson ID, Baker JA, Ter-Mikaelian M. 2003. A review of the long-term effects of post-harvest silviculture on vertebrate wildlife, and predictive models, with an emphasis on boreal forests in Ontario, Canada. *For Ecol Manage.* 177(1): 441-469.
- Thurfjell H, Ciuti S, Boyce MS. 2014. Applications of step-selection functions in ecology and conservation. *Mov Ecol.* 2(4): 1-12. doi:10.118.
- The National Forestry Database: Canada's compendium of forestry statistics. 2017. National Forestry Database. Accessed 2017 Jan 30. Available from: http://nfdp.ccfm.org/index_e.php
- Tigner J, Bayne EM, Boutin S. 2014. Black bear use of seismic lines in northern Canada. *J Wildl Manage.* 78(2): 282-292. doi: 10.1002/jwmg.664
- Udell RW. 2003. Evolution of adaptive forest management in a historic Canadian forest. Twelfth World Forestry Congress. Quebec City, Quebec, Canada. 21-28 p.
- Vander Wal E, Rodgers AR. 2012. An individual-based quantitative approach for delineating core areas of animal space use. *Ecol Modell.* 224(1): 48-53.
- Van Rensen CK, Nielsen SE, White B, Vinge T, Lieffers VJ. 2015. Natural regeneration of forest vegetation on legacy seismic lines in boreal habitats in Alberta's oil sands region. *Biol Conserv.* 184: 127-135.

- Vors LS, Schaefer JA, Pond BA, Rodgers AR, Patterson BR. 2007. Woodland caribou extirpation and anthropogenic landscape disturbance in Ontario. *J Wildl Manage.* 71(4): 1249-1256. Available from: <https://doi.org/10.2193/2006-263>
- Vors LS, Boyce MS. 2009. Global declines of caribou and reindeer. *Global change biology.* 15(11): 2626-2633. Available from: <https://doi.org/10.1111/j.1365-2486.2009.01974.x>
- Walter WD, Fischer JW, Baruch-Mordo S, VerCauteren KC. 2011. What is the proper method to delineate home range of an animal using today's advanced GPS telemetry systems: the initial step. USDA National Wildlife Research Center - Staff Publications. Paper 1375.
- Waples RS, Gaggiotti O. 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Mol Ecol.* 15(6): 1419-1439. Available from: <https://doi.org/10.1111/j.1365-294X.2006.02890.x>
- Wathen WG. 1983. Reproduction and denning of black bears in the great smoky mountains [master's thesis]. University of Tennessee. Knoxville, Tennessee, USA. 135 p.
- Weckworth BV, Musiani M, Mcdevitt AD, Hebblewhite M, Mariani S. 2012. Reconstruction of caribou evolutionary history in Western North America and its implications for conservation. *Mol Ecol.* 21(14): 3610-3624. doi:10.1111/j.1365-294X.2012.05621.x.
- Weir JN, Mahoney SP, McLaren B, Ferguson SH. 2007. Effects of mine development on woodland caribou (*Rangifer tarandus*) distribution. *Wildl Biol.* 13(1): 66-74. Available from: [http://www.bioone.org/doi/pdf/10.2981/09096396\(2007\)13\[66:EOMDOW\]2.0.CO;2](http://www.bioone.org/doi/pdf/10.2981/09096396(2007)13[66:EOMDOW]2.0.CO;2)
- Werner EE, Gilliam JF, Hall DJ, Mittelbach GG. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology.* 64(6): 1540-1548.
- Wilmers CC, Post E, Hastings A. 2007. The anatomy of predator-prey dynamics in a changing climate. *J Anim Ecol.* 76(6): 1037-1044.
- Wittmer HU. 2004. Mechanisms underlying the decline of mountain caribou (*Rangifer tarandus caribou*) in British Columbia [thesis]. University of British Columbia. Vancouver, British Columbia, Canada. 104 p.
- Wittmer HU, McLellan BN, Seip DR, Young JA, Kinley TA, Watts GS, Hamilton D. 2005a. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. *Can J Zool.* 83(3): 407-418. Available from: <https://doi.org/10.1139/Z05-034>
- Wittmer HU, Sinclair ARE, McLellan BN. 2005b. The role of predation in the decline and extirpation of woodland caribou. *Oecologia.* 144(2): 257-267. Available from: <https://doi.org/10.1007/s00442-005-0055-y>

- Wittmer HU, McLellan BN, Serrouya R, Apps CD. 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. *J Anim Ecol.* 76(3): 568-579. Available from: <https://doi.org/10.1111/j.1365-2656.2007.01220.x>
- Worton BJ. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology.* 70(1): 164-168. Available from: <http://www.esajournals.org/doi/abs/10.2307/1938423>
- Worton BJ. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *J Wildl Manage.* 59(4): 794-800.
- Young BF, Ruff RL. 1982. Population dynamics and movements of black bears in east central Alberta. *J Wildl Manage.* 46(4): 845-860. doi:10.2307/3808217
- Young Jr. DD, McCabe TR. 1997. Grizzly bear predation rates on caribou calves in northeastern Alaska. *J Wildl Manage.* 61(4): 1056-1066.
- Zager P, Beecham J. 2006. The role of American black bears and brown bears as predators on ungulates in North America. *Ursus.* 17(2): 95-108. Available from: [http://www.bioone.org/doi/abs/10.2192/1537-6176\(2006\)17\[95:TROABB\]2.0.CO;2](http://www.bioone.org/doi/abs/10.2192/1537-6176(2006)17[95:TROABB]2.0.CO;2)
- Zimmermann B, Nelson L, Wabakken P, Sand H, Liberg O. 2014. Behavioral responses of wolves to roads: scale-dependent ambivalence. *Behav Ecol.* 25(6): 1353-1364.
- Zoladeski CA, Wickware GM, Delorme RJ, Sims RA, Corns IGW. 1995. Forest ecosystem classification for Manitoba: field guide. Natural Resources Canada. Canadian Forest Service, Northern Forestry Centre. Edmonton, Alberta. Special Report 2. 205 p.
- Zwolak R. 2009. A meta-analysis of the effects of wildfire, clearcutting, and partial harvest on the abundance of North American small mammals. *For Ecol Manage.* 258(5): 539-545. Available from: <https://doi.org/10.1016/j.foreco.2009.05.033>

2.0 ROLE OF DISTURBANCE ON LAMBDA RATES FOR BOREAL CARIBOU

2.1 Abstract

The Western Canadian population of boreal caribou (*Rangifer tarandus caribou*) is of special concern and is listed as “threatened” under the Canadian Species at Risk Act (SARA). In Canada, National and Provincial boreal caribou range-based management plans are guided by the application of non-disturbance thresholds that require 65% of a given range to be maintained in a non-disturbed state. Assessing population sustainability in terms of vital rates and demography requires unambiguous range boundaries. The spatial variability in available data, empirical nature of parameter values in many models, and sheer variety in analytical approaches, results in uncertainty in delineation of range boundaries in local populations. In this study, a fuzzy classification approach was applied to a pooled telemetry dataset for 138 caribou equipped with GPS collars from 2009 to 2012 to delineate ranges for boreal caribou in northern Manitoba.

Within these ranges, patterns of disturbance across a gradient of core, peripheral and overlapping boreal caribou ranges were compared to observed caribou recruitment and mortality. Results indicated that there were no measurable differences in Lambda rates between populations and their associated disturbance regimes. The confidence interval for Lambda (λ) for populations was found to include 1 regardless of disturbance levels. This suggests that disturbance levels alone may not be an appropriate surrogate for assessing population persistence. Fuzzy K Means analysis provided a statistically rigorous approach to delineating appropriate assessment units of range use and disturbance patterns relative to animal use.

2.2 Introduction

Boreal woodland caribou have been in decline across Canada with observed range recession across the southern limits of the Canadian boreal woodland caribou zone as a result of habitat alteration and fragmentation resulting from increased linear development and landscape anthropogenic disturbance (Schaefer 2003, Vors et al. 2007). The Western Canadian population of boreal caribou (*Rangifer tarandus caribou*) is listed as “threatened” under both the Canadian *Species at Risk Act* (SARA 2002) and the *Manitoba’s Endangered Species and Ecosystem Act* (MESEA 2015). In Manitoba, there are several boreal woodland caribou ranges that are at risk of decline based on risk assessments contained in Provincial conservation and recovery strategies (Manitoba Boreal Woodland Caribou Management Committee 2015). This designation is based on range assessment criteria set forth in a scientific review to inform the identification of critical habitat for boreal woodland caribou (Environment Canada 2011). These criteria have been incorporated into the recovery of critical habitat contained in the National Recovery Strategy for Boreal Woodland Caribou (Environment Canada 2012). The cumulative relationships and pathways of effects are variable across individual boreal woodland caribou ranges and meta-populations (Environment Canada 2011). The relative effect of disturbance on boreal woodland caribou populations is dependent upon the amount and distribution of anthropogenic activity and natural disturbance patterns that can indirectly influence primary prey habitat and predator distribution (Vistnes and Nellemann 2007).

To achieve recovery of boreal caribou in Canada, National and provincial boreal caribou threat assessments and range-based management plans are guided by the

application of disturbance thresholds that require 65% of the range of a local population be maintained in a non-disturbed state to achieve a 60% probability of population persistence (Environment Canada 2011, 2012). Typical large scale anthropogenic and natural disturbance features include forestry and wildfire. Linear features that contribute to disturbance include anthropogenic development such as all weather and seasonal access roads, hydro electric transmission lines, and mineral exploration activities (Environment Canada 2011). The magnitude of landscape and linear feature disturbances can influence forest composition and structure to the benefit of wildlife species that favour early seral forests to the detriment of those that depend on older aged forest communities (Cumming and Beange 1987, Seip 1992, Boutin et al. 2012). These types of habitat shifts not only impact herbivores, but also influence how predators utilize the landscape for foraging and annual survival (Bergerud 1974, Dyer et al. 2001, McLoughlin et al. 2003).

Disturbance-related ecosystem alterations can result in adjustments to the relative predation vulnerability of primary prey relative to secondary prey caused by either an increase in the density of the primary predator (wolves) and/or a habitat-related change in the hunting strategy of the primary predator (Peek et al. 1976, Monthey 1984, Clarke et al. 2006, Zwolak 2009). The situation, in which an environmental change can result in an increase in the rate of depredation of a secondary prey species, is termed “apparent competition” (Holt 1977). The degree, to which the primary predator impacts a secondary prey, reflects the complex pattern and interrelatedness of temporal and spatial disturbance features on the landscape (Peek et al. 1976, Monthey 1984, Bergerud and Mercer 1989, Cumming 1992, McLoughlin et al. 2003, James et al. 2004, Clarke et al. 2006, Wittmer et

al. 2007, Zwolak 2009). The impact of linear features can be additive should their presence alone result in increased mortality of adults and calves, resulting in a cumulative effect where landscape and linear disturbances jointly contribute to the vulnerability of caribou (Dyer et al. 2001, McLoughlin et al. 2003, James and Stuart-Smith 2000). Where disturbances are long-term, the direct loss of habitat and/or fragmentation within individual caribou ranges may also introduce subtle ecological effects; these may include, but are not limited to, changes in the availability and use of specific resources, and the probability for encounters with predators that have the potential to influence both short- and long-term population dynamics (Bergerud 1974, Bergerud and Mercer 1989, Cumming 1992, Dyer et al. 2001, McLoughlin et al. 2003, James et al. 2004, Wittmer et al. 2007).

Boreal woodland caribou are typically found in large, un-fragmented tracts of mature coniferous dominated boreal forest with low densities of interspecific competitors and their predators (Holt 1977, Wittmer et al. 2005*b*, Latham 2009, Boutin et al. 2012). Various boreal forest caribou habitat studies specific to Manitoba and similar ecoregions in Saskatchewan have revealed winter habitat selection in mature upland spruce and/or pine forests supporting arboreal and/or terrestrial lichens and multi-season association with open and treed spruce peatlands while avoiding deciduous forest (Rettie 1998, Rettie and Messier 2000, Brown et al. 2000, Lander 2006, Schindler 2006, Metsaranta and Mallory 2007). Boreal woodland caribou occur at very low densities across landscapes, congregate into small groups during winter in traditional wintering areas, but during a period spanning late-April to mid-May, parturient females individually ‘space-out’ within lowlands in search of isolated calving and rearing sites (Bergerud et al. 1990). Calving

sites are frequently associated with nutrient poor fens that support an early flush of herbaceous plants including bogbean (*Menyanthes trifoliata*), three-leafed False Soloman's Seal (*Smilacina trifolia*), horsetails (*Equisetum spp.*) sedges (*Carex lasiocarpa*), bog willow (*Salix pedicellaris*) and bog birch (*Betula pumila glandulifera*), (Cumming and Beange 1987). Calving females have also been observed to use small islands in addition to large peatlands as isolated calving and rearing sites in northwestern Manitoba (Shoesmith and Storey 1977, Hillis et al. 1998, Armstrong et al. 2000, Pearce and Eccles 2004, Lander 2006). Cows with calves tend to maintain their pattern of isolation until mid- to late- summer, after which they begin to search for conspecifics forming small groups (Malasiuk 1999, Metsaranta and Mallory 2007). During winter, caribou select lichen rich mature upland spruce and pine stands and/or treed muskeg and avoid deciduous forests (Hillis et al. 1998, Malasiuk 1999, Armstrong et al. 2000, Pearce and Eccles 2004, Metsaranta and Mallory 2007).

The rate of population growth is expressed as λ which describes a ratio of recruitment (calf fecundity and survival) against mortality (number of surviving adult females). Although predation by wolves is widely postulated as the primary agent underlying the decline of boreal populations (Dyer 2001, 2002, Latham 2009, Boutin et al. 2012, Hervieux et al. 2013), bears are also known to be a significant factor in limiting some ungulate populations through predation of calves (Ballard 1994, DeMars 2015, Pinard et al. 2012, Leblond et al. 2016).

Ideally, resource development in boreal caribou habitat, must be planned to ensure the sustainability of local populations through management of habitat disturbance that can result in higher than natural rates of adult female mortality. Current disturbance

thresholds to ensure boreal caribou persistence may not be applicable across boreal caribou range in Canada. The objective of this chapter is to assess the effect of habitat disturbance on λ , through the assessment of adult female and calf mortality in a number of boreal caribou ranges in Manitoba, and to explore whether higher rates of anthropogenic disturbance and natural disturbance influence rates of recruitment and adult female mortality at the range level.

Disturbance and λ rates based on adult female and calf mortality were examined to determine if these relationships exist in Manitoba. Evaluation ranges were identified using current data from GPS telemetry from adult female caribou collared in 2010 through 2012. Comparisons of adult female survival and recruitment were compared to existing disturbance regimes to a control population with little anthropogenic and comparable natural disturbances. A secondary objective included application of fuzzy set theory to better delineate ranges prior to measuring disturbance patterns within and among core use areas. This approach was used in identifying sub-populations at finer scales for landscape disturbance assessment.

2.3 Study Area

The study area is located in west central Manitoba (55.02 N – 100.35 W) and includes a control area on the east side of the province near the Ontario boundary (53.20 N – 95.97 W) (Figure 2.1). The area falls mainly within the extensive Boreal Plains and Boreal Shield Ecozones. Boreal woodland caribou range delineations were originally based on the best available data descriptions provided in the 2006 Conservation and Recovery Strategy for Boreal Woodland Caribou in Manitoba (Crichton 2005). The Study

area also encompasses the proposed Bipole III Transmission Line Project, with proposed routing near known boreal woodland caribou range (Figure 2.1).

The Boreal Shield Ecozone extends across most of north-central and eastern Manitoba, and is dominated by the metamorphic gneiss bedrock, broad expanses of coniferous dominated forest, and numerous lakes; soils are typically thin, cool, acidic, and have low nutrient availability (Smith et al. 1998). The Boreal Plains Ecozone that extends as a wide band from the Peace River area of northwest British Columbia to the southeastern corner of Manitoba is differentiated from the adjacent Boreal Shield, in that it has relatively few bedrock outcrops and considerably fewer lakes. The landscape is a composite of nearly level to gently rolling plains consisting largely of hummocky and kettled to gently undulating morainal till deposits, and level to depressional glaciolacustrine sediments (Smith et al. 1998). Wetlands, including peatlands, cover between 20 - 50% of the Manitoba portion of this ecozone. Typical forest cover for both areas includes white spruce (*Picea glauca*), black spruce (*Picea mariana*), jack pine (*Picea banksiana*), tamarack (*Larix laricina*), white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*). Important predator and prey species include black bear (*Ursus americanus*), gray wolf, lynx (*Lynx canadensis*), moose, white-tailed deer, woodland caribou, beaver (*Castor canadensis*), snowshoe hare (*Lepus americanus*) and muskrat (*Ondatra zibethicus*). The zone of persistent white-tailed deer occupancy is more commonly associated with the southerly portions of the Boreal Plain that offer a more diverse land use and less severe climatic extremes. Brainworm parasite (*Parelaphostrongylus tenuis*) associated with white-tailed

deer, has been documented south of the study area on the west side of the province with low prevalence (Wasel et al. 2003).

2.4 Methods

2.4.1 Radio Collaring, Telemetry and Evaluation Range Delineation

The evaluation of the effect of range disturbances on populations of woodland caribou required the delineation and mapping of discrete ranges and the associated disturbance regime for each evaluation range. The best available information regarding caribou population distributions across Manitoba had been compiled by the Manitoba Boreal Woodland Caribou Management Committee in support of their 2005 Recovery Strategy for Boreal Woodland Caribou in Manitoba. This initial effort relied on historical observation data collected in the Reed Lake area between 1969 and 1978, and subsequent VHF telemetry observations covering the years 1995 to 2002 and GPS collar data from 1996 to 2006 for the Wabowden Range.

In this study, a refinement of the 2005 provincial ranges and range boundaries was undertaken based on GPS telemetry provided by the Manitoba Government gathered from 2010 - 2012 deployed on adult female caribou in The Bog, Wabowden, Wheadon, and Wimapedi-Wapisu evaluation ranges as well as within a control area in eastern Manitoba (Charron Lake Range). Capture and collaring was undertaken in support of the Bipole III Transmission Line Project under the authority of Manitoba Conservation. Animals were captured in January to March each year using contracted helicopter net gun capture companies. Capture and handling involved no chemical immobilization as animals were netted, secured with leg hobbles, blindfolded and then collared as per handling protocols as set forth by Manitoba Conservation (#WI-266-2009/10). Collaring locations were

based on historical distribution information and data from ongoing distribution surveys and additional reconnaissance flights. A minimum sample of 20 collared adult females in each evaluation range was maintained throughout this study based on McLoughlin et al. (2003). Blood samples were also collected from all captured females for serum progesterone analysis to determine pregnancy rates (Reproductive Physiology Laboratory, Toronto Zoo, Ontario 2011).

The GPS collars were programmed to acquire location fixes every 3 hours and data were available throughout the study period through Iridium internet satellite services. Caribou locations were downloaded approximately every two weeks and imported into Arc Info (ESRI) GIS for mapping and determining collar and animal status. Annual location data were pooled to delineate local population range boundaries using Minimum Convex Polygon (MCP) analysis as described by Burt (1943). Collars were also equipped with VHF transmitters to facilitate recruitment surveys and adult mortality site investigations when feasible.

2.4.2 Range Disturbance

The National science review update for boreal populations of woodland caribou (Environment Canada 2011) defines critical habitat as all habitat contained within the entire range of a local population, and that any activity (disturbance) that degrades any component of that habitat, either permanently or temporarily contributes to loss of critical habitat. Disturbance estimates were based on the area of the home range of a population exclusive of water bodies. Disturbance and land age metrics were facilitated through the use of an enhanced version of the Canadian Forest Service's project, Earth Observation for Sustainable Development of Forests (EOSD) and Landcover Classification of Canada

(LLC) (Wulder and Nelson 2003). The LCC was updated to include historical anthropogenic and natural disturbance areas, thereby facilitating the removal of disturbed forest areas > 40 years age from the disturbance database, as forests are not considered as “disturbed” when this threshold age is reached (Environment Canada 2011). Where buffers from disturbances overlapped one another, the buffers were combined and dissolved to reflect a single contiguous disturbance buffer. Disturbance calculations included all anthropogenic disturbance polygons, linear and fixed feature sources such as industrial forestry cutovers <40 years, roads and trails, transmission lines, mine sites, drill holes and natural disturbances (wildfires) <40 years of age. All anthropogenic disturbances include a 500 metre buffer to capture the effective zone of caribou sensitivity while natural disturbances were not buffered; the total area of disturbance was calculated as the sum of natural plus anthropogenic disturbance areas (Environment Canada 2011).

2.4.3 Fuzzy Classification

Delineation of the demographic structure of caribou populations was undertaken to provide an enhanced understanding of the spatial arrangement of disturbance within the assigned assessment ranges to provide further detail and insight into disturbance patterns. Fuzzy c-means analysis was applied using FuzMe version 3.5c (Minasny and McBratney 2002) based on Schaefer et al. (2001), Schaefer and Wilson (2002), Nagy et al. (2011), and Shuter and Rodgers (2012). Median winter (December 15 – March 15) and post summer (June 1- August 31) locations were calculated for each adult female across the study area. Fuzziness performance F index was used to assign individuals to appropriate population classes. Ranges assessed included “The Bog” as one discrete unit as it is

separated by a considerable distance from the second unit comprised of the Wimapedi-Wapisu, and Wabowden evaluation ranges. Fuzzy membership coefficients were calculated for membership groupings to determine best fit with the coefficients of 1 conveying the highest fuzzy membership. Animal IDs were then assigned to their appropriate fuzzy membership group and kernel density mapping was applied to each sub-population and the utilization distribution (UD) for each sub-population mapped. Disturbance metrics were then calculated using the same disturbance measurements described above within each of the sub-populations to illustrate disturbance levels within each sub-population overlap and non-overlap areas for each 10% Utilization Distribution contour.

