THE ROLE OF ANTHROPOGENIC CORRIDORS IN THE INTERACTIONS BETWEEN WOLVES (CANIS LUPUS), CARIBOU (RANGIFER TARANDUS CARIBOU) AND MOOSE (ALCES ALCES) IN EASTERN MANITOBA

BY
TIM J. DAVIS

A thesis submitted to the Faculty of Graduate Studies of
The University of Manitoba
in partial fulfillment of the requirements for the degree of

MASTER OF ENVIRONMENT

Department of Environment and Geography
University of Manitoba
Winnipeg, Manitoba

THE UNIVERSITY OF MANITBA
FACULTY OF GRADUATE STUDIES
****
COPYRIGHT PERMISSION

A thesis/Practicum submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

Master of Environment

Acknowledgements

To all the people involved in planning, inspiring, funding, and conducting this research, if I can remember them all.

First, Doug Schindler, for encouragement, inspiration, and tremendous in-kind support in the form of a truck, research facilities at the University of Winnipeg, flying telemetry, and accommodating a hectic work schedule. Dr. Walker and my thesis committee, Dr. James Hare, Dr. Brian Kotak, and Mrs. Kelly Leavesley for support, patience, planning, and finding funding.

The Manitoba Model Forest for providing support for securing grants. Manitoba Hydro, and Manitoba Conservation, for their respective research and development, and sustainable development innovation fund grants that supplied project resources, and a generous stipend. Manitoba Conservation also provided in-kind support though lodging in Bissett, helicopter time for surveys and participation in capture and telemetry work. The Manitoba Chapter of the Wildlife Society, and The Manitoba Big Game Trophy Association for bursary funding

All the people who helped in the field. Planning and logistics, Kelly Leavesley, Dennis Brannen, Brian Kotak, and Trevor Barker. Pilots Derek Longley and Justin Seniuk of Prairie Helicopters. Conservation Staff who assisted in field data collection, Kyle Walkowski, Ken Rebizant, Herman Dettman, and others.

To all the people who offered encouragement, support ideas and expertise until it got done, Erin McCance, Jen Ruch, Jeff and Jen Renton, Jamiee Dupont, Candace Vinke, Carla Church, Tracy Granger, Christa Rigney, Rick Baydack, and my family, who never (appeared) to get tired of hearing “no, it's not done yet”.

Abstract

In Manitoba, moose are the preferred prey species, and occupy similar landscapes to caribou. To reduce predation, caribou separate themselves from moose by selecting habitat less suitable to moose. Corridors linking caribou and moose habitat can facilitate access to caribou.

The relationship between species and linear features was assessed through radio telemetry and surveys along natural and anthropogenic corridors. Surveys were used to determine distribution of all species relative to each other, and their proximity to linear features. Wolf scat was used to determine diet. Corridor surveys showed an even distribution of use between natural and anthropogenic corridors. Surveys showed association between moose and wolves, but not caribou. Wolves and moose were closer to river and road features and farther from lakes than caribou. Wolf diet included moose and beaver, not caribou.

Caribou demonstrated partitioning from moose. Anthropogenic corridors appear to be additive, contributing to an overall wolf travel network.

Table of Contents

Acknowledgements .... **ii**
Abstract .... **iii**
Table of Contents .... **iv**
List of Tables .... **v**
List of Figures .... **vi**
Chapter 1: General Introduction **1**
    Wolves 1
    Caribou 3
    Moose 4
    Foraging Theory 5
    Human Development 8
    Objectives and Hypothesis 8
Chapter 2: Study Area **11**
    Geography/Location 11
    Natural Landscape 12
    Anthropogenic Landscape 20
Chapter 3: Spatial Distribution of Wolves, Moose and Caribou. **32**
    Abstract 32
    Introduction 33
    Methods 44
    Results 50
    Discussion 68
Chapter 4: Moose, wolf and caribou relationship to linear features **74**
    Abstract 74
    Introduction 76
    Methods 84
    Results 101
    Discussion 114
Chapter 5: Conclusion **120**
    Summary 120
    Management Implications 121
    Future Study 125
References Cited **127**

List of Tables

Table 3.1. Multispecies survey observations by year. 51

Table 3.2. Results of regression analysis of species pairs. 63

Table 3.3. Composition of wolf scat samples based on prey occurrence. 68

Table 4.1. Distance surveyed and track occurrence by feature type. 102

Table 4.2. Proportion of features surveyed and track occurrences. 103

Table 4.3. Distance of actual and random moose track locations to linear features. 103

Table 4.4. Distance of actual and random caribou locations to linear features. 104

Table 4.5. Distance of actual and random wolf locations to linear features. 106

Table 4.6. Measurements and grouping of radiocollared wolves. 107

Table 4.7. Median proximity to features by wolf. 110

Table 4.8. Summary statistics of proximity to features of wolf locations. 110

Table 4.9. Monthly Median proximity to feature classes. 111

Table 4.10. Median values of proximity to feature classes by wolf grouping. 112

Table 4.11. Median values of speed and proximity to linear features between periods. 113

List of Figures

Figure 1.1. Sigmoidal curve of prey selection relative to encounter rate. 6

Figure 1.2. Gain functions. 7

Figure 2.1. Study Area Boundaries, Game Hunting Area 26 and Multi-Species Survey Area.. 11

Figure 2.2. Climate Chart for Bissett, MB... 13

Figure 2.3. Regional Geology. 14

Figure 2.4. Ecoregion and Ecodistricts.. 15

Figure 2.5. Boreal Forest Landscape in Nopiming Park.................................. 16

Figure 2.6. Forest fire history 1928-2002. 17

Figure 2.7. Communities in the study area. 21

Figure 2.8. Linear feature access in the study area... 23

Figure 2.9. Historical forest harvest to 1980... 24

Figure 2.10. Recent forest harvest for 1991-2007. 25

Figure 2.11. Experimental Harvest area relative to caribou core area............... 26

Figure 2.12. Mining and exploration. 28

Figure 2.13. Registered Traplines. 30

Figure 2.14. Provincial Parks.. 31

Figure 3.1. Aerial multispecies survey area and transects. 46

Figure 3.2. 2006 Multispecies survey track observations by species. 51

Figure 3.3. 2008 Multispecies survey track observations by species. 52

Figure 3.4. 2009 Multispecies survey track observations by species. 53

Figure 3.5. 2006 Caribou track density... 54

Figure 3.6. 2008 Caribou track density. 55

Figure 3.7. 2009 Caribou track density. 56

Figure 3.8. 2006 Moose track density. 57

Figure 3.9. 2008 Moose track density. 58

Figure 3.10. 2009 Moose track density. 59

Figure 3.11. 2006 Wolf track density. 60

Figure 3.12. 2008 Wolf track density. 61

Figure 3.13. 2009 Wolf track density. 62

Figure 3.14. Overlain density contours of pooled species density, 2006-09. 63

Figure 3.15. Scatterplot showing moose vs. caribou tracks per km^2. 64

Figure 3.16. Scatterplot showing wolf vs. caribou tracks per km^2. 65

Figure 3.17. Scatterplot showing moose vs. wolf tracks per km^2. 66

Figure 3.18. Prey species by proportion of samples occurring excluding kill site samples. 67

Figure 3.19. Wolf killed moose from Manigotagan Lake, January 2008. 68

Figure 4.1. Survey transect routes by survey method. 86

Figure 4.2. Wolf Capture Sites, indicating date of capture and collar type. 88

Figure 4.3. Helicopter net gunning capture of wolf. 89

Figure 4.4. Captured wolf. 90

Figure 4.5. Movement path of wolf equipped with a GPS tracking collar. 96

Figure 4.6. Movement path of wolf showing analysis periods and excluded areas. 99

Figure 4.7. Movement path of the wolf during the sedentary period. 100

Figure 4.8. Moose proximity to linear features. 103

Figure 4.9. Caribou proximity to linear features. 104

Figure 4.10. Wolf proximity to linear features. 105

Figure 4.11. Radiotelemetry locations and Minimum Convex Polygons. 107

Figure 4.12. Line chart of monthly median distance to feature classes. 110

Figure 4.13. Wolf proximity to feature classes. 111

Figure 4.14. Proximity to Natural vs. Anthropogenic Features in the Sedentary Period. 113

Figure 4.15. Proximity to Natural vs. Anthropogenic Features in the Nomadic period. 114

Chapter 1: General Introduction

The use of naturally occurring linear features as travel corridors has been observed in wolves (Fritts and Mech, 1975). The corridors created by humans (anthropogenic corridors) have also been used by a number of species, including wolves (Mech and Boitani, 2003). However, anthropogenic developments, and their associated linear corridors also prove to be detrimental to a variety of wildlife, both directly and indirectly (Bradshaw et al., 1997; Thiel, 1985; Wydeven, 2001; James et al., 2004; Foreman and Alexander, 1998), including wolves (Kohn, et al., N.D.). The value of these features to wolves has not been quantified, though utilization by wolves is considered a major factor in many species' aversion to roads and other anthropogenic corridors, both by direct mortality and alterations in behaviour due to increased predation risk (Wolff and Van Horn, 2003; Ferguson et al., 1998; Lima, 1997; Dukas and Clark, 1995).

Wolves

Wolves are large terrestrial carnivores that are as varied in their preferred prey as they are in their global distribution (Mech and Boitani, 2003). Primarily focusing on ungulates and other large mammals such as moose, deer, caribou, elk, and bison (Messier, 1985; Pimlott, 1967;Carbyn, 1983), wolves have been known to feed upon livestock (sheep, cattle, pigs) (Meriggi et al., 1996), and animals from voles to black bears (Voigt et al., 1976).

The classification of wolves has been a subject of considerable debate, where recent genetic evidence has provided insight into the delineation and definition of the taxa (Wilson et al., 2003, 2009; Mech, 2010). Historically, in Canada, there were considered to be eleven subspecies of the wolf species (*Canis lupus L.*), called the gray wolf or timber wolf (Banfield, 1974). In more recent studies, eastern wolves have been reclassified as a separate species (*Canis lycaon*), that evolved independently of the gray wolf, now being referred to as the Western Wolf (Wilson, 2009).

Wolves are distributed through much of the globe, and typically occur where large ungulates such as deer, moose, and caribou are found (Young and Goldman, 1944). In North America, wolves were historically distributed across the continent until their extirpation from much of the continental United States. During this time, grey wolves were eliminated from all states except Alaska and Minnesota Mech and Peterson, 2003). Similarly, wild bison (*Bison bison*) were eliminated from the plains during this time, where they were a primary prey species for wolves, and likely represented the largest prey biomass in North America (Van Ballenberghe, 1975).

Wolves will focus on the most available/abundant food source, depending on the location, barren-ground caribou in the arctic, deer and beaver in southern and eastern Canada, and moose in north-western Canada. Wolves consume approximately 0.7 moose per month per wolf (Bergerud et al., 1983) or approximately 9 moose per wolf per year. Mech and Peterson (2003) summarized known estimates of wolf kill rates for primary prey species. Caribou were consumed at 2.5-10.2 kg/wolf/day, or 18 caribou/wolf/year. Deer were consumed at rates of 0.6-6.8kg/wolf/day, or up to 12 deer/wolf/year. Moose were consumed at rates of 1.8-24.8kg/wolf/day, or 9 per wolf/year, similar to estimates from Bergerud et al. (1983).

Wolf packs are typically composed of parent-offspring groupings (Van Ballenberghe, 1975), and yearling members often disperse as each succeeding generation grows up. Lone wolves that disperse in this way may travel extensively and form or join new packs. Pack sizes may range from as few as two, to over twenty individuals (Mech and Boitani, 2003). Pack behaviour was thought to be a mechanism to enable wolves to kill large prey, however, lone wolves have been observed to successfully bring down moose, deer and elk (Mech, 1983), and pack size is no longer thought to be beneficial to wolf hunting success beyond four wolves (MacNulty, 2012).

Caribou

Boreal woodland caribou (*Rangifer tarandus caribou* Gmelin) are members of the *Cervidae*, or deer family (Banfield, 1974). Caribou occupied North America prior to the Wisconsin glaciation, with woodland caribou becoming isolated from barren-ground populations in southern refugia during glaciation (Roed et al, 1991).

Woodland Caribou prefer older coniferous forest and bog habitat, based on lichen growth and accessibility, where younger stands tend to contain less lichen, made less accessible by winter snow (Schaefer and Pruitt, 1991). Forest succession is important on the landscape scale for caribou habitat, as stands reach greater ages, lichen production eventually declines (Schaefer, 1988).

Terrestrial and epiphytic lichens compose the majority of the caribou diet throughout the winter, though following snow melt caribou will feed extensively on nitrogen rich forbs, leaves, and sedges to increase their protein intake (Stardom, 1975). Male woodland caribou generally outweigh females by approximately twenty-five percent, weighing up to six hundred pounds, and are the largest of the caribou subspecies (Banfield, 1974). The coat of the caribou consists of hollow hairs with insulating properties, and the crescent shaped hooves and large dewclaws allow the foot of the caribou to splay out and provide better support for walking on snow (Banfield, 1974). Caribou calve during the spring, and almost always produce one calf per female each year (Banfield, 1974). Woodland Caribou in Manitoba congregate during winter months, and disperse in the spring and summer, when calves are born (Darby, 1979). This is thought to be a predator avoidance strategy (Bergerud et al., 1990). Winter group sizes range from two to over seventy (Barker, 2007, Pers. Comm.), and summer groupings rarely exceed two caribou. Wolves are the primary predator of Caribou, although Wolverine (*Gulo* gulo), Golden Eagle (*Aquila chrysaetos*), and Lynx (*Lynx Canadensis*) have been known to prey on them as well (Kelsal, 1968). Bears are also an occasional predator of caribou, Polar Bears (*Ursus maritimus*) have been known to predate arctic caribou and Svalbard reindeer (Derocher et al., 2000), and Black Bear are thought to be a major cause of calf mortality (Rettie and Messier, 1997).

Moose

Moose (Figure 1.5) are the largest members of the deer family in North America, and are widely distributed across Canada and Manitoba (Banfield, 1974). Moose range extends across the boreal forest regions of North America, and moose are adapted to the disturbance driven succession pattern of the boreal forest. Moose utilize a variety of habitat types for food and protection. Young deciduous forest and shrubs are the primary food source for moose in winter, while aquatic vegetation provides additional food and nutrients (sodium in particular) in the spring and summer (Belovsky, 1978). Older coniferous forest adjacent to food sources provide cover habitat and browse when snow is deep (Telfer and Kelsall, 1984).

The roles of early seral stages in moose habitat show its use of fire driven succession, or the similar effects of logging (Krefting, 1974; Telfer, 1974; Potvin et al., 2005). Disturbance areas selected by moose are determined by the distance to available cover and substantial clearcuts that may provide food habitat may not be utilized. Ontario Natural Resources (1998) used two hundred meters as an appropriate distance to cover to be maintained in cut blocks. Potvin et al. (2005) found that cut blocks became valuable moose browse habitat within ten years of being cut. Moose are sensitive to overheating, both in summer and winter, and utilize thermal cover to regulate their temperature in summer and by reducing their activity in winter (Timmerman and McNichol, 1988).

Moose hunting success was observed to be 19-38% by Mech (1998). Mech (1970) described the hunting outcomes of 131 encounters with moose along all stages of the hunting process. Of the total, wolves only caught up to 53 moose (41%), and only managed to kill 6 (5%).

Foraging Theory

Early study of foraging theory uses two basic models, the prey model, where prey items are discrete objects, and patch models, where contiguous units of food or habitat space are utilized (MacArthur and Pianka, 1966). General prey models offer a prey selection probability based on handling time (time spent on a prey item), how often the prey is encountered, and the net gain in energy (Charnov and Orians, 1973). Applying this concept to a two prey choice, Krebs et al. (1978) tested the threshold at which the encounter rate of superior prey dictated ignoring a lesser prey items that would previously have been taken (figure 1.1). Where caribou are almost exclusively encountered, as would be the case in the arctic (Kelsall, 1968, figure 1.1, a), they would exclusively be selected, while in the boreal, they might be more flexible in considering moose (figure 1.1,b), and where moose occur predominantly, caribou might be ignored entirely (figure 1.1, c).

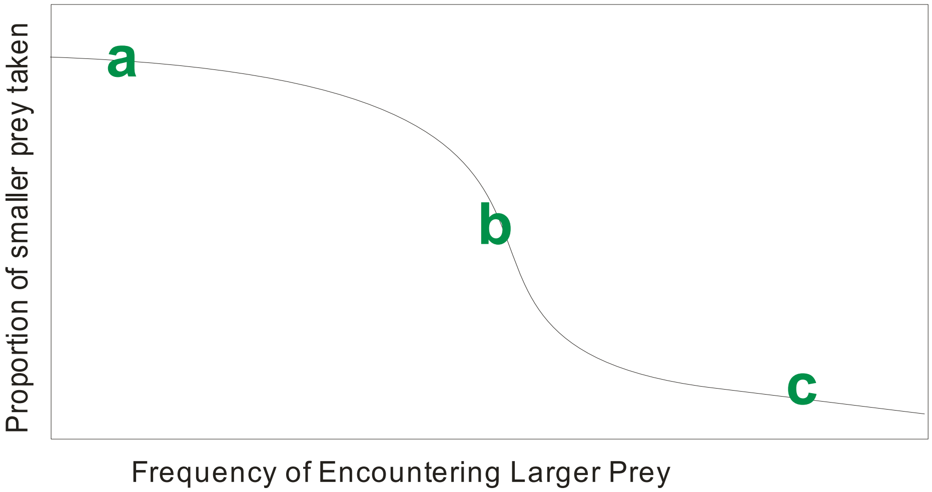


Figure 1.1. Sigmoidal curve of prey selection relative to encounter rate. Adapted from Stephens and Krebs, 1986. a) Barrenground caribou range; b) evenly distributed caribou-moose population; c) moose dominated forest.

Herbivores occupy patches when foraging, leading to net energy gain over patch residence time until the patch is depleted (Stephens and Krebs, 1986). While there is some variety in the energy gain function, it typically follows a broad pattern of increase over time to an extent as food is consumed while utilizing a patch (Figure 1.2a). Wolves however, have no gradual increase when foraging, and an encounter shows no gain function until the pursuit is successful, at which point, the gain function immediately maximizes (Figure 1.2, b).

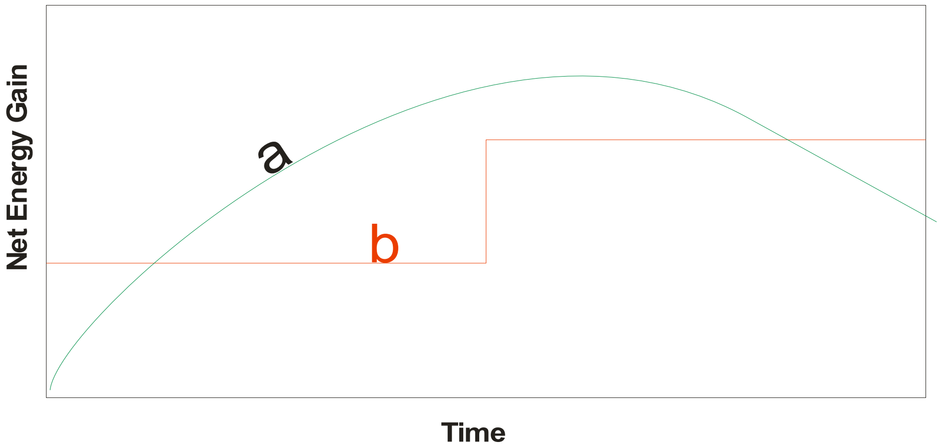


Figure 1.2. Gain functions. From Stephens and Krebs, 1986. a)humped gain of patch use by a herbivore; b)prey gain function of a predator

Owen-Smith et al. (2010) define foraging activity as an “area restricted search” for food or forage. It is understood that foraging activities are interspersed with periods of rest or engaging in other activities, such as migration to a new area or fleeing from predation (Owen-Smith et al. 2010).

The presence of predators on the landscape itself creates indirect effects on prey, where the risk of predation increases the need for vigilance (Lima and Dill, 1990). Vigilance behaviour while feeding can reduce the quantity and quality of browse by both reducing feeding rates to maintain alertness, and the use of sub-optimal habitat patches with greater security value (Holmes, 1991). The appearance of predators may have lasting effects, where the prey species remains in hiding well after the predator has moved on (Sih and Krupa, 1992). Desperation also drives risk taking behaviour, where sated prey are far less likely to forage in risk prone habitat than hungry prey (Gotceitas and Godin, 1991; Sweitzer, 1996).

Human Development

Wolves cannot subsist on the low densities of woodland caribou (a pack of five wolves could consume the Owl-Flintstone caribou in one year, based on the above estimates), however, the overlap of moose distribution will result in incidental caribou mortality (Messier, 1985). Anthropogenic disturbance can influence this. Moose prefer younger successional forest, and may occupy caribou habitat recently altered by fire or other disturbance (Rempel et al., 1997). Forest harvesting can create favourable moose habitat, resulting in an increase in both moose, and moose-dependent wolf populations. Caribou separate themselves spatially from moose by habitat selection as an anti-predation strategy (James et al., 2004). Forest harvesting into caribou habitat may increase predator access from adjacent moose habitat into previously unavailable caribou refuge areas (Cumming and Beange, 1993). As a result, forest harvesting can be doubly troubling to caribou, as it may increase access for wolves, as well as increasing the number of wolves present on the landscape.

Objectives and Hypothesis

As a threatened species, the conservation of boreal woodland caribou is critical, and research gaps must be addressed. Carnivores, as an apex predator with typically large home ranges, and complex habitat requirements, are an umbrella species that can be used as both a management tool and conservation target (Noss et al., 1996). Moose, as the primary prey species in the study area, are central in the ecology of both wolves and caribou. Managing for caribou protection, and moose population stability requires further understanding of the role of wolves, and their use of corridors, both anthropogenic and natural.

The objectives of this project are to assess the relationship of wolves, moose and caribou in the Owl-Flintstone caribou range;

Compare the relative use of linear features by wolves, and distance to features by moose and caribou.

Hypotheses

If caribou are able to partition themselves from moose and wolves on the landscape, predation on caribou should not be evident in diet assessment, thus Hypothesis A:

H_0a: Wolf distribution will not be significantly related to moose or caribou distribution

H_1a: Wolf distribution will be significantly related to moose distribution compared to caribou distribution;

And hypothesis B:

H_0b: Wolf diet will include both moose and caribou, or;

H_1b: Wolf diet will not include caribou

.

Wolves are expected to use anthropogenic corridors to the same extent that natural corridors are used, rather than preferring one type to the other, thus Hypothesis C:

H_0c: Track observations will occur on anthropogenic corridors at the same proportion that they occur on natural corridors or;

H_1c: Track observations will occur proportionally more frequently on natural features (aversion to anthropogenic corridors) or;

H_2c: Track observations will occur proportionally more frequently on anthropogenic features (preference for anthropogenic features).

Indirect use of corridors as determined by GPS and radio telemetry data was compared between feature types. Wolves were expected to be equally distributed in relation to natural and anthropogenic features, thus Hypothesis D:

H_0d: Telemetry locations will not be significantly closer to natural or anthropogenic features or;

H_1d: Telemetry locations will be significantly closer to natural features than to anthropogenic features or;

H_2d: Telemetry locations will be significantly closer to anthropogenic features than to natural features.

The relative distribution of wolves and prey species determined from aerial survey are expected to be uniformly located to linear features, thus Hypothesis E:

H_0e: Wolf, caribou, and moose observations will not be significantly nearer or farther than a random distribution of points or;

H_1e: Wolf distribution will be significantly closer than random to linear features and closer than caribou distribution.

Chapter 2: Study Area

Geography/Location

The study area lies in eastern Manitoba, between Lake Winnipeg and Ontario, from 96°25’00” W by 51°12’00” N to 95°09’00”W by 50°08’00”N. The primary study area is within Game Hunting Area 26, which contains the Owl-Flintstone caribou range, and is regularly used as a defining area for wildlife surveys in the area (Figure 2.1). Different aspects of the study involved larger and smaller areas than this, for instance, where wolves traveled beyond the study area. A select portion of the study area was the subject of repeated multi-species surveys centered on the winter portion of the Owl-Flintstone caribou range and an adjacent experimental forest harvesting area (Figure 2.1).

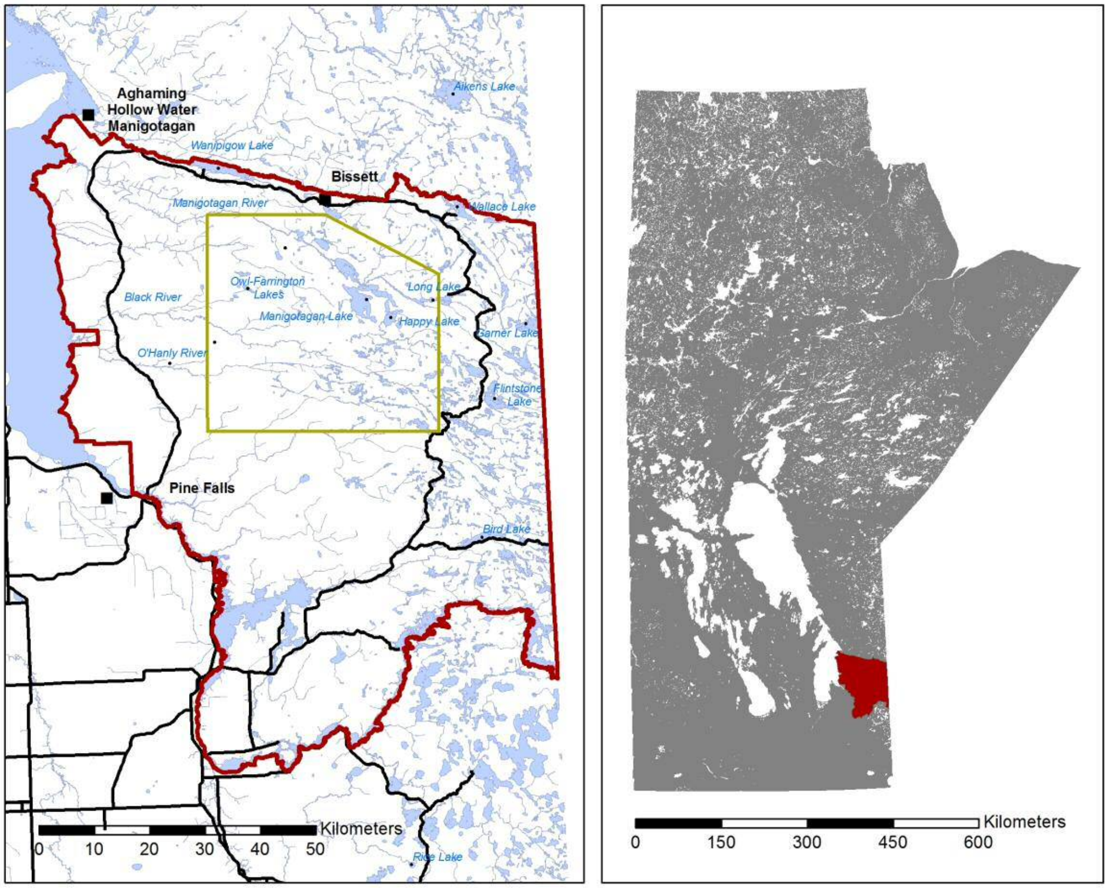


Figure 2.1. Study Area, Game Hunting Area 26 and Multi-Species Survey Area.

Natural Landscape

Climate

Mean monthly temperatures in the study area average just over one degree above freezing (1.36 ^{o}C), ranging 37.3^{o}C from -19^{o}C (January mean) to 18.3^{o}C (July mean). Average daily temperature during the winter months (1 December to 31 March) was -14.4^{o}C, and average daily summer (1 June to 31 August) temperature was 17.1^{o}C (Environment Canada, 2000). Total annual precipitation was 430mm of rain and 134cm of snowfall. Average monthly snowfall during the winter was 21cm, and snowfall is the predominant precipitation from November to March (Figure 2.2).