2.4.4 Calf Recruitment

Summer and early fall cow/calf surveys were conducted to provide an estimate of recruitment and survival rates for neonates during the critical period of expected calf mortality. Several studies have illustrated high calf mortality during the first weeks of life (Stuart-Smith et al. 1997, McLoughlin et al. 2003, Pinard et al. 2012, Bastille-Rousseau 2015, Mahoney et al. 2016), after which calf mobility and survival improves markedly (DeMars 2015). Pregnancy rates were determined from serum progesterone analyses to provide an estimate of the proportion of adult females that were pregnant in the January to March period coinciding with animal capture for collaring. Based on patterns of movement data of cows in May and June, precise calving dates were determined using step analysis procedures similar to DeMars (2015). However, for the purpose of this study, aerial recruitment surveys were conducted monthly commencing July 1 through to early September thereby providing

estimates of survival rates prior to the pre-rut grouping of animals. The July 1 start date respected low-level flight restrictions over calving areas from April 15 – July 1 as enacted by Manitoba Conservation, to minimize potential disturbance to parturient cows and cows with calves. The survey procedure involved mapping of the most recent GPS locations of collared females, thereby refining the search area using standard VHF telemetry techniques to visually locate females. On subsequent flights approximately 10% of cows without calves from previous surveys were resampled to verify lost calves.

Recruitment rates were calculated for each evaluation range as the number of radio-collared female caribou with calves in September divided by the number of adult females with active collars at that time, expressed as calves/100 cows. Standard deviations for the overall parturition rate and for recruitment rates of each population were calculated from the binomial distribution (Sokal and Rohlf 1981).

2.4.5 Adult Female Mortality

During the course of the study, bi-weekly acquisition of GPS collar data were downloaded and inspected for possible mortality clusters. Cluster events of multiple location fixes suggesting no movement, were all subject to field investigations in an effort to verify a cause of death, the timing of which was governed by a host of factors including the cost and availability of helicopters in remote locales, but ranged from two weeks to several months.

Annual survival rates were calculated using a biological year commencing 17 - May, the average calving date as determined using step function analyses (DeMars 2015) and terminating on 17-May the following year (e.g., May 17, 2010 to May 16,

2011). The number of live caribou exposure days for each monitored adult female was calculated for each year as were total adult female mortalities for each evaluation range. In the case of collars that failed with no associated mortality cluster the live exposure days included the date of the last movement data. Survival rates and 95% confidence intervals were calculated in MICROMORT (Heisey and Fuller 1985) based on Mayfield (1975). Data were pooled to provide a two-year survival analysis.

2.4.6 Lambda

For each caribou population in this study, λ was calculated using the female survival rate and variance estimated from MICROMORT and observed calf-cow ratio from field reconnaissance based on Caughley (1977). To obtain confidence limits on λ , a randomization algorithm was developed in CRAN-R (R Core Team 2016). This function calculated a random expectation for both the survival and calf-cow ratio and variance derived from MICROMORT in the λ formula. The observed female survival and variance were used as arguments for the CRAN-R function `rnorm` and `rbinom` in the `stats` package to generate a random survival value from observed number of cows and observed calf-cow ratio for each population as arguments. For each population randomization was repeated a minimum of 10,000 times to calculate a mean and standard deviation. Confidence intervals were constructed for each population for alpha ($\alpha = 0.05$) using the standard deviation from the random simulations.

2.4.7 Disturbance and Lambda

For each range, the total disturbance was calculated for all anthropogenic sources (e.g. linear features buffered by 500 m, forest harvest and mining) and fire. The choice of a 500 m buffer on each side of the linear feature follows the criteria set forth by

Environment Canada as the distance of effect determined for linear feature disturbance assessment (Environment Canada 2012). Disturbance was then expressed as a percentage of the total area of each evaluation range. To determine whether or not there was a relationship between λ and disturbance, the observed λ values for each evaluation range was regressed against disturbance in CRAN-R. Although the Caribou Recovery Strategy considers thresholds based on total disturbance, the influences of each source of disturbance (natural and anthropogenic) as well as the total disturbance was examined using standard regression statistics.

Discrete examination of disturbance patterns was undertaken to assess levels of anthropogenic and natural disturbance within each utilization distribution (UD) isopleth for fuzzy range delineations. Total area for each disturbance source was converted to percentages using bin classes defined by pairs of isopleths from the kernel described previously (e.g. disturbed and undisturbed area within the 10th to 20th percentile of the kernel volume, 20th to 30th and so on expressed as percentage). These percentages were further divided into two groups: non-overlapping (area within an isopleth that did not overlap with another fuzzy range) and overlapping (the area was shared among ranges).

To summarize trends in total disturbance across each range, percentage of disturbance was plotted against isopleth and standard regression was performed. This was then repeated for only those isopleths (and portions thereof) that overlapped an adjacent range to examine the pattern of disturbance in areas coincident among ranges. To examine the pattern of disturbance source and types with respect to location within the ranges, a PCA was performed treating each isopleth (reshaped by summarizing the mean for all ranges by isopleth and grouping by non-overlapping/overlapping) as samples and

source/type as variables. A biplot summarizing the first two axes was constructed. To examine whether disturbance in overlapping portions of ranges was greater than non-overlapping areas, a multiple discriminant analysis (MDA) was performed on the data used in the PCA analysis (see Legendre and Legendre 2012, for a complete description of these methods). The discriminant scores for the groups on the canonical variate axis were graphed using a box-plot.

2.5 Results

2.5.1 Delineation of Evaluation Ranges

Telemetry data collected in the evaluation ranges provided an update to the ranges originally identified by the Manitoba Boreal Woodland Caribou Management Committee (2006). The updated evaluation ranges included The Bog (5,583 km²), Wheadon (6,299 km²), Wabowden (5,589 km²), and Wimapedi-Wapisu (10,009 km²). The Charron Lake Control Area is approximately 21,000 km² (Figure 2.2). Fuzzy ranges were defined based on the coefficient memberships which were closest to 1 for The Bog (Bog 1 and Bog 2) and the Wabowden, Wheadon, Wimapedi-Wapisu were combined in the analysis and sub-populations were identified as WWW-A, WWW-B and WWW-C (Table 2.1). Kernel density estimates and areas of overlap between fuzzy populations were mapped to illustrate membership among The Bog evaluation range and the WWW assignment group as identified through the fuzzy cluster analysis (Figure 2.3).

2.5.2 Range Disturbance

No evaluation range exceeded the 65% critical disturbance threshold identified by Environment Canada (2012). The nature and extent of disturbance for all the evaluation ranges, including the Charron Lake control area, is summarized in Table 2.2. Figure 2.4

provides an example of mapped extent of natural wildfire, anthropogenic disturbances and linear features within an evaluation range. Total disturbance including anthropogenic and natural sources accounted for a low of 14% (820 km²) of the area of The Bog to a range of 26% to 24% for the Wabowden, Wheadon, Wimapedi-Wapisu ranges and the Charron Lake control area (Table 2.2). Burns <40 years age are the dominant landscape disturbance feature affecting 20-40% of most ranges with the exception of The Bog (3%) and Wabowden (17%) ranges. Linear features are the primary source of anthropogenic disturbance largely restricted to The Bog and Wabowden ranges, the extent of which does not exceed 7% in any single range.

Examination of disturbance within the Fuzzy population ranges using a multiple line plot indicates disturbance is not uniform (Figure 2.5). For most ranges disturbance is lowest in the core use area (isopleth 0-20) and increases towards the edge of the range. The Bog ranges are notable in that percentage disturbance remains relatively similar throughout. The WWVA fuzzy range has the largest change in disturbance from the core to the edge of the range.

Patterns of disturbance by type is compared using PCA with isopleths grouped into overlapping and non-overlapping areas to provide a confidence ellipse (Figure 2.6 A) Note these ellipses are based on statistics generated from the first two axes scores and group was not a factor used in the PCA calculation itself and are for the purpose of display and interpretation. The component scores on the PCA first axis (42% of overall variance) are associated primarily with areas identified as overlapping vs non-overlapping. Isopleths that were shared between or among ranges generally have larger component scores. Most disturbance variables are positively associated with areas found

as shared between ranges. With the exception of railways all disturbance types trend positively on the first axis with natural disturbance having the strongest trend. Anthropogenic sources of disturbance trend positively (drill holes and mine and transmission lines) or negatively (roads and harvest) on the second axis, except for railways. An LDA performed on these data was consistent with the trends detected on first axis of the PCA in that percentage disturbance between overlapping and non-overlapping was significantly different and consistently higher in the former (Figure 2.6 B).

2.5.3 Calf Recruitment

The results of recruitment surveys demonstrated a high incidence of calf mortality within all ranges progressing from mid-May to September (Table 2.3). Fall recruitment rates varied from 0.00 to 0.29 with an overall average of 0.10 (Table 2.4).

2.5.4 Adult Female Survival

The estimated survival rates for each evaluation range are presented in Table 2.5. In 2010, survival rates range from 1.0 (Charron Lake) to 0.88 (Wabowden). Survival rates range from 0.84 (Charron Lake) to 0.94 (Wabowden) in 2011. The data indicated a consistent decline in the adult survival across all ranges excepting Wheadon between 2010 and 2011. The data suggest a consistent decline in the adult survival across all ranges except Wheadon between 2010 and 2011.

2.5.5 Disturbance and Lambda

The results indicate variability in population growth rates both among years and among evaluation ranges (Table 2.6). For all populations except The Bog (2010) and Wimapedi-Wapisu (2010) λ was less than the replacement value 1, however the

confidence intervals for λ determined through simulation all overlapped 1. Evidence that the populations were in decline over the years studied is thus weak, but the consistently low values are suggestive. The relationship between disturbance and λ rates are presented in Table 2.7 and Figure 2.7. There were no significant relationships found for any of the regressions of λ against percentage landscape disturbance. Total Disturbance and Natural Disturbance were non-significant with overall P-values of 0.16 and 0.35 respectively and had a positive slope (Figure 2.7 A, C). Anthropogenic disturbance was also non-significant, but results may be considered suggestive with a P= 0.07 (Figure 2.7 B).

2.6 Discussion

Within this region of Manitoba, combined natural and anthropogenic disturbance rates were not correlated with overall adult female survival, calf recruitment or population growth. Although the λ is below 1 for all populations, the SEs all overlap 1, suggesting that populations growth may be slightly negative during the period of this study. Despite the fact that adult survival was less than 85% in 6 of 7 tracked populations, a biologically significant threshold, the sample size was too small to detect statistical significance for these observations. The slope for total disturbance was positive which is counter-intuitive but with a p-value of over 3 likely anomalous. Lack of any relationship between disturbance and λ is contrary to what has been found in several studies reported in Alberta by Hervieux et al. (2013). However, the total disturbance in all ranges in this study rarely exceeds 25% of the land area, whereas disturbance levels for comparable studies often exceeded more than 50% of the range (Hervieux et al. 2013). When specific sources of disturbance were considered (anthropogenic vs. natural), results were still not statistically significant (P>0.05). The relationship was positive for natural disturbance (i.e. more

disturbance increases lambda) which is counterintuitive but likely also anomalous given the large p-value.

While calf recruitment can be variable from year to year and also between geographic regions and landscapes with different vegetative composition (McCarthy et al. 2011), the rates observed in this study were comparatively lower relative to other boreal caribou populations studied (Rettie and Messier 1998, McLoughlin et al. 2003). The low calf recruitment can also not be explained by pregnancy rate as determined through the serum progesterone analysis, which was 87%, and consistent with other boreal shield populations in Saskatchewan (86.2% in 2012 and 93.3% in 2015) (McLoughlin et al. 2016). The adult female survival rates observed in 2010 were also consistent with other boreal populations (Hervieux et al. 2013, McLoughlin et al. 2016).

Lambda was consistently low for all of the populations in this study, largely because of high observed calf mortality (up to 90%). Although calf surveys were not conducted until July, with the exception of 2010, evidence of early calf mortality was evident which is consistent with other studies assessing early calf mortality (Dussault et al. 2012, Pinard et al. 2012, Lewis and Mahoney 2014, DeMars 2015, Mahoney et al. 2016, Leblond et al. 2016, Bastille-Rousseau et al. 2016). The low recruitment rates in the evaluation ranges studied (6% -29%) cannot be explained by either anthropogenic or natural disturbance.

Utilization of fuzzy classification for final population assignment of captured animals provided an improved delineation of range boundaries and a refined estimate of range overlap. The higher percentage of disturbance in areas of fuzzy range overlap (20-50%), represents a trend in range fragmentation for the sub-populations studied.

Similarly, disturbance within the core of caribou ranges, could disperse animals to less preferred habitats and more disturbed habitat at the edge of a range. This too could contribute to higher than expected rates of predation mortality especially if disturbance increases access and attracts predators to calving grounds (DeMars et al. 2011).

The role of disturbance in the literature tends to focus on negative impacts, often on landscapes that are highly disturbed. This study demonstrated a weak trend in a reduction of lambda for those ranges where anthropogenic disturbance was greater. Given that the total area of natural disturbance well exceeded other types of disturbance, it is important to note that recent fire mapping in the Province is done using remotely sensed imagery. Kansas et al. (2016) provided evidence that interpretations of fire disturbance using LANDSAT data tended to overestimate areas of fire disturbance by approximately 32% given the extensive distribution of unburned residual areas within gross fire area boundaries, thereby reducing the cumulative impact of this type of disturbance on caribou populations in northern Saskatchewan. It is possible in this study that disturbance estimates might also be biased and higher than the true values.

Refined delineation of discrete subranges is considered to have potential benefits in resource planning, mitigation and effects monitoring (Shuter and Rodgers 2012). Through the examination of disturbance regimes of discrete populations and assessing the associated demographics of boreal caribou range, it may be possible to focus land management and mitigation options to increase the probability of boreal caribou persistence on managed landscapes. For example, a concentration of disturbance on the fringe of local population ranges may result in a higher incidence of core area avoidance as a result of anthropogenic disturbance and fragmentation of habitat (Polfus et al. 2011).

The ability to identify more explicitly potential impacts of disturbance across a gradient of animal use within its range can contribute to the identification of potential land-use planning and mitigation opportunities in boreal caribou range (Polfus et al. 2011).

All disturbance regimes within local boreal caribou ranges (natural and anthropogenic) contribute to a probability of persistence indicator, with an explicit understanding that anthropogenic disturbances present much greater threats than natural disturbance regimes (Polfus et al. 2011). Resource development within boreal caribou range requires the protection and management of critical habitat. Delineation of discrete ranges to establish baselines against which the impacts of anthropogenic and natural disturbance can be adequately measured against population metrics including adult survival and recruitment are required (Environment Canada 2012).

Rates of immigration and emigration between adjacent and overlapping local populations and the disturbance within these overlaps may occur at high levels while overall disturbance regimes within the range remains well within the thresholds outlined by Environment Canada (2012). However the effect of localized variation in the concentration of disturbance within ranges on population metrics are difficult to isolate statistically. The increase in disturbance observed towards the outer isopleths of overlapping fuzzy ranges, suggests a higher degree of functional fragmentation. Although the overall disturbance ratio may be well below the thresholds established by Environment Canada (2011). Similarly, higher proportional rates of disturbance within core areas of home ranges, may assist in assessing fragmentation effects, and the degree to which local populations are being affected. A more complete appreciation of these factors may also provide an opportunity to refine both mitigation and effects monitoring

programs such as the construction of linear developments and/or disturbance associated with wildfires and industrial forest management operations.

The failure to identify effective mitigation of neonate mortality limits the delivery of effective management in the conservation of caribou. Furthermore, constraining industry based on other unsubstantiated potential threats, may not be an optimal allocation of resources given the combined concerns of uncertainty respecting efficacy of treatments, and extended time frames for assessment of effects.

Due to the status of boreal caribou in Manitoba, resource developers are required to assess the long-term effects of their activities as well as considering the cumulative effects of other development on local populations. Assessing sustainability and the probability of persistence of local boreal caribou populations can be significantly enhanced through the collaring and tracking of an adequate sample of individuals in a local population. The assessment of disturbance levels as they relate to rates of adult female mortality and calf survival based on more accurate range delineations provides opportunities for resource managers to assess anthropogenic disturbance at a finer scale and promote an understanding of the spatial characteristics of current and proposed resource development relative to core use areas and in overlapping populations. Understanding the context of disturbance in relation to survival and recruitment in Manitoba can assist resource managers and resource developers in the process of boreal woodland caribou recovery.

The examination of disturbance regimes for discrete populations and subpopulations, and improving the assessment of associated demographics of boreal caribou occupying these ranges, can improve the efficacy of land-management decisions

and mitigation options designed to increase the probability of boreal caribou persistence on landscapes where industrial development is occurring.

2.7 Conclusion

When examining Lambda (λ) within these evaluation ranges, adult female survival rates during the study period were within the range of expected levels found in previous studies in Canada (McLoughlin et al. 2003). Conversely, spring to fall recruitment surveys found that calf survival was low, with high calf mortality within the first weeks of life. This finding is consistent with reported literature (Blake 2006, Dussault et al. 2012, Bastille-Rousseau et al. 2015, DeMars 2015) and low recruitment rates were the main contributor to low λ in the evaluation ranges studied. No significant relationship was detected between disturbance and Lambda and disturbance was low in the ranges studied. Anthropogenic disturbance ranged from 1% to 11%, and natural disturbance between 3% and 24%. No range studied exceeded the 35% total disturbance necessary to suggest a demographic response and observed disturbance was typically well below the Environment Canada threshold. That said, a weak relationship was found between anthropogenic disturbance and lambda.

Assessment of range disturbance at a finer scale using fuzzy analysis to define range use at a sub-population level, found higher rates of disturbance within areas of overlap, with anthropogenic features being the most dominating disturbance feature. The sub-population ranges typically had more disturbances at the periphery than in the core and disturbance was not uniform within ranges. The spatial pattern of disturbance within ranges may be critical and more research needs to be done to determine whether disturbance in overlapping portions of the ranges affect sub-population dynamics. Given

that total disturbance as a single factor does not explain low lambda values, management of these populations should consider location of disturbance, as well as the influence of predators, especially when planning new large-scale projects.

2.8 References

- Armstrong TR, Racey GD, Bookey N. 2000. Landscape-level considerations in the management of forest-dwelling woodland (*Rangifer tarandus caribou*) in northwestern Ontario. *Rangifer*. 12: 187-189.
- Ballard WB. 1994. Effects of black bear predation on caribou - a review. *Alces*. 30: 25-35.
- Bastille-Rousseau G. 2015. Demography and habitat selection of Newfoundland caribou [dissertation]. Trent University. Peterborough, Ontario, Canada.
- Bastille-Rousseau G, Potts JR, Schaefer JA, Lewis MA, Ellington EH, Rayl ND, Mahoney SP, Murray DL. 2015. Unveiling trade-offs in resource selection of migratory caribou using a mechanistic movement model of availability. *Ecography*. 38(10): 1049-1059. doi: 10.1111/Ecog.01305
- Bastille-Rousseau G, Rayl ND, Ellington EH, Schaefer JA, Michael JL, Peers, Mumma MA, Mahoney SP, Murray DL. 2016. Temporal variation in habitat use, co-occurrence, and risk among generalist predators and a shared prey. *Can J Zool*. 94(3): 191-198. dx.doi.org/10.1139/cjz-2015-0127
- Bergerud AT. 1974. Decline of caribou in North America following settlement. *J Wildl Manage*. 38(4): 757-770. Available from: <http://www.jstor.org/stable/3800042>
- Bergerud AT, Mercer WE. 1989. Caribou introductions in eastern North America. *Wildlife Society Bulletin (1973-2006)*. 17(2): 111-120.
- Bergerud AT, Ferguson R, Butler HE. 1990. Spring migration and dispersion of woodland caribou at calving. *Anim Behav*. 39(2): 360-368.
- Blake J. 2006. Coyotes in insular Newfoundland: current knowledge and management of the islands newest mammalian predator. Department of Environment and Conservation Wildlife Division, Government of Newfoundland and Labrador, Canada. 11. Available from: www.env.gov.nl.ca/env/publications/wildlife/51f40a0ed01.pdf
- Boutin S, Boyce MS, Hebblewhite M. 2012. Why are caribou declining in the oil sands? Peer-reviewed letter. *Wildlife Biology Faculty Publications*. The Ecological Society of America. Paper 22.
- Brown WK, Rettie WJ, Wynes B, Morton K. 2000. Wetland habitat selection by woodland caribou as characterized using the Alberta wetland inventory. *Rangifer*. 12: 153-157. Available from: <http://www.cabdirect.org/abstracts/20013018835.html>
- Burt WH. 1943. Territoriality and home range concepts as applied to mammals. *J Mammal*. 24(3): 346-352.
- Caughley JG. 1977. Analysis of vertebrate populations. Wiley Interscience, London.