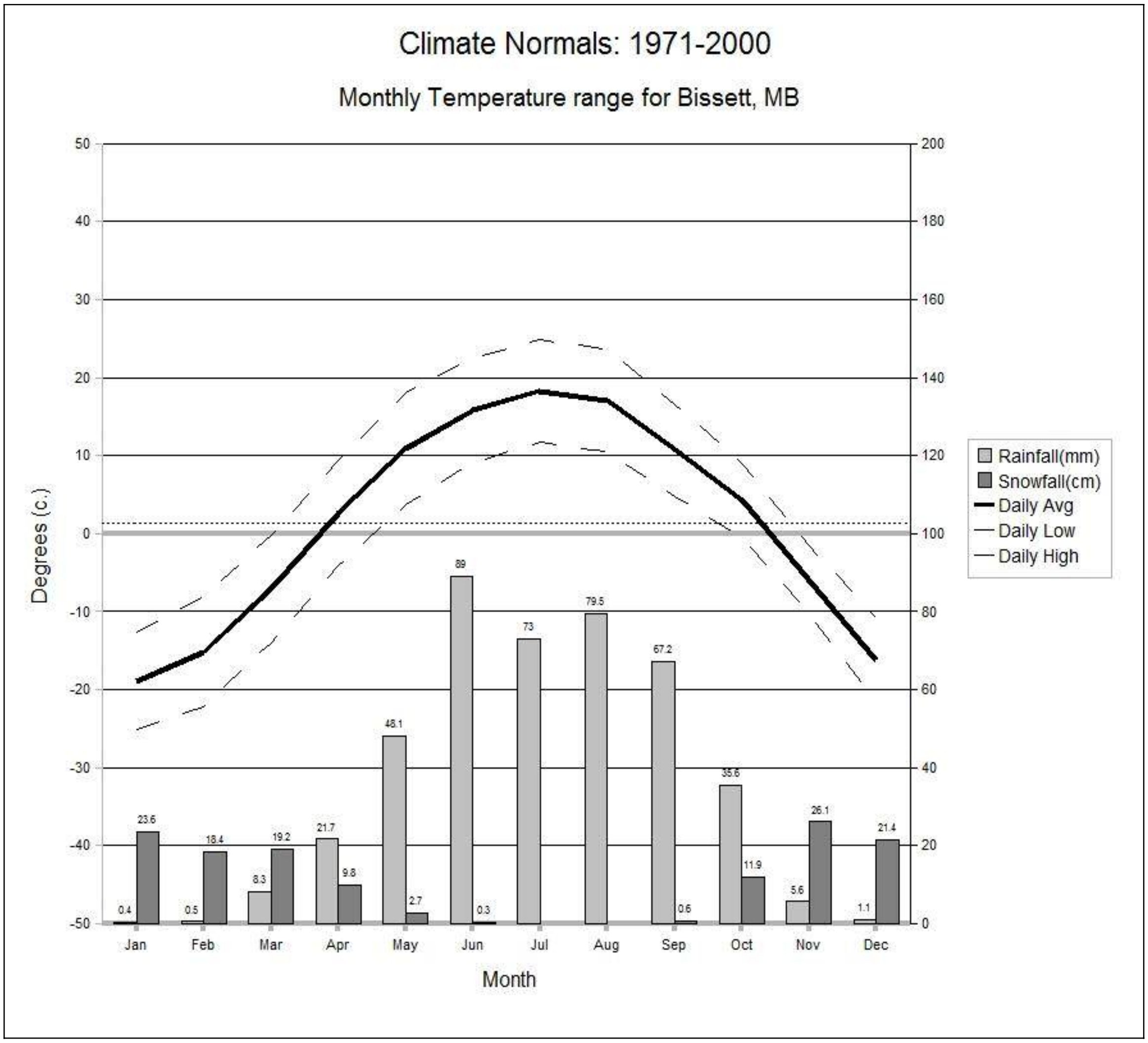


Figure 2.2. Climate Chart for Bissett, MB. Environment Canada, 2000

Geology

The study area lies upon the Superior Province of the Precambrian shield geological region (Manitoba Mines, Energy and Innovation, 2009). The area is primarily composed of metamorphosed early intrusive rock (tonalite, gneiss, gabbro, granite), late intrusive rock (granite, granodiorite), and the metavolcanic and metasedimentary rock found in the Rice Lake Group (basalt, greywacke, conglomerate, ultramafic rocks) located along the Wanipigow River corridor (Bannatyne and Teller, 1984, Figure 2.3).

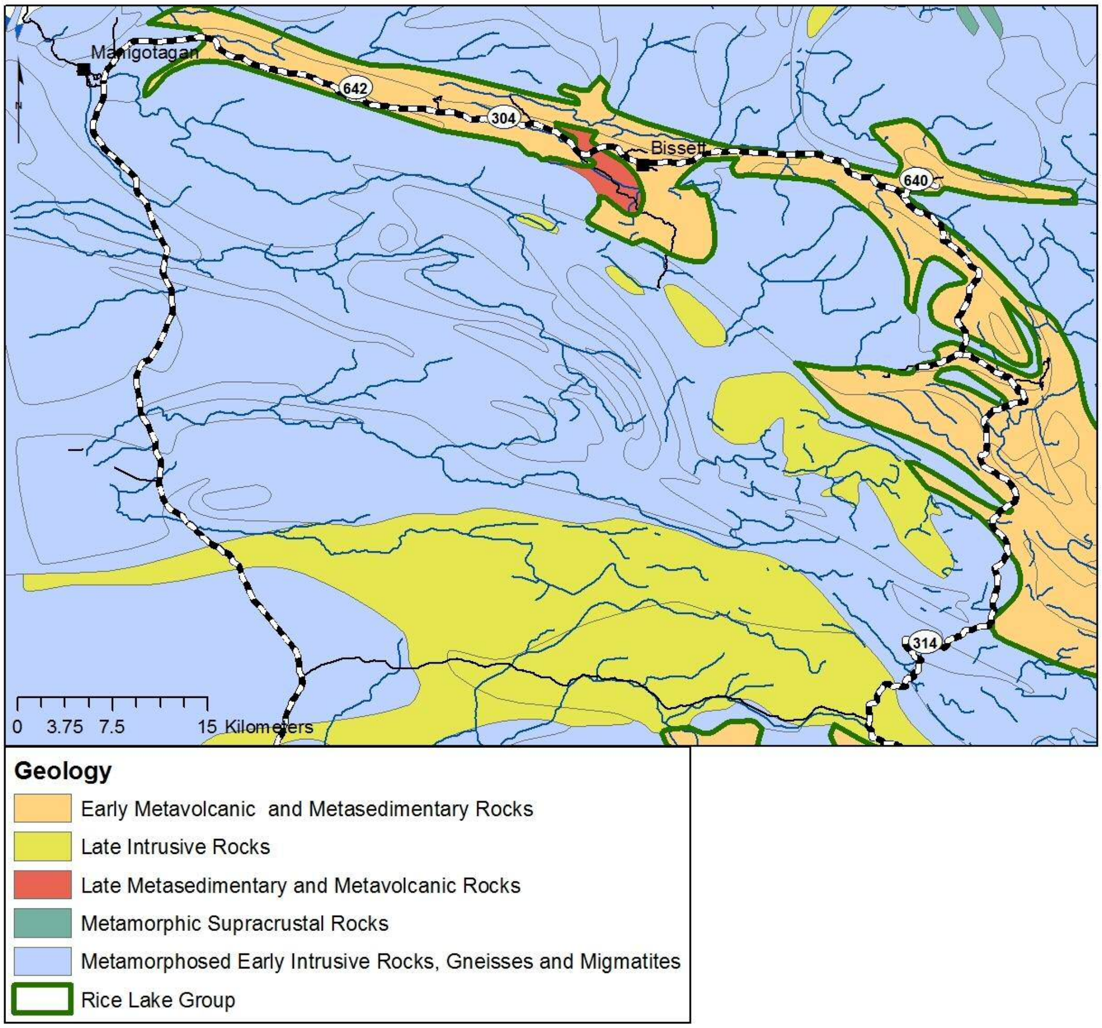


Figure 2.3. Regional Geology. Data from Manitoba Mines Energy and Innovation, 2009

Vegetation

The Study area is within the boreal forest ecozone (Ecological Stratification Working Group [ESWG], 1995), dominated by coniferous forest, exposed bedrock, and deep organic deposits (Scott, 1995). The region is classified as the Lac Seul Upland Ecoregion, and is composed of three smaller Ecodistricts (Figure 2.4). The study area is located within two of these Ecodistricts, the Wrong Lake Ecodistrict and the Nopiming

Ecodistrict (ESWG, 1995).

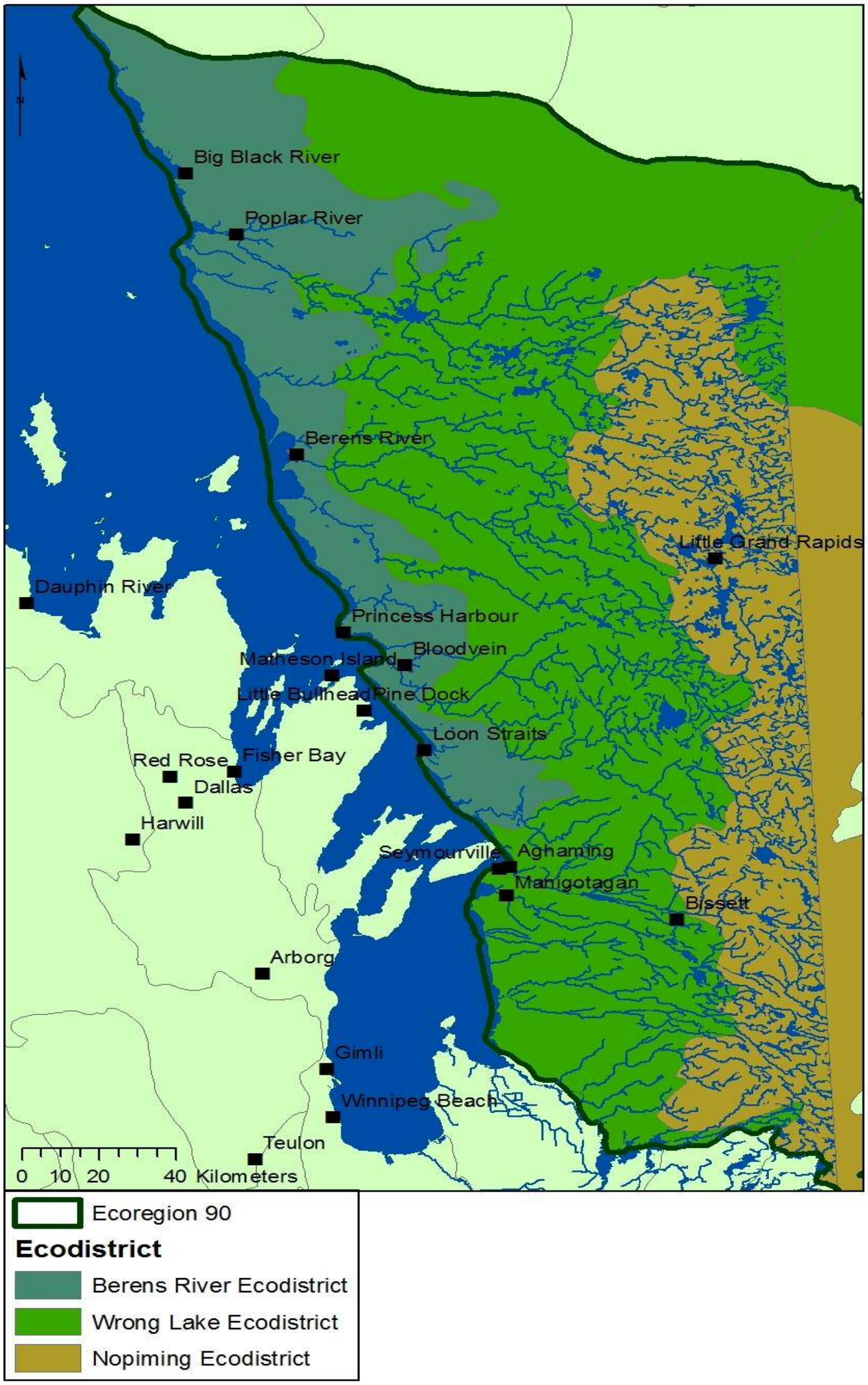


Figure 2.4. Ecoregion and Ecodistricts of the study area. ESWG, 1995

The Nopiming Ecodistrict is dominated by granite outcrops with thin glacial deposits and remnant beaches and gravel ridges from glacial Lake Agassiz (Smith et al., 1998). The sparse soil cover in the district is largely organic, with localized occurrences of dystric brunisols and gray luvisols. The dominance of exposed bedrock and thin, well drained soils is reflected in the typical vegetation, Jack Pine (*Pinus banksiana*), and lichen dominated ground cover (Figure 2.5)(Smith et al., 1998). Sphagnum moss-dominated bogs compose the wetland areas in the district, with Black Spruce (*Picea mariana*) being the typical tree cover (Smith et al., 1998). Balsam Fir (*Abies balsamea*), White Spruce (*Picea glauca*), and Trembling Aspen (*Populus tremuloides*) occupy areas with deeper soils (Smith et al., 1998).

Figure 2.5. Boreal Forest Landscape in Nopiming Park. T. Davis, 2004

The Wrong lake Ecodistrict is an intermediate area between the Nopiming district, and the colder, wetter Berens River Ecodistrict to the west, which is dominated by low lying bog and fen formations (Smith et al., 1998). The occurrence of thicker layers of glaciolacustrine till and mineral soils, and greater amounts of low lying organic deposits cause Black Spruce to be the dominant tree species, with Jack Pine and Trembling Aspen occurring less frequently, on upland sites (Smith et al., 1998).

Disturbance (Fire)

The boreal forest is a fire driven ecosystem, where both animal and plant species rely on forest fires to feed or propagate. Fire history in the study area has been recorded since 1928. From 1928 to 2002, approximately 450,000 hectares or 50.6% of the Forest Management License 1 area, which approximates the GHA 26 area was burned, largely in the Nopiming ecodistrict, which contains more upland forest than the Wrong Lake ecodistrict, which contains extensive wetland complexes. On an annual basis, the average burn area is approximately six thousand hectares (0.6% of the land area). Based on this annual burn period, the entire area (not counting areas not subject to major fire disturbance) would burn in approximately two hundred years. Fires in earlier decades tended to be much larger, while extensive fire suppression in more recent years has prevented most catastrophic large fires from occurring. Some exceptions include major fires in the 80s and 90s around Beresford Lake and Manigotagan (Figure 2.6)

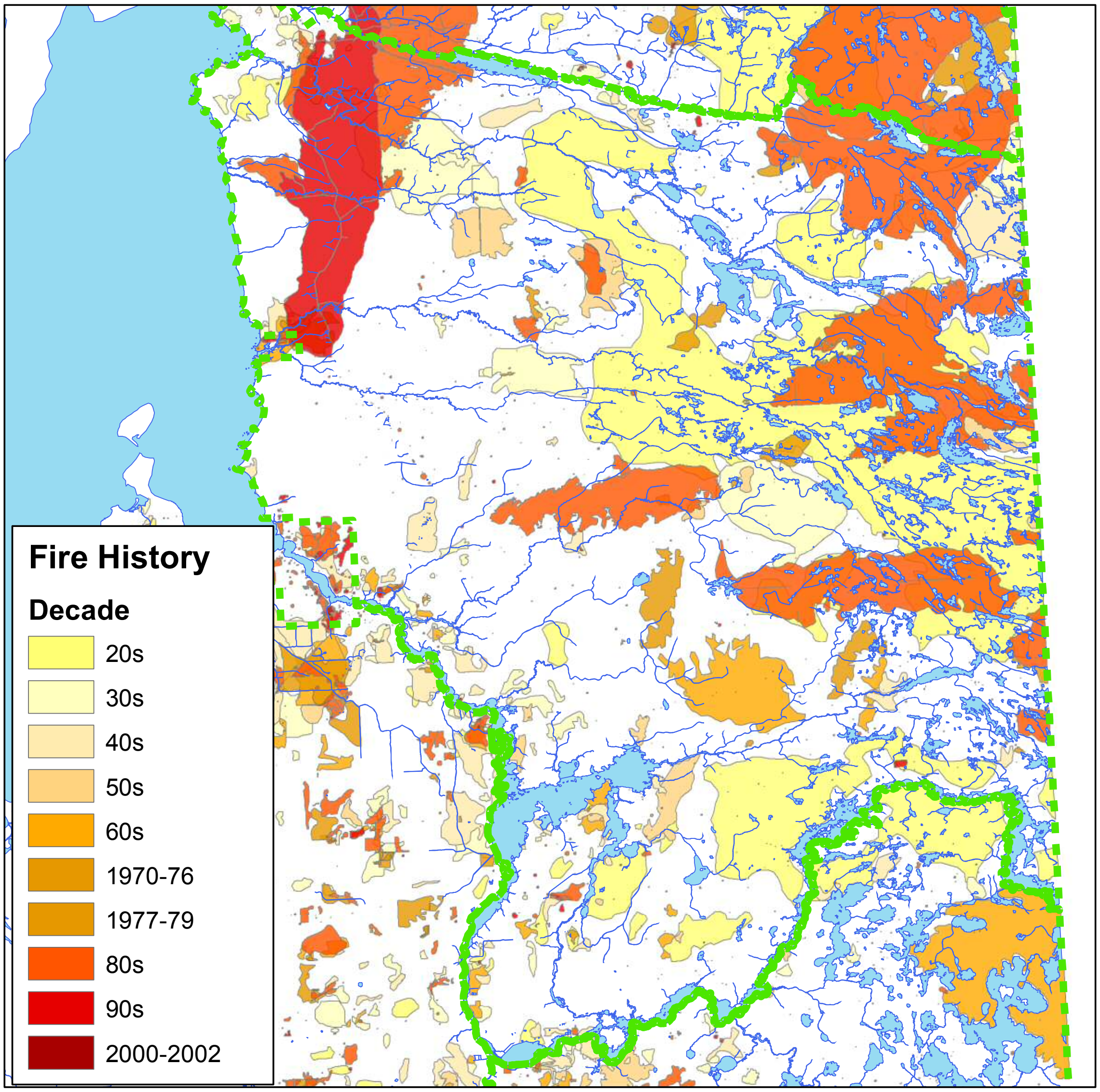


Figure 2.6. Forest fire history of the study area, 1928-2002.

Wildlife

The study area supports a variety of wildlife (MC, 2009) including over 167 bird species (WRCS et al., 1997). Big game species include Black Bear (*Ursus americanus*), Wolf, Moose, White-tailed Deer (*Odocoileus virginianus*), and woodland caribou.

Wolves

Wolves in the region have not been extensively studied or monitored until recently, with most observations being incidental during moose or caribou related surveys. In 2007 a dedicated wolf survey was flown in the northern portion of GHA 26, containing the Owl-Flintstone caribou winter range, observing 38 individuals, and additional unassociated tracks (Barker, Pers Comm.). Based on the minimum count for the surveyed area, the wolf population density is approximately 11 wolves/1,000km^2. The 2007 wolf survey was also conducted in game hunting area 17A (adjacently north of the study area), and a minimum count of 32 wolves led to a density of 7.6 wolves/1,000km^2. Observations during and prior to the study observed wolves in groups of one to seven, while trappers in the area had observed groupings of as many as 21 wolves (Weiss, Pers. Comm).

Moose

Moose occur throughout the study area, and are the primary target of hunters, as well as wolves. Surveys for moose have occurred somewhat regularly in GHA 26, beginning in 1993, where the population was estimated at 1,657 moose, while a 2000 survey estimated 2,350 moose. Surveys in 2006 and 2010 indicated decreased populations of 1,553 and 823 moose, respectively (Manitoba Model Forest, 2011).

Caribou

The Owl-Flintstone Caribou range occupies a central portion of the study area. The winter range is located towards Owl Lake in the west, and the summer range in the east is located nearer to Flintstone Lake and Nopiming Park. The population has been monitored extensively, and in recent years, the population has remained stable at approximately 75 animals. Radio telemetry and aerial surveys have been used to track these caribou since the 1970's, and GPS and satellite technology have recently been used to provide more detailed and up to date information.

Anthropogenic Landscape

Settlement

Settlement in the area is limited to several communities along Lake Winnipeg, and the town of Bissett. The Sagkeeng, Black River, and Hollow Water First Nations, as well as the communities of Aghaming, Seymourville, and Manigotagan are located along the lakeshore (Figure 2.7). Mining and logging have occurred in the region for the last hundred years at varying levels of intensity. Trapping, hunting, fishing, camping and cottaging also contribute to the local economy.

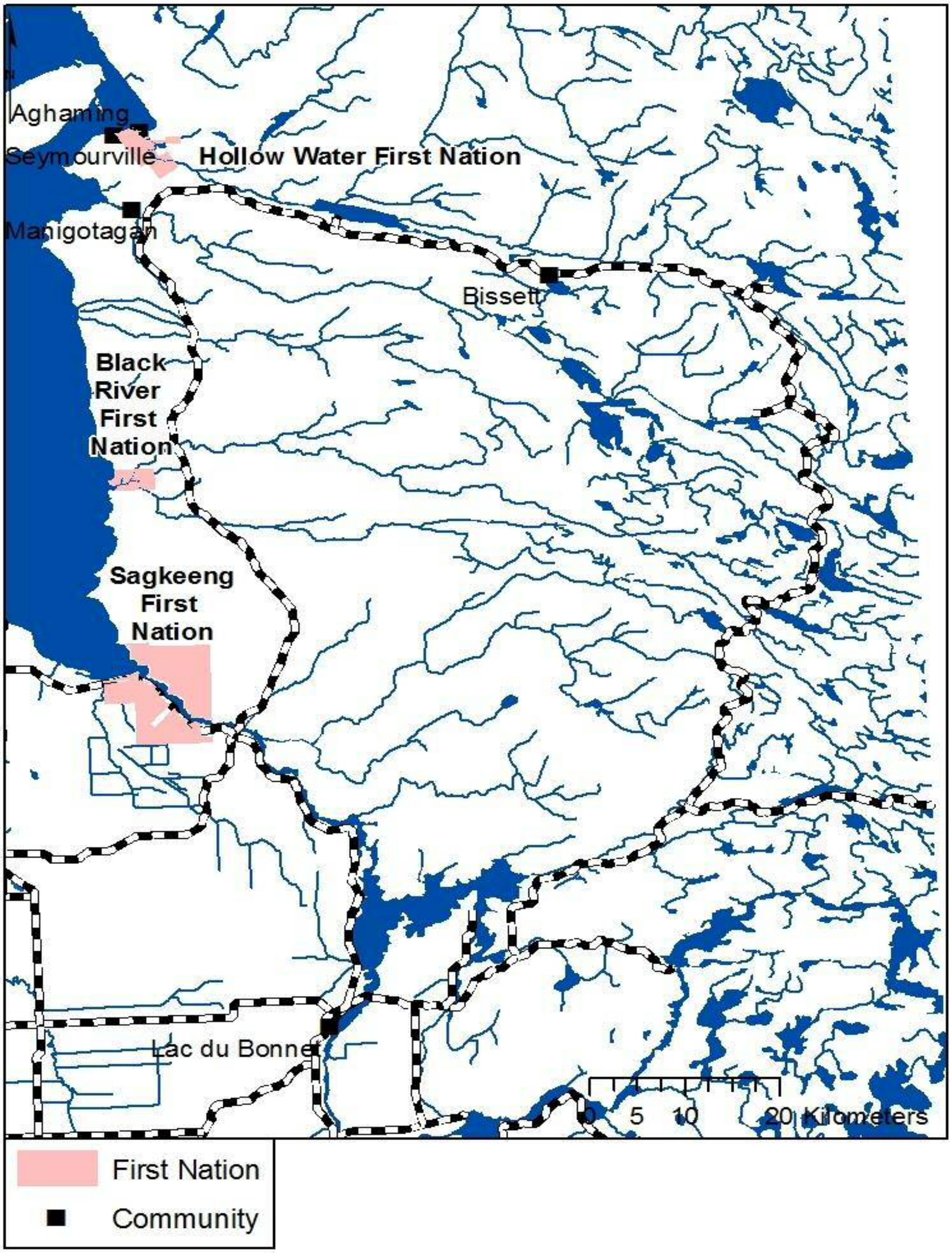


Figure 2.7. Communities in the study area.

Forestry and access

Forestry operations in the study area were mainly driven by the need for pulpwood to supply Tembec's newsprint mill in Pine Falls, adjacent to the study area. Forest management License Area 1 includes the study area, and was the supply area for the mill. Commercial forest harvesting in the region began in 1925 and was conducted by several companies, with Tembec being the final license holder. Spruce and to a lesser extent, pine were the primary materials required for mill operations (the mill can function on a mix of up to 40% pine with 60% spruce (Tembec, 2009). In recent years (1991-2007), 28,542 hectares from, 2,292 harvest blocks of 9-20 hectares were logged to supply the mill. Of this, over 1.5 million cubic meters of spruce, and over 800,000 cubic meters of pine were harvested. In 2009, the mill was closed, and operations have ceased (Tembec, 2009). Tembec had administered logging operations in Forest Management License One, which includes the study area, and had harvested a substantial area, and established extensive road access into the interior (Figures 2.8, 2.9 and 2.10). Over the same period, 179km of road was constructed. Most forestry roads are short-lived, and decommissioned soon after work is complete, but some permanent roads have been established. The decommissioning of roads can be a simple as ceasing to maintain, or as elaborate as plowing and replanting (MC, 2005). The trans-license road has been developed as a public use road, and is largely permanent. Major routes providing access to the Owl-Flintstone range have been decommissioned or have regulated access. The Black River Road and Sand River Road were decommissioned, and the Happy Lake Road was managed as the only vehicular access route into the area. Decommissioning of access routes is intended to prevent most human access, and is typically limited in the spatial extent and effort expended. Infrastructure at water crossings are removed, and shorelines restored, and the first two kilometers of access are plowed and barricades with boulders or millstones (Tembec, 2009). On a practical level, the sustainable harvesting of timber depends on forest regeneration, and repeated use of the landscape rather than constant expansion. As such, decommissioning of major access routes is limited with the intent to redevelop roads. Both the Sand River Road and Black River Road were scheduled for potential re-commissioning (Tembec, 2009). These routes may remain functional to predators and hunters for many years, as ATV access is still often feasible, and predators are not restricted by access controls.

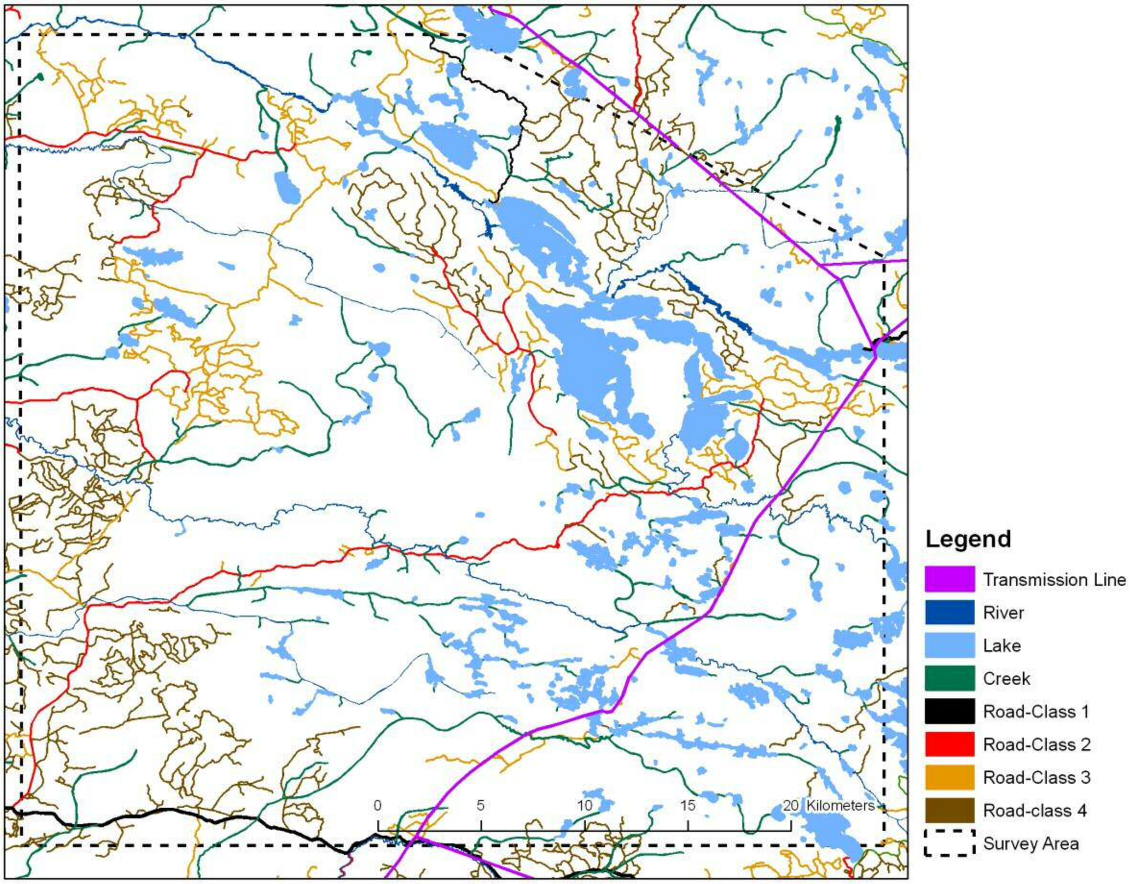


Figure 2.8. Linear feature access in the study area.