- Clarke DJ, Pearce KA, White JG. 2006. Powerline corridors: degraded ecosystems or wildlife havens? *Wildl Res.* 33(8): 615-626. Available from: <http://www.publish.csiro.au/?paper=WR05085>
- Crichton V. 2005. Manitoba's conservation and recovery strategy for boreal woodland caribou (*Rangifer tarandus caribou*). Manitoba Conservation. 22 pp.
- Cumming HG, Beange DB. 1987. Dispersion and movements of woodland caribou near Lake Nipigon, Ontario. *J Wildl Manage.* 51: 69-79.
- Cumming HG. 1992. Woodland caribou: facts for forest managers. *The Forestry Chronicle.* 68(4): 481-491.
- DeMars C, Thiessen C, Boutin S. 2011. Assessing spatial factors affecting predation risk to boreal caribou calves: implications for management. Annual Report. University of Alberta and Ministry of Natural Resource Operations de la Colombie-Britannique. 1-35 p. Available from: <http://scek.ca/sites/default/files/documents/RA-2011-01-Assessing-Spatial-Factors-Affecting-Predation-Risk-Boreal-Caribou-Calves-Dec-1-11.pdf>
- DeMars CA. 2015. Calving behavior of boreal caribou in a multi-predator, multi-use landscape [dissertation]. Department of Biological Sciences, University of Alberta. 215 p.
- Dussault C, Pinard V, Ouellet JP, Courtois R, Fortin D. 2012. Avoidance of roads and selection for recent cutovers by threatened caribou: fitness-rewarding or maladaptive behaviour?. *Proc Roy Soc B.* 279: 4481-4488.
- Dyer SJ, Neill JPO, Wasel SM, Boutin S. 2001. Avoidance of industrial development by woodland caribou. *J Wildl Manage.* 65(3): 531-542.
- Dyer SJ, O'Neill JP, Wasel SM, Boutin S. 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. *Can J Zool.* 80(5): 839-845. Available from: <https://doi.org/10.1139/Z02-060>
- Environment Canada. 2011. Scientific assessment to inform the identification of critical habitat for woodland caribou (*Rangifer tarandus caribou*), Boreal Population, in Canada: 2011 update. Ottawa, Ontario, Canada. 102 pp. plus appendices.
- Environment Canada. 2012. Recovery strategy for the woodland caribou (*Rangifer tarandus caribou*), boreal population, in Canada. Update. <https://doi.org/10.2307/3796292>
- Heisey DM, Fuller TK. 1985. Evaluation of survival and cause specific mortality rates using telemetry data. *J Wildl Manage.* 49: 668- 674.
- Hervieux D, Hebblewhite M, DeCesare NJ, Russell M, Smith K, Robertson S, Boutin S. 2013. Widespread declines in woodland caribou (*Rangifer tarandus caribou*) continue in Alberta. *Can J Zool.* 91(12): 872-882. doi:10.1139/cjz-2013-0123

- Hillis TL, Mallory FF, Dalton WJ, Smiegielski AJ. 1998. Preliminary analysis of habitat utilization by woodland caribou in northwestern Ontario using satellite telemetry. *Rangifer*. 18(5): 195-202.
- Holt RD. 1977. Predation, apparent competition, and the structure of prey communities. *Theor Popul Biol*. 12(2): 197-229.
- James ARC, Stuart-Smith AK. 2000. Distribution of caribou and wolves in relation to linear corridors. *J Wildl Manage*. 64(1): 154-159.
- James ARC, Boutin S, Hebert DM, Rippin AB. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. *J Wildl Manage*. 68(4): 799-809. Available from: [http://www.bioone.org/doi/abs/10.2193/0022-541X\(2004\)068\[0799:SSOCFM\]2.0.CO;2](http://www.bioone.org/doi/abs/10.2193/0022-541X(2004)068[0799:SSOCFM]2.0.CO;2)
- Kansas J, Vargas J, Skatter HG, Balicki B, McCullum K. 2016. Using landsat imagery to backcast fire and post-fire residuals in the Boreal Shield of Saskatchewan: implications for woodland caribou management. *Int J Wildland Fire*. 25: 597-607.
- Lander CA. 2006. Distribution and movements of woodland caribou on disturbed landscapes in west-central Manitoba: implications for forestry [dissertation]. University of Manitoba. Winnipeg, Manitoba, Canada.
- Latham ADM. 2009. Wolf ecology and caribou-primary prey-wolf spatial relationships in low productivity peatland complexes in northeastern Alberta [dissertation]. University of Alberta. Edmonton, Alberta, Canada.
- Leblond M, Dussault C, Ouellet JP, St-Laurent MH. 2016. Caribou avoiding wolves face increased predation by bears – caught between Scylla and Charybdis. *J Appl Ecol*. 53(4): 1078-1087.
- Legendre P, Legendre L. 2012. *Numerical Ecology*. 3rd Edition. Amsterdam, The Netherlands, Amsterdam. Elsevier B. V. 990 pp.
- Lewis KP, Mahoney SP. 2014. Caribou survival, fate, and cause of mortality in Newfoundland: a summary and analysis of the patterns and causes of caribou survival and mortality in Newfoundland during a period of rapid population decline (2003-2012). Technical Bulletin No. 009, Sustainable Development and Strategic Science. Government of Newfoundland and Labrador. St. John's, NL.
- Mahoney SP, Lewis KP, Weir JN, Morrison SF, Luther GJ, Schaefer JA, Pouliot D, Latifovic R. 2016. Woodland caribou calf mortality in Newfoundland: insights into the role of climate, predation and population density over three decades of study. *Popul Ecol*. 58(1): 91-103. Available from: <https://doi.org/10.1007/s10144-015-0525-y>
- Malasiuk JA. 1999. Aboriginal land use patterns in the boreal forest of north-central Manitoba: applications for archaeology [master's thesis]. University of Manitoba. Winnipeg, Manitoba, Canada.

- Manitoba Boreal Woodland Caribou Management Committee. 2006. Conservation and Recovery Strategy for Boreal Woodland Caribou (*Rangifer tarandus caribou*). Government of Manitoba, Conservation Branch.
- Manitoba Boreal Woodland Caribou Management Committee. 2015. Conserving a Boreal Icon, Manitoba's Boreal Woodland Caribou Recovery Strategy. Manitoba Conservation and Water Stewardship. Winnipeg, Manitoba. 30 p.
- Mayfield HF. 1975. Suggestions for calculating nest success. *Wilson Bulletin*. 87: 456–466.
- McCarthy SC, Weladji RB, Doucet C, Saunders P. 2011. Woodland caribou calf recruitment in relation to calving/post-calving landscape composition. *Rangifer*. 31(1): 35-47.
- McLoughlin PD, Dzus EH, Wynes B, Boutin S. 2003. Declines in population of woodland caribou. *J Wildl Manage*. 67(4): 755-761. Available from: <http://www.jstor.org/stable/3802682>
- McLoughlin PD, Stewart K, Superbie C, Perry T, Tomchuk T, Greuel R, Singh K, Truchon-Savard A, Henkelman J, Johnstone JF. 2016. Population dynamics and critical habitat of woodland caribou in the Saskatchewan Boreal Shield. Interim Project Report 2013–2016. Department of Biology. University of Saskatchewan. Saskatoon, Saskatchewan, Canada. 162 p.
- MESEA (Manitoba Endangered Species and Ecosystem Act). 2015. Government of Manitoba.
- Metsaranta JM, Mallory FF. 2007. Ecology and habitat selection of a woodland caribou population in west-central Manitoba, Canada. *Northeastern Naturalist*. 14(4): 571-588. Available from: [https://doi.org/10.1656/1092-6194\(2007\)14\[571:EAHSA\]2.0.CO;2](https://doi.org/10.1656/1092-6194(2007)14[571:EAHSA]2.0.CO;2)
- Minasny B, McBratney AB. 2002. FuzME version 3.0. Australian Centre for Precision Agriculture. University of Sydney. Sydney, Australia.
- Monthey RW. 1984. Effects of timber harvesting on ungulates in northern Maine. *J Wildl Manage*. 48(1): 279-285. Available from: <http://www.jstor.org/stable/3808489>
- Nagy JA, Johnson DL, Larter NC, Campbell MW, Derocher AE, Kelly A, Dumond M, Allaire, Croft B. 2011. Subpopulation structure of caribou (*Rangifer tarandus* L.) in arctic and subarctic Canada. *Ecol Appl*. 21(6): 2334-2348.
- Pearce J, Eccles G. 2004. Characterizing forest-dwelling woodland caribou distribution in Ontario, Canada. Canadian Forest Service. Sault Ste Marie, Ontario.
- Peek JM, Urich DL, Mackie RJ. 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. *Wildlife Monographs*. 48: 3-65.
- Pinard V, Dussault C, Ouellet JP, Fortin D, Courtois R. 2012. Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. *J Wildl Manage*. 76(1): 189-199. Available from: <https://doi.org/10.1002/jwmg.217>

- Polfus JL, Hebblewhite M, Heinemeyer K. 2011. Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain woodland caribou. *Biol Conserv.* 144(11): 2637-2646. Available from: <http://doi.org/10.1016/j.biocon.2011.07.023>
- R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: <https://www.R-project.org/>
- Rettie WJ, Messier F. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. *Can J Zool.* 76(2): 251-259. Available from: <https://doi.org/10.1139/cjz-76-2-251>
- Rettie WJ. 1998. The ecology of woodland caribou in central Saskatchewan [Ph.D. thesis]. University of Saskatchewan. Saskatoon, Saskatchewan.
- Rettie WJ, Messier F. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography.* 23(4): 466-478. Available from: <https://doi.org/10.1034/j.1600-0587.2000.230409.x>
- SARA (Species At Risk Act). 2002. Bill C-5, An act respecting the protection of wildlife species at risk in Canada. Available from: <http://laws.justice.gc.ca/PDF/Statute/S/S-15.3.pdf>
- Schaefer JA, Veitch AM, Harrington FH, Brown WK, Theberge JB, Luttich SN. 2001. Fuzzy structure and spatial dynamics of a declining woodland caribou population. *Oecologia* 126(4): 507-514.
- Schaefer JA, Wilson CC. 2002. The fuzzy structure of populations. *Can J Zool.* 80(12): 2235-2241. Available from: <https://doi.org/10.1139/Z02-184>
- Schaefer JA. 2003. Long-term range recession and the persistence of caribou in the Taiga. *Conserv Biol.* 17(5): 1435-1439. Available from: <https://doi.org/10.1046/j.1523-1739.2003.02288.x>
- Schindler DW. 2006. Home range and core area determination, habitat use and sensory effects of all weather access on boreal woodland caribou (*Rangifer tarandus caribou*) in eastern Manitoba [master's thesis]. University of Manitoba. Winnipeg, Manitoba, Canada. 165 p.
- Seip DR. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Can J Zool.* 70(8): 1494-1503. Available from: <https://doi.org/10.1139/z92-206>
- Shoemith MW, Storey DR. 1977. Movements and associated behaviour of woodland caribou in central Manitoba. Manitoba Department of Renewable Resources and Transportation Services. Research Manuscript No. 77-15. 74 p.
- Shuter JL, Rodgers AR. 2012. Delineating demographic units of woodland caribou (*Rangifer tarandus caribou*) in Ontario: cautions and insights. *Rangifer.* 32(2): 159-181.

- Smith RE, Veldhuis H, Mills GF, Eilers RG, Fraser WR, Lelyk GW. 1998. Terrestrial ecozones, ecoregions and ecodistricts of Manitoba: An ecological stratification of Manitoba's natural landscapes. No. Technical Bulletin 9E. Research Branch: Agriculture and Agri-Food Canada. Brandon Research Centre. Brandon, Manitoba, Canada.
- Sokal RR, Rohlf FJ. 1981. Biometry: the principles and practice of statistics in biological research, 2nd edition. Freeman: San Francisco. 859 p.
- Stuart-Smith AK, Bradshaw CJA, Boutin S, Hebert DM, Rippin AB. 1997. Woodland caribou relative to landscape patterns in northeastern Alberta. *J Wildl Manage.* 61(3): 622-633. Available from: <http://www.jstor.org/stable/3802170>
- Vistnes I, Nellemann C. 2007. Impacts of human activity on reindeer and caribou: The matter. *Rangifer.* 27(3): 47-56. doi.org/10.1007/s00300-007-0377-9
- Vors LS, Schaefer JA, Pond BA, Rodgers AR, Patterson BR. 2007. Woodland caribou extirpation and anthropogenic landscape disturbance in Ontario. *J Wildl Manage.* 71(4): 1249-1256. Available from: <https://doi.org/10.2193/2006-263>
- Wasel SM, Samuel WM, Crichton V. 2003. Distribution and ecology of meningeal worm, *Parelaphostrongylus tenuis* (*Nematoda*), in northcentral North America. *J Wildl Dis.* 39: 338-346.
- Wittmer HU, Sinclair ARE, McLellan BN. 2005b. The role of predation in the decline and extirpation of woodland caribou. *Oecologia.* 144(2): 257-267. Available from: <https://doi.org/10.1007/s00442-005-0055-y>
- Wittmer HU, McLellan BN, Serrouya R, Apps CD. 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. *J Anim Ecol.* 76(3): 568-579. Available from: <https://doi.org/10.1111/j.1365-2656.2007.01220.x>
- Wulder M, Nelson T. 2003. EOSD land cover classification legend report, version 2. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre. Victoria, British Columbia, Canada.
- Zwolak R. 2009. A meta-analysis of the effects of wildfire, clearcutting, and partial harvest on the abundance of North American small mammals. *For Ecol Manage.* 258(5): 539-545. Available from: <https://doi.org/10.1016/j.foreco.2009.05.033>

2.9 Tables

Table 2.1 Confusion matrix of fuzzy cross classifications indicating fuzzy membership

MaxCls	Bog 1	Bog 2	WWW A	WWW B	WWW C
Bog 1	0.9867	0.0133	0.0000	0.0000	0.0000
Bog 2	0.0004	0.9976	0.0000	0.0000	0.0020
WWW A	0.0000	0.0001	0.9999	0.0000	0.0000
WWW B	0.0003	0.0000	0.0004	0.9993	0.0000
WWW C	0.0000	0.0006	0.0000	0.0000	0.9994

Table 2.2 Summary of current disturbance regime for the Charron Lake control area, and the Wheadon, The Bog, Wabowden, and Wimapedi-Wapisu evaluation ranges

	Charron Lake		Wheadon		The Bog		Wabowden		Wimapedi-Wapisu	
	Area (km ²)	Range (%)								
Total Range Area	21,346		6,299		5,583		5,589		10,009	
Total Linear Features Buffer - no overlap	162	1	186	3	314	6	389	7	291	3
Harvested Forest <40 yrs	0	0	9	0	279	5	86	2	67	1
Natural Disturbance - Fire<40yrs Gross	5,572	28	1,555	28	186	3	948	17	2,009	20
Natural Disturbance - Fire<40yrs Net (all other buffer overlap removed)	4,741	24	1,350	24	179	3	889	16	1,974	20
Drill Holes - 250m buffer, not in Disturbance	1.37	0	2	0	0	0	7	0	12	0
Total Disturbance - water and overlap removed	4,905	25	1,547	27	820	14	1,432	26	2,344	24

Table 2.3 Summary of calves observed during June through September recruitment surveys

Range	Number of Calves Observed				Total
	June	July	August	Sept	
Charron Lake				4	
Harding Lake	3	3	2	2	10
The Bog	3	1	1	1	6
Wabowden	3	3	3	2	11
Wheadon	8	4	3	3	18
Wim/Wap	8	8	7	6	29

Table 2.4 Mean annual recruitment rates expressed as calves/cow for September and late winter surveys of radio-collared animals and winter range surveys of random portions of each evaluation range

Evaluation Range	Adult Females 'n'	Sep-2010 Calves/Cow (SD)	Adult Females 'n'	Winter 2010-2011 Calves/Cow (SD)	Adult Females 'n'	Sep11 Calves/Cow (SD)	Adult Females 'n'	Winter 2011-2012 Calves/Cow (SD)
Charron Lake	0	ND	0	ND	17	0.24 (0.11)	0	ND
The Bog	20	0.13 (0.07)	41	0.10 (0.05)	14	0.06 (0.06)	74	0.07 (0.03)
Wabowden	15	0.00 (0.00)	24	0.00 (0.00)	13	0.13 (0.09)	80	0.08 (0.03)
Wheadon	17	0.00 (0.00)	0	No data	18	0.15 (0.08)	15	0.00 (0.00)
Wimapedi-Wapisu	21	0.00 (0.00)	32	0.03 (0.03)	18	0.29 (0.10)	131	0.07 (0.02)
Overall	79	0.03 (0.02)	97	0.05 (0.02)	96	0.16 (0.04)	300	0.07 (0.01)

Table 2.5 Caribou evaluation range annual survival rates from radio-collared animals. Values represent survival from 17 May of the nominal year until 16 May of the following year (06 April 2012 in the case of 2011 rates). Values in parentheses are 95% confidence limits

Evaluation Range	2010	2011	Pooled 2010-11
Charron Lake	1.00 (1.00 - 1.00)	0.84 (0.68 - 1.00)	0.88 (0.76 - 1.00)
The Bog	0.94 (0.84 - 1.00)	0.77 (0.59 - 0.99)	0.85 (0.75 - 0.98)
Wabowden	0.94 (0.83 - 1.00)	0.78 (0.59 - 1.00)	0.87 (0.75 - 1.00)
Wheadon	0.88 (0.74 - 1.00)	0.94 (0.84 - 1.00)	0.91 (0.82 - 1.00)
Wimapedi-Wapisu	1.00 (1.00 - 1.00)	0.80 (0.64 - 1.00)	0.90 (0.82 - 1.00)

Table 2.6 Caribou evaluation range annual growth rates (expressed as both r_s and λ) based on survival and recruitment estimates where both were available. Values of r_s above zero indicate proportional annual increase and those below zero indicate proportional annual decline. Values in parentheses are 95% confidence limits

Evaluation Range	r_s 2010	r_s 2011	λ 2010	λ 2011
Charron Lake	No data	-0.07	No data	0.94 (0.75-1.13)
The Bog	0	-0.23	1.00 (0.88-1.12)	0.79 (0.61-0.98)
Wabowden	-0.06	-0.19	0.94 (0.84-1.03)	0.83 (0.62-1.05)
Wheadon	-0.13	0.01	0.88 (0.74-1.02)	1.01 (0.88-1.13)
Wimapedi-Wapisu	0	-0.09	1.00 (1.00-1.00)	0.92 (0.72-1.11)

Table 2.7 Comparison of disturbance and Lambda (λ) rates for all Evaluation Ranges

Evaluation Range	Disturbance and Lambda (λ) Rates			
	Natural %	Anthropogenic%	Total%	λ^*
Wheadon	24	4	28	0.94
Wabowden	16	9	25	0.90
Wimapedi-Wapisu	20	4	24	0.96
The Bog	3	11	14.7	0.90
Charron Lake	24	1	25	0.94

2.10 Figures

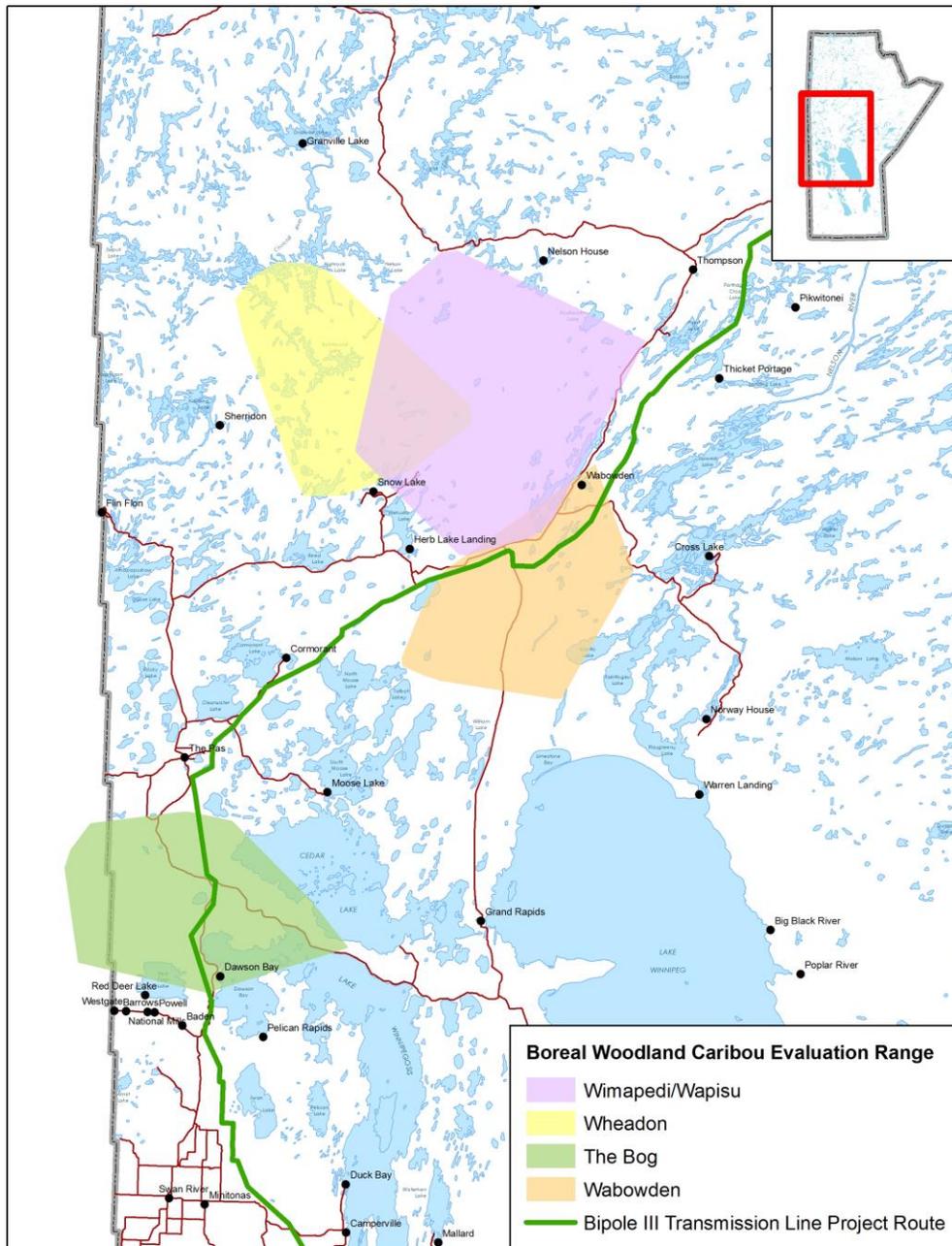


Figure 2.1 Boreal caribou evaluation ranges identified through telemetry data and Minimum Convex Polygon (MCP) analysis and in relation to the Bipole III Transmission Line Project

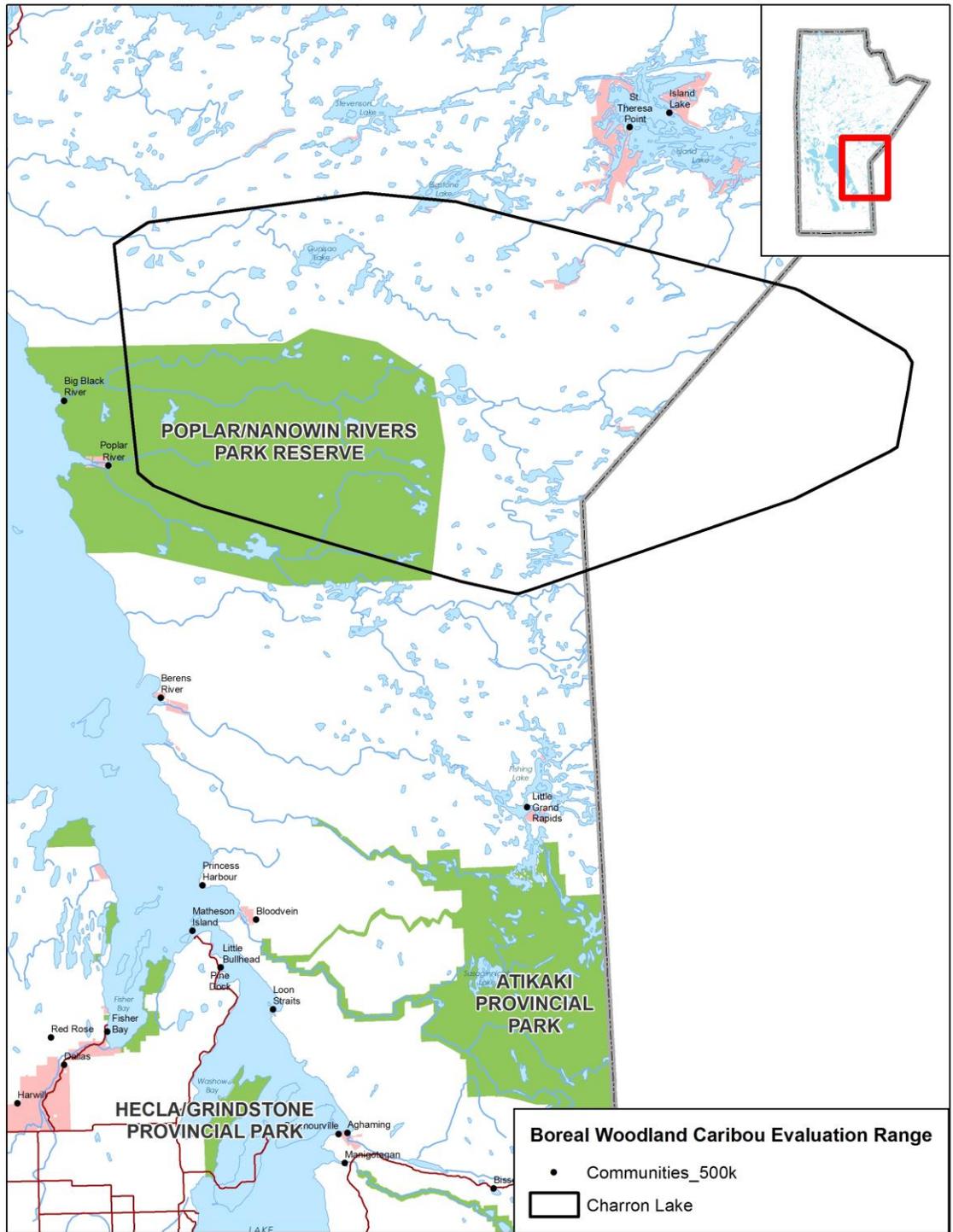


Figure 2.2 Location of Charron Lake Evaluation Range

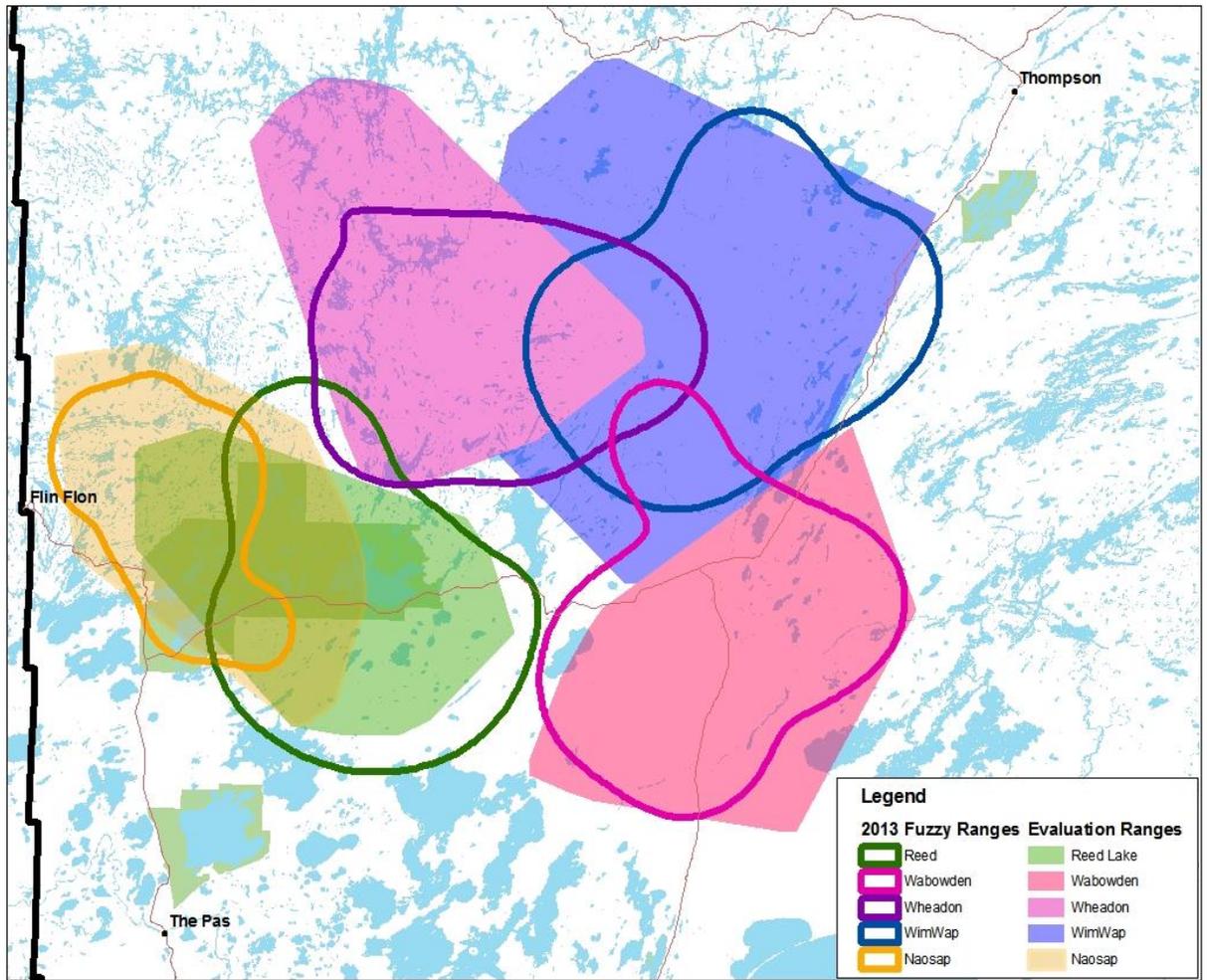


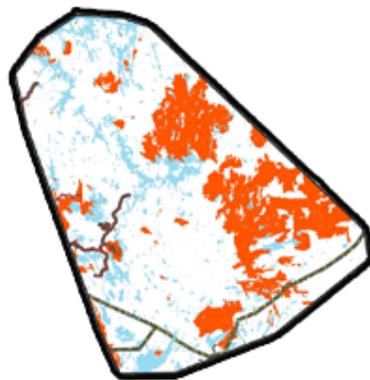
Figure 2.3 Evaluation ranges and fuzzy classified range boundaries



THE BOG RANGE
 5583 Square Kms (100%)
 Disturbance 820 Square Kms (15%)



WABOWDEN RANGE
 5,589 Square Kms (100%)
 Disturbance 1,432 Square Kms (26%)



WHEADON RANGE
 5,554 Square Kms (100%)
 Disturbance 1,547 Square Kms (26%)



Figure 2.4 Examples of disturbance mapping for the Bog, Wabowden and Wheadon boreal caribou ranges

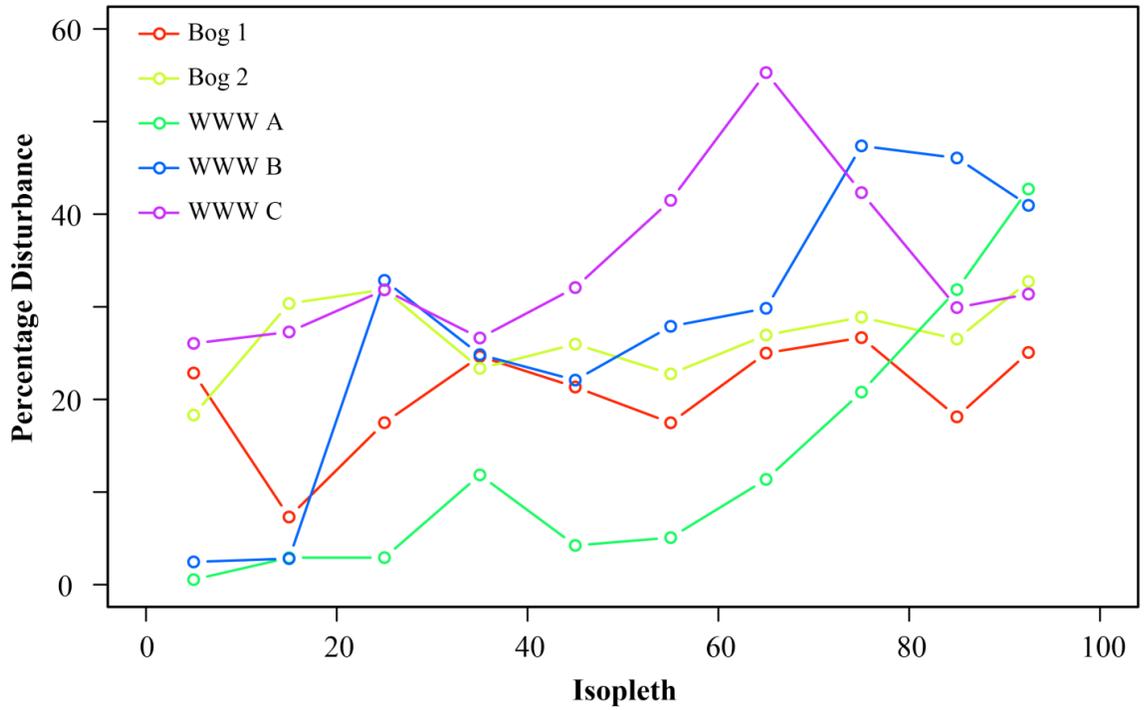


Figure 2.5 Percentage disturbance as a function of the kernel density isopleths. Note that this represents probability contours for the distribution and can be interpreted as the ‘distance’ from the core use area (i.e. smaller values are in the core). In general, disturbance increase with distance from the core, with the range periphery having greater disturbance

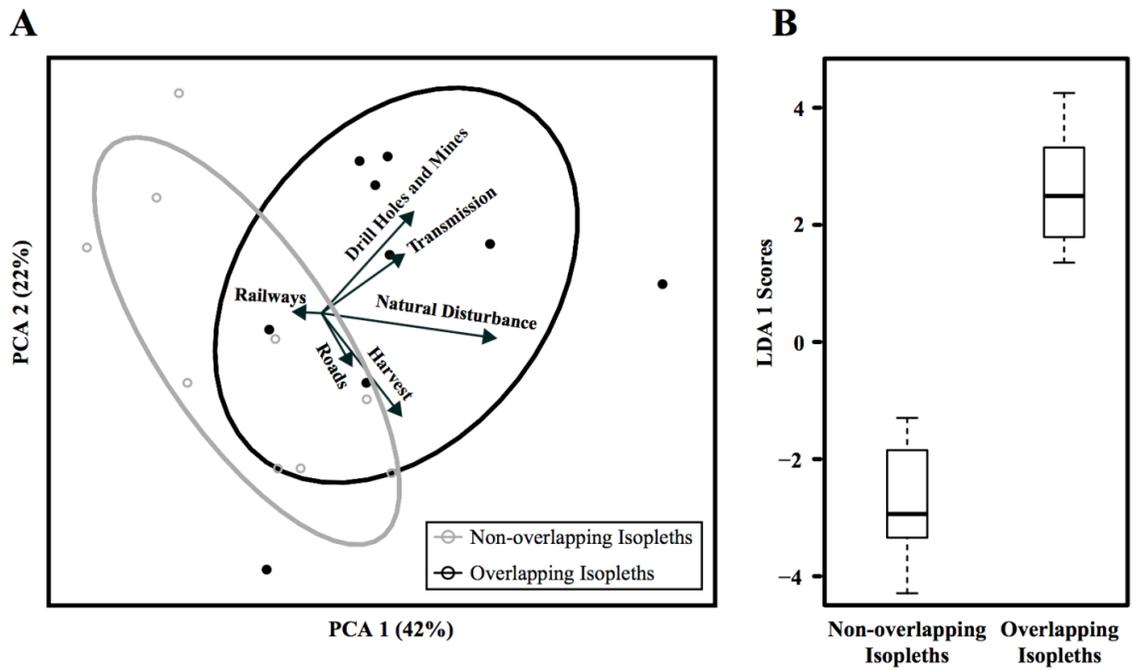


Figure 2.6 (A) Principal Component Analysis biplot of overlapping (black circles) and non-overlapping (grey circles) portions of caribou ranges as typified by disturbance. Ellipses represent one standard deviation. (B) Boxplots of Linear Discriminant Analysis (LDA) scores treating the nonoverlapping/overlapping areas as separate classes

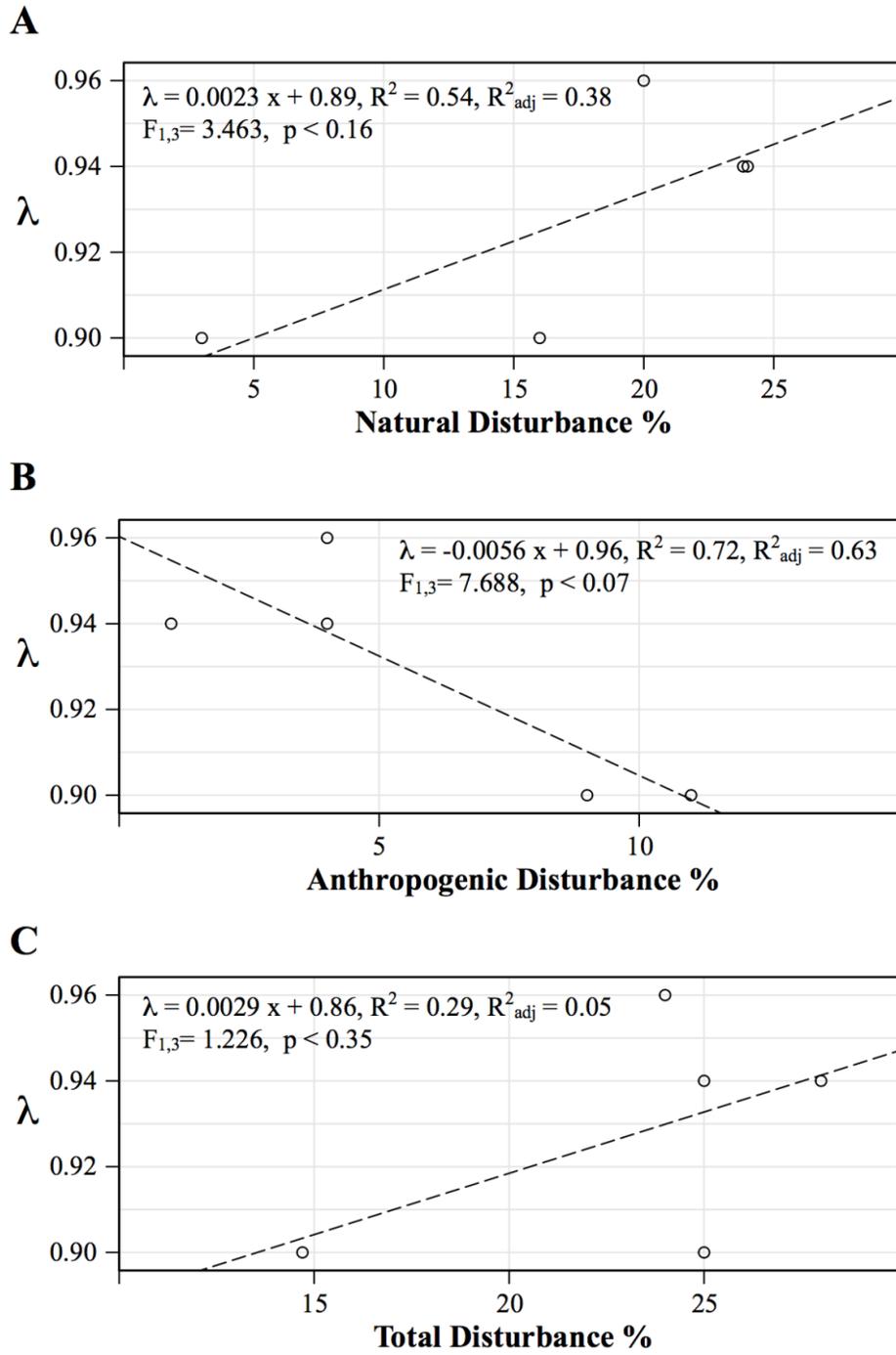


Figure 2.7 Regression of lambda (λ) against percentage of landscape disturbance for (A) Natural sources, (B) Anthropogenic sources, and the Total (C). None of the slopes were significant and only anthropogenic disturbance has the expected negative relationship with disturbance

3.0 ASSESSMENT OF GREY WOLF (*Canis lupis*) AND BOREAL CARIBOU (*Rangifer tarandus caribou*) HABITAT SELECTION AND INTERACTION DURING CALVING AND CALF REARING

3.1 Abstract

Ensuring sustainability of boreal caribou (*Rangifer tarandus caribou*) populations is challenging within industrially impacted landscapes because of their sensitivity to disturbance and often low replacement rates. High neonatal mortality in the first weeks of life is the most frequently cited explanation for negative growth rates, and this is often attributed to the effects of predation by grey wolves (*Canis lupis*). Sixty-five wolves and 138 caribou were GPS collared in northwestern Manitoba from 2009 to 2012 to assess resource selection and habitat use for both species during the critical calving and calf-rearing period. To examine habitat and resource selection a comprehensive 1 km scale GIS database of natural (landcover and hydrology) and anthropogenic (roads and rights-of-way, clear cuts) features was developed. To determine likely location of calf birthing and of calf mortality a step analysis was performed and supplemented by aerial surveys. To better understand predator-prey relationships trail cameras were deployed in the study area. Aerial recruitment surveys of collared animals yielded high rates of mortality during the early weeks of neonate life. Telemetry from this period, when compared with the habitat layers, indicate that wolves are more gregarious than caribou in habitat usage but do not frequent the same landcover types. Based on resource selection models using GPS telemetry data for both grey wolf and boreal caribou, there is significant separation in habitat selection during the calving and calf rearing period, in particular habitat where calf mortalities occurred is not primarily selected by wolves. Results of simultaneous trail camera trials in calving complexes and control areas indicate that presence of black bear

(*Ursus americanus*) in boreal caribou calving complexes is significant. This suggests that mortality of boreal caribou neonates by black bears requires further investigation to assist regulatory agencies and industrial proponents in better understanding both natural and anthropogenic causes of boreal caribou decline.