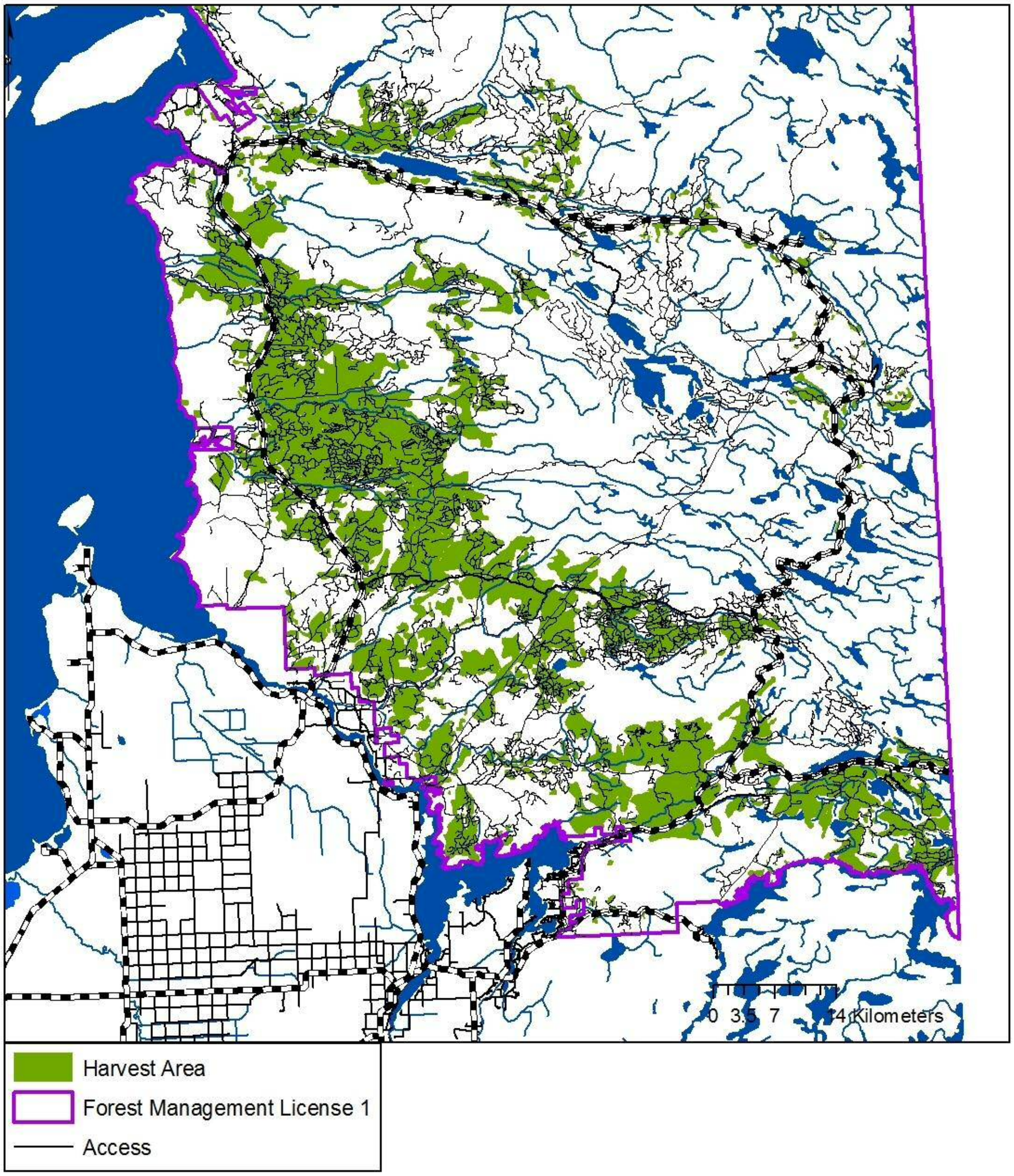
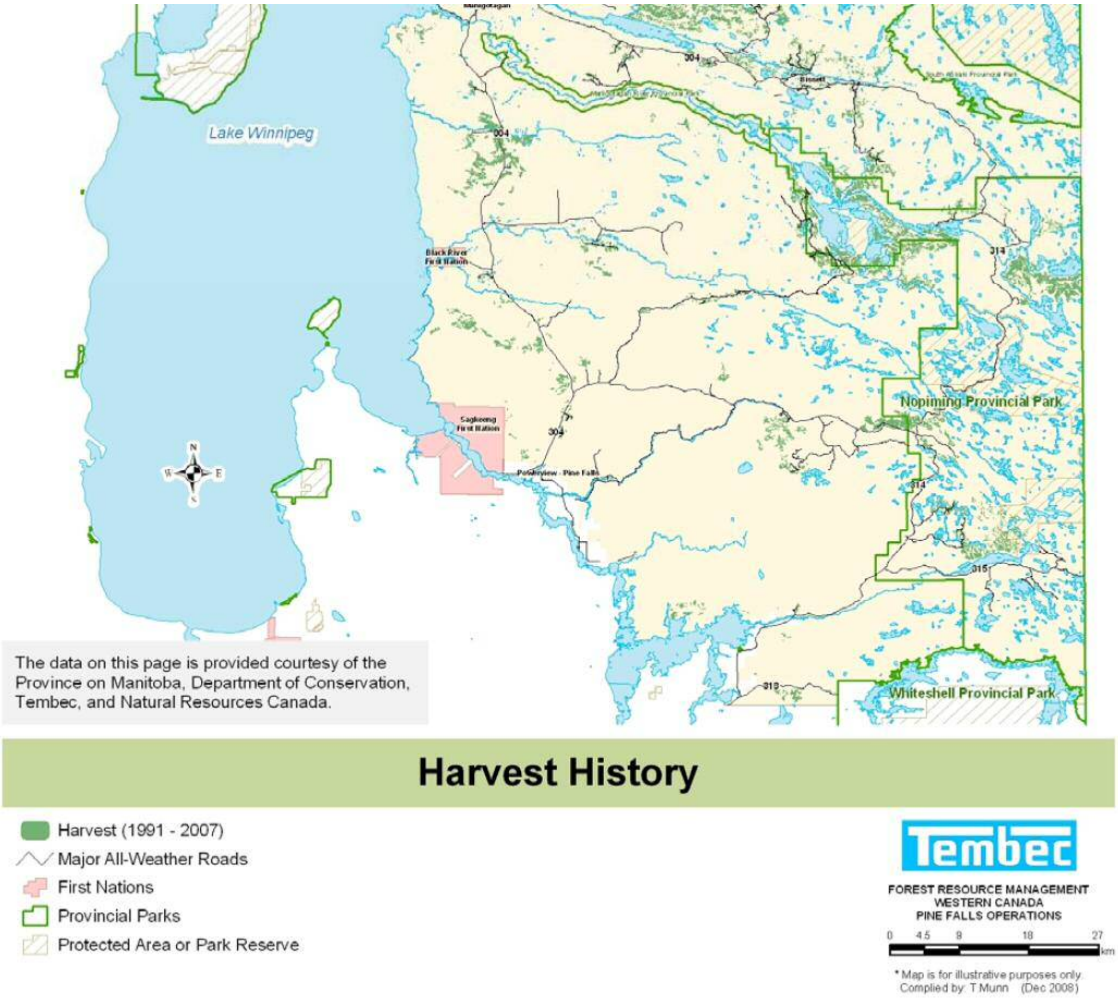


Figure 2.9. Historical forest harvest and access in the study area from 1940 to 1980.



The data on this page is provided courtesy of the Province on Manitoba, Department of Conservation, Tembec, and Natural Resources Canada.

* Map is for illustrative purposes only.
Complied by: T.Munn (Dec 2008)

Figure 2.10. Recent forest harvest in the study area for 1991-2007. From Tembec, 2009

In 1995, the Manitoba Model Forest engaged in some small experimental forest harvest designs on the edge of the Owl-Flintstone caribou range (Manitoba Model Forest, 1995). These sites were developed to test potential harvest designs that would not impinge upon caribou habitat as substantially as standard logging practices, and allow for integrated forestry and wildlife habitat on the landscape. The Owl-Flintstone range is composed of substantial high quality habitat, primarily more mature forest, which becomes less suitable as it ages through forest succession. Due to a history of intensive forest fire suppression, the natural mode of habitat cycling in the region has been removed. The role of forestry in an integrated environment was thought to be one that could substitute for fire disturbance and allow habitat cycling without large-scale impact on the landscape. The Owl-Flintstone range had previously been delineated into several management zones, caribou overall winter (zone 1B) and core winter (zone 1A). The integrated management strategy established a rule that required 67% of high quality caribou habitat in the overall winter range (zone 1B) be maintained at all times, allowing for a substantial habitat buffer in the case of a catastrophic forest fire event (Manitoba Model Forest, 1995, Figure 2.11).

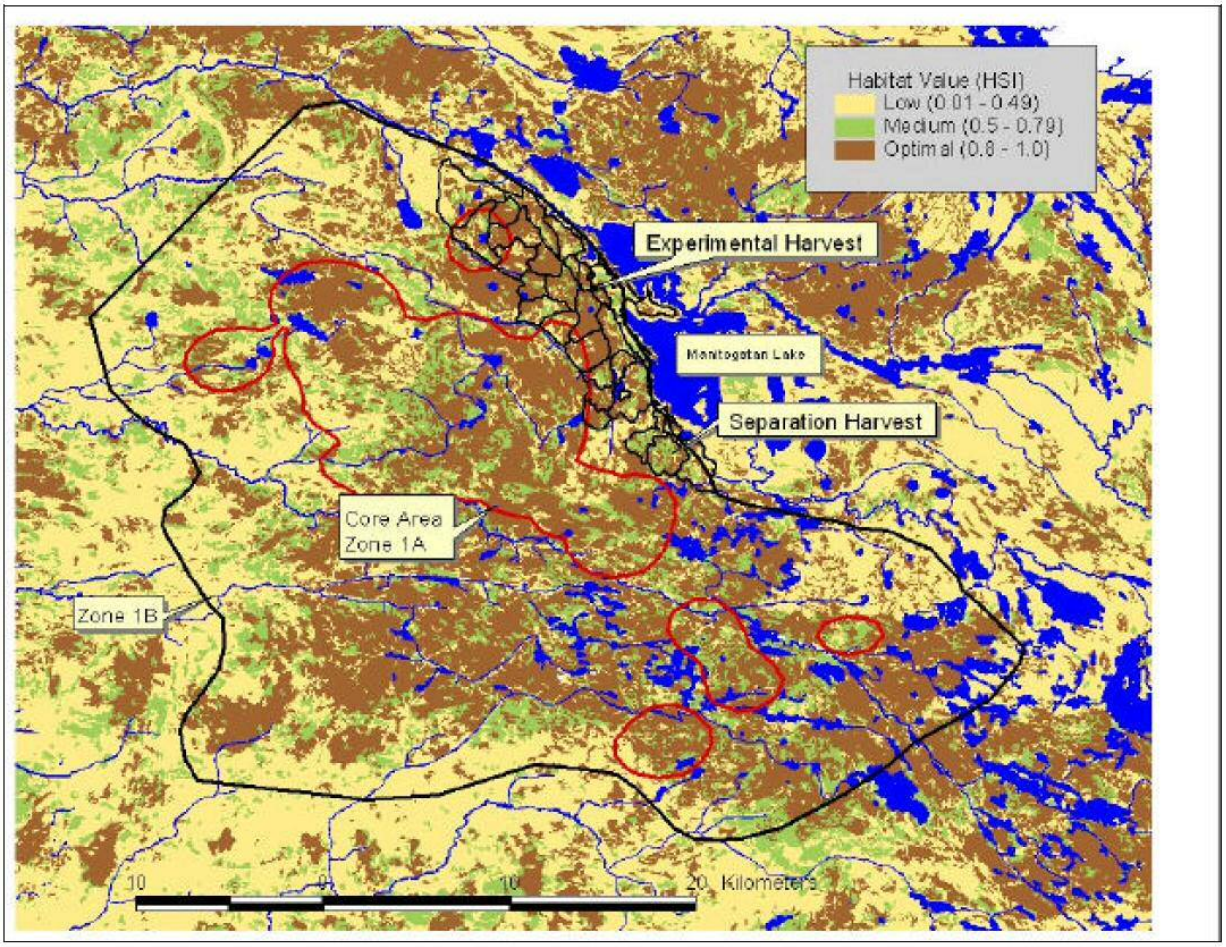


Figure 2.11. Experimental Harvest area relative to caribou core area. From Manitoba Model Forest, 2005

Mining

The first mine shaft in the region was dug in 1915, and marked the start of a gold rush, leading to the establishment of numerous gold mines (Manitoba Mines, Energy, and Innovation, 2008). In addition to gold, copper, cilver, nickel and tin have been mined along the Rice Lake Group, as well as lithium and rare earth elements in the Bernic Lake area to the south (Manitoba Mines, Energy, and Innovation, 2009). Active mining centers around Bissett (gold, silver) and Bernic Lake (tantalum, cesium), while mining claims cover much of the Rice Lake Group and adjacent areas (Figure 2.12)

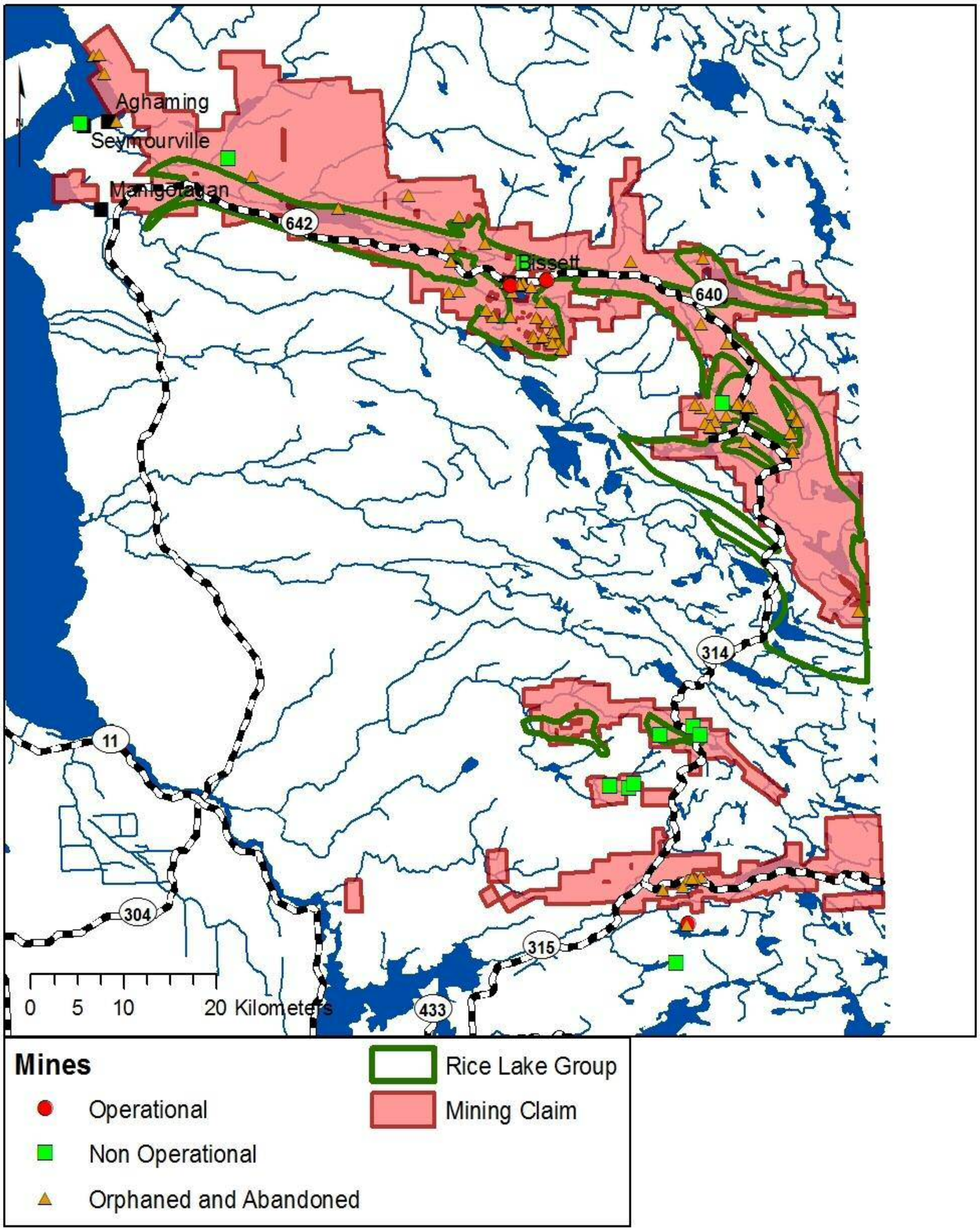


Figure 2.12 Mining activity in the study area. From Manitoba mines, energy and innovation, 2008

Trapping

Trapping in the region has been a traditional activity for thousands of years, and remains a regular recreational and commercial activity. Twenty registered traplines in the Lac Du Bonnet trapping section are active in the area (Figure 2.13), and a variety of species are caught, mainly Marten (*Martes americana*). Wolves are occasionally trapped, but the fluctuation of value makes it an unstable species to pursue (Weiss, pers. Comm.).

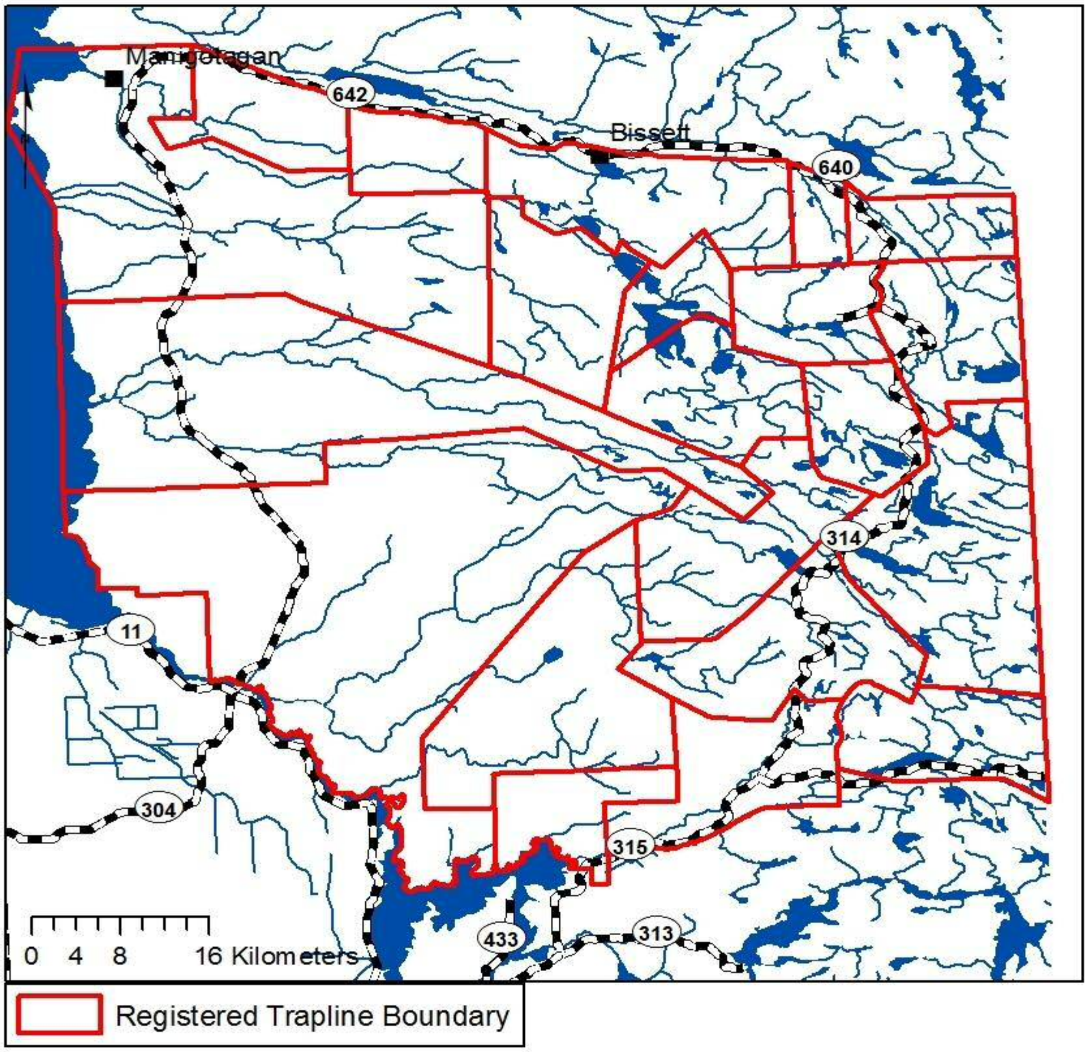


Figure 2.13. Registered Traplines

Recreation

Two major parks occur in the study area (Figure 2.14). Nopiming Provincial Park is the largest recreational area in the study area, occupying the entire eastern side. Manigotagan River Provincial Park crosses through the northern portion of the study area. Both parks are classified as Natural Parks, which are intended "both to preserve areas of a natural region and to accommodate a diversity of recreational opportunities and resource uses" (MC, 1998). Land use categories within the parks designated what types of Recreational and resource use are permitted. Manigotagan River Park is primarily categorized for backcountry camping, and allows limited resource use, such as trapping, but not mining, forestry, or hydro development. Nopiming Park is primarily classed as Resource Management, where development may occur within the confines of the park classification. Nopiming Park provides opportunities for backcountry and drive-in camping, boating, and cottaging, as well as hiking and canoeing routes.

Cottage developments have been established in Manigotagan, Bissett, Bird Lake and Long Lake. Additional camping opportunities are available in a series of regional parks on the Wanipigow River system. Fishing and hunting opportunities are available throughout the study area.

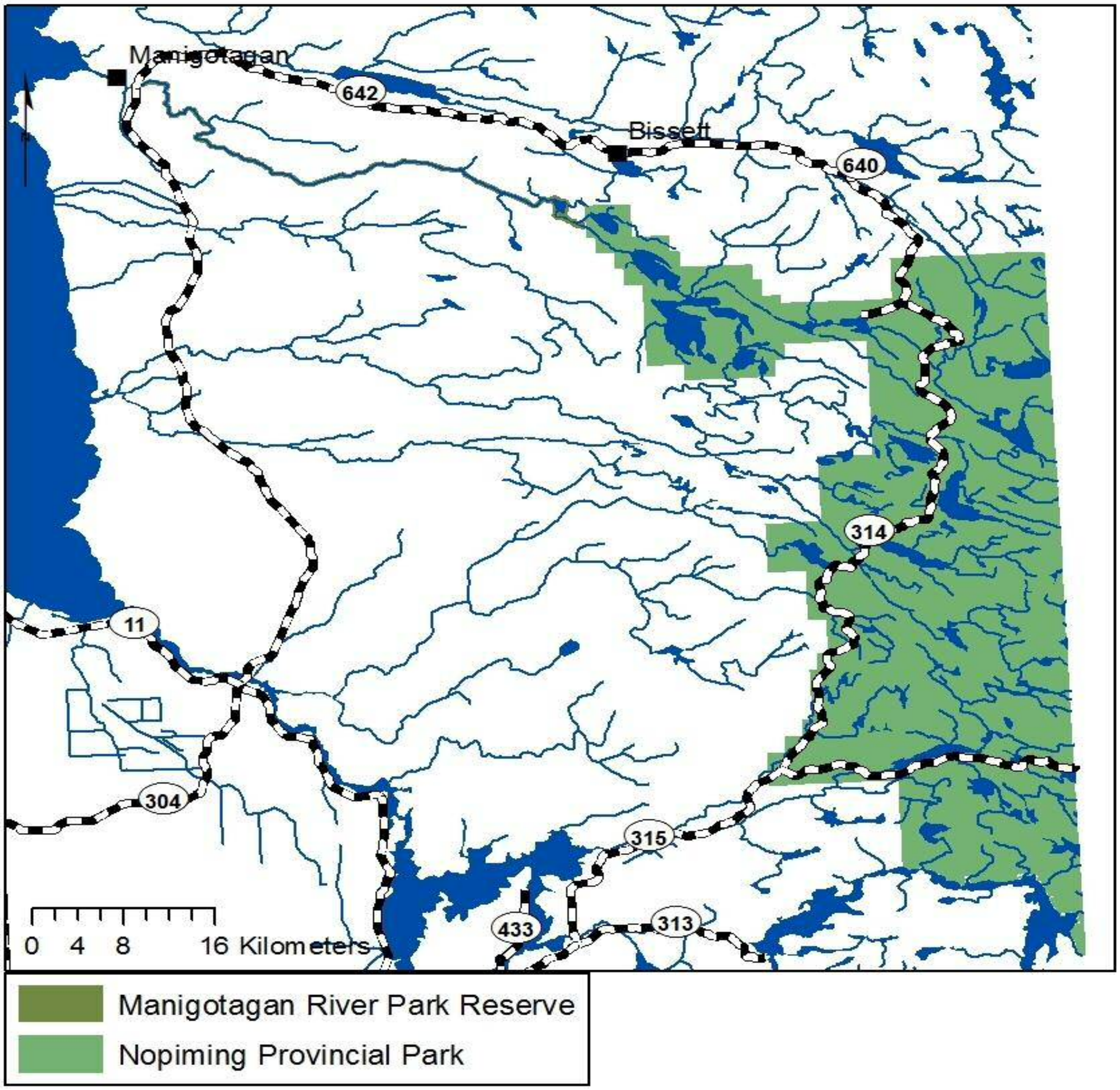


Figure 2.14. Provincial Parks in the study area.

Chapter 3: Spatial Distribution of Wolves, Moose and Caribou.

Abstract

The distribution of wolves, caribou and moose are highly related in the Canadian boreal forest. Wolves select prey based on availability, vulnerability, and net energy gain, which make moose a primary prey species. Woodland caribou avoid moose as a method of reducing predation risk from wolves. This study used transect-surveys and diet analysis to test for spatial partitioning of moose and caribou, and its effectiveness in minimizing predation by wolves. Species track observations were converted to density surfaces and compared with linear regression to assess overlap between species. Scat samples were collected to assess the proportion of caribou in the local wolf diet. Wolf distribution was highly related to moose distribution (coefficient 4.967, $P<0.001$), while caribou distribution was negatively related to moose and wolf distribution (coefficient -0.058, $P<0.001$ and coefficient -0.004, $P = 0.024$). Caribou remains were not observed in wolf scats, while moose remains occurred in 85% of samples. Distribution patterns show a strong pattern of spatial partitioning between caribou and moose, more pronounced than caribou avoidance of wolves themselves. The lack of apparent wolf predation on caribou suggests that avoiding moose may help to reduce caribou mortality and that protection of caribou populations could be achieved by preserving this partitioning through landscape management.

Introduction

Species distribution

Species distribution can be described at multiple spatial and temporal scales, from global distribution to individual movement. Wolves are distributed through much of the globe, and typically occur where large ungulates such as deer, moose, and caribou are found (Young and Goldman, 1944). In North America, wolves were historically distributed across the continent until their extirpation from much of the continental United States (Mech, 1970). During this time, grey wolves were eliminated from all states but Alaska and Minnesota (Mech, 1970). Similarly, wild bison were eliminated from the plains during this time, where they were a primary prey species and likely represented the largest prey biomass in North America (Van Ballenberghe, 1975). Between the extirpation of bison and predator aggressive control programs, wolves were virtually absent from the lower United States, until reintroduction efforts were undertaken in the Yellowstone ecosystem (Bangs and Fritts, 1997). In addition to direct reintroduction, recolonization by adjacent wolf populations has further expanded wolf range in Minnesota, Michigan and Wisconsin (Mladenhoff, 1995). In Canada, wolf distribution extends across the country, primarily in undeveloped areas (Carbyn, 1981).

Moose are widespread across the boreal forest, while caribou occur in both the boreal and arctic regions (Banfield, 1974). Caribou occurring in the arctic form large herds consisting of hundreds of thousands of animals and typically form the primary prey of arctic wolves (Kelsall, 1968). In the boreal forest, woodland caribou form smaller groups of few individuals, and are less likely to be the primary prey of wolves (Rettie and Messier, 1997).

Partitioning and habitat

Species distribution relates the characteristics of the animal (diet, mobility, reproduction and dispersal), and the ecological properties of the landscape, to define what is considered the niche (Grinell, 1917). The relative distribution of species shows how predators or competitors affect the ecological niche as much as landscape variables (Soberon et al., 2007). A species that is excluded from parts of the landscape by competition, but continues to coexist by utilizing a separate habitat niche and often sacrificing optimal habitat is considered partitioning (Tilman, 1987).

Partitioning occurs at a variety of spatial and temporal scales, among a variety of species. Predators of different sizes (Paquet, 1991,1992; Fortin et al., 2007; Fuller and Keith, 1981; Berger and Gese, 2007; Atwood and Gese, 2010; Kitchen et al., 1999); ungulates (Stewart et al., 2002, 2003, 2005; Torstenson et al., 2006; Jenkins, 1988; Cumming et al., 1996); and birds (Yahner, 1982) exhibit partitioning across landscape, time, food resources, and vertical divisions.

Predators often partition themselves from larger, more dangerous predators through spatial, temporal, and resource partitioning. Bears in British Columbia were observed to exhibit spatial and resource partitioning around salmon runs, where black bears rarely attempted to hunt salmon where their range overlapped with grizzly bears (Fortin et al., 2007). Instead, black bear diet was primarily vegetation (berries), which was only a minor component of grizzly bear (*Ursus arctos horriblus*) diet (Fortin et al., 2007). This pattern of spatial and diet partitioning was observed between brown and black bears in Alaska (Belant et al., 2010). Coyotes (*Canis latrans*), as a mid-sized predator, are often included in partitioning studies, as they frequently overlap with both wolves and smaller predators. Paquet (1991, 1992) observed resource and temporal partitioning by coyotes, due to the serious risk of mortality by wolves. Coyotes in Riding Mountain National Park would select smaller prey, and only occasionally pursue ungulates such as deer (Paquet, 1992). At the same time, coyotes would occupy the same spatial range as wolves, but would temporally partition themselves to avoid aggression and to scavenge on wolf kills (Paquet, 1991). In Alberta, Fuller and Keith (1981) found coyote home ranges did not spatially overlap with wolf territories. Berger and Gese (2007) found that this relationship had a limiting effect on coyote abundance and distribution. When the coyote was the larger predator on the landscape, Kitchen et al. (2005) found that Swift Foxes (*Vulpes velox*) suffered high coyote related mortality when at the edge of their home range. Spatio-temporal partitioning was not present, but dietary partitioning did occur.

Ungulates exhibit a variety of partitioning effects among other ungulates, as well as with domestic cattle on rangeland. Torstenson et al. (2006) identified that while mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*) and cattle showed substantial spatial overlap, elk and deer showed dietary partitioning (deer selected shrubs/forbs, vs. Elk selecting grasses). Elk and cattle showed dietary overlap, but temporal partitioning on the same landscapes (cattle used sagebrush grassland in summer/fall, elk in spring/winter). Predation pressure can also be manipulated by partitioning, as noted by Cooley et al. (2008), who observed that white -tailed deer would seasonally adjust their spatial distribution into areas unfavourable to cougars, leaving Mule deer as the more vulnerable target.