3.2 Introduction

Predation is known to be the primary limiting factor on boreal caribou populations through the manifestation of apparent competition resulting from anthropogenic disturbance leading to landscape conditions that favour higher densities of browsing ungulates, resulting in increases in associated wolf populations that predispose caribou to higher risk of predation mortality (Thomas 1995, James and Stuart-Smith 2000, Dyer et al. 2001, Courbin et al. 2009). Predation by wolves is largely considered the main cause of population decline (Dyer et al. 2001, 2002, Wittmer et al. 2005a, 2005b, 2007, Hervieux et al. 2013, 2014) and the potential for increased incidental predation on calves can impose significant population trends through slight decreases in Lambda (λ) with the primary cause being predation (Courtois et al. 2007, Pinard et al. 2012, Lewis and Mahoney 2014).

Woodland caribou are at risk to decline as they are vulnerable to population threats where increases in adult mortality are accompanied by a high incidence of predation-related calf mortality, the latter of which defines many woodland caribou populations across their range (Environment Canada 2011, Hayek et al. 2016). The vulnerability of woodland caribou to high early calf predation mortality has also been known since the earliest field investigations in Newfoundland in the late 1950's (Bergerud 1971). Evidence of high rates of calf predation in the early weeks of life is well

understood. Edmonds (1988) tracked 24 radio-collared southern mountain and boreal range adult caribou in west-central Alberta in the 1980's and reported high rates of calving success, but fall recruitment estimates of only 14.5% calves with the assumption that early calf mortality was attributable to wolves. Pinard et al. (2012) placed VHF radio collars on 64 calves whose fate was tracked from mid-May to the end of August in each year 2004-2006 resulting in an estimated fall recruitment rate of approximately 46 calves/100 cows. Similarly, of the 36 calves that died, 61% were due to predation (95% bears, 5% wolves) in the first 2 weeks of life; 23% of the calves were believed to have died from natural causes with the remaining 16% undetermined.

Boreal woodland caribou largely occupy large peatlands or expansive rugged forested areas of the Canadian Shield where parturient cows 'space out' across extensive landscapes to calve as a predator avoidance strategy to separate themselves from moose and their main predator, wolves (McLoughlin et al. 2005, Latham et al. 2011). For boreal caribou inhabiting Shield ranges in Saskatchewan, Manitoba, Ontario and Quebec, the predator-prey dynamic consists of moose as the primary prey species of wolves and black bears with boreal caribou being a secondary prey in the presence of moose (Rettie and Messier 2000).

When considering boreal caribou conservation and management, calf recruitment is critical to population growth rates and maintaining stable high adult female survival is balanced against inherent low recruitment rates (Environment Canada 2011). Lambda (λ) rates in boreal caribou populations, expressed as the ratio of recruitment (calf fecundity and survival) against mortality (number of surviving adult females) make their sustainability tenuous when higher than normal rates of calf mortality persist. In

Manitoba, low lambda rates and very low calf survival have been observed (see Chapter 2), but the reason for high calf mortality is not yet established.

The degree to which wolves contribute to boreal caribou calf mortality during the first weeks of life and through the critical calf rearing period is not well understood in Manitoba. Adult female collar data do not provide direct information on calves. Calf survival studies require intensive aerial tracking of adult females during the early weeks of calf life, and are often accompanied by follow up collaring and tracking of calves to determine fate and cause of mortality (Gustine et al. 2006, Whitten et al. 1992, DeMars et al. 2011, Pinard et al. 2012). Presence of pregnancy hormones can also be used to infer potential calf production, but must be supplemented by intensive aerial surveys to determine recruitment (McLoughlin et al. 2003). Step analysis using GPS collar data collected at frequent intervals provides an opportunity for researchers to quantify both date and precise locations of calving and calf mortality locations without the need for expensive and invasive field surveys (DeMars et al. 2013). This approach uses individual-based *a priori* models that represented movement patterns for non-parturient females, females with surviving calves and females that lost their calves. This method is still indirect but does have the potential for delineating timing and location of important life-history events during calving and calf rearing (DeMars et al. 2013).

The objective of this paper is to assess grey wolf and boreal caribou habitat selection and interaction during calving and calf rearing. To address this objective, step analysis was performed to more precisely identify the locations of calving and of possible mortality of calves. For the latter, this study seeks to establish whether there is evidence that wolf are present in, and using habitat associated with, calf mortality locations.

3.3 Materials and Methods

3.3.1 Study Area

The region of interest was associated with the potential effects of the proposed Bipole III High Voltage Direct Current (HVDC) project on boreal caribou that is being routed from northern Manitoba to Winnipeg on the west side of Lake Winnipeg. The study area is located in west central Manitoba and falls mainly within the extensive Boreal Plains and Boreal Shield Ecozones. Boreal woodland caribou evaluation range delineations were modified from ranges outlined in the 2006 Conservation and Recovery Strategy for Boreal Woodland Caribou in Manitoba (Crichton 2005) based on current telemetry data gathered as part of this overall research described in Chapter 2. The specific area used in the analysis was delineated using 3 overlapping boreal caribou evaluation ranges located near the proposed transmission line project. A combined Minimum Convex Polygon (MCP) was generated from the union of an MCP for all spring and summer wolf relocations with the caribou ranges, that was then further buffered by 10 kilometers to reflect a movement potential distance for caribou outside the MCP (following Gustine et al. 2006, Figure 3.1 A). This area also corresponds to the habitat database that is part of ALCES (A Landscape and Cumulative Effects Simulator) coverage for Manitoba (see Methods, Figure 3.1 B).

3.3.2 Collaring

Caribou and wolf monitoring were conducted using satellite Iridium Track3D satellite tracking collars (Lotek Wireless Inc. Newmarket, Ontario) as part of the Bipole III Transmission Line Project. Capture and collaring was performed under the authority of Manitoba Conservation with animals captured in January to March each year using

contracted helicopter net gun capture companies. Capture and handling involved no chemical immobilization as animals were netted, secured with leg hobbles, blindfolded and then collared as per handling protocols as set forth by Manitoba Conservation (#WI-266-2009/10). Fix rates averaged 3 hours and data were remotely retrieved through the Iridium satellite network. Data from 86 boreal caribou and 23 wolves that were found to occur in the study area from May to September 1 during 2010 and 2012 were used in the analysis.

3.3.3 Construction of Habitat and Telemetry Database

The Land Cover Classification for Canada (LCC) developed by the Canadian Forest Services (Wulder and Nelson 2003) was utilized in all habitat analyses. These data have been harmonized between Federal Departments involved in land management or land change detection and were the most current and consistent habitat classification available. This database is provided as a spatial polygon layer with a land cover attribute consisting of 31 classes: 12 forest; 3 shrubland; 7 tundra/grasslands; 7 developed land types including cropland, mosaic and built-up areas; and 2 water cover types (http://ftp.maps.canada.ca/pub/nrcan_rncan/vector/geobase_lcc_csc/shp_en/). The LCC was enhanced by incorporating the National Stratification Working Group ecological framework database (Smith et al. 1998) with the addition of wetland features, Manitoba forest harvest and fire layers. Analysis was not performed directly on this enhanced layer, instead these layers were aggregated and incorporated in the landscape indicator database for ALCES which has been developed for Manitoba by the ALCES Group (www.alces.ca) and D. Schindler (Joro Consultants). ALCES is an online tool that includes a comprehensive suite of terrestrial and aquatic indicators. ALCES includes

anthropogenic (e.g. roads, transmission lines, mining, and total footprint) and natural features and conditions (e.g. large and small rivers, fire, slope, elevation). ALCES provides data aggregated at several scales: cover parameters are expressed as proportional amounts, slope and elevation as means, and linear features as lineal intercept in km² (see Figure 3.1 B for example habitat layer). Analyses presented here use the 1 km ALCES grid downloaded in geotif format, imported into ArcGIS 10.4 and clipped using the MCP described above. The clipped raster layers were spatially joined to a vector layer of cells of 1 km size matching the ALCES geotifs to generate an attribute table that contained the resource selection parameters used in this study.

Telemetry data for caribou calving and calf mortality sites, and all wolf data were joined to the vector cell habitat attribute layer to provide counts of wolves and caribou occurring in each cell. These data were also segregated into monthly time sequences (May, June, July and August) to reflect the period when caribou calves are born and when wolves emerge from dens and over the period in which young for both species become more mobile. Within the MCP some cells contained both wolves and caribou, wolves without caribou, or neither; all cells were retained in the database. Thus, the final joined layer contained habitat indicators, anthropogenic and natural features, and telemetry counts for all wolves and caribou in total and by month including those MCP cells with zero counts (42,404 cells and 48 variables). Hereafter this database will simply be referred to as the ALCES 1 km database or dataframe from which (through various reshaping methods as described below) all analyses were based (with the exception of step analysis). This database was then exported as a text table for analysis and imported into CRAN-R (R Core Team 2016) as a dataframe.

3.3.4 Determination of calving and calf mortality sites

In this study, aerial recruitment surveys in 2010 were conducted once per month from May through September. In 2011, provincial restrictions on conducting surveys in calving areas were limited to July, August and September. Although recruitment rates could be determined from these survey data, it was not possible to determine information on the location of calving or mortality.

A series of step analyses following DeMars et al. (2013), were performed to identify calving sites and locations where calf mortality occurred. We used a script written in CRAN-R (R Core Team 2016) provided by DeMars (personal communication, n.d.), which included individual-based *a priori* models representing movement patterns for non-parturient females, females with surviving calves and females that lost their calves. This analysis generated ltraj objects (Calenge 2006) from which 3-day movement averages were determined. From these, the three *a priori* models and thresholds were applied to predict dates and locations where females likely had calves and when they were likely to be lost.

3.3.5 Habitat Use by Caribou and Wolves from Calving to Late Summer

To assess and compare habitat use by caribou and wolves over the critical summer months from calving until late August a Linear Discriminant Analysis (LDA) was performed. LDA (also referred to as Canonical Variates Analysis), is a linear modeling method used to detect and test the separation of two or more *a priori* natural classes/groups. It computes linear combinations of the explanatory variables that best separate those classes and in so doing, provides weights indicating their overall contribution to discrimination. Re-substitution of the original data into the derived linear

relationships provides component scores for sites that can be used in a biplot (for analyses involving more than two groups) or as boxplots for single variate solutions (see Legendre and Legendre 2012). LDA can be used in resource selection analyses and provides results highly correlated with other methods such as logistic regression (Manly et al. 2002).

To specifically examine how habitat use changed over time for wolves and caribou, the ALCES 1 km data frame was reshaped and subsampled in CRAN-R by species (wolf/caribou) and month (May to August). Only the cells containing telemetry data were retained for this analysis and a grouping variable (species-month combination) was created (11,465 cells, 12 variables, 8 groups [two species x four months]). Analysis was performed in CRAN-R using the *lda* function from the MASS package and the significance test used the *F* approximation for Wilks' λ calculated using MANOVA in the statistics package. Variables used included treed wetlands, shrubland, total deciduous forest, herb wetlands, sparse conifer forest, dense conifer forest, mixedwood, lakes, rivers, roads, transmission lines (as linear features) and landscape age. The mean score for each group (species by month) was calculated using the function *aggregate* (stats package) for the canonical scores derived from *lda.predict* (MASS package). These were plotted as connected centroids over time (trajectories) on a biplot that included the structure correlations for the predictor variables.

3.3.6 Caribou Calving, Calf Mortality and Wolf Habitat Use

LDA's were also used to isolate differences in habitat characteristics between calving locations or where calf mortalities occurred, and habitats utilized by wolves over that same period. For this analysis, the ALCES 1 km dataframe was subsampled and reshaped, primarily by extracting only cells corresponding to locations identified in the

step analysis where ‘calving’ or calf ‘mortality’ occurred. Wolf cells from the ALCES 1 km dataframe were extracted that correspond to the time period over which calving took place (hereafter referred to as wolf May, wolf June, etc.) and when calf mortality occurred (hereafter referred to as wolf June). Step analysis was not performed on the wolf telemetry, as wolf use cells represent all locations visited by wolves over the defined periods. For each cell included in the analysis, the habitat and variables examined included treed swamp, shrubland, total deciduous forest, total herbaceous wetlands, dense and sparse conifer forest, total mixedwood forest, total rivers and lakes, total road and transmission lines and land age. Using these parameters in lda, the following specific LDAs were performed: i) a global test of calving vs mortality vs wolves, ii) May vs wolves June (does overall habitat use differ for caribou calving, mortality, and that of wolves over the same period n= 664, groups=4 [calving=82, mortality=58, wolves May=568, wolves June=466], p=12 [land cover and feature types]), iii) calving vs mortality (does habitat differ between calving sites and mortality sites, n= 140, groups=2 [calving=82, mortality=58], p=12 [land cover and feature types]), iv) calving vs wolf May (does habitat where calving occur differ from that utilized by wolves over the same period, n=650, groups=2 [calving=83, wolves May=568], p=12 [land cover and feature types]) and v) mortality vs wolf June (does habitat where calf mortality occur differ from that utilized by wolves over the same period, n=524, groups=2 [mortality=58, wolves June=466], p=12 [land cover and feature types]). The latter three sets of tests represent a subset of pair-wise comparisons for the global test. The function manova was used to test significance using the *F* approximation to Wilks’ λ for these models in CRAN-R.

3.3.7 Development of Habitat Prediction Maps

Caribou and wolf selection analysis was based on the assumption that usage reflects the resources required by each species during the calving and early summer period. In this study, caribou “used” cells, data were extracted from the ALCES 1 km dataframe corresponding to the cells with calving locations from the step analysis (described above). All grid cells where caribou were never observed (i.e. cell was never visited at any time during the May through August period) were considered the full pool of “unused” cells. For wolves the dataframe “wolfMay”, which included all wolf locations in May, was considered “used” cells (described above). Locations where no wolves were observed during the period of the study were considered the full pool of “unused” cells. As there were substantially more “unused” than “used” cells in the study area, for the caribou and wolf analyses, a sample of random “unused” cells were selected from the ALCES 1 km dataframe (following Manley et al. 2002). For each species, a random sample of a size equal to the number of “used” cells was extracted; these extracted cells differed between species, but for a given species the same random set was used for each analytical run to eliminate potential confounding that might occur in comparing models developed from different random subsets.

Resource selection probabilities/predictions were calculated using two different approaches (LDA and Resource Selection Function analysis, RSF) performed on both caribou calving cells (used vs unused) and May wolf cells (used vs unused). LDA was performed in CRAN-R and followed the methods described above and using a two group structure (used/unused). The variables used for the LDAs included habitat cover types: wetland swamp, wetland herb, shrub land, total deciduous forest, sparse and dense conifer

forest, mixedwood forest; human linear features: total roads and transmission lines, and; natural features: rivers, lakes and forest age (which is a measure of fire disturbance history). Sample size for the caribou data set was 164 cells ($g=2$, used=82, unused=82 random subset) with the twelve cover types and features described ($p=12$). Sample size for the wolf data set was 164 cells ($g=2$, used=82, unused=82 random subset) with the twelve cover types and features described above plus slope ($p=13$).

The parameters identified to be of biological (known life history requirements) and statistical importance (in particular variable weights from LDA were examined) to boreal caribou resource selection were used in construction of the base equation for multiple Resource Selection Function models in CRAN-R. The RSFs utilized Logistic Regression with a logit link function (Manly et al. 2002) using `glm` (in package `stats`). The variables in the candidate models (see below) were permuted using the `dredge` function from package `MuMin` (Barton 2016) and assessed using Akaike Information Criterion (Bozdogan 1987). Candidate models used the `glm` function from `stats` with family set to binomial. The most parsimonious models with a ΔAIC of less than 4 were identified and used as a subset for the `model.avg` function in `MuMin`. For the caribou calving RSF the variables used in the candidate models included habitat cover types: shrubland, total deciduous forest, herb wetland, and sparse and dense conifer; human and natural linear and other features: total roads, transmission lines and lakes ($p=9$). For the wolf RSF using May telemetry (corresponding to the calving period for caribou) the variables used in the candidate models included habitat cover types: wetland swamp, shrubland, sparse conifer, and mixedwood forest; human and natural linear and other landscape features: total roads, transmission lines and rivers as well as land age and slope ($p=9$).

The predict functions appropriate to LDA (`predict.lda` in package `stats`) and the RSF method (`predict.averaging` from `MuMIn`) were used to obtain predictions for the input data. The results of two modeling approaches were compared (following Manly et al. 2002, p.176). For this comparison, the predictions of the averaged top parsimonious models for the RSF analyses were compared to the predictions from LDA (using the full set of input parameters without reduction, unlike Manly et al. 2002 where identical model terms are used). This facilitated comparison of both RSF and LDA approaches in developing resource selection models. In the latter case, the complete sets of coefficients (discriminant weights) is desirable for landscape change simulation purposes in ALCES, as cover must add to 100% (these results are not presented in this chapter, however the goal of further research is to model climate change and cumulative effects). To examine map agreement (i.e. do the maps adequately predict which cells are being used), the predicted values obtained from re-substitution of the original ALCES 1 km cell data subset into the models were tested using Welch's two-sample t-tests. We chose t-tests rather than a classification metric such as kappa to reflect how these maps will be incorporated and used within GIS for conservation and management purposes (with LDA class labels could have been assigned instead, but this is not how they are mapped). Final prediction maps were produced for the LDA and RSF results by substituting the full set of ALCES 1 km grid cells for the study area in the appropriate predict functions. For the LDA analyses, symbology was applied in ArcGIS to the caribou "used" likelihood attribute (`predict.lda` in `MASS` provides likelihoods for each class, but only "used" was considered for symbology in GIS). For RSF the fit values output from `predict.glm` in package `stats` were symbolized. Symbology was based on a yellow-red 'heat' color ramp using Jenks natural breaks optimization (Jenks 1967).

3.3.8 Preliminary assessment of predator presence

Preliminary assessment of predator (black bear and wolf) presence in relation to calving areas was conducted using trail camera traps. Seventy-two trail cameras were deployed between the dates of May and August in 2010 and 2011 within the Wimapedi, Wapisu, and Wabowden evaluation ranges. The calving and control areas were determined through assessment of spring GPS collar location data and were placed in clusters of 3-5 cameras per location. Control areas were selected based on the identification of similar habitat types to known calving areas, but not known or considered to be calving areas. Note that these controls represent habitat favourable to caribou but not used (i.e. calving site controls), not predator controls, and no predator management or removal was done at these sites. Cameras were deployed and retrieved by helicopter and photos were coded as to the species and number of individuals observed. For the purpose of this thesis, presence absence per camera was tabulated and used to calculate frequency (i.e. a camera recording at least one or more occurrences of a caribou, wolf or bear is counted as a presence, for example, if 10 out of 30 deployed cameras record at least one or more bears the frequency is $10/30=.33$ bears).

3.4 Results

Step analysis resulted in the identification of 42 and 43 calving locations in 2011 and 2012 respectively. Of these, 29 and 30 calves were found to have died during the first 4 weeks of life. The average calving date was 19 May in both years. Table 3.1 summarizes the analysis of female caribou that: did not calve (M0), had calves that survived >4 weeks (M1), and females that lost their calves (M2). Figure 3.2 illustrates an example of path movements used in the determination of calving and calf mortality

events that were utilized in the RSF and LDA modeling to compare resource selection between caribou and wolves during the calving period.

There is evidence that habitat use by caribou and wolves differs over the period from calving to late summer (Figure 3.3). When examining the full set of wolf and caribou occupied cells, the first axis from the LDA (94% of canonical discrimination) separates species (Wilks $\lambda=0.65$; $F_{84,70110}=59.5$; $P<<.001$). Wolf cells are typified by a higher proportion of deciduous and mixedwood cover as well as linear features such as roads and rivers. Caribou are associated with wetland cover types, especially herbaceous wetland, which in this region is often fen. Habitat use by wolves and caribou changed during the summer months although much less so for caribou. Wolf trajectories diverge from that of caribou, with late season wolf habitat use associated with increasingly negative canonical axis scores (left side of biplot). Caribou canonical axis scores are positive with trajectories that change little on the first axis with a slight positive increase on the second axis.

An analysis of habitat characteristics of calving locations and calf mortality sites (from the step analysis) provide evidence that wolves utilize the landscape differently over the May-June period that encompasses caribou calving and early calf-rearing May-June period (Figure 3.4). The Linear Discriminant Analysis of these relationships was significant (Wilks $\lambda=0.80$; $F_{36,3425}=7.50$; $P<.0001$) and comparable in overall trends to the analysis of the full set of caribou and wolf occupied cells (as presented in Figure 3.3). The first axis primarily separates species, while monthly habitat usage overlaps with little separation. As with the previous analysis, linear features and deciduous cover dominate wolf-occupied cells and wetlands and sparse conifer typify areas occupied by

caribou. The pair-wise canonical relationship between calving and mortality cell habitat was not significant (Wilk's $\lambda=0.95$; $F_{12,129}=0.69$; $P=0.73$; Figure 3.5 A) indicating that caribou calves are born and die (if depredated in the first month of life) in essentially the same habitat. Calving and wolf May habitat use (Wilk's $\lambda=0.83$; $F_{12,637}=10.60$; $P<.0001$), as well as caribou mortality and wolf locations in June (Wilk's $\lambda=0.80$; $F_{12,511}=10.70$; $P<.0001$) were statically significant (Figure 3.5 B, C). This recapitulates the overall trend identified in Figure 3.4 and provides evidence that wolves are not utilizing the same habitat during calving, or in the first month of life where typically the highest calf mortality occurs.

The resource selection maps based on Linear Discriminant and Resource Selection Function Analysis are presented in Figure 3.6 for caribou calving and wolf May telemetry. The LDA habitat model for caribou calving presented on the map in Figure 3.6 was significant (Wilk's $\lambda=0.64$; $F_{12,151}=7.00$; $P<.0001$) with transmission lines, rivers, deciduous forest ranked the most negatively and sparse conifer forest positively scored (Table 3.2). This compares favourably with the top model selected for RSF that retained, deciduous forests, lakes, rivers, shrubland and transmission lines as avoided features with sparse conifer forest as a positively selected habitat cover type (Table 3.3). The wolf use of habitat in May LDA analysis was also significant (Wilk's $\lambda=0.89$; $F_{13,1122}=10.09$; $P<.0001$). Discriminant coefficients for linear features such as roads and rivers were the most positively weighted while mixedwood forest was the most negatively weighted (Table 3.2). The most parsimonious RSF model for wolves also had high coefficients for rivers and roads suggesting selection of these features on the landscape (Table 3.4). In general, the caribou calving and wolf models developed using LDA and RSF tended to

have strong agreement with each other (Figure 3.7 A, B). The predicted RSF values and LDA likelihoods for “use” are strongly correlated ($r = .94$ for both species). The predicted values obtained from re-substitution of the original ALCES 1 km cell data subset into the models compare favourably with known use of habitat by caribou and wolves. For caribou calving the mean RSF value for cells known to be used was 0.90 and -1.37 for unused cells and use was significantly predicted $t_{122.8} = -8.8269$, $p\text{-value} < .001$. The comparison of predicted mapped likelihoods for used and unused cells based on the LDA model was also significant ($t_{158.91} = -9.9864$, $p\text{-value} < .001$) with a mean likelihood of 0.71 in areas of known use and 0.33 in areas not known to be used. Comparison of the predicted wolf May habitat use based on RSF was significant ($t_{1128.5} = -11.044$, $p\text{-value} < .001$) with means for used (0.23) and unused cells (-0.22). The mean LDA likelihood for known used cells was 0.55 and unused mapped cells had a mean of 0.45 and was significant ($t_{1133.9} = -11.456$, $p\text{-value} < .001$).

The number of cameras deployed in calving and control areas are provided on Table 3.5. We detected a high frequency of caribou use (0.81) in calving complexes during the calving and calf rearing period compared to control areas (0.21) (Table 3.6). Observed predator (black bear and wolf) presence in relation to known calving areas found that predators were present in calving areas. Bears occurred slightly more frequently in calving areas vs. control areas (0.39 vs 0.10) than wolves (Table 3.6), which were found in almost equal numbers in both (0.21 vs 0.13).

3.5 Discussion

The results indicate that boreal caribou are successful in separating themselves from wolves during the critical calving period and the weeks that follow when calf mortality is

high. As found in Table 3.3 caribou are mainly selecting sparse conifer forest whereas wolves are positively correlated with roads, wetland swamp, rivers and to a lesser degree sparse conifer forest. The most significant parameters in the RSF model contained deciduous forest, rivers and shrublands. The results of the LDA for caribou calving and wolf-may indicate different habitat selection for roads (1.016), rivers (0.702), wetland swamp (0.514), shrublands (0.290), transmission lines (0.267), and sparse coniferous (0.245). Calving caribou were found to be negatively correlated with all positive wolf parameters, with the exception of sparse coniferous (0.267), which is slightly more favoured by caribou. Similarly, locations where calves were estimated to have died occurred in the same habitats where they were born. The results of LDA as illustrated in Figure 3.3 also indicate that as summer progresses, wolf habitat use shifts away from caribou.

Overall, the results of the LDA provided a more fine-grained classification of caribou complexes that corresponds with field observations. Mapping of habitat values based on the coefficients generated from RSF or LDA as found in Figure 3.6, illustrate some visual differences. Mapping with multi class simulations in LDA may have more utility as parameter reduction in RSF does not occur. As seen in Figure 3.6, the output is highly correlated with RSF methods (Figure 3.7). There may be an advantage in using fully parameterized models when simulating landscape change, tools such as ALCES (ALCES A Landscape & Land-Use Ltd 2017) designed to work with a suite of landscape indicators in performing cumulative effects analysis.

The wolf telemetry data from this study would also suggest that wolves are selecting habitat near water, creeks and rivers, where there are likely other foraging

opportunities such as beaver that are susceptible to wolf predation during spring (DeMars 2015). Caribou typically did not select these features and indeed tended to remain in the same wetland complexes throughout the study. Although the original study design was based on examining the role of wolves in calf mortality we observed very little evidence that wolves are depredating calves in the region. Instead, we detected bear presence in many of the aerial reconnaissance flights and on trail camera images. This was not expected, the camera trap component was originally designed not as a predator study *per se* but to capture habitat use in calving complexes compared to areas not currently used. Capturing and obtaining counts of predators was anticipated, however we did not foresee the number of bears observed or interactions of bears with equipment. During study pre-trail camera deployments, we did capture trail imagery (Figure 3.8) that was suggestive of this outcome, but not appreciated at the time. We did observe many more individual bears than most other predators (not published), however, bears knocked many cameras off alignment making individual counts difficult. The principal reason why counts of individuals are not presented (presence-absence frequencies are instead) is because of bear tampering with cameras.

Bears have long been identified as major predators of moose, elk, and/or deer calves across all ranges occupied by bears in North America (Zager and Beecham 2006) including Newfoundland (Mahoney et al. 1990), Alaska (Ballard et al. 1981), Saskatchewan (Stewart et al. 1985), and Alberta (Nolan and Barrett 1985). In northeastern Minnesota, both wolves and bears were reported to share in the predation of white-tailed deer fawns (Kunkel and Mech 1994). Black bears were identified as an important predator of caribou calves in the late 1980's in Newfoundland (Mahoney et al.

1990, Mahoney and Virgil 2003), although wolves had been extirpated from Newfoundland in the early 1900s. However, bears have received limited attention by the research communities outside of Newfoundland and Quebec (Hervieux et al. 2013, Johnson et al. 2015).

The recent publications of DeMars (2015) in Alberta, and LeBlond et al. (2016) and Bastille-Rousseau et al. (2016) in Quebec, combined with the observations of black bear movements from upland to wetland habitats in the spring coinciding with the calving season (Latham et al. 2011), suggest the likelihood of bears as the probable primary predator of boreal caribou calves on many ranges. The evidence from Manitoba of extremely low annual recruitment rates of <10 calves/100 cows in some years, combined with robust annual adult survival of 95-100% (see chapter 2) mirrors early calf mortality estimates for ranges in Newfoundland (Lewis and Mahoney 2014), Quebec (Pinard et al. 2012) and British Columbia (DeMars 2015). DeMars (2015) and LeBlond et al. (2016) also demonstrated the nature of spatial separation of calving habitat with wolves and overlap with black bears. In particular, DeMars (2015) highlighted the fact that both black bears and woodland caribou selected poor fens during the caribou calving season for boreal plain lowlands. It may be of significance that parturient caribou also selected for poor fen habitats for calving within the boreal shield. Both studies also showed a distinct avoidance of these same habitats by wolves at this particular season, and both suffered from high rates of post-natal mortality. In the expansive boreal shield ranges of northern Saskatchewan, McLoughlin et al. (2016) made a case that wolves existed at very low densities in line with low densities of prey (moose and caribou), but that despite very high pregnancy and very low adult female mortality rates, calf mortality was high (annual

recruitment rates <20 calves/100 cows); wolves were not shown to be implicated in the deaths of any calves. LeBlond et al. (2016) believed that wolf-avoidance strategies predisposed calving woodland caribou to an ecological trap leading to higher early spring encounter rates with black bears.

In planning the timing for aerial recruitment surveys, three Canadian studies were considered: Ferguson and Elkie (2004) that determined the calving period in northwestern Ontario from 17 May to 14 July based on 3-day sequences of low movement patterns of radio-collared animals, in Saskatchewan from 5 May – 25 May based on observational data (Rettie and Messier 2001), and Reed Lake Manitoba, between 17 May to 31 May, observed on calving islands using radio-collars (Shoesmith and Storey 1977). Assessment of 3 day average movement rates of all collared females in this study, an average calving date of 17 May was determined. The application of the step analysis yielded a mean calving date of 19 May, which is consistent with other calving period reported on above. Calving and calf mortality sites defined by through step analysis provided an efficient alternative to direct measures (aerial surveys or calf collaring) of parturition and mortality.

3.6 Conclusion

Contemporaneous collection of grey wolf and boreal caribou telemetry for multiple overlapping ranges was examined in this study allowing direct comparison of habitat selection of a predator and prey species during calving and calf rearing. Step analysis was used to predict the locations and timing of parturition and mortality events. This resulted in the identification of 42 and 43 calving locations in 2011 and 2012 respectively. The average calving date was 19 May in both years and 29 and 30 calves died during the first 4 weeks of life. The predicted mortality events were consistent with aerial reconnaissance

undertaken as part of recruitment surveys. Step analysis was found to be a practical technique for identifying locations of life history events not easily obtained by reconnaissance alone. Habitat in which calving and calf mortality occurs were found to be significantly different from habitat utilized by wolves. Wolf habitat selection over the calf rearing period showed a divergent trend to that of caribou, with a long trajectory on the discriminant analysis biplot. Caribou remained in substantially similar habitat over this period suggesting that calves are in calving complexes when mortality occurs.

The RSF and LDA models provided mapped distributions of habitat selection consistent with the discriminant analyses. The derived RSF and LDA mapped values, log-likelihoods and likelihoods for the 'used' class respectively, were tested against known caribou and wolf locations and found to significantly predict greater selection. For both methods, landscape units predicted to be highly selected by boreal caribou were not typically predicted to be selected by wolves and thus the mapped distributions of these species differed. The RSF and LDA models made comparable predictions that were highly correlated, and the model coefficients for cover types were consistent for those parameters that occurred in both. In landscape modeling, and for simulation in software such as ALCES where habitat covertypes add up to 100%, having coefficients for all parameters is essential and LDA is a suitable and under-utilized tool. These findings of this study further suggest that the early mortality of neonates is not easily explained as a function of wolf predation. Camera deployments observed predator (black bear and wolf) presence in known calving areas, but recorded more bear activity than wolves. Tampering of the cameras by bears, make assessment of significance problematic, but based on these findings, it is recommended that black bears activity in calving complexes be studied.

Predator management, which currently focuses on wolves may have no effect on predation rates of calves, and thus not be a useful tool in achieving desired management outcomes.

3.7 References

- ALCES Landscape & Land-Use Ltd. 2017. A collaboration of environmental scientists, ecologists, planners and management consultants. ALCES Online is a web based ecological cumulative effects modeling platform designed for wildlife researchers and resource managers. Developed by Joro Consultants Inc. in Manitoba.
- Ballard WB, Spraker TH, Taylor KP. 1981. Causes of neonatal moose calf mortality in south central Alaska. *J Wildl Manage* [Internet]. 45(2): 335-342. Available from: <http://www.jstor.org.proxy2.lib.umanitoba.ca/stable/pdf/3807916.pdf>
doi:10.2307/3807916
- Barton K. 2016. MuMIn: multi-model inference. R package version 1.10.0. Available from: <https://cran.r-project.org/web/packages/MuMIn/index.html>
- Bastille-Rousseau G, Rayl ND, Ellington EH, Schaefer JA, Michael JL, Peers, Mumma MA, Mahoney SP, Murray DL. 2016. Temporal variation in habitat use, co-occurrence, and risk among generalist predators and a shared prey. *Can J Zool*. 94(3): 191-198. [dx.doi.org/10.1139/cjz-2015-0127](https://doi.org/10.1139/cjz-2015-0127)
- Bergerud AT. 1971. The population dynamics of Newfoundland caribou. *Wildlife monographs*. 25: 3-55.
- Bozdogan H. 1987. Model selection and Akaike's information criterion (AIC): the general theory and its analytical extensions. *Psychometrika*. 52(3): 345-370.
- Calenge C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecol modell*. 197(3): 516-519.
- Courbin N, Fortin D, Dussault C, Courtois R. 2009. Landscape management for woodland caribou: the protection of forest blocks influences wolf-caribou co-occurrence. *Landsc Ecol*. 24(10): 1375-1388. Available from: <https://doi.org/10.1007/s10980-009-9389-x>
- Courtois R, Ouellet JP, Breton L, Gingras A, Dussault C. 2007. Effects of forest disturbance on density, space use, and mortality of woodland caribou. *Ecoscience*. 14(4): 491-498. Available from: [https://doi.org/10.2980/1195-6860\(2007\)14\[491:EOFDOD\]2.0.CO;2](https://doi.org/10.2980/1195-6860(2007)14[491:EOFDOD]2.0.CO;2)
- DeMars C, Thiessen C, Boutin S. 2011. Assessing spatial factors affecting predation risk to boreal caribou calves: implications for management. Annual Report. University of Alberta and Ministry of Natural Resource Operations de la Colombie-Britannique. 1-35 p. Available from: <http://scek.ca/sites/default/files/documents/RA-2011-01-Assessing-Spatial-Factors-Affecting-Predation-Risk-Boreal-Caribou-Calves-Dec-1-11.pdf>
- DeMars CA, Auger-Méthé M, Schlägel UE, Boutin S. 2013. Inferring parturition and neonate survival from movement patterns of female ungulates: a case study using woodland caribou. *Ecol Evol*. 3(12): 4149-4160. doi.org/10.1002/ece3.785

- DeMars CA. 2015. Calving behavior of boreal caribou in a multi-predator, multi-use landscape [dissertation]. Department of Biological Sciences, University of Alberta. 215 p.
- Dyer SJ, Neill JPO, Wasel SM, Boutin S. 2001. Avoidance of industrial development by woodland caribou. *J Wildl Manage.* 65(3): 531-542.
- Dyer SJ, O'Neill JP, Wasel SM, Boutin S. 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. *Can J Zool.* 80(5): 839-845. Available from: <https://doi.org/10.1139/Z02-060>
- Edmonds EJ. 1988. Population status, distribution, and movements of woodland caribou in west central Alberta. *Can J Zool.* 66(4): 817-826.
- Environment Canada. 2011. Scientific assessment to inform the identification of critical habitat for woodland caribou (*Rangifer tarandus caribou*), Boreal Population, in Canada: 2011 update. Ottawa, Ontario, Canada. 102 pp. plus appendices.
- Ferguson SH, Elkie PC. 2004. Seasonal movement patterns of woodland caribou (*Rangifer tarandus caribou*). *J Zool.* 262(2): 125-134. doi.org/10.1017/S0952836903004552
- Gustine DD, Parker KL, Lay RJ, Gillingham MP, Heard DC. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife monographs.* 165: 1-32.
- Hayek T, Lloyd N, Stanley-Price MR, Saxena A, Moehrenschrager A. 2016. An exploration of conservation breeding and translocation tools to improve the conservation status of boreal caribou populations in western Canada: pre-workshop document. Centre for Conservation Research. Calgary Zoological Society. Calgary, Alberta, Canada.
- Hervieux D, Hebblewhite M, DeCesare NJ, Russell M, Smith K, Robertson S, Boutin S. 2013. Widespread declines in woodland caribou (*Rangifer tarandus caribou*) continue in Alberta. *Can J Zool.* 91(12): 872-882. doi:10.1139/cjz-2013-0123
- Hervieux D, Hebblewhite M, Stepnisky D, Bacon M, Boutin S. 2014. Managing wolves (*Canis lupus*) to recover threatened woodland caribou (*Rangifer tarandus caribou*) in Alberta. *Can J Zool.* 92(12): 1029-1037. dx.doi.org/10.1139/cjz-2014-0142
- James ARC, Stuart-Smith AK. 2000. Distribution of caribou and wolves in relation to linear corridors. *J Wildl Manage.* 64(1): 154-159.
- Jenks GF. 1967. The Data model concept in statistical mapping. *International yearbook of cartography.* 7(1): 186-190.
- Johnson CJ, Ehlers LP, Seip DR. 2015. Witnessing extinction - Cumulative impacts across landscapes and the future loss of an evolutionarily significant unit of woodland caribou in Canada. *Biol Conserv.* 186: 176-186.
- Kunkel KE, Mech LD. 1994. Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. *Can J Zool.* 72(9): 1557-1565.

- Latham ADM, Latham MC, Boyce MS. 2011. Habitat selection and spatial relationships of black bears (*Ursus americanus*) with woodland caribou (*Rangifer tarandus caribou*) in northeastern Alberta. *Can J Zool.* 89(4): 267-277.
- Leblond M, Dussault C, Ouellet JP, St-Laurent MH. 2016. Caribou avoiding wolves face increased predation by bears – caught between Scylla and Charybdis. *J Appl Ecol.* 53(4): 1078-1087.
- Legendre P, Legendre L. 2012. *Numerical Ecology*. 3rd Edition. Amsterdam, The Netherlands, Amsterdam. Elsevier B. V. 990 pp.
- Lewis KP, Mahoney SP. 2014. Caribou survival, fate, and cause of mortality in Newfoundland: a summary and analysis of the patterns and causes of caribou survival and mortality in Newfoundland during a period of rapid population decline (2003-2012). Technical Bulletin No. 009, Sustainable Development and Strategic Science. Government of Newfoundland and Labrador. St. John's, NL.
- Mahoney SP, Abbott H, Russell LH, Porter BR. 1990. Woodland caribou calf mortality in insular Newfoundland. In: Transactions of the 19th international union of game biologists congress. Trondheim. 19: 592-599.
- Mahoney SP, Virgl JA. 2003. Habitat selection and demography of a nonmigratory woodland caribou population in Newfoundland. *Can J Zool.* 81(2): 321-334. Available from <http://article.pubs.nrc-cnrc.gc.ca/ppv/RPViewDoc?issn=1480->
- Manly BFL, McDonald L, Thomas D, McDonald TL, Erickson WP. 2002. Resource selection by animals: statistical design and analysis for field studies. *J Anim Ecol.* January 2002, DOI: 10.2307/5247
- McLoughlin PD, Dzus EH, Wynes B, Boutin S. 2003. Declines in population of woodland caribou. *J Wildl Manage.* 67(4): 755-761. Available from: <http://www.jstor.org/stable/3802682>
- McLoughlin PD, Dunford JS, Boutin S. 2005. Relating predation mortality to broad-scale habitat selection. *J Anim Ecol.* 74(4): 701-707.
- McLoughlin PD, Stewart K, Superbie C, Perry T, Tomchuk T, Greuel R, Singh K, Truchon-Savard A, Henkelman J, Johnstone JF. 2016. Population dynamics and critical habitat of woodland caribou in the Saskatchewan Boreal Shield. Interim Project Report 2013–2016. Department of Biology. University of Saskatchewan. Saskatoon, Saskatchewan, Canada. 162 p.
- Nolan JW, Barrett MW. 1985. A preliminary study of moose calf mortality in northeastern Alberta. Alberta Environmental Centre, Vegreville.
- Pinard V, Dussault C, Ouellet JP, Fortin D, Courtois R. 2012. Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. *J Wildl Manage.* 76(1): 189-199. Available from: <https://doi.org/10.1002/jwmg.217>

- R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: <https://www.R-project.org/>
- Rettie WJ, Messier F. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography*. 23(4): 466-478. Available from: <https://doi.org/10.1034/j.1600-0587.2000.230409.x>
- Rettie WJ, Messier F. 2001. Range use and movement rates of woodland caribou in Saskatchewan. *Can J Zool*. 79(11): 1933-1940. Available from: <http://doi.org/10.1139/cjz-79-11-1933>
- Shoesmith MW, Storey DR. 1977. Movements and associated behaviour of woodland caribou in central Manitoba. Manitoba Department of Renewable Resources and Transportation Services. Research Manuscript No. 77-15. 74 p.
- Smith RE, Veldhuis H, Mills GF, Eilers RG, Fraser WR, Lelyk GW. 1998. Terrestrial ecozones, ecoregions and ecodistricts of Manitoba: An ecological stratification of Manitoba's natural landscapes. No. Technical Bulletin 9E. Research Branch: Agriculture and Agri-Food Canada. Brandon Research Centre. Brandon, Manitoba, Canada.
- Stewart RR, Kowal EH, Beaulieu R, Rock TW. 1985. The impact of black bear removal on moose calf survival in east central Saskatchewan. *Alces*. 21: 403-418.
- Thomas D. 1995. A review of wolf-caribou relationships and conservation implications in Canada. In: Carbyn LN, Fritts SH, Seip DR, editors. *Ecology and conservation of wolves in a changing world*. Canadian Circumpolar Institute, Occasional Publication No. 35. Edmonton, Alberta, Canada. 261-273 p.
- Whitten KR, Garner GW, Mauer FJ, Harris RB. 1992. Productivity and early calf survival in the Porcupine caribou herd. *J Wildl Manage*. 56(2): 201-212.
- Wittmer HU, McLellan BN, Seip DR, Young JA, Kinley TA, Watts GS, Hamilton D. 2005a. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. *Can J Zool*. 83(3): 407-418. Available from: <https://doi.org/10.1139/Z05-034>
- Wittmer HU, Sinclair ARE, McLellan BN. 2005b. The role of predation in the decline and extirpation of woodland caribou. *Oecologia*. 144(2): 257-267. Available from: <https://doi.org/10.1007/s00442-005-0055-y>
- Wittmer HU, McLellan BN, Serrouya R, Apps CD. 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. *J Anim Ecol*. 76(3): 568-579. Available from: <https://doi.org/10.1111/j.1365-2656.2007.01220.x>
- Wulder M, Nelson T. 2003. EOSD land cover classification legend report, version 2. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre. Victoria, British Columbia, Canada.