In all the above predator partitioning cases, separation was driven by avoidance of aggression and mortality. The spatial separation of herbivores is not typically driven by avoidance of direct mortality, and the precise nature of partitioning can be harder to assess, while separation could appear to be spatially driven, or resource driven, or both. Spatial separation could be a function of resource distribution that favours partitioning, or resource selection could be an adaptation to spatial segregation. Resource selection (see chapter 4) is generally predicted largely or entirely by observations of species distribution, which prevents discriminating habitat as cause or effect of partitioning. The role of partitioning in moose-caribou-wolf interactions was studied by Cumming et al. (1996), using multispecies track surveys in northwestern Ontario. Using modified transect survey data and converting into track density surfaces, broad cells of 3 km^2 were used to compare relative distribution of each species over 4 winters. Overlap analysis was used to assess the relatedness of species distributions. Wolves and moose showed substantial spatial overlap, while caribou were inversely correlated with moose and wolf density. Nearest neighbour analysis of species distributions showed wolf locations three times farther from caribou locations than moose locations.

In 1995, the Manitoba Model Forest engaged in some small experimental forest harvest designs on the edge of the Owl-Flintstone caribou range (Manitoba Model Forest, 1995). These sites were developed to test potential harvest designs that would not impinge upon caribou habitat as substantially as standard logging practices, and allow for integrated forestry and wildlife habitat on the landscape. The Owl-Flintstone range is composed of substantial high quality habitat, primarily more mature forest, which becomes less suitable as it ages through forest succession. Due to a history of intensive forest fire suppression, the natural mode of habitat cycling in the region has been removed. The role of forestry in an integrated environment was thought to be one that could substitute for fire disturbance and allow habitat cycling without large-scale impact on the landscape. The Owl-Flintstone range had previously been delineated into several management zones, caribou overall winter (zone 1B) and core winter (zone 1A). The integrated management strategy established a rule that required 67% of high quality caribou habitat in the overall winter range (zone 1B) be maintained at all times, allowing for a substantial habitat buffer in the case of a catastrophic forest fire event (Manitoba Model Forest, 1995).

Following initial experimental harvests near Farrington Lake and Happy Lake, a 2005 update of the integrated management strategy was completed, which called for more elaborate experimental design and more thorough assessment of the results. The revised design called for an extensive test area (approximately 2,000 ha of cuts) along the western edge of Manigotagan Lake and Quesnel Lake, with separate designs for caribou habitat retention (harvest designed to result in brief or no displacement of caribou), natural landscape (emulating disturbance to create future high quality habitat), and separation cutting (reduced quality habitat for moose and deer to reduce the movement of these species into other test cuts) (Manitoba Model Forest, 2005).

Monitoring goals of this project were extensive. Pre-and Post-harvest lichen response was monitored, caribou were monitored via GPS and radio telemetry in and out of the harvest blocks to assess response and population effects, and winter aerial surveys were used to assess distribution and population trends in alternate prey (moose, deer), and predator (wolf) species (Manitoba Model Forest, 2005).

Predation (hunting, prey selection/preference)

Wolf predation can be broken into several stages: location/searching; stalking; encounter; chasing; and rushing (Mech, 1970).

Locating prey consumes much of a wolf's daily activity and involves travelling across the pack territory seeking prey (Peterson et al., 1977). Searching ends when prey is detected, either directly, by scent, chance encounter, or indirectly, by locating prey tracks or sign (Mech, 1970).

Once located, the stalking stage begins, where the wolf or wolves utilize stealth to get as near as possible to the prey species without being detected (Mech, 1970). Wolves utilize stalking to achieve visual confirmation of the prey, and to minimize the distance needed to engage (Mech, 1970).

The encounter phase begins when the prey detects the wolves, sometimes not until the wolf has physically reached them (Mech, 1970). At this stage, the responds to the wolf. The following stage, the rush, is where the wolf begins to engage the prey following a decision to flee at the encounter stage. At this stage, the benefit of effective stalking is most important, as the ability to close distance with the prey in the rush depends on the prey not having enough time to escape (Mech, 1970).

Hunting success

Wolf success in hunting is thought to be relatively minimal, as prey species have a wide variety of methods to reduce mortality at all stages of the hunting process (described below). Mech and Peterson (2003) synthesized overall success rates across a variety of prey species, noting a range of 10-49% success rates, with the highest being Alaskan caribou in summer (49%, but 15% success in winter), and the lowest being bison in winter (10%, but 33% in summer). Moose hunting success was observed to be 19-38% by Mech (1998). Mech (1970) described the hunting outcomes of 131 encounters with moose along all stages of the hunting process. Of the total, wolves only caught up to 53 moose (41%), and only managed to kill 6 (5%).

Pack size plays a role in hunting success, but not to the extent previously thought (Macnulty, 2012, Mech and Boitani, 2003). Lone wolves have been observed to hunt, attack, and kill most prey, even their largest prey species (moose, bison, and muskoxen) (Thurber and Peterson, 1993; Carbyn et al., 1993; Gray, 1970). While they may not expand the number of prey species available to wolves, packs increase hunting success, but only to a certain size (2-4 wolves), at which point, additional wolves engage in following behaviour, or "free riding" (Macnulty, 2012). This is often due to pack age structure, but free riding behaviour is not limited to young or inexperienced wolves.

Prey selection

Wolf distribution relative to available biomass suggests broad scale selection for prey species (Fuller, 1989). Wolf hunting behaviour suggests that at a fine scale, practical choices of prey are made based on estimating the relative vulnerability of the individual (Keith, 1983). Prey vulnerability and selection is a major part of hunting success, where age, disease/malnourishment/injury and defensive behaviour make animals more or less susceptible to predation (Mech and Peterson, 2003).

Prey selection is a consideration at most levels of the hunting process. Locating prey while travelling across the pack territory may lead to detection of sign or scent of numerous species, requiring a choice of pursuing or ignoring. When stalking prey, further information is gained about the individual or herd, allowing the opportunity of continuing or abandoning they prey (Mech, 1970). At the encounter stage, wolves may gauge the vulnerability of prey based on their response to the arrival of predators, either to stand their ground or flee, where a defensive or aggressive response from prey typically leads to wolves abandoning the attack, at least temporarily (Peterson and Ciucci, 2003). The rush and chase stages are where wolves have dedicated themselves to pursuit of the prey, and they can identify vulnerabilities, and select weaker looking prey from groups (Mech, 1970)

As noted above, prey biomass, vulnerability and availability are major selection factors. An additional factor, handling time, is equally important, and related to biomass and vulnerability. Edible biomass is important, as it is the measure of gross energy gain, and would select the largest prey species (edible mass) as the ideal choice, in this case the moose. However, alone, biomass does not address the costs associated with large prey, such as mortality risk, chance of success, and energetic cost.

Handling time, or the energetic cost of catching and killing prey, influences prey selection. Where smaller prey, and prey with additional vulnerabilities may require less time, biomass gained from easy prey may not be sufficient to justify even limited hunting efforts.

The combination of biomass and handling time can be combined to determine the net energy gain of a prey item, allowing variable prey sizes to be compared. While smaller prey may be easier to obtain, the increase in energy expenditure to pursue larger prey may be greatly exceeded by the potential gain (Stephens and Krebs, 1986).

Vulnerability can be observed at the species and individual level. Numerous ailments can affect individuals, such as disease, injury, malnourishment, or the use of unfavourable escape habitat (limiting available antipredator tactics, described below). Species level vulnerabilities relate to landscape variables such as snow cover,and how they respond to them. Ungulates species adapt to snow conditions in different ways; White-tailed deer and moose have relatively high foot loading (g/cm^2 foot area) compared to wolves, while caribou have spreading hooves that reduce their foot loading (Telfer and Kelsall, 1984). Increasing snow depth can be a major vulnerability to deer, and to a lesser extent moose (due to their height) (Telfer and Kelsall, 1984).

Prey response to predation risk (anti-predator tactics)

Counter to vulnerabilities of prey, species sharing a landscape with predators evolve adaptations to reduce their vulnerability. Methods of reducing predation occur in different physical and behavioural categories (fighting, hiding, escape, caution, and landscape use) (Peterson and Mech, 2003).

Moose and other larger ungulates utilize defensive responses to predation, using size and aggression and large antlers to deter wolves (Peterson, 1977), particularly in the case of defending calves. Mech (1998) observed female moose defending already dead calves aggressively for over a week, a behaviour observed once in this study. Larger herding species such as bison and muskoxen use grouping and formation to protect calves from predators (Gray, 1987; Carbyn and Trottier, 1988). Aggressive defence is an effect deterrent to predators, as noted by Mech (1970), of 131 moose-wolf encounters, no moose that responded aggressively were attacked, with stand-offs rarely lasting more than a few minutes.

Smaller ungulates, while equipped with antlers and hooves that can kill attacking wolves (Mech and Nelson, 1985), are more likely to rely on hiding, fleeing or avoiding contact. Rather than aggressive defence of calves, hiding is used by deer to protect calves from harm, and calves are adapted to avoiding detection visually (colouration) and a lack of odour (Lent, 1974; Severinghaus and Cheatum, 1956).

Caribou utilize a variety of tactics to avoid predation at the landscape level. Barren-ground caribou migrate hundreds to thousands of kilometers, and woodland caribou use landscape factors to reduce predation risk and increase escape potential (James et al., 2004; Kunkel and Pletscher, 2000; Ferguson et. al., 1988; Ferguson, 2005).

Escape habitat for caribou may take the form of steep slopes (Bergerud et al., 1984), islands and lakes (Ferguson, 2005; Bergerud, 1985; Shoesmith and Storey, 1977), or bog and fen complexes (Stuart-Smith et al., 1997; Schindler, 2006; Brown et al., 1986) where wolves are less capable of pursuit.

Based on GPS telemetry (James et al., 2004), and track survey data, caribou are also thought to distribute themselves apart from other species such as moose (Cumming et al., 1996; Brown et al., 1986). Spacing apart (from other caribou) has been observed, notably in the spring during calving, which increases searching time between caribou for predators, and reduces their apparent availability (Bergerud et al., 1990; Seip, 1991; Rettie and Messier, 2000, Davis, unpubl. data). Calves and female caribou during calving are at their most vulnerable stage and use habitat such as islands (Shoesmith and

Storey, 1977; Bergerud, 1985; Cumming and Beange, 1987; Davis 2006) and bog complexes (Hirai, 1998; James et al., 2004). Additionally, caribou calving occurs over a short period, from two to four weeks (Gustine et al., 2006; Adams et al., 1995; Post et al., 2003), with GPS data analysis in the Owl-Flintstone range identifying a twenty-one day range between expected calving dates from 10-31 May from 2002-2005 (Davis, 2006). The compounded difficulty presented to wolves by these tactics make caribou a less favourable choice at their most vulnerable period, where they must travel a greater distance in a short period of time between available vulnerable cows and their calves.

Objectives

This study compares the distribution of wolves and two potential ungulate prey species, moose and woodland caribou, as well as the local diet of wolves in the study area. Aspects of availability, vulnerability, net energy gain determine prey selection, so by reducing value in all these factors, a species can make themselves less valuable to predators. If caribou are able to partition themselves from moose and wolves on the landscape, predation on caribou should not be evident in diet assessment, thus:

Ha0: Wolf distribution will not be significantly related to moose or caribou distribution

Ha1: Wolf distribution will be significantly related to moose distribution compared to caribou distribution

Hb0: Wolf diet will include both moose and caribou, or;

Hb1: Wolf diet will not include caribou

Methods

Track surveys

Aerial surveys were conducted in 2006, 2008, and 2009 by Manitoba Conservation to observe the distribution of ungulates and prey over an experimental harvest study zone. Transects across the study area were flown in a north-south orientation at approximately 400m altitude, at 1.75 km apart, over an area approximately 40km by 40km, or 1600 km^2 (Figure 3.1). Surveys were conducted in January of each year over 2-4 days: 4-6 Jan. in 2006, 22-23 Jan. in 2008, and 12-15 Jan. in 2009. Multiple trained observers on board a helicopter used handheld GPS units to record tracks and sightings along transects. Moose, wolf and caribou tracks were recorded, as well as white-tailed deer, which occurred very rarely (three tracks observed in 2006 and 2009), and wolverine (three tracks seen in 2006). Deer and wolverine tracks were not included in the analysis. Observations and tracks were pooled as overall locations. Instances where multiple animals were recorded at a single location were not weighted by number, as no similar data were collected for track sightings, which could also represent multiple animals.

Multispecies survey methods reflect those used by Cumming et al. (1996), albeit at a finer scale (1.75 vs. 3 km interval). Cumming et al. converted track observations per species into continuous density surfaces, or cellular grids, to quantify species distributions. This study also used a density surface approach, at a finer scale. Density surfaces for each species and year were generated using ArcGIS Spatial Analyst Density Tool, using 250m cell sizes, for improved visualization of density contours (ESRI, Redlands, CA). A search neighbourhood of 10 km was selected to avoid bias from survey edges (outlying cells have reduced search neighbourhoods), and transect line bias where a small search radius would reflect transect line distribution rather than track locations. A radius of 10 km avoids this by ensuring that all cells include a neighbourhood encompassing at least four transect lines. Use of a density surface creates a homogenous dataset of equal size for each variable (one cell equals one record) from location records with uneven counts between years and species. Each annual surface was tabulated and pooled by species, creating three variables for comparison. Relationships between each variable (species) were compared using linear regression (Bowman et al., 2010; Zar, 1984). Three regressions were conducted, between wolf and caribou density, wolf and moose density, and caribou and moose density.

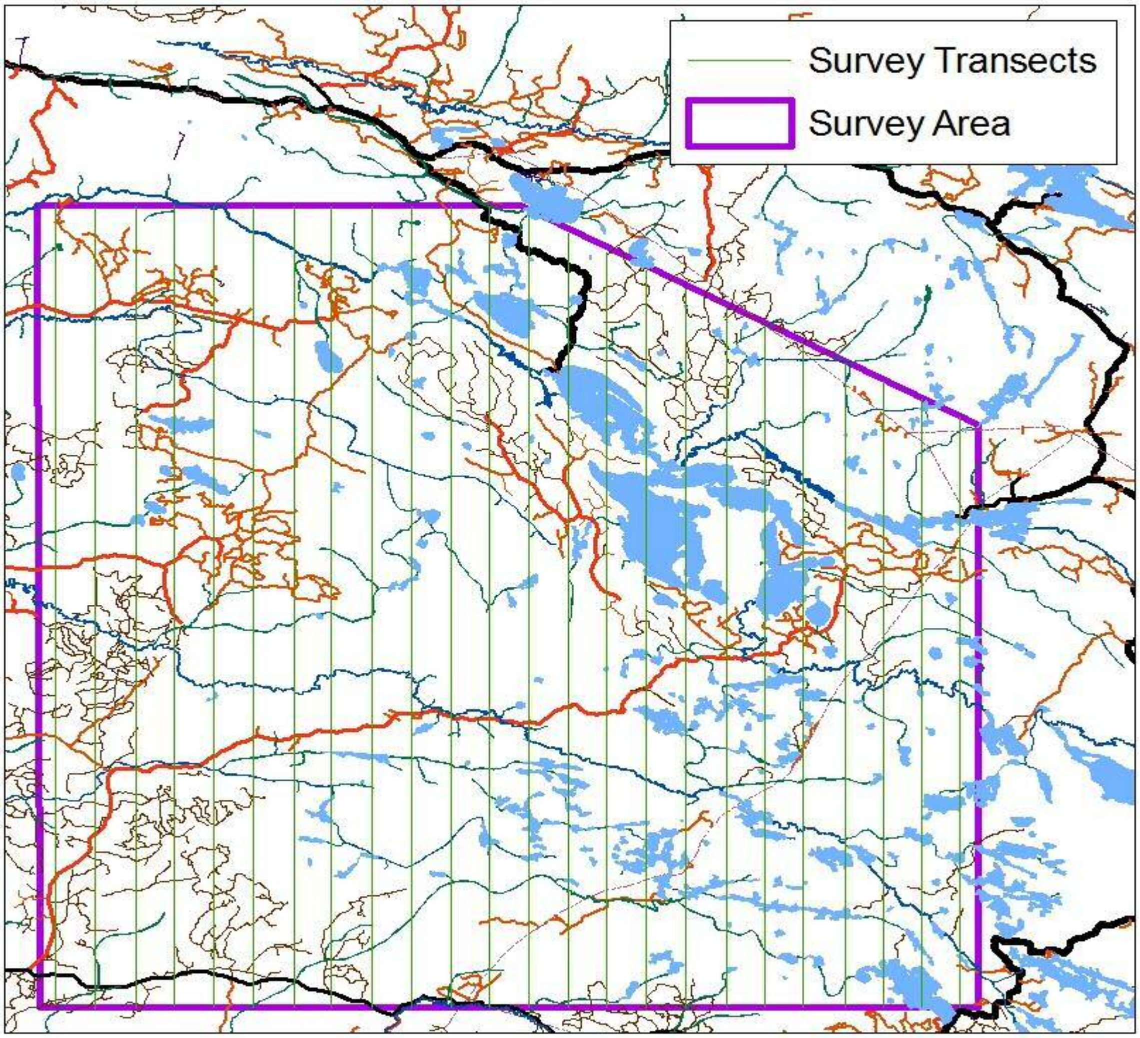


Figure 3.1. Aerial multispecies survey area and 1.75 km spaced transects.

Diet analysis

Wolf diet was assessed to identify potential caribou predation in the study area. Scat samples were collected opportunistically, when encountered during corridor surveys and wolf collaring efforts (see chapter 4). Supplemental data of wolf predation sites were noted during the study period, and assessed by Manitoba Conservation wildlife staff to identify prey species.

Scats collected were identified by size, composition, and locational evidence (proximity to kill sites, observation of animals or tracks present). Scats can be highly variable depending on the parts being consumed, with scats from largely digestible flesh being almost entirely liquid, with little other matter. Scats from the later portion of feeding, when more hair and skin is consumed than meat, become more solid, and form longer, tapered cylinders, typically over one inch diameter (Weaver and Fritts, 1979). Wolf scats can be similar to those of other species, such as other canids (coyote), large felids (cougar), or bears (Murie and Elbroch, 2005). Coyote scats resemble wolf scats in shape and content, but are typically smaller, with most measuring under one inch diameter, while 95% of wolf scats measured greater than one inch diameter (Weaver and Fritts, 1997). While coyotes do not frequently occur in the study area, scats smaller than one inch in diameter were rejected, however large coyote scats could not be discounted entirely. Cougar are considered extremely rare, and have not been observed in the study area. Scat from cougars resembles that of wolves in form and content, but often occurs in broken or segmented portions (Murie and Elbroch, 2005). No scats were discounted as potential cougar scats. Black bear are frequent in the study area, and under some conditions may have scats that resemble wolf scat. Bear scat will typically be blunt ended, and unless a substantial volume of meat has been consumed, will contain a greater amount of vegetative and digested matter than wolves, and will typically be larger in diameter (Murie and Elbroch, 2005).

Scats were collected, kept frozen until processing, cleaned, and separated. Cleaning and separating have had numerous methods attempted, ranging from hand separating, to blenders and washing machines (Chavez and Gese, 2005). In this study, samples were kept intact, frozen, and initially boiled, to reduce risk of exposure to transmittable parasites.

Wolves frequently consume indigestible material when feeding on prey, which remains intact when scats are excreted later on. Hair and bone fragments and other matter (seeds, feathers, human garbage) can be extracted and identified to determine what items prey have consumed. Hair characteristics have long been known to be different between prey species (Hausman, 1920; Mathiak, 1938; Stains, 1958; Mayer, 1952). Length and width of hair are variable between species, but not sufficient for confirmation. Hair pattern, as observed in the cuticular scales along the length of the hair can be used to identify the species of origin (Adjoran and Kolenosky, 1969; Kennedy and Carbyn, 1981). The combination of hair length and diameter, as well as scale pattern can differentiate between mammals likely to be encountered in the study area. A description of a few select species is included, see Adjoran and Kolenosky (1969), Wallis (1993), for detailed species identification, and De Marinis and Asprea (2006) or Meyer et al. (2002) for additional examples of European species and photographic examples.

Beaver (*Castor Canadensis*), moose, caribou, and snowshoe hare (*Lepus americanus*) were considered to be the most probable prey items, and are described below (as per Adjoran and Kolenosky, 1969).

Beaver guard hairs are typically 65mm long, up to 190 um width and crenate (wavy)-imbricate (discontinuous) scales. Caribou hairs are up to 60mm long, 150-220 um width, with ovate-imbricate scales.Moose guard hairs are 150-160 mm long, 290-550 um width, with ovate imbricate scales.

Snowshoe hare guard hairs are 30-40mm long, and up to 100 um width, elongate (chevron)-imbricate scales.Moose hairs were easily identifiable without microscopy due to their length and thickness, while hare and beaver were distinguishable by length and distinct scale patterns (Adjoran and Kolenosky, 1969).

Forbes and Theberge (1992) assessed moose predation using wolf scat samples based on the methods in Adjoran and Kolenosky, (1969) and Swanson (1989), to estimate prey proportions by identifying three (3) sample hairs from each scat. Swanson (1989) found that more than three hairs resulted in additional species occurrence. Point-frame methods, such as used in quadrat sampling of plant communities, has been applied to hair identification, by spreading out samples and randomly selecting items by pin drops, which resulted in comparable results to intensive hand separation methods, but a dramatic reduction in processing time of 85% (Ciucci et al., 2004). A complete sampling is not found to be necessary, however, because the purpose of this study was intended to identify caribou predation, larger sampling proportions were used. Trites and Joy (2005) found that >59 scats would be sufficient to identify principal prey species, while >94 would be necessary to conduct any comparative analysis.

In addition to keys from Adjoran and Kolenosky (1969) and Wallis (1993), the use of local representative samples was recommended (Pruitt Jr., Pers. Comm), and was collected during the study as existing sets were no longer available locally (Pruitt Jr., Pers. Comm).

In this study, scats were examined coarsely following boiling, and grouped according to apparent homogeneity of hairs. Homogenous samples were broken in half lengthwise, and five samples were taken from four sides, both ends, and from each half of the interior, for a total of forty (40) per scat. The sampled hairs were identified at macro or microscope level as needed. Microscope analysis required creating casts of each hair in glue, and viewing the scale pattern under a microscope (Adjoran and Kolenosky, 1969).

Dissecting microscopes with adequate lighting were found to be capable of allowing the viewing of hair scales on actual samples rather than casts in some cases, but dissecting microscopes were generally not used.

Heterogeneous samples were sampled in the same manner as above, but with increased sample sizes (twenty per location) and additional samples. Additional samples were selected by separating the sample completely on a tray, and identifying notably different hairs based on length and width.

Results

Track Observations

The survey resulted in a total of 2,565 locations of observations or track for all species in all years, 1,004 in 2006, 836 in 2008, and 725 in 2009 (Figures 3.2-3.4). Table 3.1 below shows the distribution of points by species.

Table 3.1. Multispecies survey observations by year

Year	Total		Moose		Caribou		Wolf	
	Tracks	Animals	Tracks	Animals	Tracks	Animals	Tracks	Animals
2006	1004	34(63)	745	33(47)	193	1 (15)	66	0
2008	836	22(56)	497	19(41)	190	1(7)	149	2(8)
2009	725	18(58)	447	15 (40)	129	1(14)	149	2(4)
Total	2565	74(177)	1689	53(128)	383	3(36)	364	4(12)

**Numbers in Parentheses indicate the number of individuals observed among locations*

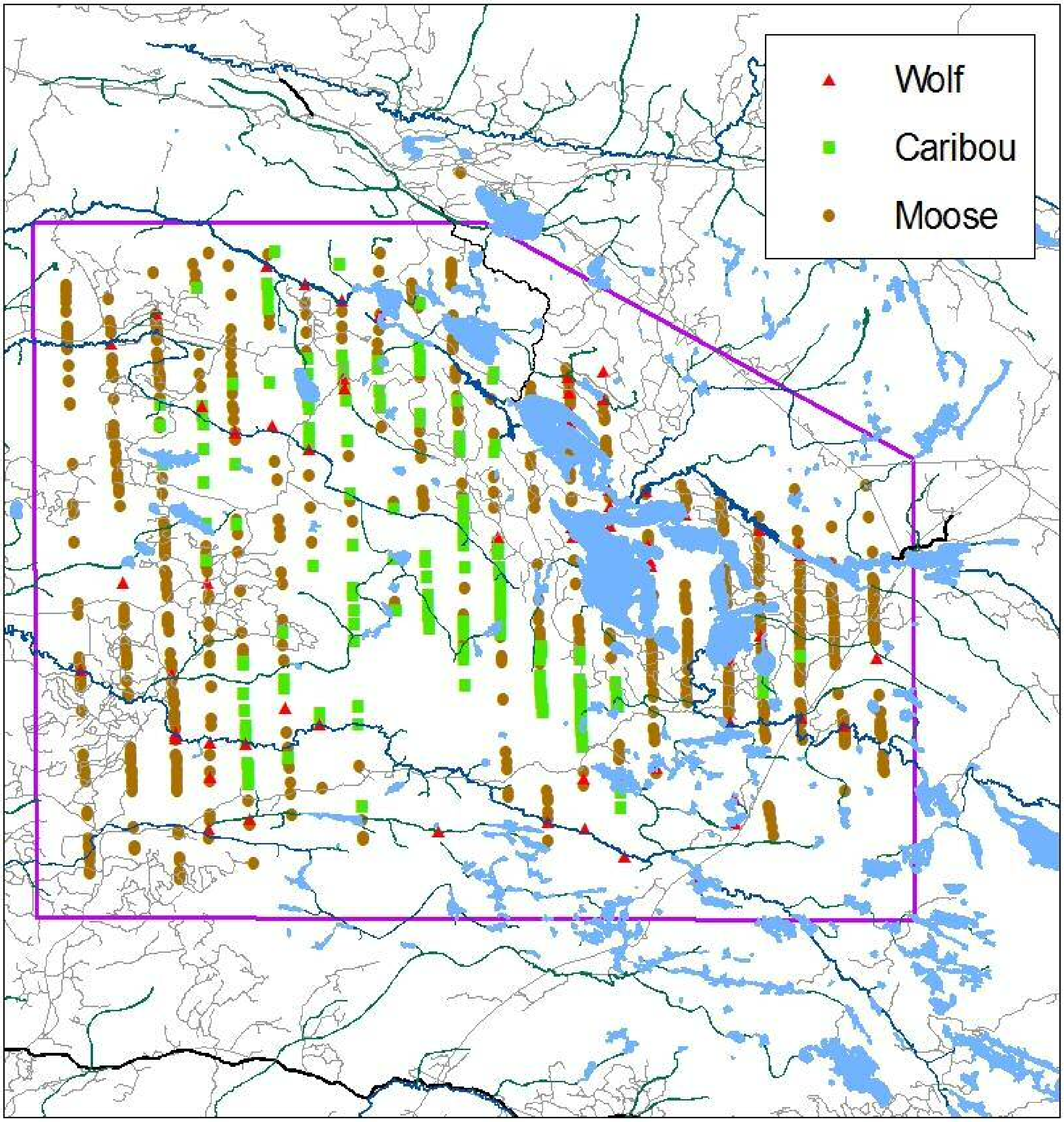


Figure 3.2. 2006 Multispecies survey track observations by species.

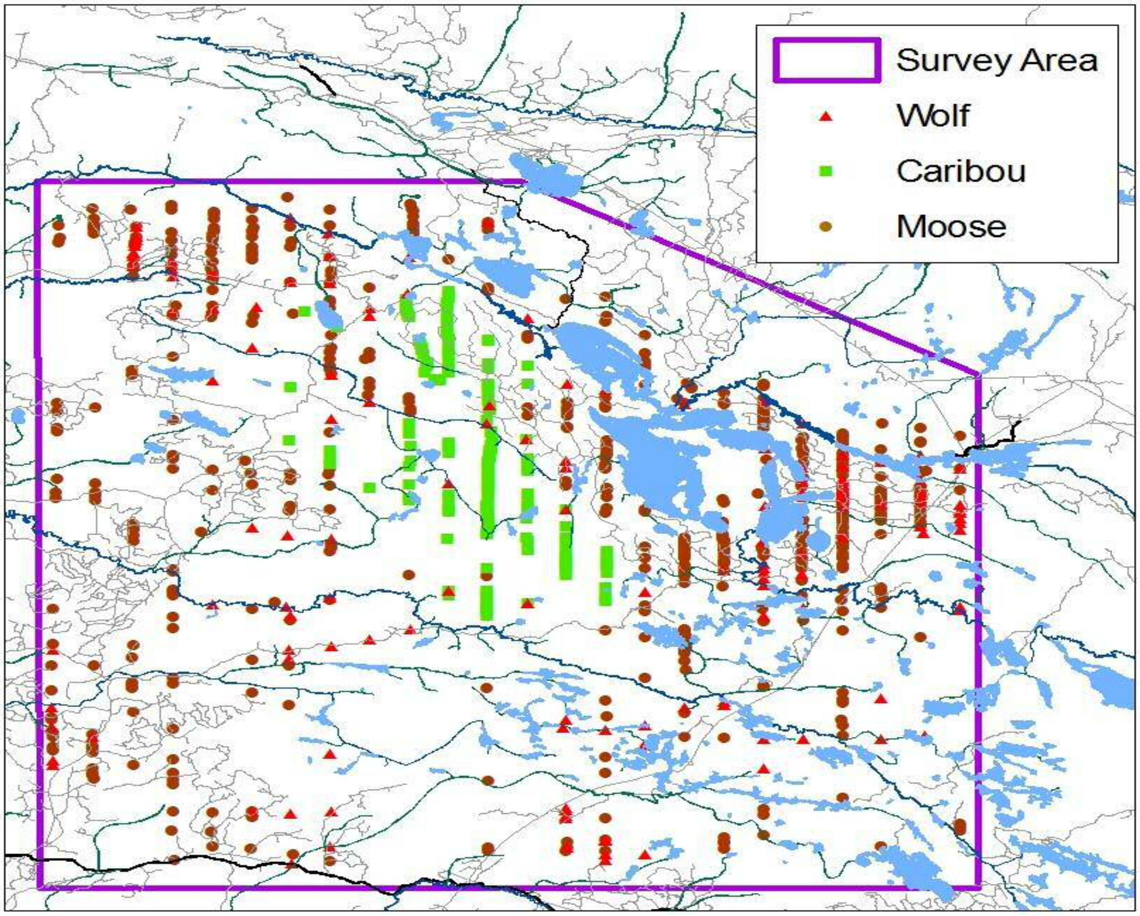


Figure 3.3. 2008 Multispecies survey track observations by species.