Zager P, Beecham J. 2006. The role of American black bears and brown bears as predators on ungulates in North America. *Ursus*. 17(2): 95-108. Available from: [http://www.bioone.org/doi/abs/10.2192/1537-6176\(2006\)17\[95:TROABB\]2.0.CO;2](http://www.bioone.org/doi/abs/10.2192/1537-6176(2006)17[95:TROABB]2.0.CO;2)

3.8 Tables

Table 3.1 Results of Step Analysis

Calving Events				
	M0	M1	M2	Total
2011				
Wabowden	4	3	5	12
Wapisu	5	5	16	26
Wheadon	3	5	8	16
Total	12	13	29	54
2012	M0	M1	M2	Total
Wabowden	1	4	12	17
Wapisu	4	3	12	19
Wheadon	1	6	6	13
Total	6	13	30	49

Table 3.2 Linear Discriminant analysis parameter coefficients for the caribou calving and wolf May data used in developing the habitat models

Parameter	Caribou Calving	Wolf May
Wetland Swamp	-0.109	0.514
Shrubland	-0.356	0.290
Roads	-0.343	1.016
Deciduous Forest	-0.532	-0.006
Herbaceous Wetland	0.070	0.169
Rivers	-0.905	0.702
Sparse Conifer Forest	0.267	0.245
Mixedwood Forest	-0.064	-0.105
Dense Conifer Forest	-0.205	-0.007
Lakes	-0.309	0.159
Transmission Lines	-1.374	0.267
Landscape Age (post fire)	0.020	0.063
Slope	-	0.652

Table 3.3 Caribou Calving RSF Model parameter estimates and standard errors. The base, top and average models are presented. For the average model the adjusted standard error, number of models that include the term and parameter weights are provided

Parameter	Base Model	Top Model	Average Model
(Intercept)	0.788 (0.673)	0.943 (0.441)**	0.962 (0.719)
Sparse Conifer Forest	0.332 (0.161)**	0.241 (0.146)*	0.217 (0.195, 19, 1)
Deciduous Forest	-1.017 (0.385)***	-1.093 (0.378)***	-1.064 (0.380, 19, 1)***
Lakes	-0.273 (0.151)*	-0.347 (0.138)**	-0.303 (0.179, 19, 1)*
Rivers	-1.964 (0.645)***	-2.134 (0.6a12)***	-2.057 (0.636, 16, 0.93)***
Shrubland	-0.506 (0.165)***	-0.508 (0.157)***	-0.529 (0.168, 16, 0.88)***
Transmission Lines	-3.516 (3.516)	-3.702 (3.030)	-3.295 (3.247, 13, 0.71)
Dense Conifer Forest	-0.153 (0.147)	-	-0.057 (0.117, 8, 0.38)
Herbaceous Wetland	0.158 (0.159)	-	0.077 (0.143, 8, 0.35)
Roads	-1.469 (6.312)	-	-0.312 (2.887, 7, 0.22)

Standard errors in parentheses. * Significant at 10%; ** significant at 5%; *** significant at 1%

Table 3.4 Wolf May RSF Model parameter estimates and standard errors. The base, top and average models are presented. For the average model the adjusted standard error, number of models that include the term and parameter weights are provided

Parameter	Base Model	Top Model	Average Model
(Intercept)	-1.638 (0.635)***	-1.393 (0.202)***	-1.516 (0.378)***
Sparse Conifer Forest	0.121 (0.048)**	0.136 (0.047)***	0.129 (0.048, 15, 1)***
Mixedwood Forest	-0.099 (0.060)*	-0.093 (0.058)	-0.055 (0.065, 15, 1)
Rivers	0.451 (0.111)***	0.462 (0.110)***	0.453 (0.110, 15, 1)***
Roads	0.797 (0.172)***	0.800 (0.171)***	0.796 (0.171, 15, 1)***
Shrubland	0.163 (0.054)***	0.171 (0.043)***	0.173 (0.047, 15, 1)***
Wetland Swamp	0.301 (0.054)***	0.289 (0.052)***	0.300 (0.053, 8, 0.58)***
Transmission Lines	0.169 (0.149)	-	0.070 (0.127, 7, 0.41)
Slope	0.379 (0.350)	-	0.110 (0.256, 7, 0.34)
Landscape Age (post fire)	0.030 (0.125)	-	0.009 (0.066, 7, 0.26)

Standard errors in parentheses. * Significant at 10%; ** significant at 5%; *** significant at 1%

Table 3.5 Total numbers of trail cameras deployed within calving and non-calving areas by evaluation range.

Evaluation Range	Number of Calving Area Camera Clusters	Number of Control Area Camera Clusters	Number of Cameras Deployed		
			Calving Areas	Control Areas	Total Deployed
Wabowden	4	4	17	20	37
Wimapedi-Wapisu	4	4	16	19	35
Total	8	8	33	39	72

Table 3.6 Pooled results from all trail cameras within calving and control areas, number of sites that recorded caribou, bear, and wolf occurrences and frequency of occurrences relative to camera deployments.

Area	Number of Cameras	Number of Caribou Occurrences	Caribou Frequency	Number of Bear Observations	Bear Frequency	Number of Wolf Observations	Wolf Frequency
Calving Areas	33	27	0.82	13	0.39	7	0.21
Control Areas	39	8	0.21	4	0.10	5	0.13
Total	72	35	0.49	17	0.24	12	0.17

3.9 Figures

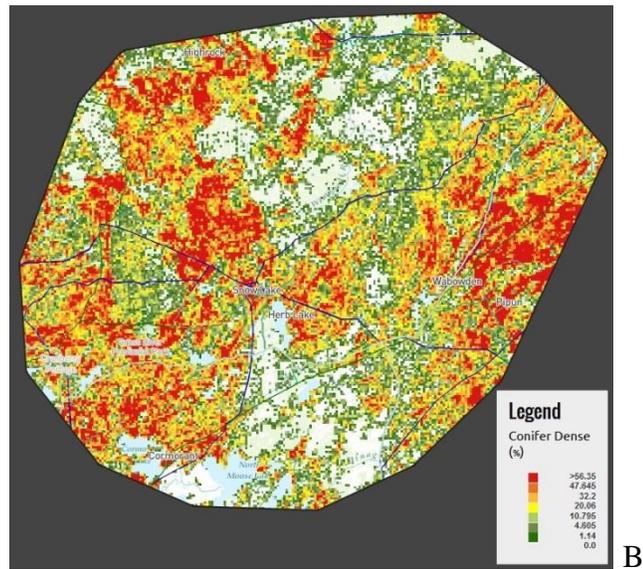
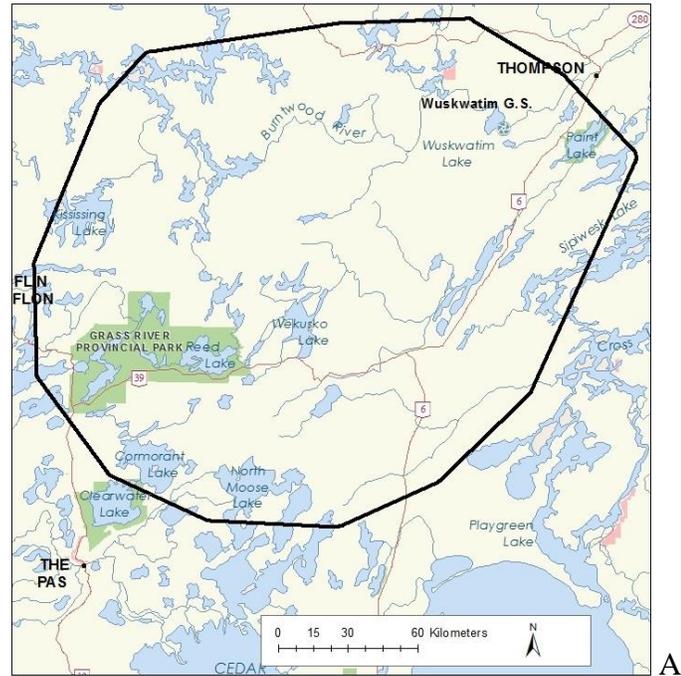


Figure 3.1 (A) The study area MCP for the caribou calving and wolf habitat use and resource selection models. (B) Example of ALCES raster 1 km grid showing proportion of Dense Conifer Forest (blue green = 0 % per sq km color ramp to red = 100% per sq km) described in the methods section

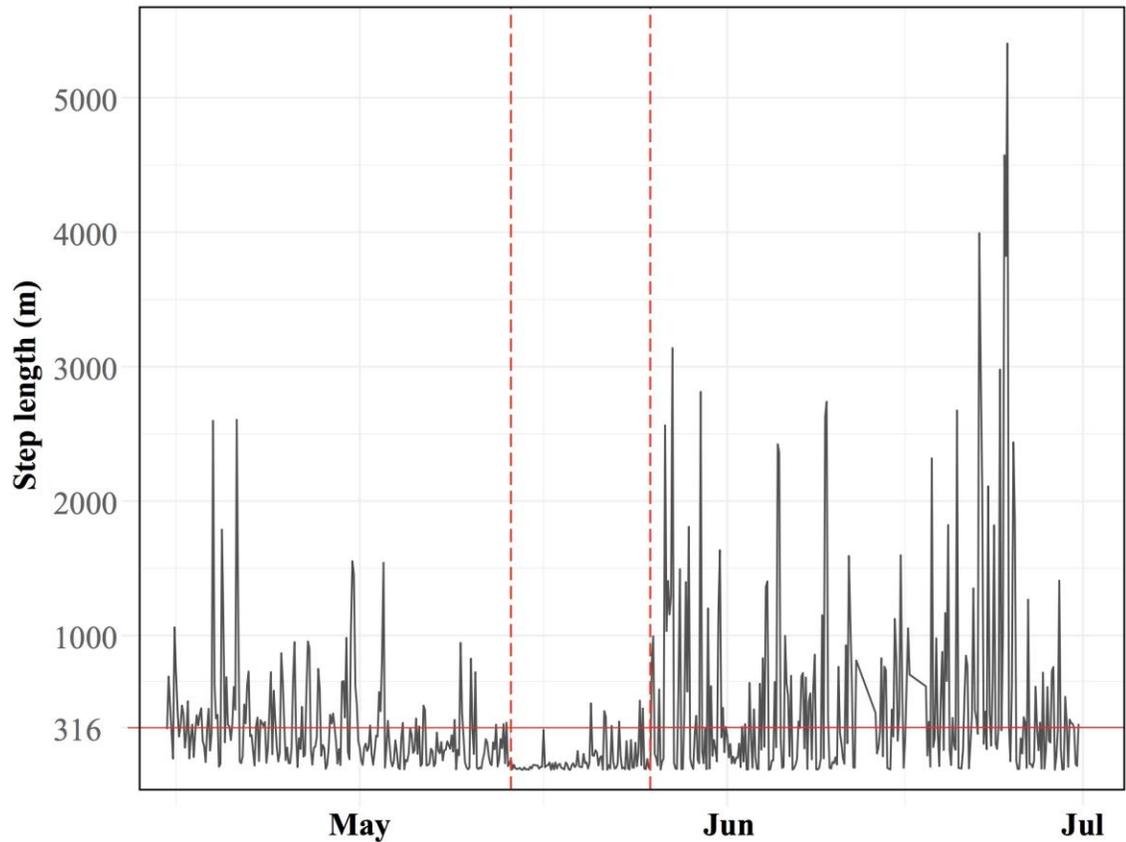


Figure 3.2 Example of the individual-based method of inferring parturition and offspring survival status in female woodland caribou as described in DeMars et al. (2013). The black line illustrates the daily movement pattern of a female caribou and from 1-May to 1- July that gave birth on approximately 13- May and lost her calf on 25-May. The red horizontal line represents the mean step length for 1-May through 1-July. The vertical dashed red lines represent the estimated break points indicating that the female calved and then lost the calf. The lower step length between the two vertical lines illustrates female movement with the surviving calf.

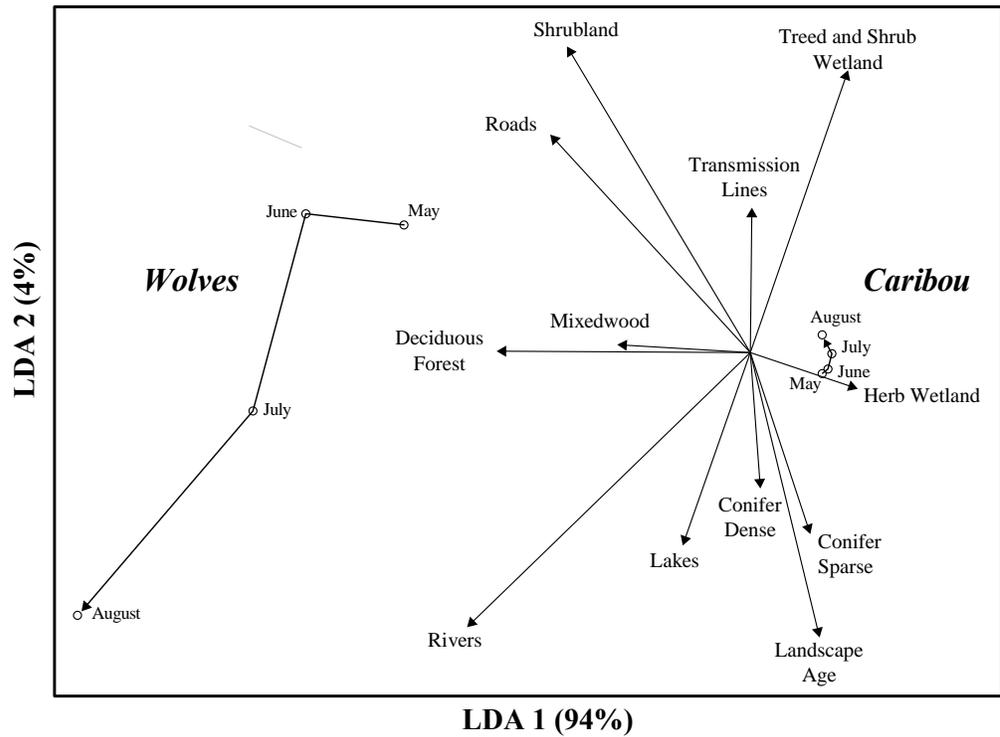


Figure 3.3 Linear Discriminant Analysis of all wolf and caribou cells in the ALCES 1 km database for the study area grouped by species and month Graph shows component scores aggregated by species and month (i.e. monthly centroids). These are connected as trajectories over time. Structure correlations for variables used in discrimination are presented.

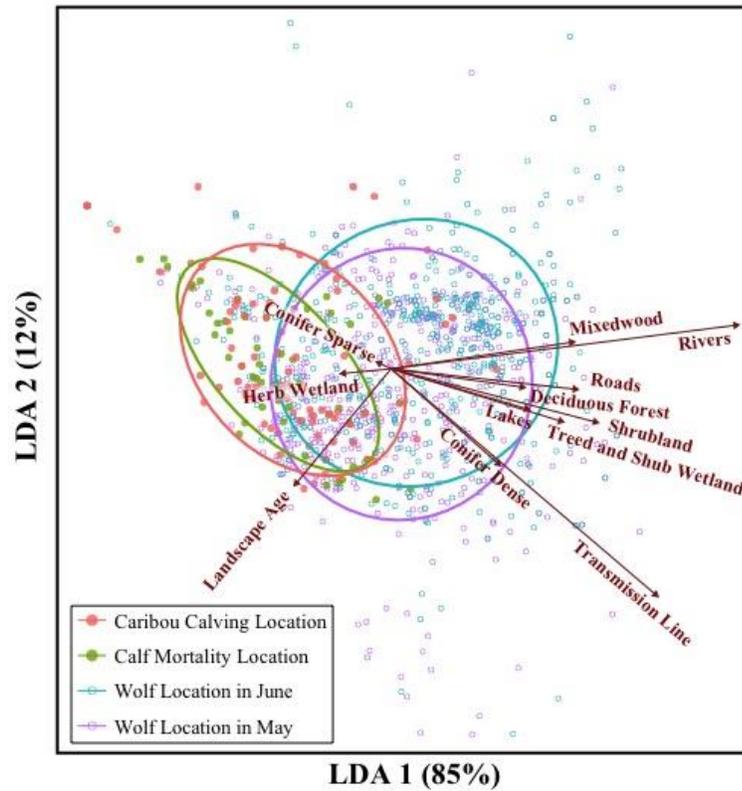


Figure 3.4 Linear Discriminant Analysis of habitat locations (cells from ALCES 1 km database) where caribou calving and mortality occurred (from the step analysis) and landscape cell locations utilized by wolves in May and in June (concurrent with calving and mortality respectively). Structure correlations of the variables with the canonical axes are provided.

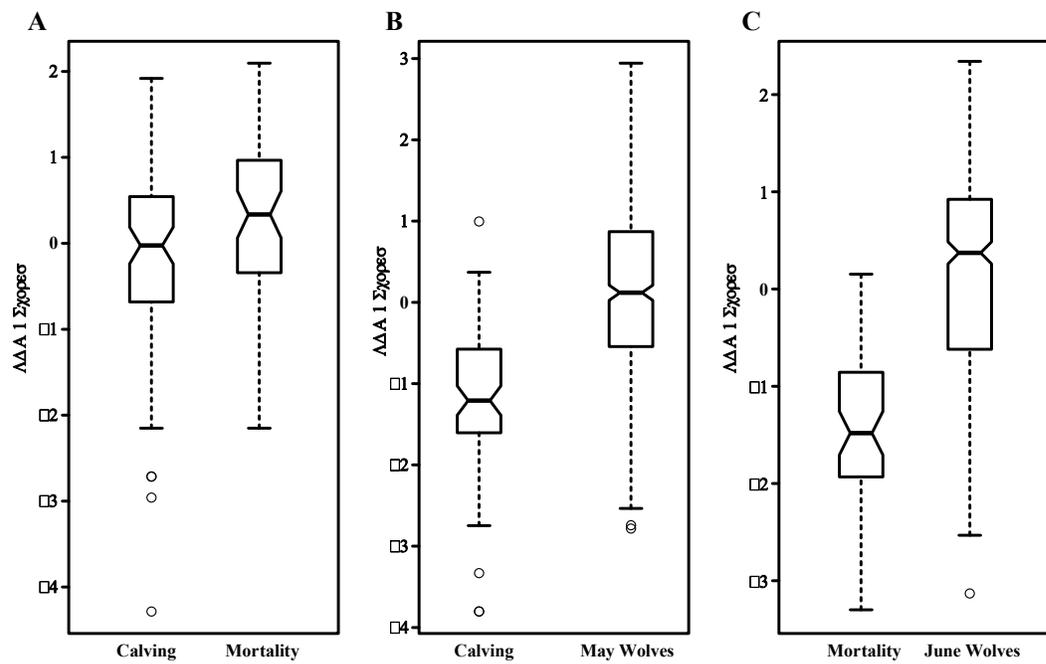


Figure 3.5 Linear Discriminant Analysis boxplots summarizing scores on the canonical variate axis. (A) Comparison of calving vs. mortality habitat (not significant, see text); (B) calving vs May wolf habitat use, and; (C) habitat in which a calf mortality occurred vs June wolf habitat use (the latter two were significant, see text).

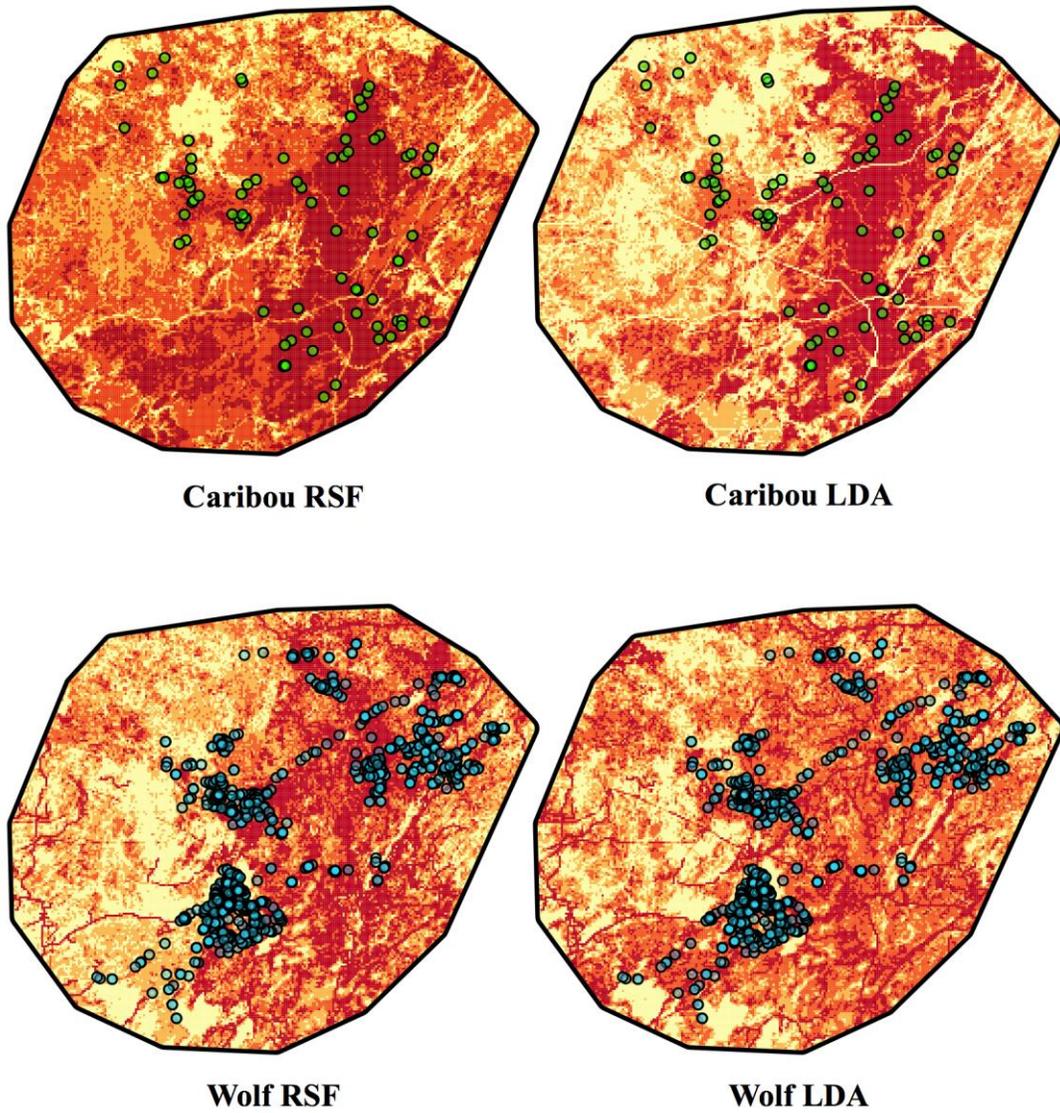


Figure 3.6 Resource selection maps of the study area for the caribou calving period. Caribou maps are based on the RSF and LDA approaches using the step analysis locations for calving and all cells occupied by wolves during the May calving period.