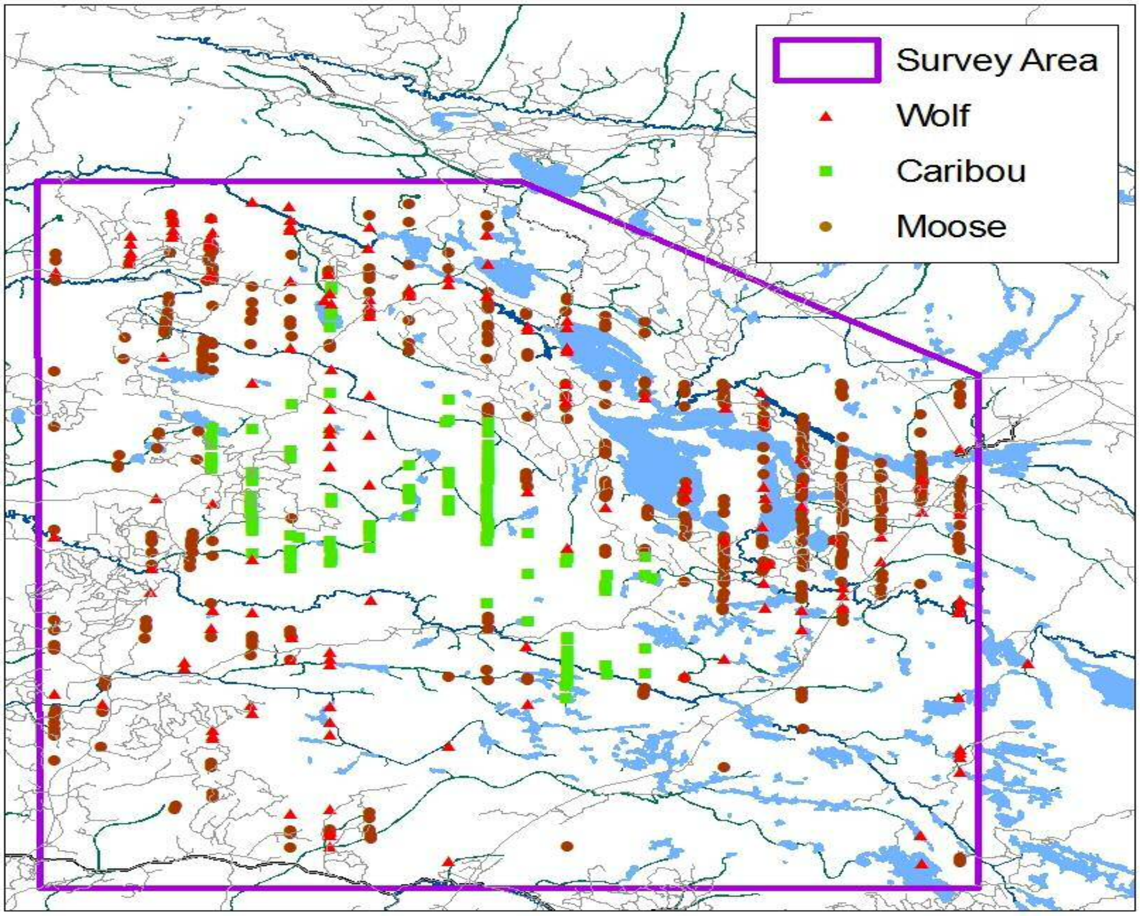


Figure 3.4. 2009 Multispecies survey track observations by species

Track Density

For each year, density surfaces were generated for each species. Each surface contains 21,042 cells matched to a common cell ID for each surface. Each surface was combined in Excel and each density was averaged among years, by species. Caribou track density ranged from zero to 0.682 tracks/km^2 in 2006 (Figure 3.5); from 0 to 0.988 tracks/km^2 in 2008 (Figure 3.6); and from 0 to 0.521 tracks/km^2 in 2009 (Figure 3.7). Moose track density ranged from 0 to 1.614 tracks/km^2 in 2006 (Figure 3.8); from 0 to 1.14 tracks/km^2 in 2008 (Figure 3.9); and from 0 to 1.236 tracks/km^2 in 2009 (figure 3.10). Wolf track density ranged from 0 to 0.142 tracks/km^2 in 2006 (Figure 3.11); from 0 to 0.368

tracks/km^2 in 2008 (Figure 3.12); and from 0 to 0.252 tracks/km^2 in 2009 (figure 3.13). Wolf density was generally lower, with yearly maximum density not exceeding 0.4 tracks/km^2, than either caribou (maximum densities between 0.5 and 1.0 tracks/km^2), or moose (maximum densities above 1.0 track/km^2).

Caribou tracks were concentrated in the center of the study area in all years. Moose density was highest along the northern, eastern, and western edges, with the Happy Lake vicinity being the highest density area in all years. Wolf distribution was concentrated on the north, east and western edges of the study area, with Happy Lake and Drummer Lake areas being consistently high density in all years.

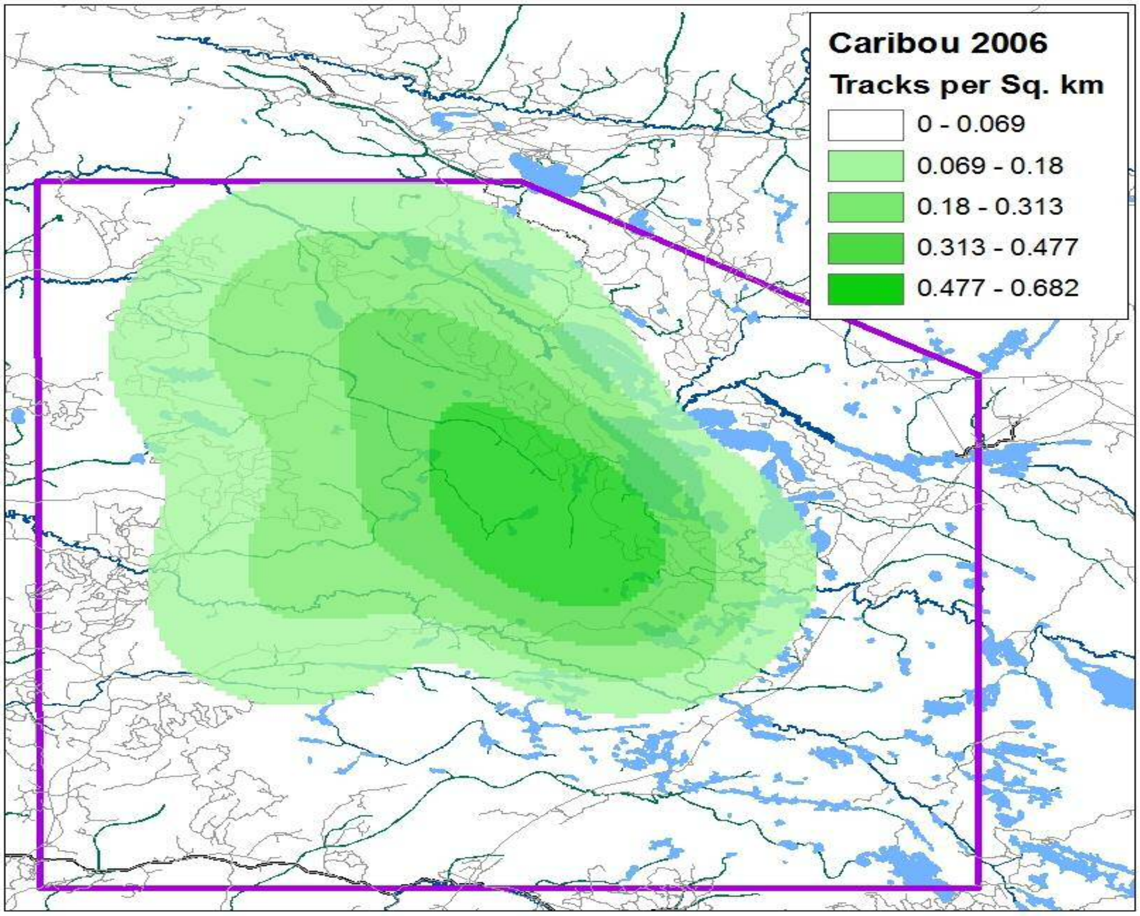


Figure 3.5. 2006 Caribou track density from aerial survey observations.

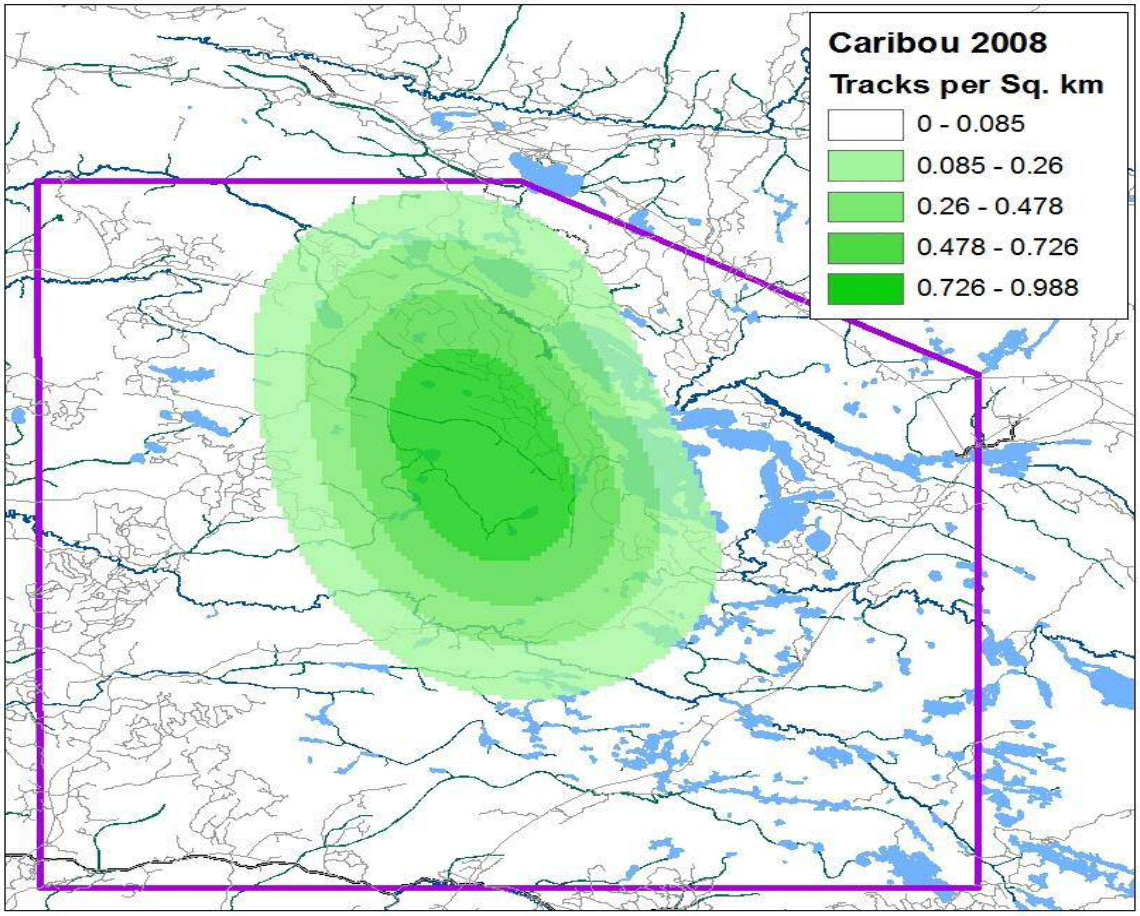


Figure 3.6. 2008 Caribou track density from aerial survey observations.

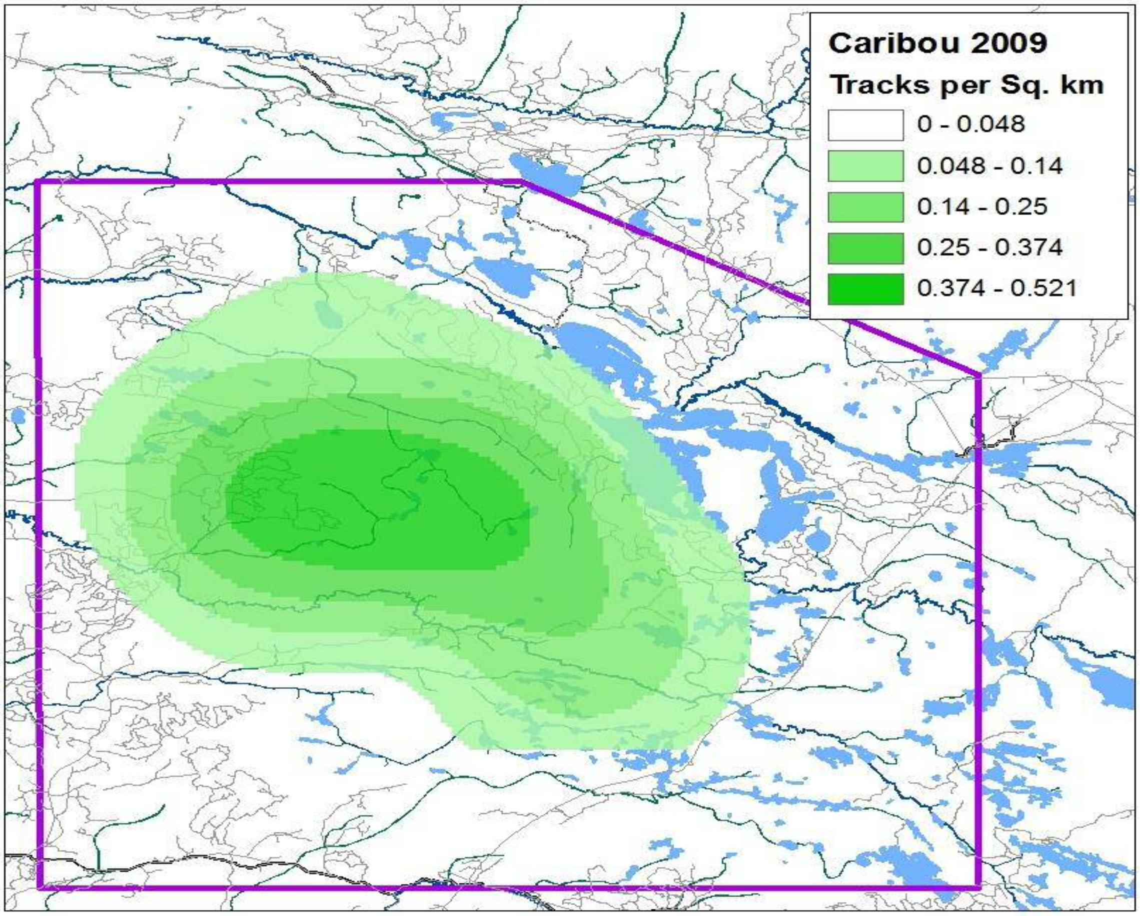


Figure 3.7. 2009 Caribou track density from aerial survey observations.

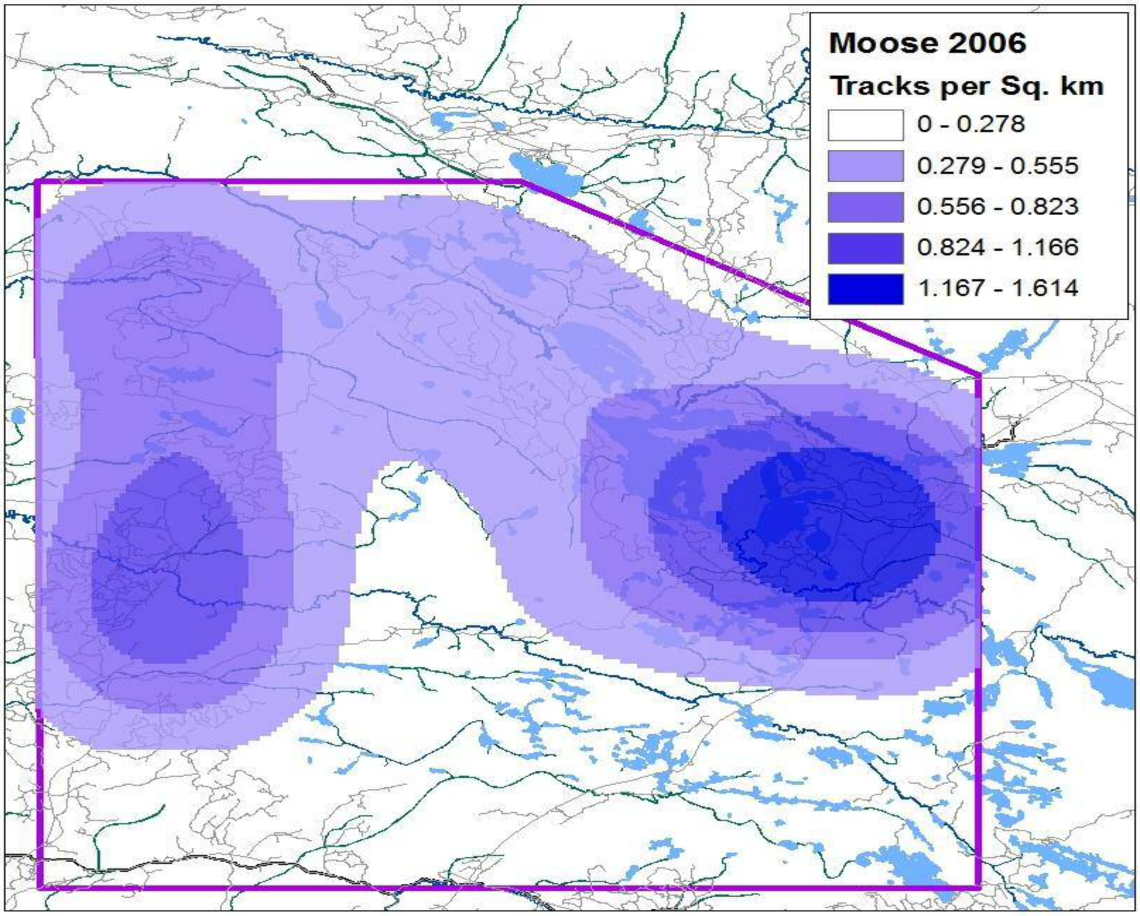


Figure 3.8. 2006 Moose track density from aerial survey observations.

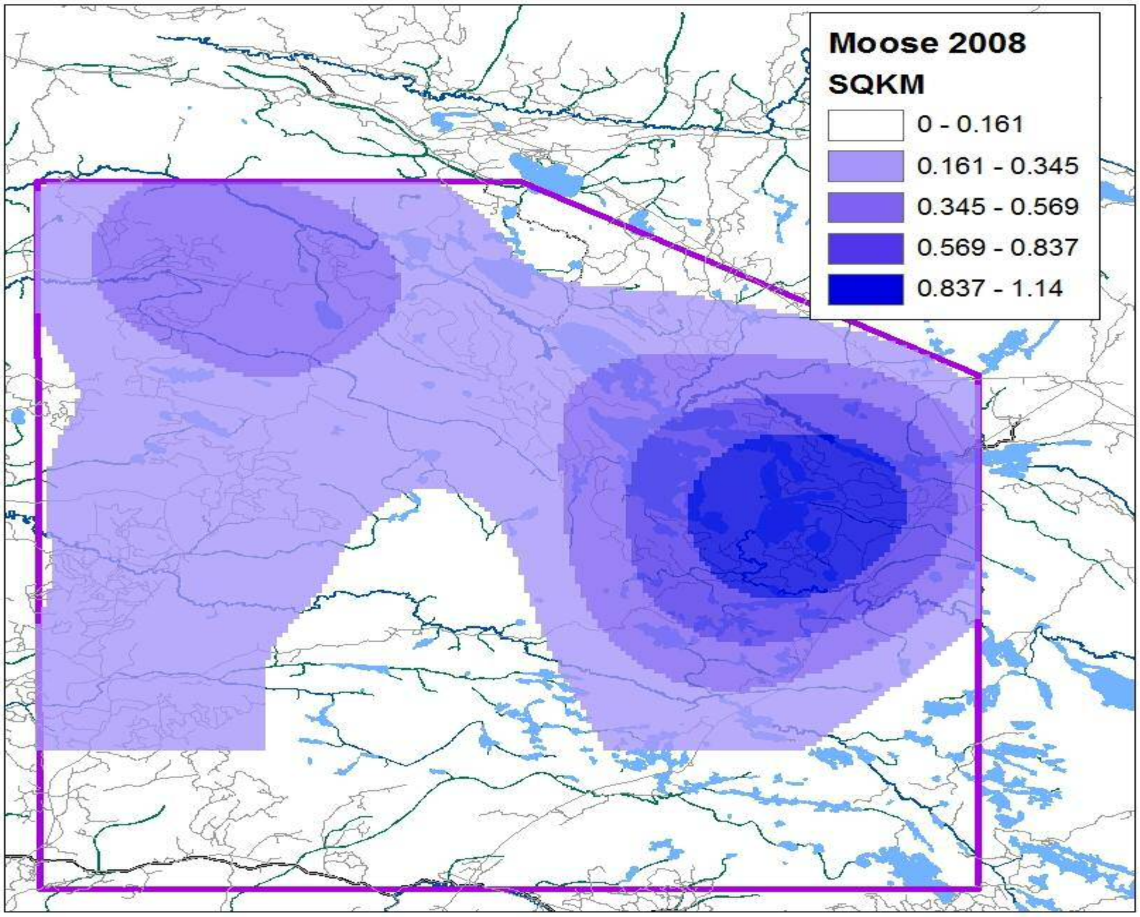


Figure 3.9. 2008 Moose track density from aerial survey observations.

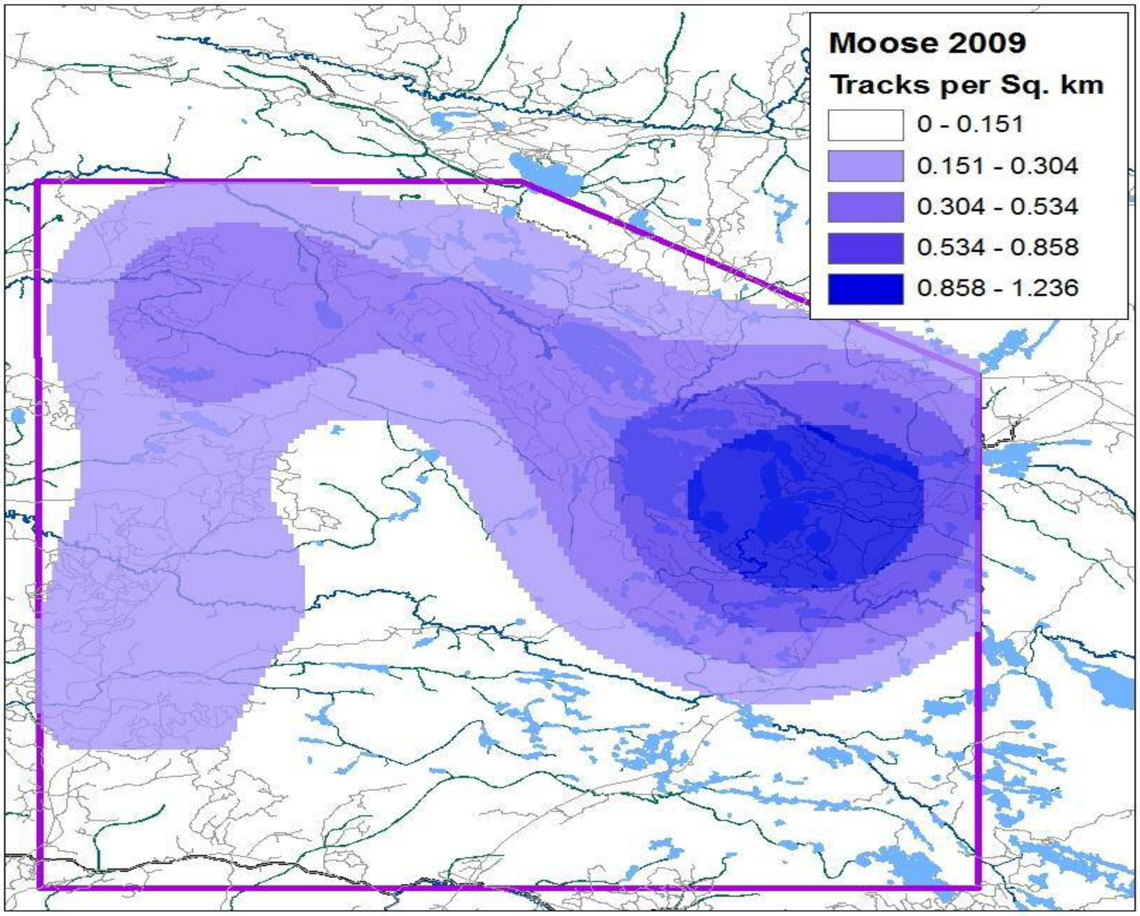


Figure 3.10. 2009 Moose track density from aerial survey observations.

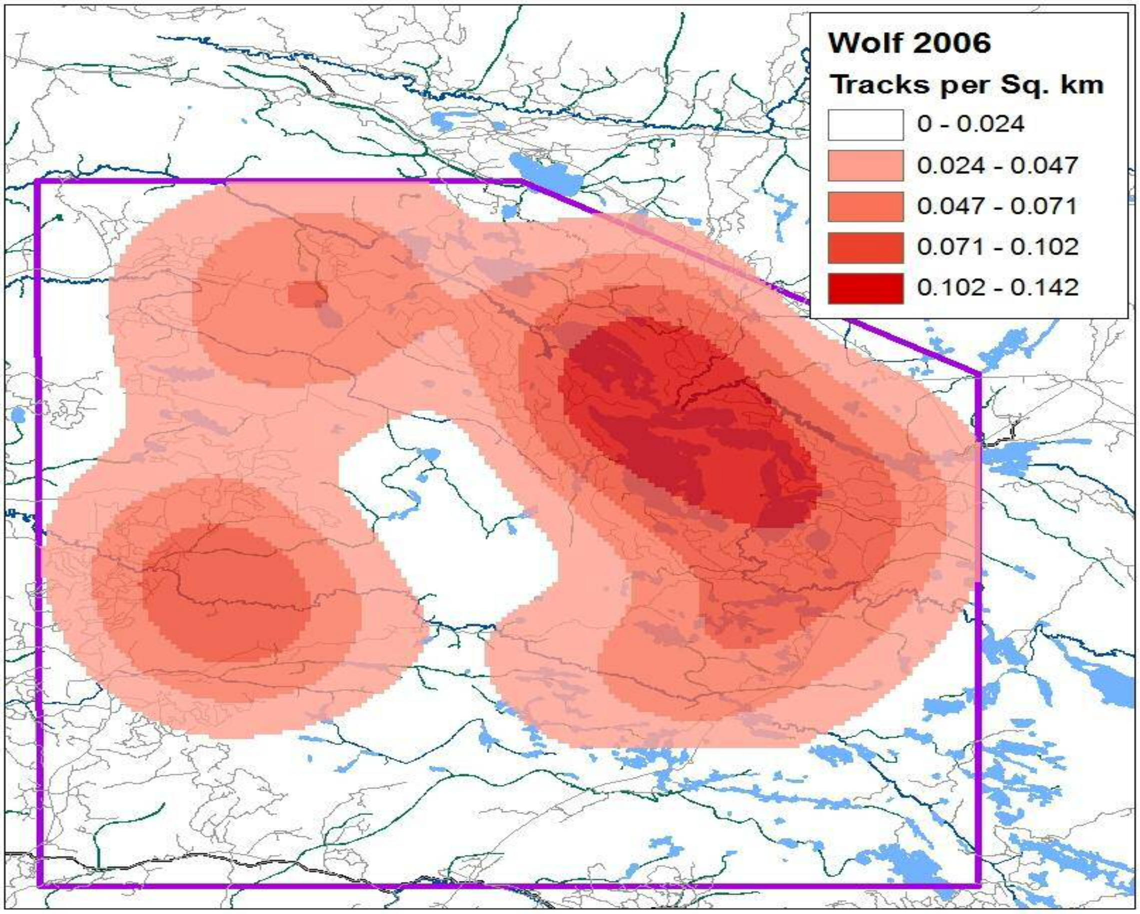


Figure 3.11. 2006 Wolf track density from aerial survey observations.

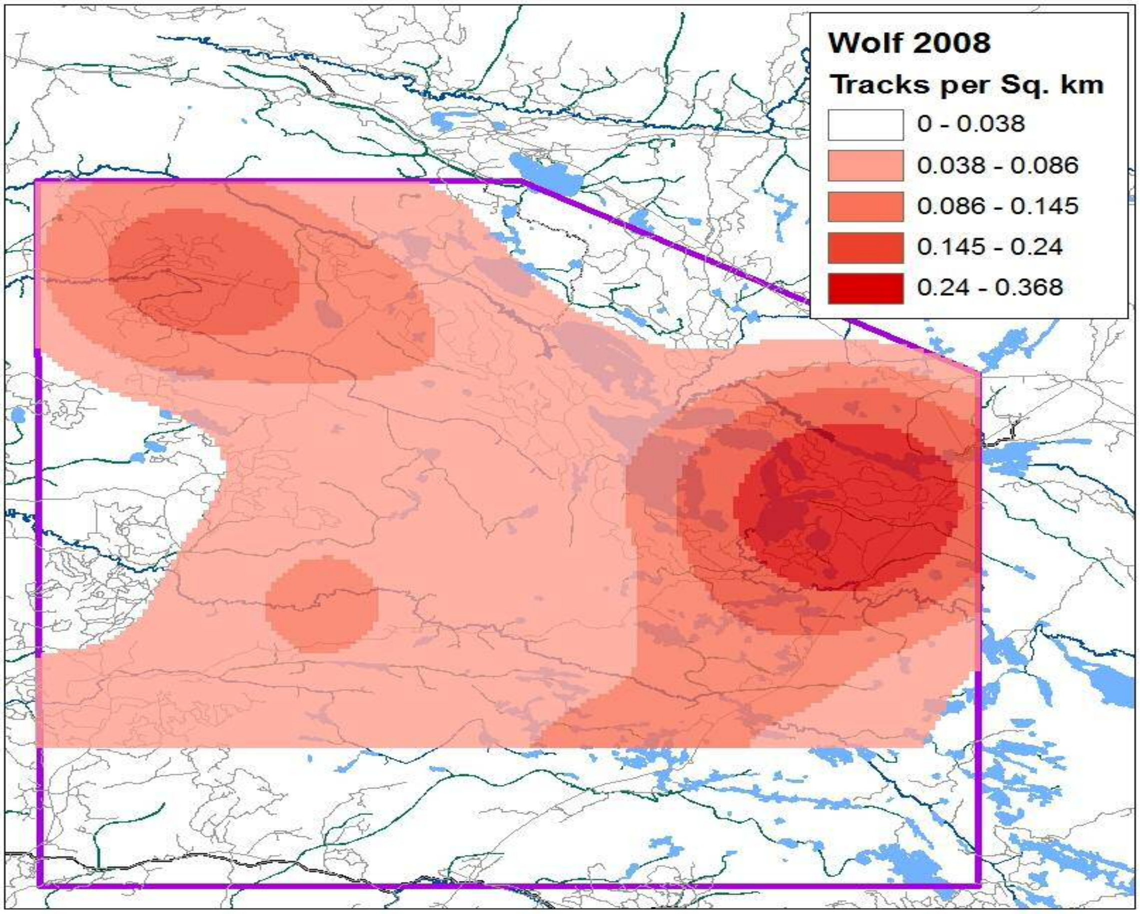


Figure 3.12. 2008 Wolf track density from aerial survey observations.

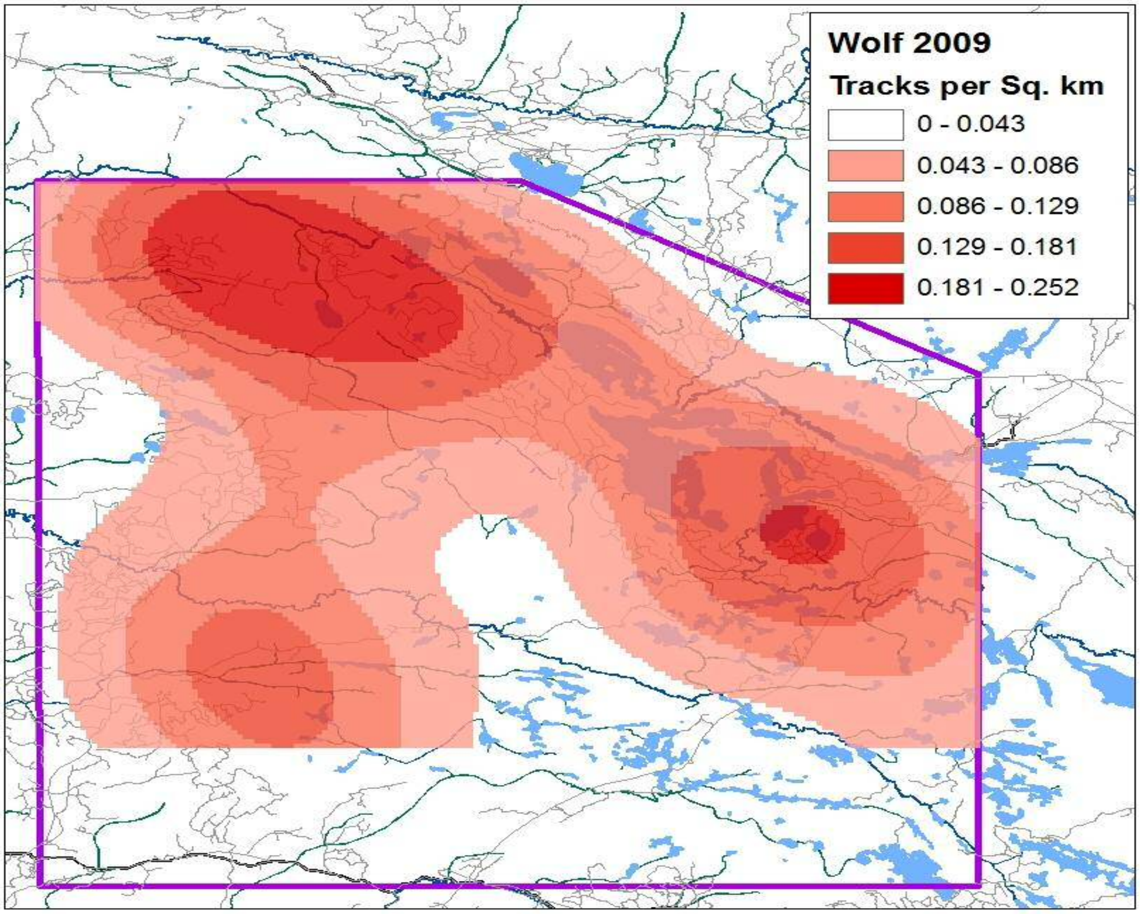


Figure 3.13. 2009 Wolf track density from aerial survey observations.

Pooled data for each year per species was overlain and mapped to illustrate the relative distribution of moose, caribou, and wolves (Figure 3.14). Regression analysis between species showed a weak negative relationship between moose and caribou density (Figure 3.15) and caribou and wolf density (Figure 3.16), but a strong positive correlation between wolf and moose density (Figure 3.17; Table 3.2). The negative relationship between caribou and moose (coefficient -0.05820) was more pronounced than that of caribou and wolves (coefficient -0.00419).

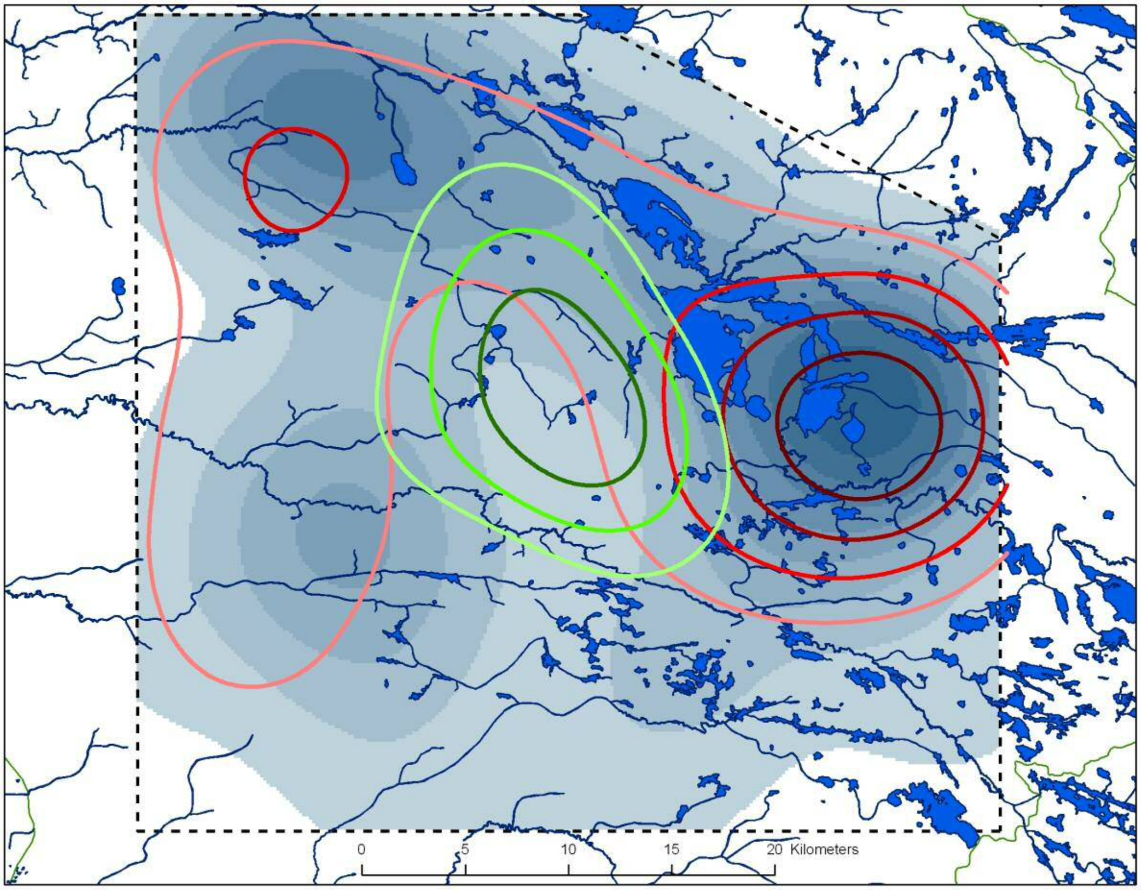


Figure 3.14. Overlain density contours of pooled species density, 2006-09. (Moose in shaded blue, caribou in green lines, and wolf in red lines. Darker shades/lines indicate greater density.

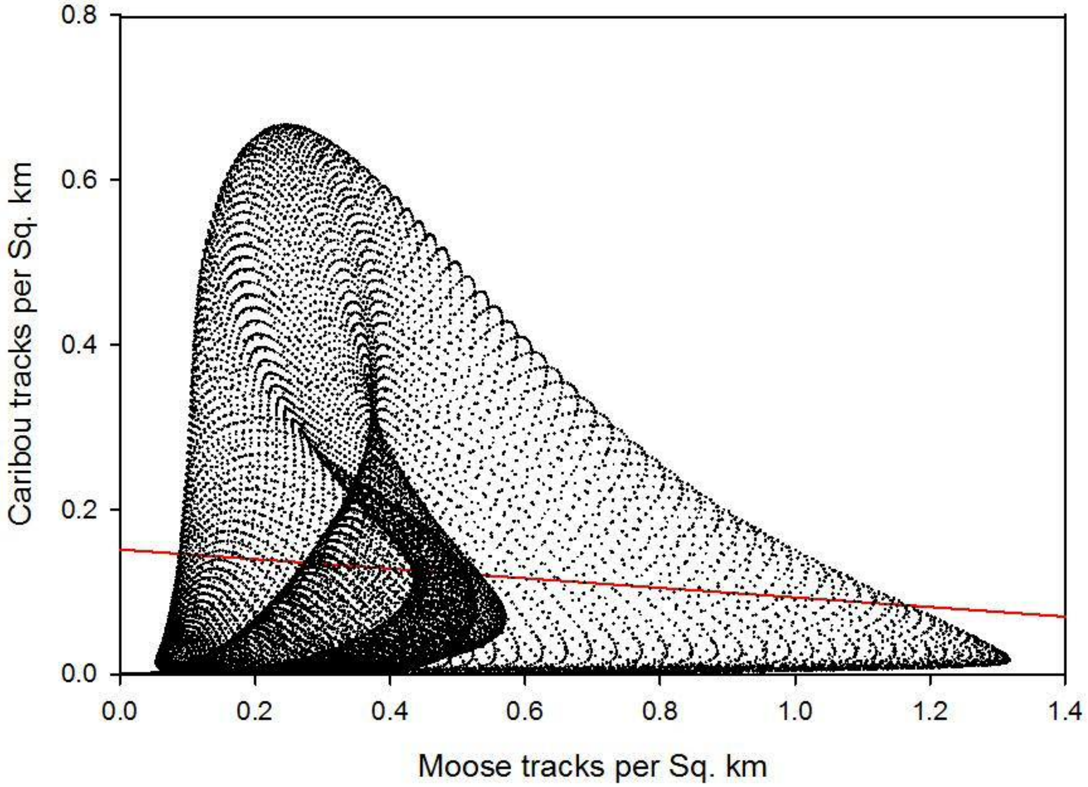


Figure 3.15. Scatterplot showing moose vs. caribou tracks per km^2

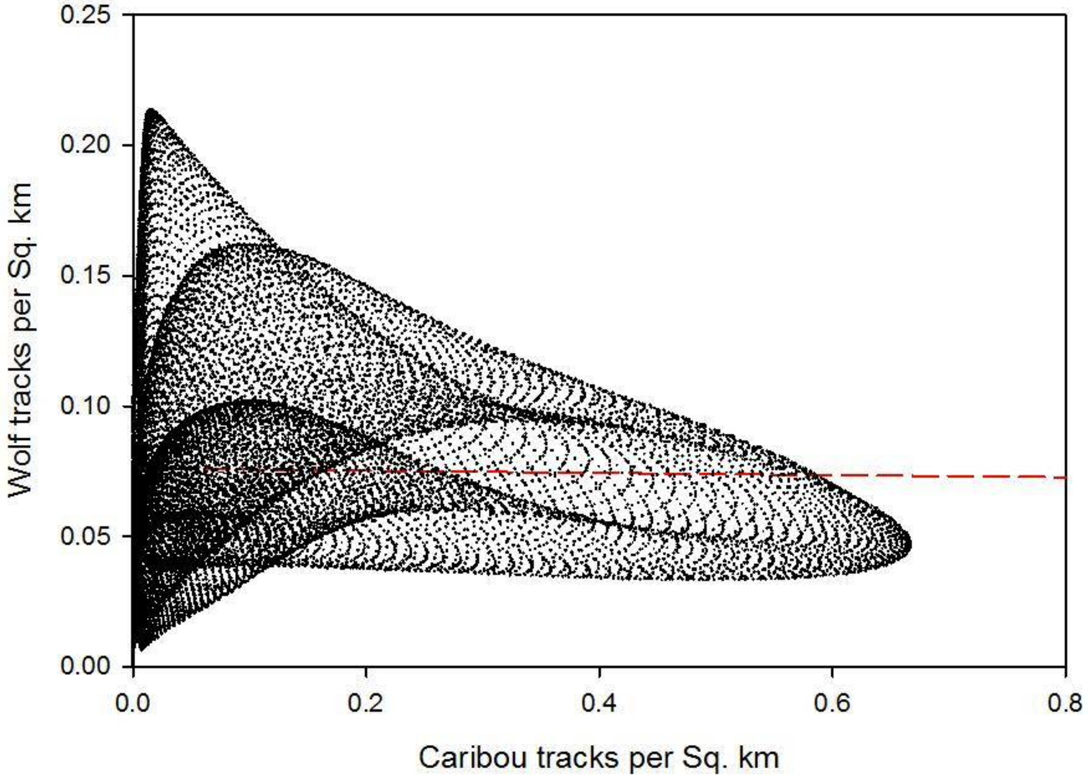


Figure 3.16. Scatterplot showing wolf vs. caribou tracks per km^2

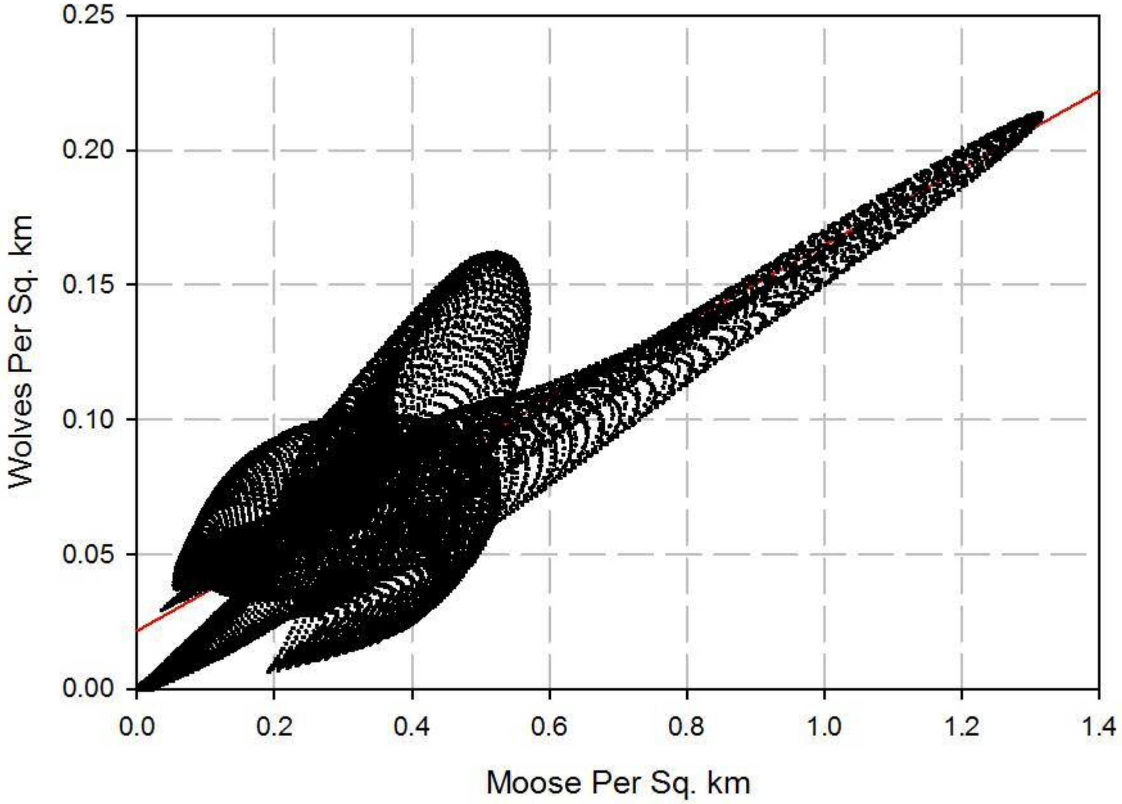


Figure 3.17. Scatterplot showing moose vs. wolf tracks per km^2

Table 3.2. Results of regression analysis of species pairs.

Species Pair	Coefficient	Standard Error	R-Squared	P-Value (CI 95%)
Caribou-Moose	-0.058200	0.004370	0.008510	<0.001
Caribou-Wolf	-0.004190	0.001850	0.000246	0.024000
Moose-Wolf	4.974000	0.022500	0.703000	<0.001

Diet

Of the 185 sampled scats, three prey species were identified (Table 3.3). Moose were the most frequently occurring prey species identified in scats at 96%. Discounting the samples obtained near kill sites, moose still occurred in all but eight scats, or 85% of the total, with beaver being the second most common (9.6%), and hare the third prey item at 5.8% (Figure 3.18). Caribou were not identified in scats during the study period.

Heterogenous samples were added to the results based on the most frequently occurring species, in both cases, beaver. The first heterogenous sample was composed of 56 (80%) beaver, and 14 (20%) moose. The second heterogenous sample was composed of 39 (56%) beaver, and 31 (44%) moose.

Table 3.3. Composition of wolf scat samples based on prey occurrence.

Collection Area	Examined samples	Prey Species Present		
		Moose	Beaver	Hare
Kill Site	133	133	0	0
Trail	40	36	1	3
Den Site	12	8	4	0
Total	185	177	5	3
Total Percentage	100.00%	96.00%	3.00%	1.00%

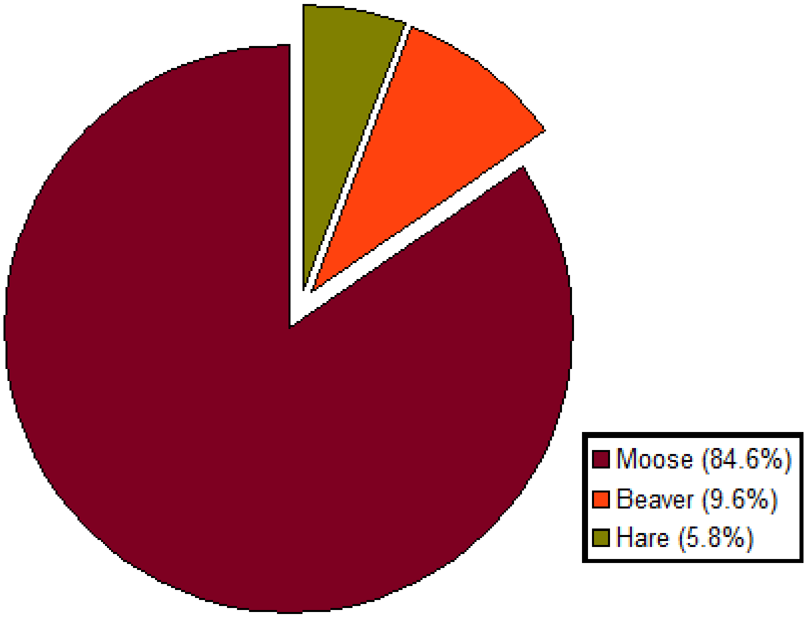


Figure 3.18. Prey species by proportion of samples occurring excluding kill site samples.

Kill site observations noted or reported during 2008-09 field work included fourteen moose (Figure 3.19), and one grouse. No caribou were observed or reported during the study period. Kill sites located during ground and aerial surveys were found on Manigotagan Lake, Drummer Lake, along Highway 304 near Wanipigow Lake, and a live moose surrounded by wolves was observed near Wallace Lake and later found killed. The remaining observations were not personally observed, or were not marked.

Figure 3.19. Wolf killed moose from Manigotagan Lake, January 2008. T. Davis

Discussion

Species Distribution

The pattern of distribution of species in the study area shows a strong tendency for wolves and moose to occur in the same places, and caribou to occur in places less likely to be used by wolves or moose. This supports previous observations of partitioning theory between moose and caribou, as a predator avoidance pattern (Cumming et al., 1996; James et al; 2004; Bergerud, 1990), and the idea that wolves select prey based on availability, vulnerability, and net energy gain (Keith, 1981; Seip, 1992).

The distinct association between wolf and preferred prey as exemplified by the wolf-moose relationship shown in this study demonstrate the suitability of prey distribution as a key component in modelling wolf habitat (Mladenhoff et al. 1999). Considering the limited availability of landscape variables available to predict wolf habitat (primarily only associated with roads or human development), the use of prey distributions, or prey habitat selection as surrogate habitat variables for predicting wolf distribution could be applicable.

Moose tracks were far more common on survey transects than wolf or caribou tracks (~ four times greater). While wolf and caribou track numbers were quite similar, peak track density was much higher for caribou than wolves, indicating a more concentrated distribution. The wider distribution of wolves across the study area, and occasional presence in caribou areas (2009, Figure 3.4), may suggest that wolves may travel through caribou areas, but not necessarily utilize them.

Moose in the greater study area are in decline (Manitoba Conservation, 2011), and the Owl-Flintstone caribou population has remained relatively stable (Leavelsley, Pers. Comm.), while less is known about wolf population trends in the area. The tracks observed for both moose and caribou showed a decline from year to year (actual moose observations also declined), while wolf tracks increased from 2006 to 2009. The inverse trend in rising predator track occurrence and the decline in their primary prey suggest that wolf populations may not have begun to respond to the decline in moose, creating an environment where increased predation pressure may influence the remaining moose, driving further decline. Moose track counts remained higher than caribou counts, which suggest that even with population reduction, they remain the preferred prey species. Potvin et al. (1988) observed that wolves would continue to preferentially prey on deer in the winter when their numbers declined below that of moose. Hayes et al. (2000) observed that wolves continued to focus on moose when caribou numbers increased, and population density was only slightly lower (78%) than moose, compared to 25% in this study.

Kittle et al. (2008) observed wolf prey selection and habitat selection by ungulates in a multi prey environment, and found predation risk (from wolf distribution) was not a direct influence of prey distribution. Prey species selected habitat based on combinations of anti-predator tactics to reduce vulnerability, rather than on wolf distribution (Kittle et al., 2008). This would suggest that while caribou distribution was negatively related to wolf distribution, other factors, such as spacing away from moose, and the use of escape habitat drive caribou distribution. The greater overlap of caribou and wolf distribution compared to caribou and moose distribution indicate that it is moose that are being avoided, though the goal may be to reduce wolf encounters.

The use of multispecies surveys is limited compared to the wealth of location data provided by GPS tracking. However, it provides a systematic, repeatable, consistent approach. It allows for more direct comparison of distribution between species and over time across a constrained area, reducing bias of individual behaviour, and autocorrelation that may arise in utilizing GPS data (Cagnacci et al., 2010; Otis and White, 1999; Hemson et al., 2005).

Diet

The assessment of wolf diet did not show any evidence of caribou predation. While limited in number, scats were collected across the study area, in areas expected to be occupied by moose and caribou, but scats were primarily composed of moose hair (85%). Hayes et al. (2000) showed a similar proportion of moose (89%) based on locating kill sites in a moose-caribou system in the Yukon Territory. Secondary prey species, beaver and hare, occurring in scats were expected, as observed in Quebec (Tremblay et al., 2001), Yukon Territory (Theberge and Cottrell, 1977), Finland (Yliopisto, 2000), and Minnesota (Van Ballenberghe, 1975). In summer, beaver are occasionally the principal prey species in Ontario (Voigt et al., 1978), and Latvia (Andersone, 1999), where in a depression of cervid populations, beaver consumption increased.

Caribou did not occur in samples, and scats were not found during surveys in areas of high caribou density. Seasonality may influence the presence or absence of caribou in scats. Wolves are thought to prey heavily on caribou calves where possible, which would not be observed in winter scat collection. Collection of scats in other seasons requires extensive ground survey time, or the aid of radiotelemetry or dogs to effectively locate samples (Wasser et al., 2004). Moose kills occurred most often in open spaces, and naturally would be more evident to observers in the air or travelling along open corridors. Caribou are both smaller, and more apt to be found under taller cover, leading to the possibility that kill sites may be missed. However, extensive effort to locate caribou during capture work, telemetry, and aerial surveys was made, and these efforts led to much greater scrutiny of caribou areas and habitat. Estimating populations of caribou was another aspect of the field that would include locating uncollared caribou. Attempting to locate caribou and wolves on capture and telemetry flights also requires following tracks until animals are found, in open and covered areas. Following tracks of both species with this level of intensity would seem to reduce the likeliness that caribou kills would be overlooked to a greater degree than moose. While tracks were observed during corridor surveys within caribou range, scats were not found, which could indicate permeability of caribou range as a travel area, rather than as a hunting ground. Previous examination of wolf scats in the region were conducted by Pruitt, in which he indicated a miniscule proportion of caribou hair occurring (<1%), and attributed it to scavenging of poached caribou discovered at a similar time (Pruitt Jr., Pers. Comm.). Unfortunately, the scope and extent of scat sampling was not published or made available.

Hypotheses

The null hypotheses of this analysis proposed that species distributions would not be significantly different, and that caribou predation by wolves would be evident due to a lack of partitioning. This hypothesis was rejected in favour of the alternate hypothesis that wolf distribution would be positively correlated with moose distribution, and not with caribou distribution, and that apparent partitioning would lead to a lack of evidence of caribou predation by wolves. While a more robust diet survey would more fully describe the food habits of wolves in the study area, the present study indicates that caribou are either absent, or figure very minimally in wolf predation.

The partitioning of caribou and moose, as observed by Cumming et al. (1996), James et al. (2004), and noted as a possible anti-predator tactic in mountain caribou by Bergerud et al. (1984), is clearly evident in this study. The lack of scats observed in surveys in caribou range, and the lack of caribou hairs observed in scats from adjacent areas suggest that this partitioning may be effective in reducing caribou mortality from wolf predation

Chapter 4: Moose, wolf and caribou relationship to linear features

Abstract

Wolves utilize corridors for travel and hunting. This has been well documented, but not specifically quantified. Caribou utilize spatial partitioning from moose and wolves. Caribou selection for and against landscape features inversely to moose selection may be part of how caribou effectively avoid moose.

Multi-species transect surveys were used to compare moose, wolf and caribou distribution relative to natural and anthropogenic features using distance-based selection. Wolf tracking via corridor surveys and telemetry was used to further explore the role of linear corridors in wolf movement on the landscape. Preference for linear natural or anthropogenic features was compared using distance-based comparison of paired samples.

Wolves and moose selected river and road features, while caribou avoided them. Caribou selected lakes, as potential escape habitat. Highways and transmission corridors were too rare on the landscape to be effectively analyzed. Wolf telemetry showed no preference for natural or anthropogenic features for wolves in pack territory. Lone, dispersing wolves showed a preference for natural features when making extensive movements.

Caribou avoidance of features associated with moose demonstrates partitioning as well as one possible mechanism involved in reducing predation risk. The role of anthropogenic corridors for wolf travel appears to be additive rather than compensatory, with both contributing to the overall travel network. The fragmentation of the landscape by this network increases wolf encounter rates with prey and reduces refuge habitat available to both moose and caribou. Caribou habitat partitioning has been effective so far, due to

management efforts to preserve it, but declining moose numbers suggest that combined hunting and predation pressures will ultimately make available refuge habitat insufficient.

Introduction

Wolf use of anthropogenic corridors has been studied relative to road/traffic density (Thiel, 1985, Mech et al., 1988; Lesmerises et al., 2011), crossing/barrier effects (Thurber et al., 1994; Whittington et al., 2005; Percy, 2003), and habitat/resource selection (Latham et al., 2011; Mladenhoff et al. 1995; Houle et al., 2009; Kuzyk et al., 2004). The direct use of these corridors by wolves has been documented, but has not been quantified specifically. In the course of this study, wolf use of a variety of features has been further documented and assessed for both direct and indirect value.