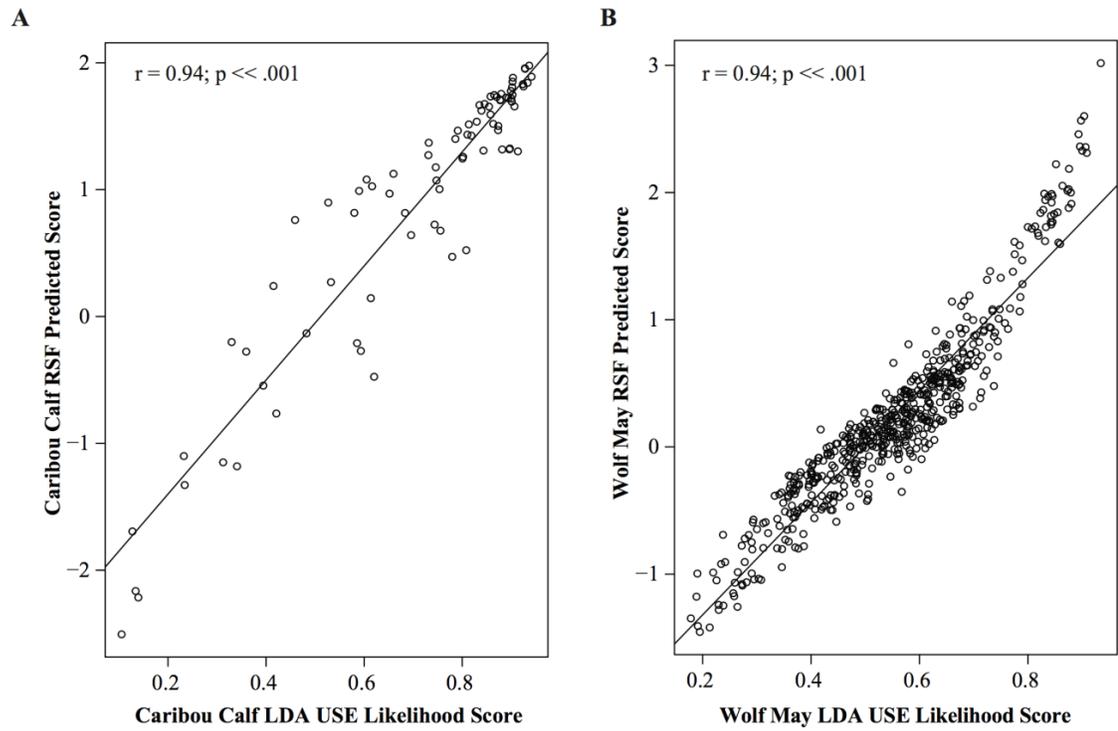


Figure 3.7 Comparison of predicted RSF selection vs likelihood score for “USE” for (A) the caribou calving model and (B) the wolf May habitat model. Correlations between model outputs are significant, the least-squares fit line is provided for reference.



Figure 3.8 Trail camera example for Reed Lake (N 53.3826, W 101.0188) collected during a pre-trial deployment for monitoring predators in calving areas. Bear occurred on August 9, 2009 and caribou on August 12, 2009, three days and two hours apart.

4.0 CONTRIBUTION TO KNOWLEDGE

Environment Canada was mandated in the mid-2000's to lead an inclusive consultation process with the provinces to advance the formulation of recovery strategies for boreal caribou populations across Canada, based on a guiding principle that self-sustaining local populations are essential to improve the likelihood of maintaining boreal caribou in the wild. A cornerstone of the Environment Canada Science Review (Environment Canada 2011) recommended procedures for the estimation of total disturbance within ranges, and the setting of disturbance thresholds necessary to ensure self-sustaining populations. Disturbance metrics included natural disturbance (fire) and anthropogenic development; linear features and area-based disturbances such as forestry and mining. These disturbance thresholds were determined through a national meta-analysis of boreal caribou demographics and disturbance regimes in areas where sufficient data on adult female mortality, recruitment and disturbance existed. These metadata were typically available for boreal caribou populations that were thought to be declining, and have been the focus of intensively funded monitoring in the face of ongoing pressure from resource development. When the sum of these disturbance levels exceeds 65%, risk of apparent competition results in higher than natural rates of adult female mortality and reduced recruitment from predators (mainly wolves), followed by population decline (Environment Canada 2011).

My research focused on expanding the knowledge of the relationship between disturbance and its effect on adult female survival and calf recruitment, and to assess habitat selection of wolves and caribou during the critical calving period. I also wanted

to examine the National Strategies assumptions of boreal caribou persistence in a Manitoba Landscape, knowing that thresholds of disturbance (natural and anthropogenic) are a consideration in regulatory approvals of resource development. I envisioned the lessons learned from this research may provide management options and identify research needs to advance boreal caribou conservation in Manitoba and other boreal landscapes.

Disturbance and Boreal Caribou

The first part of my research dealt with examining disturbance rates in well-defined ranges using current GPS telemetry data. The evaluation ranges identified were generated using the best available data and resulted in modifications to existing provincial range designations representing demographic units that provided optimum comparisons between populations, something which has not been conducted in Manitoba. When comparing Lambda (λ) to disturbance within these evaluation ranges, I found adult female survival rates between 88% and 91% during the study period that were within the range of expected levels found in previous studies in Canada (McLoughlin et al. 2003). Conversely, spring to fall recruitment surveys and associated step analysis demonstrated that calf survival was found to be low (often less than 10 %), with high calf mortality within the first weeks of life. The low recruitment rates found within the evaluation ranges studied, which were below the Environment Canada threshold of disturbance, was not expected. High rates of calf mortality in the first weeks of life were found to be consistent with reported literature (Blake 2006, Dussault et al. 2012, Bastille-Rousseau et al. 2015, DeMars 2015). Low recruitment rates were the main contributor to low λ in the evaluation ranges studied, including the Charron Lake Range, which only has 1%

anthropogenic disturbance. In my study area, anthropogenic disturbance ranged from 1% to 11% and natural disturbance between 3% and 24% and no range studied exceed the 35% total disturbance necessary to suggest a demographic response resulting in expected population decline or λ rates below 1.0.

My work with woodland caribou populations in western Manitoba also augments the scientific record regarding the nature of the relationships between the type of range disturbance and λ , including the persistence of small populations well below the established standard of 300 animals (Environment Canada 2011). As stated, adult survival was very high in 2010 and populations persisted in the face of low recruitment; conversely in 2011 slight improvements in recruitment offset a trend towards higher adult mortality. In all years, λ was below 1.0, however confidence intervals did overlap 1.0.

In examining the influence of disturbance on lambda no statistically significant relationships were observed for the ranges studied. There is, at best, a suggested trend for the influence of anthropogenic disturbance, however, wildfire is the most significant form of disturbance within all of the ranges I studied. This situation is unlike many other published studies where boreal caribou populations are experiencing decline in Canada, where anthropogenic disturbance is high (Hervieux et al. 2013). This suggests that there is value in further investigating how the nature of the disturbance (anthropogenic vs. natural) might influence lambda over a range of disturbance regimes especially at levels that are below and approaching the threshold. While my work showed that disturbance was clearly below the critical thresholds, it also demonstrated that in the face of very high pregnancy rates and high adult survival, calf survival was very low during the years of study and that there was no sensitivity based on disturbance, the source of which was

primarily natural (fire). Added to this, pregnant cows exhibited calving site selection behaviours indicative of calving success. Based on the comparisons of disturbance to λ rates, low calf recruitment cannot be explained by disturbance, and suggests other factors such as predation might be the controlling factor.

Fine Scale Disturbance and Landscape Mosaic

My work also points to a need to appreciate how caribou use their ranges at finer scales through the assessment of disturbance in fuzzy classified ranges. This particular analysis is unique in that I assessed potential range fragmentation in overlapping fuzzy boundaries and found higher rates of disturbance, suggesting potential range fragmentation for sub-populations. I found evidence for separate grouping of caribou on the west and east sides of Highway 10 suggestive of distinct subpopulations. Until this research project, The Bog was treated as a single range (Manitoba Boreal Woodland Caribou Management Committee 2015). Understanding why these animals are at times found in close association with this significant linear corridor and the role it may have in influencing or even affecting these sub populations should be examined. This study found that for the ranges studied, disturbance increased towards the edge of ranges and was typically greatest between ranges. This suggests that the spatial pattern and location of disturbance might have a role in delineating range extent and raises an important question: in general, are the populations that overlap, but where sub-populations can be recognized, experiencing fragmentation from disturbance in overlapping areas? Further study is needed to determine the influence of the spatial pattern of disturbance in population and metapopulation dynamics in these ranges. From a management perspective, we need to understand whether the impact of cumulative disturbance effects

might tend to be multiplicative rather than additive in these areas and whether specialized management prescriptions/mitigations might be required (e.g. restricting the kind and timing of activities taking place, degree of impact allowed). Fuzzy analysis is also recommended as a useful analytical tool for researchers/managers in assigning individuals to subpopulations where ranges overlap.

The potential role of low-level (moderate disturbance) in maintaining a landscape mosaic should be further studied. Concepts of “landscape equilibrium” related to spatial and temporal disturbance patterns and recovery (Turner et al. 1993) are generally not considered in boreal caribou habitat recovery planning. Caribou landscapes in the study area also include populations of moose and other early seral adapted wildlife, and these populations have existed over many decades. Landscape disturbance effects can be measured by rate, size and the life history characteristics of the species (Turner et al. 1993). Focusing on total disturbance without considering the ecological role of disturbance, the spatial pattern of disturbance within and between ranges, the source and type of disturbance, and then treating this continuum of disturbance as a single threshold ‘tipping point’ is likely an oversimplification. Understanding natural and anthropogenic disturbance, and how they relate to the Natural Range of Variability (NRV) resulting from natural disturbance regimes (which vary across ecosystems), is necessary in evaluating cumulative anthropogenic effects and management (Wong & Iverson 2004). Management is better informed by on-going monitoring of the landscape and outcomes better achieved by a broader ecosystem-based approach in maintaining population of terrestrial wildlife on landscapes (Suring et al. 2011). The results of this study suggest

both further study and also the value of a more nuanced approach in management with respect to disturbance.

Wolf and Caribou Habitat Selection

One of the unique contributions of this study was the contemporaneous collection of grey wolf and boreal caribou telemetry for multiple overlapping ranges. This afforded an opportunity to directly compare habitat selection of a predator and prey species during the critical calving and calf rearing period of the latter. In examining the role of predation on caribou one of the challenges is to determine the exact location and timing of parturition and calf mortality (should the calf be predated). This study used recently developed step analysis to predict the locations of these critical events. The locations identified as likely calving sites (calving complexes) were subsequently used for calving habitat selection models and the predicted mortality events were consistent with aerial reconnaissance undertaken as part of recruitment surveys. These results contribute to the growing body of literature demonstrating the utility and reliability of path analytical approaches in telemetry studies.

An important finding of the study is that habitat in which calving and calf mortality occurs was significantly different from habitat utilized by wolves during parturition and calf rearing. Wolves do occur in these areas, as confirmed by trail camera images, but the individuals studied spend little time in this habitat. In fact, wolf habitat selection over the same period showed a divergent trend to that of caribou, with a long trajectory on the discriminant analysis biplot used to visualize selection. Caribou remained in substantially similar habitat over the entire early calf-rearing period, and it was found that the habitat

where calves died was not significantly different from where they were born. This suggests that calves are most often still in calving complexes when mortality occurs. In examining the trends in wolf habitat selection, trail camera imagery and also when plotting wolf telemetry locations on maps of the region, it is clear that wolves are gregarious, but there is little evidence that wolves are selecting habitat in calving complexes.

The results of Resource Selection Function (RSF) analysis and Linear Discriminant Analysis (LDA) modeling also demonstrated separation between wolves and caribou habitat selection during the calving and calf rearing period. Both RSF and LDA are constrained analyses and different forms of the general linear model. RSF is typically the preferred method for determining selection in the literature, as it finds the most parsimonious model of factors, which are normally a subset of candidate parameters. This aids in identifying the key resources of a species and those that might be potentially limiting. However, with the future goal of landscape simulation in mind, I also performed LDA as a method for selection analysis as it provides coefficients for all parameters. This application is by no means new, but because of the predominance of RSF in the habitat selection literature, and the value of comparing these methods for consistency, a dual analytical approach was undertaken. The predictions were comparable and the coefficients were consistent for those parameters that occurred in both RSF and LDA models for the species. In landscape simulation modelling in GIS, where habitat covertypes add up to 100%, having coefficients for all parameters is essential and I found LDA to be suitable to the task. Also, parameterizing the more comprehensive coefficients derived from LDA can be accommodated in landscape and cumulative effects models

such as ALCES and ALCES Online (AO), as opposed to a less robust set of coefficients derived from RSFs.

The findings of this study suggest that the early mortality of neonates was either not related to predation by wolves, and/or, that some other predator was likely responsible or another unstudied autecological factor is responsible. Research from Newfoundland has demonstrated that black bears accounted for essentially half of the predator-related mortality of calves (Blake 2006, Bastille-Rousseau et al. 2015). In a study by Rayl et al (2015), that mapped the spatio-temporal pattern of predator and prey relationships, the authors found that black bears were the major mechanism of population decline through calf predation. This research followed and supported a previous study (Rayl et al. 2014) that suggested, based on caribou telemetry, that bears were a significant predator. The findings in Newfoundland are supported in other jurisdictions; mortality for one Quebec range (Dussault et al. 2012), suggested that bears accounted for 95% of predator-related mortality. Despite these studies, the role of bears has been generally overlooked as a serious predator of caribou calves in most of the rest of Canada. Trail cameras, although not originally deployed to survey bears, recorded more bear activity in calving areas in this study than most other predators and especially more than wolves. Tampering of the cameras by bears, and lack of a true control for predators make assessment of significance problematic, but based on these findings, I highly recommend that work be undertaken to study the extent of the co-occurrence of black bears and calving woodland caribou during the sensitive period from early May to mid-June.

Management and Recovery

The study of small populations presents unique challenges to detect statistically significant effects to changes to either recruitment or survival, thereby increasing the need for vigilance to ensure long-term sustainability. Boreal caribou populations are naturally small and within Manitoba have remained relatively stable at low levels with no evidence of rapid increase, although some decline has been observed. In this study, Lambda had a value very close to 1, thus it does not take many calf or cow mortalities to bring it below that value. Under these conditions, the pattern and concentrations of disturbance within ranges may exert a greater local impact on populations or subpopulations than would be expected. For example, high rates of disturbance in zones of overlap between populations or subpopulation groups, or within functional core areas like calving complexes, could contribute to population or subpopulation isolation, thereby increasing the risk of those isolated groups to stochastic events, or, may increase the vulnerability of caribou calves to higher rates of predator-induced mortality. It must also be noted that it does not take much of an improvement in survival for lambda to exceed 1. It is therefore tempting regardless of the levels of disturbance (or indeed because of high levels of disturbance) to use predator control as a primary tool for management of at-risk populations. Control measures have been implemented in a number of jurisdictions to reduce wolf populations to assist caribou (and in some areas moose) recovery. For the latter species this approach, while subject to public and political debate, may have merit. But I found little evidence that wolves are selecting caribou habitat and may not account for calf mortality, and adult survival was quite high. Wolf culling may have no effect on predation rates of calves, and thus not be a useful tool in achieving desired management outcomes.

The overall results of this research suggest that standards for disturbance as established by the science review (Environment Canada 2011) should not necessarily be universally applicable across all caribou ranges or at least they are an oversimplification of a more complex dynamic. There is no doubt that excessive habitat loss can result in extirpation, but the unquestioning application of threshold levels is problematic. Ecosystem management that considers pattern of disturbance and maintenance of a landscape mosaic within the range of historic natural variability should be the approach used to achieve recovery. It is also clear that other factors and in particular neonate mortality, requires further research as low lambda rates were found in this study in the absence of significant disturbance. As previously stated, predator management approaches focused on wolf culling may have little conservation value. There is little evidence that wolves are primarily responsible for calf mortality, but mortality is high. If predator management is to be considered as part of a recovery strategy, it is highly recommended that a substantial research effort to examine the role of bears be completed first.

4.1 References

- Bastille-Rousseau G, Potts JR, Schaefer JA, Lewis MA, Ellington EH, Rayl ND, Mahoney SP, Murray DL. 2015. Unveiling trade-offs in resource selection of migratory caribou using a mechanistic movement model of availability. *Ecography*. 38(10): 1049-1059. doi: 10.1111/Ecog.01305
- Blake J. 2006. Coyotes in insular Newfoundland: current knowledge and management of the islands newest mammalian predator. Department of Environment and Conservation Wildlife Division, Government of Newfoundland and Labrador, Canada. 11. Available from: www.env.gov.nl.ca/env/publications/wildlife/51f40aed01.pdf
- DeMars CA. 2015. Calving behavior of boreal caribou in a multi-predator, multi-use landscape [dissertation]. Department of Biological Sciences, University of Alberta. 215 p.
- Dussault C, Pinard V, Ouellet JP, Courtois R, Fortin D. 2012. Avoidance of roads and selection for recent cutovers by threatened caribou: fitness-rewarding or maladaptive behaviour?. *Proc Roy Soc B*. 279: 4481-4488.
- Environment Canada. 2011. Scientific assessment to inform the identification of critical habitat for woodland caribou (*Rangifer tarandus caribou*), Boreal Population, in Canada: 2011 update. Ottawa, Ontario, Canada. 102 pp. plus appendices.
- Hervieux D, Hebblewhite M, DeCesare NJ, Russell M, Smith K, Robertson S, Boutin S. 2013. Widespread declines in woodland caribou (*Rangifer tarandus caribou*) continue in Alberta. *Can J Zool*. 91(12): 872-882. doi:10.1139/cjz-2013-0123
- Manitoba Boreal Woodland Caribou Management Committee. 2015. Conserving a Boreal Icon, Manitoba's Boreal Woodland Caribou Recovery Strategy. Manitoba Conservation and Water Stewardship. Winnipeg, Manitoba. 30 p.
- McLoughlin PD, Dzus EH, Wynes B, Boutin S. 2003. Declines in population of woodland caribou. *J Wildl Manage*. 67(4): 755-761. Available from: <http://www.jstor.org/stable/3802682>
- Rayl, N. D., Fuller, T. K., Organ, J. F., McDonald, J. E., Mahoney, S. P., Soulliere, C., ... Murray, D. L. (2014). Mapping the distribution of a prey resource: neonate caribou in Newfoundland. *Journal of Mammalogy*, 95(2), 328–339. <http://doi.org/10.1644/13-MAMM-A-133.1>
- Rayl, N. D., Fuller, T. K., Organ, J. F., McDonald, J. E., Otto, R. D., Bastille-Rousseau, G., ... Mahoney, S. P. (2015). Spatiotemporal variation in the distribution of potential predators of a resource pulse: Black bears and caribou calves in Newfoundland. *Journal of Wildlife Management*, 79(7), 1041–1050. <http://doi.org/10.1002/jwmg.936>

- Suring LH, Gaines WL, Wales BC, Mellen-McLean K, Begley JS, Mohoric S. 2011. Maintaining populations of terrestrial wildlife through land management planning: A case study. *J Wildl Manage.* 75(4): 945-958. Available from: <https://doi.org/10.1002/jwmg.114>
- Turner MG, Romme WH, Gardner RH, O'Neill RV, Kratz TK. 1993. A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. *Landsc Ecol.* 8(3): 213-227.
- Wong C, Iverson K. 2004. Range of natural variability: Applying the concept to forest management in central British Columbia. *BC J Ecosyst Manage.* 4(1): 1-14.