Wolf Habitat

As a top predator, wolf distribution is related to prey distribution at different scales. Globally, wolf distribution is associated with large ungulate distribution (Young and Goldman, 1944), while at regional levels, wolf density directly relates with prey biomass (Fuller, 1989). Wolf population and distribution are regulated by the availability of prey, that is, present and vulnerable to predation (Keith, 1983). Because of this, landscape pattern and composition, which is more readily observed and relatively more permanent, is not easily associated with wolf distributions, compared to herbivorous species (Mladenhoff, 1999).

Wolf habitat preferences are often dependent on the scale and landscape pattern. While road density is considered a limiting factor to, and effective predictor of wolf distribution (Mladenhoff, 1995, 1999), Bowman et al. (2010) found wolf distribution positively correlated with road density in Ontario at a broad scale, and wolves have been found to occupy areas with higher road densities, so long as there was adjacent forest cover

(Mech, 1989).

Moose Habitat

Moose range extends across the boreal forest regions of North America and moose are adapted to the disturbance driven succession pattern of the boreal forest (Banfield, 1974). Moose utilize a variety of habitat types for food, nutritional needs, protection, and thermal cover. Young deciduous forest and shrubs are the primary food source for moose in winter, while aquatic vegetation provides additional food and nutrients (sodium in particular) in the spring and summer (Belovsky, 1978). Older coniferous forest adjacent to food sources provide cover habitat and browse when snow is deep (Telfer and Kelsall, 1984). The roles of early seral stages in moose habitat show its use of fire driven succession, or the similar effects of logging (Krefting, 1974; Telfer, 1974; Potvin et al., 2005). Disturbance areas selected by moose are determined by the distance to available cover and substantial clearcuts that may provide food habitat may not be utilized. Ontario Natural Resources (1998) used two hundred meters as an appropriate distance to cover to be maintained in cut blocks. Potvin et al. (2005) found that cut blocks became valuable moose browse habitat within ten years of being cut. Moose are sensitive to overheating, both in summer and winter, and utilize thermal cover to regulate their temperature in summer and by reducing their activity in winter (Timmerman and McNichol, 1988).

Caribou Habitat

Woodland Caribou utilization of landscape can be described at multiple spatial and temporal scales. Habitat characteristics, as well as other factors, including predators, and other prey species influence caribou distribution and home range. Woodland caribou as a species occur across Canada in the boreal forest, while different ecotypes occupy a variety of sub-regions, from mountainous to coastal (CWS, 2005). At the range scale, caribou occupy landscapes with large areas, allowing them to space out, reducing predation risk (Bergerud and Page, 1987; Stuart-Smith et al., 1997). In winter, Caribou select areas with large and complex lakes (Ferguson and Elkie, 2005), peatland and black spruce complexes (Rettie and Messier, 2000; Bradshaw et al., 1995), Pine and spruce forest (Antoniak and Cumming, 1998), and avoidance of moose habitat (James et al., 2004; Cumming et al., 1996) and wolf predation (James and Stuart-Smith, 2000) Avoidance of moose and their habitat is thought to be a predator avoidance strategy (James et al., 2004) Calving and summer habitat is largely similar to winter habitat, utilizing peatlands, black spruce, and pine forest, but in smaller ranges (Rettie and Messier, 2001). The Owl-Flintstone caribou show an association to bog and treed rock, as well as 60-70 year old pine forest, shrub cover and deciduous stands were avoided (Schindler, 2006). Disturbance on the landscape influences caribou habitat selection through fragmentation and alteration (Smith et al., 2000). Moose often select disturbed sites (Potvin et al., 2005), resulting in caribou avoidance (James et al., 2004). Linear disturbances fragment forest habitat, and are often avoided by caribou due to risk of predation (James and Stuart-Smith, 2000).

Human development and corridors

Human activity can have great consequences for ecosystems and wildlife populations from direct mortality, habitat destruction, contamination and fragmentation, and the introduction or removal of species (Ledig, 1992). Development and alteration of the landscape for agriculture and settlement has removed vast amounts of habitat available to wildlife (Richards, 1990), while corridor and road development has caused change far beyond its areal extent (Forman and Alexander, 1998). Road development effects include hydrological alteration, wildlife barrier effects (refusal or hesitancy to crossing), avoidance, human mortality (vehicular collision, environmental contaminants, or increased hunting), invasive species pathways (bringing disease, competition), and loss of diversity (Forman and Alexander, 1998; Fahrig and Rytwinski, 2009).

Caribou, moose, and wolves respond to linear developments, often both positively and negatively (Laurian et al., 2008; Johnson et al., 2005). Caribou generally avoid roads and trails at coarse and fine scales (James and Stuart-Smith, 2000; Bradshaw et al., 1997; Dyer et al., 2001, 2002; Bowman et al., 2010), though Noel et al. (2004) found an oilfield road had little influence on caribou distribution. Moose tend to avoid or reluctantly cross roads under most conditions (Laurian et al., 2008; Dussault et al., 2007); however, maintained roads can provide a source of sodium from de-icing salt that moose may utilize (LeBlond et al., 2007). Wolves often find roads and trails to be a semi-permeable barrier, only crossing occasionally (Whittington et al., 2004, 2005; Percy, 2003; Thurber et al., 1994), while other studies have associated wolves with features (Bowman et al., 2010; Houle et al., 2009) or implicated wolves using linear features in increases in caribou mortality (James and Stuart-Smith, 2000; McLoughlin et al., 2003; Darby and Duquette, 1986). A repeated theme of these analyses involve traffic, where corridor use by wolves is mainly associated with low use landscapes such as seismic exploration lines, seasonal roads and trails, or pipelines, and barrier effects are most strongly observed in high traffic areas and features. Studies of wolf distribution show wolf populations not being supported in environments of higher road density. Thiel (1985) identified this threshold at 0.58km/km^2 for a period from 1926-60, and indicated that public opinion regarding wolves and predators would influence wolf persistence. Potvin et al. (2005) developed a model for wolf distribution in northern Michigan based on deer density because existing models (Mladenhoff, 1995; 1999) depended entirely on road density, did not reflect prey availability, and greatly overestimated potential habitat. The Potvin et al. (2005) model considered road densities above 0.7km/km^2 to be the threshold of wolf habitation.

Resource selection and comparison

Identifying habitat preference, or resource selection, can be accomplished by comparing use of landscape variables relative to their availability (Manly, 2002). Habitat availability is the range of landscape components that an animal is able to select. Home range boundaries such as density kernels or minimum convex polygons generally form the overall extent of available habitat when individuals can be defined (Johnson, 1980). Where home ranges cannot be estimated, or it is used to define selection, the study area defines availability (Thomas and Taylor, 2006). Manly (2002) identifies three aspects of selection, use (whether a species is present at the resource), selection (where the species chooses to use a resource), and preference (where the species selects resources where it is equally available to other habitat). Assessment of use can be determined by overlapping relocations (or buffered relocations) upon habitat variables, or comparing density surfaces, or distance-based analysis, where rather than occurrence in habitat patches, proximity to features is used (Thomas and Talyor, 2006). Advantages of distance-based assessment include reduced influence of patch sizes in selection, less influenced by locational error, greater recognition of linear and edge effects, and value in determining specific preference (habitat a vs. habitat b) (Conner et al., 2003). Limitations of distance-based analysis include uncertainty in use (being near, rather than in habitat) and potential confounding by associated habitats (Dussault et al., 2005). Habitat availability within the home range or study area is quantified from either areal proportion (percent of land cover), or through the use of random selection (Manly, 2002). Comparison of actual locations to random locations can be applied to both compositional and distance-based analysis. Distance-based analysis can also be used to assess preference without the use of availability, due to having every location having a value for each variable present (Thomas and Taylor, 2006). Pairwise comparison using hypothesis testing or regression approaches can be used on distance-based data (Conner et al., 2003). Paired t-tests and Wilcoxon tests can be used to assess preference between two resources, where single locations with multiple attributes are available (Powell and Collier, 2000; Sagedhpour and Ginnett, 2011; Buehler et al., 1991).

Distance-based analysis against random locations has been used to study mammals, such as moose (Ollsen et al., 2011), bears (Fecske et al., 2002; Sagedhpour and Ginnett, 2011; Obbard et al., 2010; Wieglus et al., 2002), caribou (Schaefer and Mahoney, 2007), as well bird species such as eagles (Buehler et al., 1991), and Plover (Powell and Collier, 2000).

Since wildlife location data are rarely distributed normally, data must be either transformed, or compared using non-parametric testing methods (Thomas and Taylor, 2006).

Wilcoxon tests use signed ranks, where one variable is assigned a negative, and the other a positive, and then ranked by absolute value. The ranks are then tallied, to determine whether negative ranks outweigh positive ranks (Zar, 1999). This approach can indicate preference between two feature types by identifying if locations are consistently nearer to one feature type. Mann-Whitney U tests compare two sets of values using a rank sum method, where values from both sets are ranked together, and the sum of rank values are compared (Zar, 1999). Kruksal-Wallis tests are a non-parametric equivalent to ANOVA (Analysis of variance) tests, based on Mann-Whitney rank sum tests, but applied to multivariate datasets (Zar, 1999).

Objectives

The study uses linear corridor surveys to assess the direct use of linear corridors by wolves. Wolves are expected to use anthropogenic corridors to the same extent that natural corridors are used, rather than preferring one type to the other, thus Hypothesis A:

H0a: Track observations will occur on anthropogenic corridors at the same proportion that they occur on natural corridors or;

H1a: Track observations will occur proportionally more frequently on natural features (aversion to anthropogenic corridors) or;

H2a: Track observations will occur proportionally more frequently on anthropogenic features (preference for anthropogenic features).

Indirect use of corridors as determined by GPS and radio telemetry data was compared between feature types. Wolves were expected to be equally distributed in relation to natural and anthropogenic features, thus Hypothesis B:

H0b: Telemetry locations will not be significantly closer to natural or anthropogenic features or;

H1b: Telemetry locations will be significantly closer to natural features than to anthropogenic features or;

H2b: Telemetry locations will be significantly closer to anthropogenic features than to natural features.

The relative distribution of wolves and prey species determined from aerial survey are expected to be uniformly located to linear features, thus Hypothesis C:

H0c: Wolf, caribou, and moose observations will not be significantly nearer or farther than a random distribution of points or;

H1c: Wolf distribution will be significantly closer than random to linear features and closer than caribou distribution.

Methods

Data Collection

Field research commenced with the deployment of radio telemetry collars in February-March 2008, with subsequent monitoring conducted for the following year. Corridor surveys were primarily conducted in winter 2009, while data from transect surveys were obtained from Manitoba Conservation occurring in January of both years, as well as an initial survey in 2006.

Corridor surveys were conducted along a variety of feature types within the study area (Figure 2.5). Features were categorized based on existing road classes defined by Manitoba Conservation and described by the Manitoba Model Forest (Manitoba Model Forest, 1994; Manitoba Conservation, 2005), Class 1 is defined as all season permanent public roads including highways; class 2 defined as long term (20+ year) all season access roads; class 3 defined as seasonal, temporary (1-10 year) harvesting roads; and class 4 defined as smaller temporary winter roads and smaller trails.

Both ground surveys via snowmobile and automobile and aerial surveys via helicopter were conducted. Surveys were conducted in the study area following snowfall events. Ten survey periods of 1-3 days between January and March 2009 were conducted, until ice and snow conditions were unfavourable. Helicopter surveys were made as available, while ground surveys depended on snow conditions. Track surveys began within 1-2 days of a snowfall, to allow time for tracks to accumulate (Alexander et al., 2005). Each survey involved 1-3 days of surveys, pending weather conditions and routes were not repeated until a new snowfall. Helicopter surveys did not depend on snow cover, because they were used to visit routes less reachable on the ground, and thereby not likely to result in duplicate track counts.

Tracks were identified and the start and end of tracks were recorded using handheld GPS units while traveling on snowmobile. Repeated surveys were conducted by snowmobile along two main routes in the study area: Bissett to Long Lake via Quesnel and Manigotagan Lake and Bissett to Turtle Lake. The Black and Sand Rivers were surveyed twice aerially, as well as part of the Maniogtagan River. The Sand River Road was surveyed by snowmobile, Highway 314, Trans-license Road, and Happy Lake Road were surveyed by automobile and air (Figure 4.1).

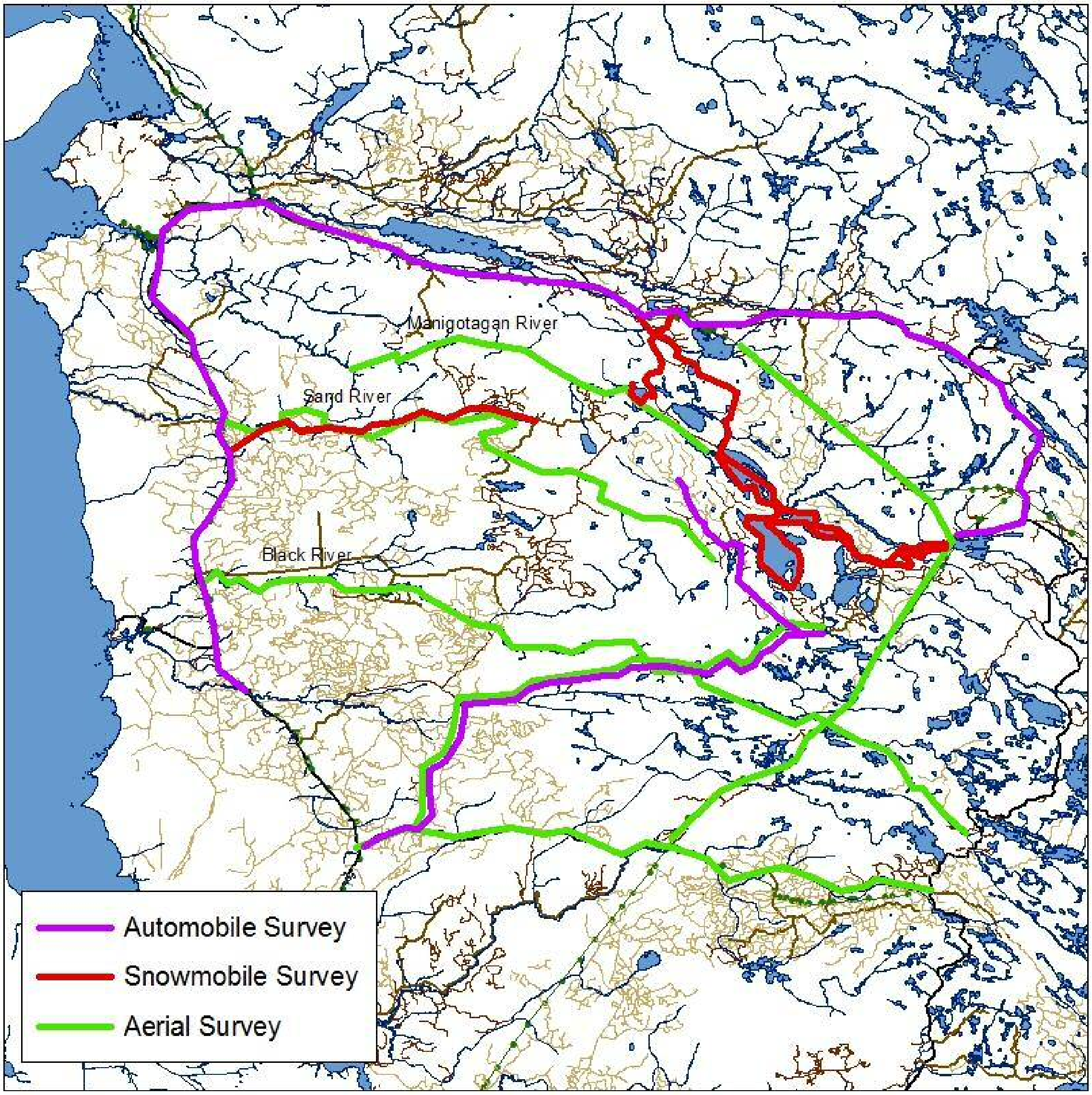


Figure 4.1. Corridor survey transect routes by survey method used.

Transect surveys

Aerial surveys were conducted in 2006, 2008, and 2009 by Manitoba Conservation to observe the distribution of ungulates and prey over a small experimental study zone as described in Chapter 3.

Transects across the study area were flown in a north-south orientation at approximately 400m altitude, at 1.75 km apart, over an area approximately 40km by 40km, or 1600 km^2

(Figure 3.1). Surveys were conducted in January of each year over 2-4 days: 4-6 Jan. in 2006, 22-23 Jan. in 2008, and 12-15 Jan. in 2009. Multiple trained observers on board a helicopter used handheld GPS units to record tracks and sightings along transects, for the three species, as well as white-tailed deer, which occurred very rarely (three tracks observed in 2006 and 2009), and wolverine (three tracks seen in 2006), and were not included. Observations and tracks were pooled as overall locations. Instances where multiple animals were recorded at a single location were not weighted by number, as no similar data was collected for track sightings, which could also represent multiple animals.

Eight wolves were captured and equipped with tracking collars in 2008 concurrently with caribou collaring efforts in the Owl-Flintstone range. Two GPS2000 Global Positioning System (GPS) tracking collars and six Very High Frequency (VHF) radio collars (Advanced Telemetry Systems Inc, Isanti, MN) were deployed to monitor wolf activity in the study area. The GPS collars and four VHF collars were placed in a large pack in the study area, eleven animals observed during captures. Two additional VHF collars were placed on a pair of wolves in the Wallace Lake area to the northeast (Figure 4.2).

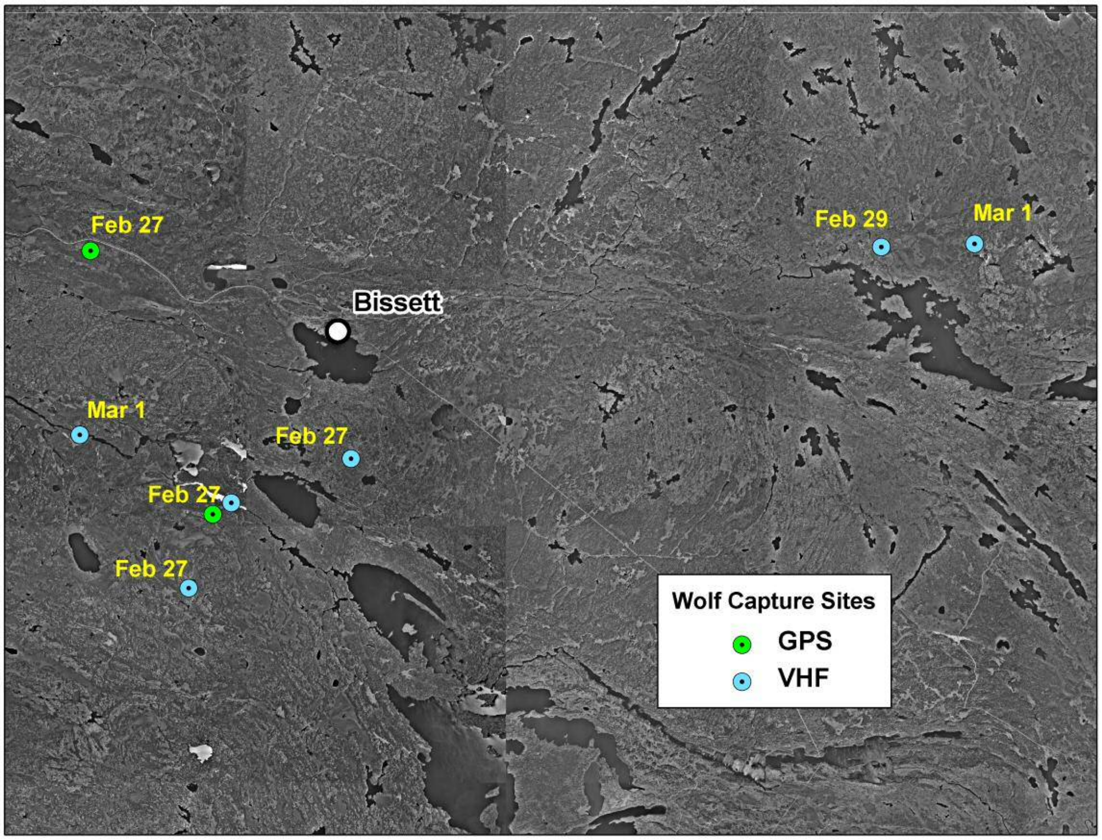


Figure 4.2. Wolf collaring capture sites, indicating date of capture and collar type.

Wolf captures were conducted by professional handlers via helicopter net gunning (Figure 4.3). Captures were conducted according to Manitoba Conservation wildlife handling guidelines for animal health and safety. Conservation wildlife staff and additional trained personnel monitored all captures from a second helicopter, as well as on the ground at capture sites, to ensure the safety protocol was followed and provide assistance to reduce overall handling time. Capture via net gun did not involve the use of tranquilizers and animals were controlled and restrained by one crew member before support staff approached to assist (figure 4.4). Restraint involved securing fore and back legs with belting, securing the jaw with rope and face mask.

Figure 4.3. Helicopter net gunning capture of wolf. T. Barker, 2008

Figure 4.4. Captured wolf being removed from net. T. Davis 2008

Once secured, wildlife staff would assist in processing the wolf, from collaring, assessing the health and age of the wolf, taking measurements, and extracting a blood sample for contribution to genetic study of wolves. Measurements included total length, shoulder height, and chest girth. Weight was not measured, as it was not feasible under field conditions, or required for any study aspect.

Radiotelemetry has become a major component of wildlife studies, and satellite tracking has made further advances in the amount and quality of spatial data available (Rogers, 2001). While satellite (GPS) telemetry has been so readily selected, radio telemetry remains valuable as its own right and as a key aspect in the use of GPS tracking.

Radio telemetry consists of attaching a radio transmitter keyed to a specific frequency in the VHF range to an animal via a collar or other device. Researchers can then use a receiver to locate the animal by the radio pulse emitted by the transmitter when sufficiently close (White and Garrott, 1990). Telemetry receivers can be used on the ground with handheld antennas to either track, or triangulate the location by taking fixes (bearings) of signals from several locations. Receivers and antennas can be mounted on aircraft and used to locate and record animal locations, as well as obtaining visual confirmation of animal condition. GPS collars are generally also equipped with radio transmitters to assist in recovering collars following study completion.

Satellite tracking became commercially available for research in 1991 following development of the Global Positioning System satellite network for military applications (Rodgers, 2001). Early testing of GPS collars on wildlife in forested environments was conducted in the Owl Lake area on caribou (Terrestrial and Aquatic Ecosystem Management, 1999). GPS collars use triangulation relative to geostationary satellites to determine a spatial location. Data are recorded on the collar and either collected when collars are recovered, or remotely collected via UHF radio or satellite transmission, if so equipped. Collars used in this study were either standard VHF radio collars or store-on-board GPS collars.

GPS tracking collars were set up to record locations every 80 minutes (1.3 hours), in order to extend the functional life of the collar to just over a year (estimated life 410 days), to provide a complete year’s data of one wolf and its associated pack. GPS collars can be programmed to provide fine or coarse scale temporal resolution, depending on the study objectives. As this was an exploratory attempt to assess wolf movement in the study area, a coarser scale was selected to maximize duration, rather than assess fine scale movements.

Radio telemetry was conducted by aircraft by Manitoba Conservation wildlife staff or qualified biologists to locate and observe wolves. Telemetry flights were conducted concurrently with caribou telemetry to locate and observe calving status on a monthly basis for population studies. Wolves were located, and visually inspected to confirm any mortalities and count uncollared wolves in company.

Both GPS tracking collars disappeared from the study area early into the study. One was located by a trapper in Ontario, and eventually returned, while the second was never located.

Data Analysis

Corridor surveys were conducted along 735km of a variety of features, using 500m units to describe presence or absence of travel along corridors after Beier and Cunningham, 1995; Alexander et al., 2004; 2005, in their analysis of cougar tracks as a population index. For each survey period, the total distance surveyed of each feature type was recorded, as was the distance of wolf tracks recorded. Because of the variation in the surveyed distance of each feature or survey period, results were pooled into either natural features or anthropogenic features. Pooled results were converted to proportions of track presence on each feature type. The null hypothesis states that there should be no difference between the proportions of surveyed routes to the proportion of track observations in each category. A Chi-square with Yates' correction factor was used to compare the expected (surveyed) proportion of natural and anthropogenic features to observed (track observation) proportions (Zar, 1999)

Transect Survey

Multispecies survey data were used to compare proximity to natural and anthropogenic feature types of moose, caribou, and wolves. Using a Euclidean distance-based approach (Conner at al., 2003; Perkins and Conner, 2004; Schaefer and Mahoney, 2007; Obbard et al., 2010), actual locations for each species were measured to eight classes of linear feature. Actual locations were compared against randomly distributed locations amounting to one hundred times the number of actual points for each species. Obbard et al. (2010) generated random locations for comparison and used cumulative average distances to two habitat types to identify a levelling off point of means, to determine the necessary number of features for comparison without biased distribution. Schaefer and Mahoney (2007) also identified levelling off points for their random locations relative to logging activity. Ollson et al. (2011) used 50,000 points, though no rationale was given. Schaefer and Mahoney (2007) found mean distance levelled off at ~2,000 random locations, while Obbard et al. (2010) found in two habitat types, distance levelled off within 150-175 random locations. I compared distances of random locations in the study area to two feature types that were well distributed (Class 3 roads and rivers) by randomly sorting and generating cumulative means and repeating three times. Cumulative means would level off at approximately 500 points in all cases. In order to ensure that random locations reflected availability in terms of survey methods, all points were located along transect lines. Random locations were measured to the nearest features of the eight classes and merged with actual locations in single datasets for each species. Values for actual and random locations for each species-feature class were compared with Mann-Whitney Non-parametric rank sum tests to compare two groups (Zar, 1999).

Telemetry survey

Radiotelemetry data were collected from the eight collared wolves and location data were used to compare proximity to natural and anthropogenic features. Using Arcmap Spatial Join Tool (ESRI, Redlands, CA), each wolf location was measured to the nearest of each type of linear feature, creating paired data samples as in Sadeghppour and Ginnett (2011). Seasonality of data was assessed by comparing the distance to natural and anthropogenic features of monthly locations using Kruksal-Wallis ANOVA tests for non-parametric multivariate data (Zar, 1999). Effects of individuals on the overall dataset were also compared using a Kruksal-Wallis test. After factoring for individual effects, the difference between wolves associated with the pack were compared against lone wolves with a Mann-Whitney U test to compare two groups (Zar, 1999).

To test whether wolves showed a preference for anthropogenic or natural features, wolves of the Sand River pack, Pairwise comparisons were performed using Wilcoxon tests (P= 0.05) as in Sadeghpour and Ginnett (2011).

GPS Telemetry

GPS telemetry from a single wolf was collected, providing 6225 locations over one year and ten days. Locations were collected every 1.3 hours, with an overall success rate of

92% (6225 of a possible 6734 locations). Data from the wolf had a total travel distance of 3116 km and spanned two provinces and one state (Figure 4.5).

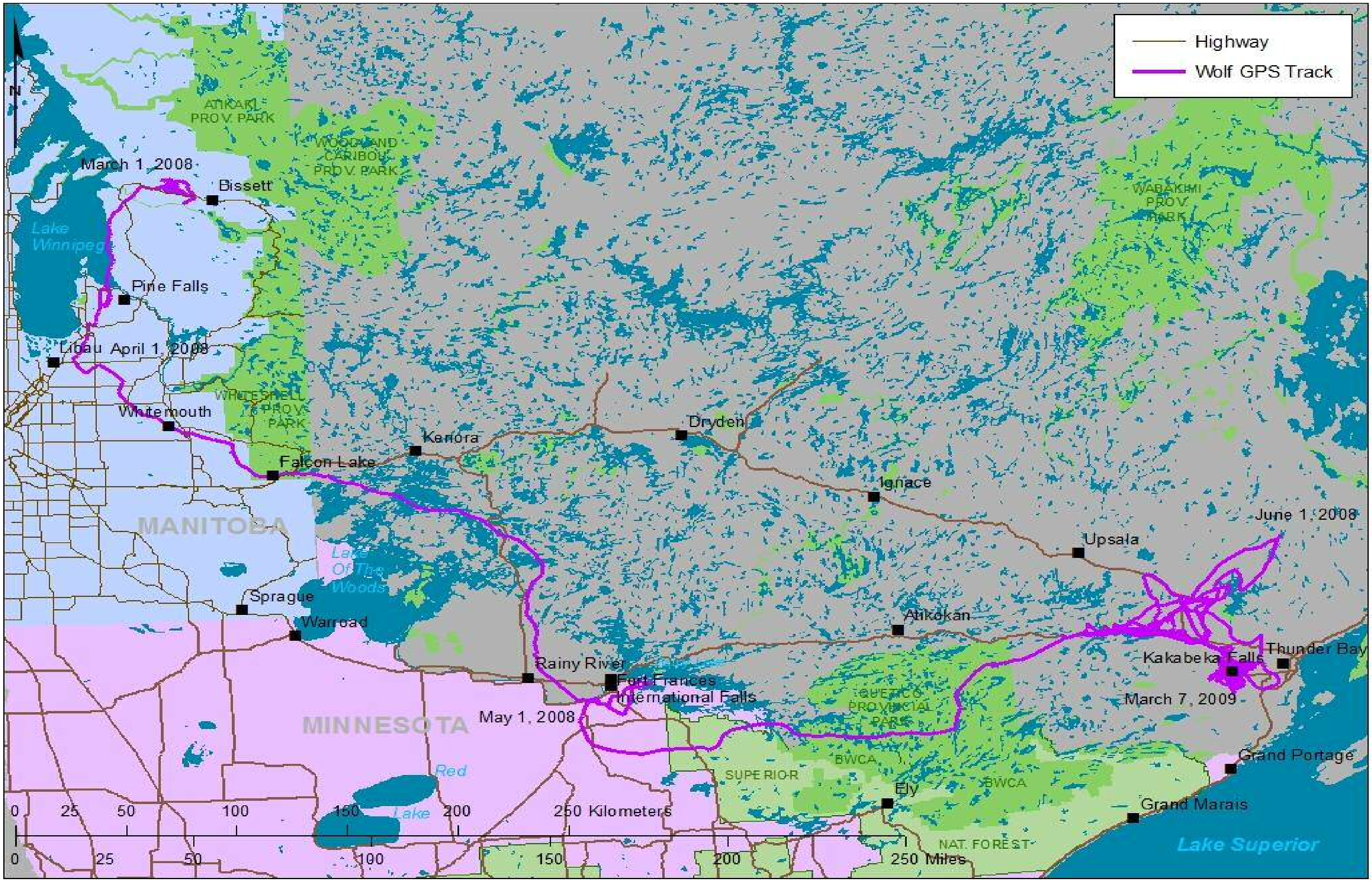


Figure 4.5. Movement path of wolf equipped with a GPS tracking collar.

GPS tracking data were analyzed similarly to the radiotelemetry data, by pairwise comparison to assess a preference for one class of feature or the other. A compositional analysis or resource selection was not chosen due to the extensive dispersal behaviour of the wolf. The substantial movements over a wide area make determining a home range area for comparison difficult (Sagedhpour and Ginnett, 2011) and make availability harder to judge. A major dispersal movement such as this also suggests unfamiliarity with the landscape, which limits decision making to the options immediately available. Seasonal habitat variation is accounted for in satellite telemetry studies of caribou (James et. al, 2004; Schindler, 2006; Schaefer and Mahoney, 2007; Post et al., 2003; Ferguson and Elkie, 2004; Saher and Schmieglow, 2004) and wolves (Houle et al., 2009; Theuerkauf et al., 2003; Musiani et al., 2005), in particular, because other methods (track surveys, scat collections) are far more difficult outside of winter. Wolf seasonal behaviours mark distinct changes in movement, which tend to be related to pack dynamics, Houle et al., (2009) used three seasons, denning, rendezvous, and nomadic. These periods do not reflect the behaviour of a dispersing wolf, so alternate delineations of movement patterns were assessed from the GPS data. The most notable change for a dispersing wolf is likely the switch from nomadic to sedentary, open selection of a new territory, by joining or forming a pack (Mech and Boitani, 2003). The GPS data appeared to indicate such a shift, where in the first half of the dataset, there was a relatively constant rise in dispersal distance from previous points as the wolf travelled east (Figure 4.6). In August, the wolf began to travel in a concentrated area, around Kakabeka Falls, Ontario, and remained there for the remainder of the collar's operating life. The nomadic period prior to this was composed of 2,206 locations and an MCP area of 90,620km^2, while the sedentary period included over one thousand additional points (3314), but an MCP area of only 245km^2 (Figure 4.7). The MCP of the sedentary period occurs entirely within the nomadic MCP, and represents 0.3% of its area, but describes 60% of locations.

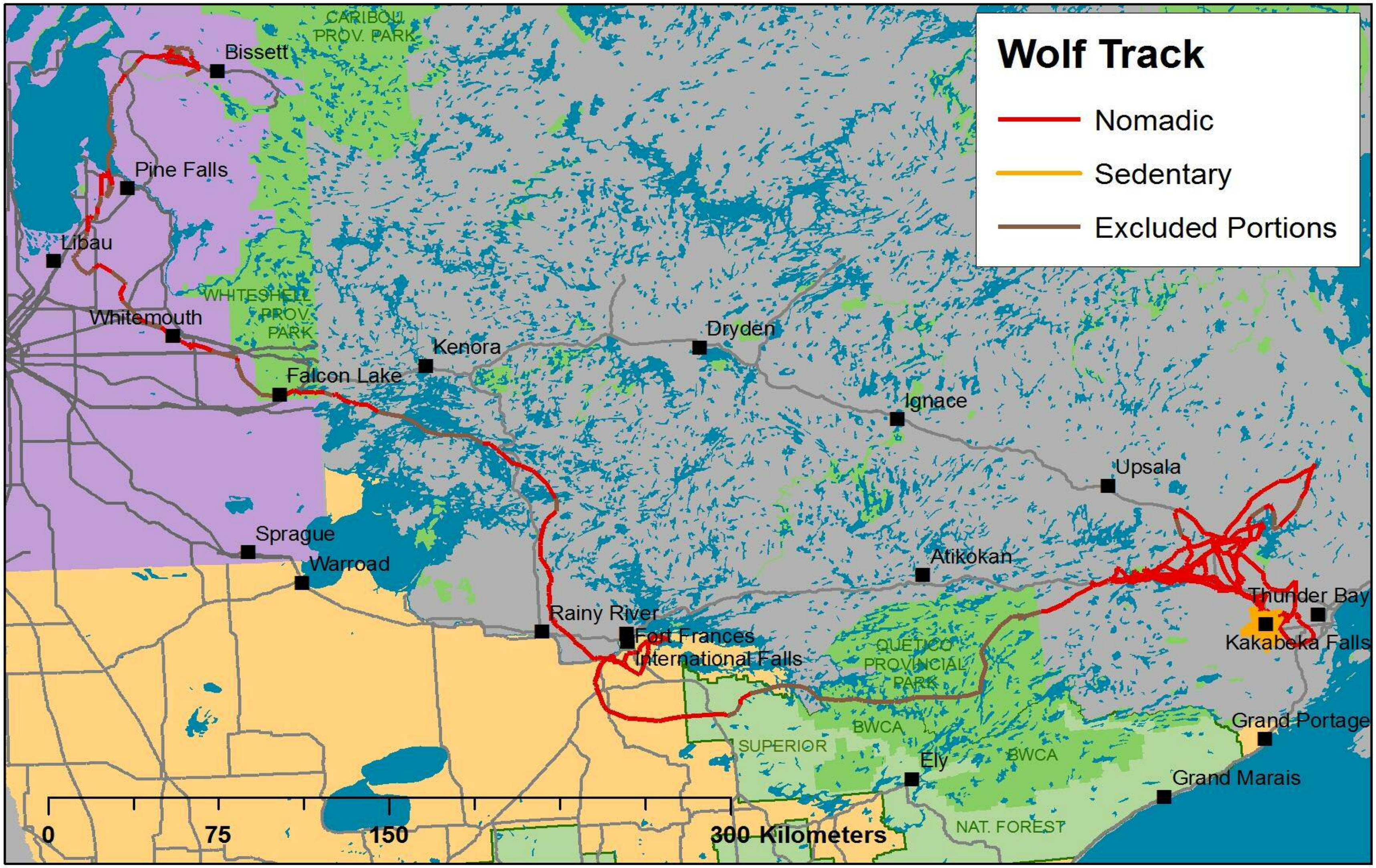


Figure 4.6. Movement path of wolf showing nomadic and sedentary periods and excluded areas.

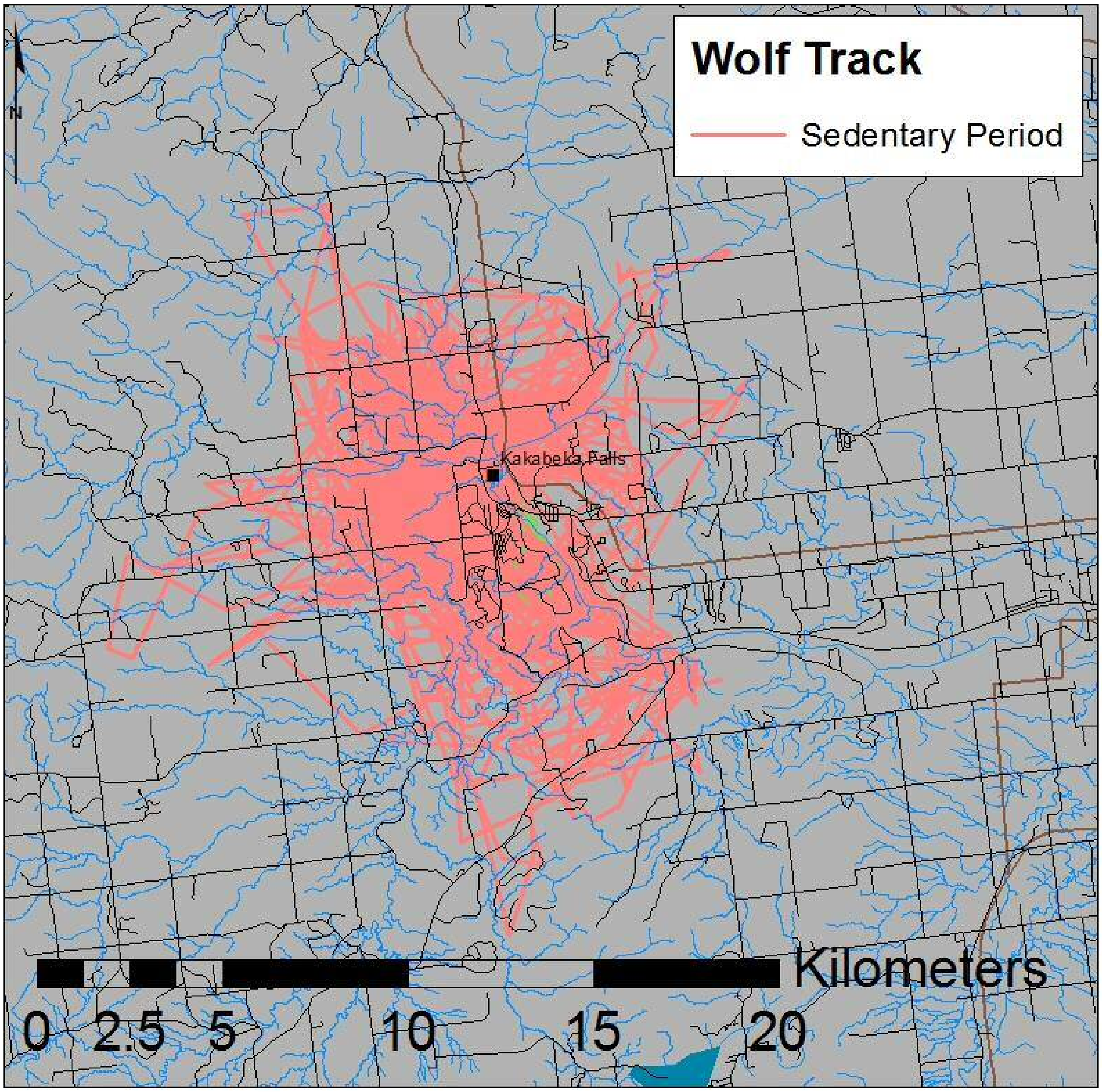


Figure 4.7. Movement path of the wolf during the sedentary period.

Given the substantial change in movement behaviour, the two periods were analyzed as separate groups. In much of the nomadic period, the wolf traveled in areas free of road development, such as the roadless wilderness of Quetico Provincial Park and while travelling on Lake Winnipeg and Lake of The Woods (Figure 4.6). As a result of the probable unfamiliarity, and likely unintentional use of these areas, wolf locations beyond 3km of anthropogenic features were discounted from comparison. The dataset used for analysis was 5520 points, or 86% of the total track record.

Pairwise comparison using Wilcoxon tests was conducted to compare between anthropogenic and natural feature proximity in the overall dataset, the sedentary period and the nomadic period. Mann-Whitney U tests were used to compare the difference between nomadic and sedentary periods for movement rates, and distance to both anthropogenic and natural features (Zar, 1999).

Results

Corridor Survey

Of the 711km surveyed along transects, 212km (29.8%) of track observations were recorded. Four hundred and ten kilometers of natural features were surveyed and 301.5km of anthropogenic features were surveyed (Table 4.1). Track observations were 127km and 85km for natural and anthropogenic features, respectively.

Table 4.1. Distance surveyed and track occurrence by feature type.

Feature Class	Length Surveyed	Tracks observed
Natural	410.5km	127km
Anthropogenic	301.5km	85km
Total	711km	212km

Pooled survey results were converted to proportions to identify differences between expected (surveyed) distance and observed (track occurrence) distance. Natural features accounted for ~60% of both surveyed distance and observed distance. Anthropogenic features accounted for ~40% of survey distance and track occurrence distance. The difference between observed and expected proportions was less than two percent. Proportions were compared with a Yates' corrected Chi-Square test. The Chi-Square value of 0.03 was less than the critical value of 3.84, indicating that the observed values (track occurrence) were not significantly different than expected (surveyed) values.

Table 4.2. Proportion of features surveyed and track occurrences by feature type.

Feature Class	Percent of surveyed length	Percent of tracks observed
Natural	57.7%	59.91%
Anthropogenic	42.3%	40.09%
Total	100.00%	100.00%

Transect Survey

Moose

Actual moose track observations were significantly closer to rivers, creeks, and class 2-4 roads (Table 4.3). Tracks were significantly farther than random to class 1 roads (Figure 4.8). Lake and transmission line feature distances were not significantly different between actual and random locations.

Table 4.3. Distance of actual and random moose track locations to linear features

Feature type	Actual distance (m)	Random distance (m)	Nearer/ Farther?	Significant ?	P-Value
River	**1876**	**2131**	**N**	**Y**	**<0.001**
Creek	**1047**	**1078**	**N**	**Y**	**<0.001**
Lake	1168	1116	F	N	0.0540
Road1	**9141**	**8865**	**F**	**Y**	**<0.001**
Road2	**2059**	**3413**	**N**	**Y**	**<0.001**
Road3	**922**	**1912**	**N**	**Y**	**<0.001**
Road4	**1002**	**1694**	**N**	**Y**	**<0.001**
Transmission	7566	7987	N	N	0.27

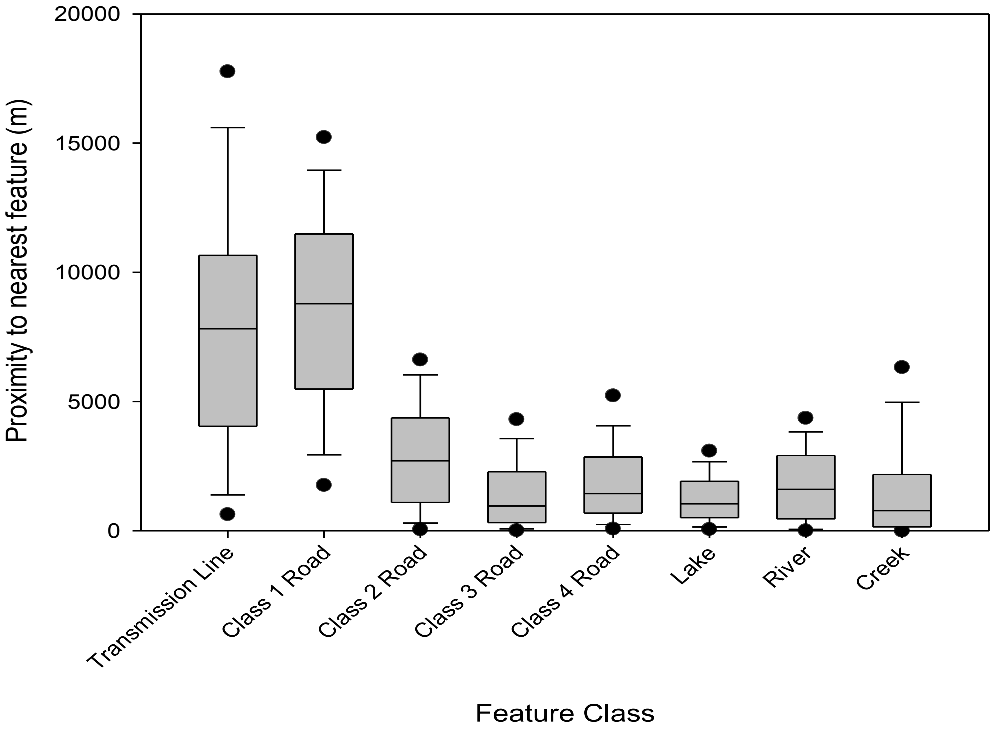


Figure 4.8. Boxplot of moose track proximity to linear features

Caribou

Caribou tracks were significantly closer to lakes, and significantly farther from rivers, transmission lines, and class 3 and 4 roads (Table 4.4). Tracks were not significantly different than random locations from creeks and class 1 and 2 roads (Figure 4.9).

Table 4.4. Distance of actual and random caribou locations to linear features

Feature type	Actual	Random	Nearer/ Farther?	Significant?	P-Value
River	**2361**	**1973**	**F**	**Y**	**<0.001**
Lake	**1014**	**1332**	**N**	**Y**	**<0.001**
Creek	1172	1127	F	N	0.9440

Road1	10790	11109	N	N	0.0080
Road2	2485	2834	N	N	0.0130
Road3	**1614**	**1212**	**F**	**Y**	**<0.001**
Road4	**2602**	**1795**	**F**	**Y**	**<0.001**
Transmission	**13717**	**8534**	**F**	**Y**	**<0.001**

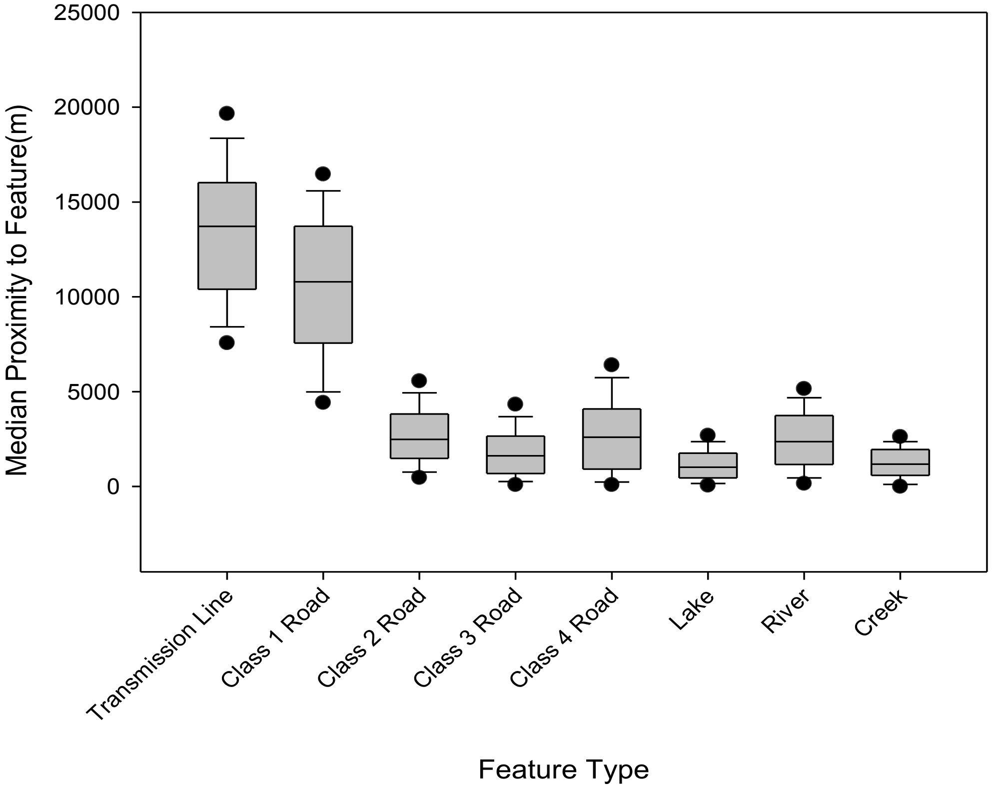


Figure 4.9. Boxplot of caribou track proximity to linear features

Wolf

Wolf track locations were significantly closer than random locations to rivers, creeks, and class 2 and 3 roads (Table 4.5). Tracks were not significantly distant from lakes, transmission lines, or class 1 and 4 roads (Figure 4.10).

Table 4.5. Distance of actual and random wolf locations to linear features

Feature type	Actual distance (m)	Random distance (m)	Nearer/Farther?	Significant?	P-Value
River	**1599**	**2149**	**N**	**Y**	**<0.001**
Creek	**773**	**1083**	**N**	**Y**	**<0.001**
Lake	1043	1098	N	N	0.0240
Road1	8786	8765	F	N	0.4670
Road2	**2707**	**3421**	**N**	**Y**	**<0.001**
Road3	**955**	**1925**	**N**	**Y**	**<0.001**
Road4	1437	1669	N	N	0.3770
Transmission	7815	7195	N	N	0.1210

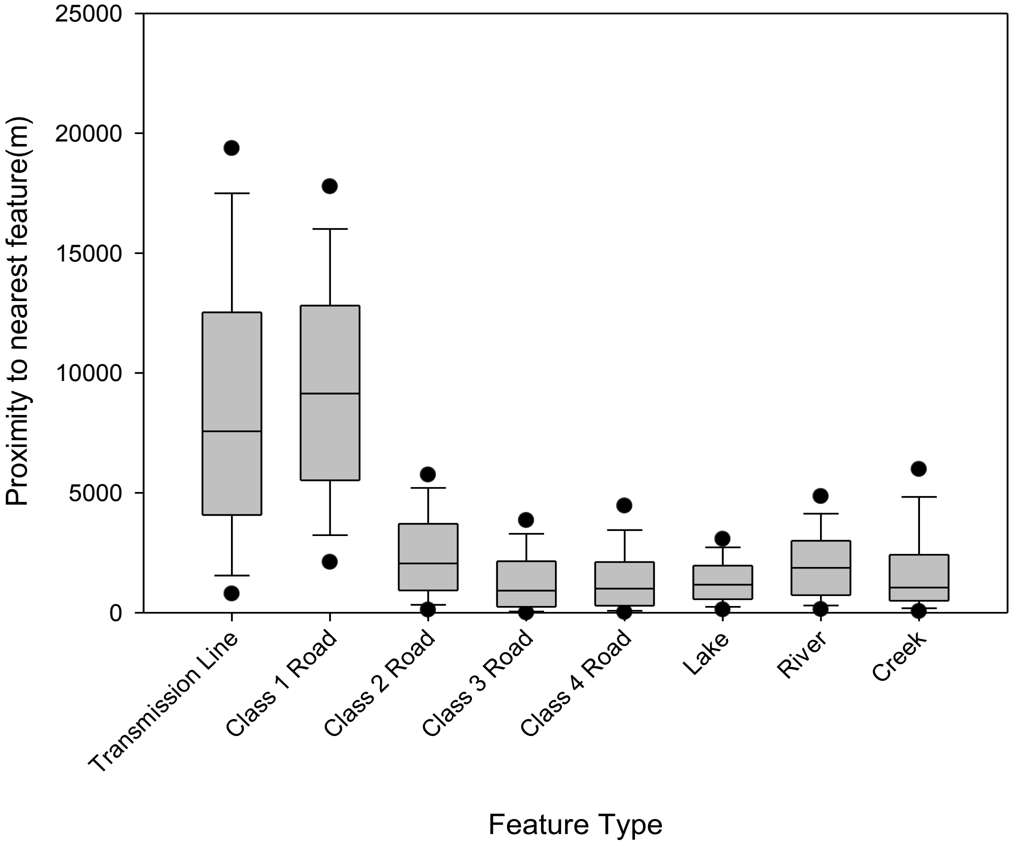


Figure 4.10. Boxplot of wolf track proximity to linear features

Telemetry Survey

During radiocollaring, wolves were identified as members of a pack after being observed together, or as lone wolves, after being observed independently (Table 4.6). The two wolves observed alone were later seen together. Telemetry data showed that following capture, they occupied entirely distinct ranges, and were indeed lone wolves.

Table 4.6. Measurements and grouping of radiocollared wolves

Animal ID	Pack/Group	Gender	Total Length (cm)	Chest Girth (cm)	Shoulder Height (cm)
GPS1	Sand River?	m	189	84	75
VHF2	Sand River	m	164	62.5	75
GPS3	Sand River	f	171	72	79
VHF4	Sand River	m	173	81	83
VHF5	Sand River?	f	166	66	78
VHF6	Wallace Lake	m	180	76	89
VHF7	Sand River	m	183	79	80
VHF8	Wallace Lake	m	na	na	na

Wolves grouped as pack animals and the two lone wolves were mapped, and home range size determined by Minimum Convex Polygons (MCPs, Mohr, 1947) as shown in Figure 4.11. Lone wolves showed a much larger home range (1570 and 1331 sq. km for VHF8 and VHF6, respectively) than the combined MCP of all pack animals (620 sq. km).

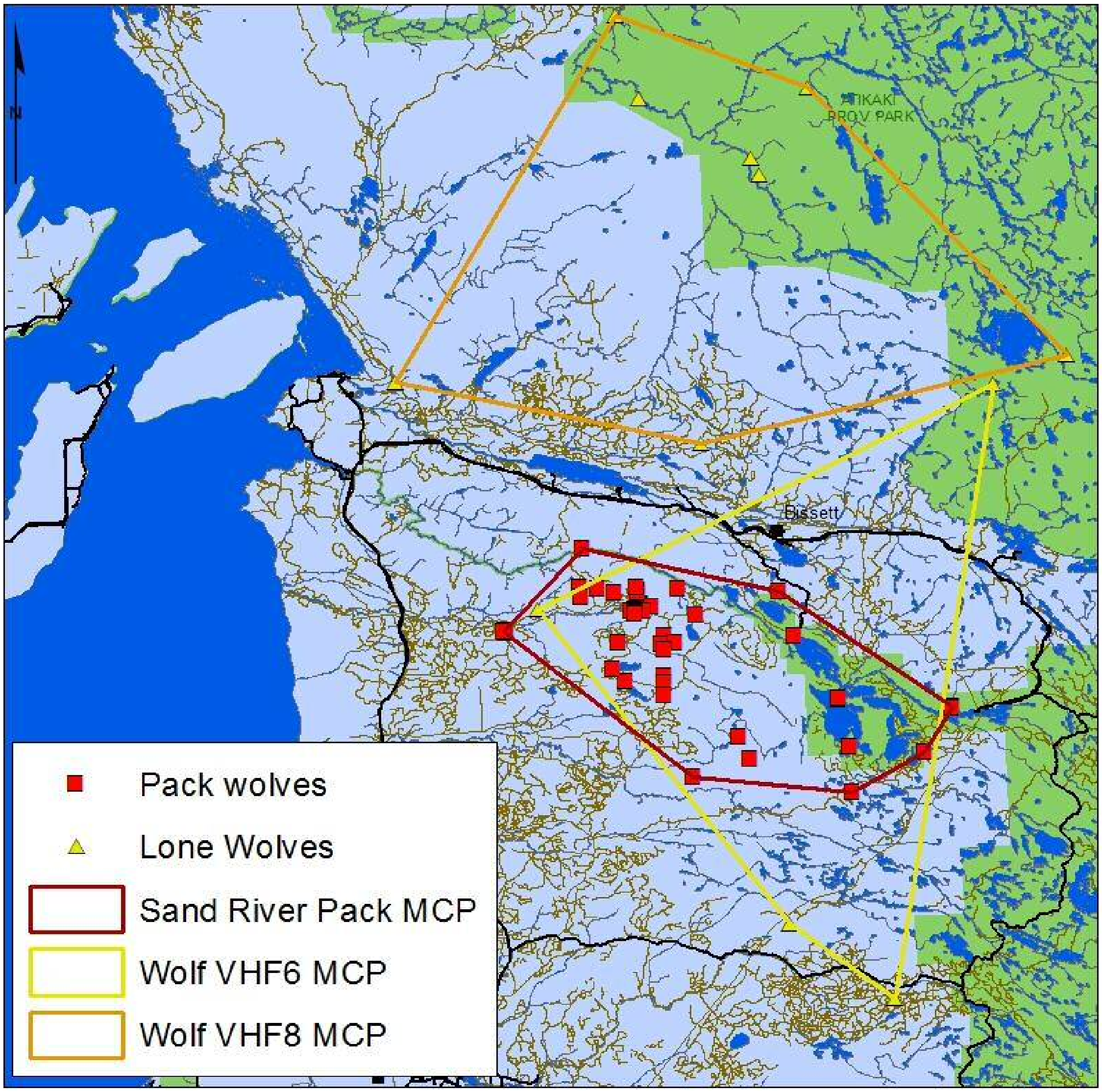


Figure 4.11. Radiotelemetry locations and Minimum Convex Polygons of collared wolves.

Individuals showed no significant difference in their proximity to either feature class (Table 4.7). The mean values of proximity were 1777m for anthropogenic features and 649m for natural features, while the median values were 342m for anthropogenic and 509m for natural features (Table 4.8). The Kruksal-Wallis (95%) test found no significant difference in the proximity to either natural ($P = 0.533$) or anthropogenic ($P = 0.081$) features among individuals, though wolf VHF8 showed much greater distances from roads, as its range was in the Atikaki wilderness area, with little road access (Figure 4.11).

Table 4.7. Median proximity of telemetry locations to features by wolf

Wolf ID	Median Distance to Natural Features	Median Distance to Anthropogenic Features
GPS1	545	2066
VHF2	664	173
VHF4	731	278
VHF5	344	493
VHF6	364	729
VHF7	574	305
VHF8	275	6639

Table 4.8. Summary statistics of proximity to features of wolf locations

Feature type	Mean Distance	Median Distance	Minimum Distance	Maximum Distance	Standard Error
Natural	649	509	0	2240	71
Anthropogenic	1777	342	15	20055	504

Seasonal differences in proximity were compared by month with a Kruksal-Wallis test (Alpha= 0.05) (Table 4.9) and indicated no significant difference among months and median proximity to anthropogenic features (P = 0.440), but did find a significant difference among proximity to natural features (P = 0.019). September and November were significantly different (Figure 4.12). Overall, winter locations were closer (Mean 177m) to natural features than summer locations (mean 658m), while anthropogenic features remained similarly from summer to winter at 729m, and 579m, respectively.

Table 4.9. Monthly Median proximity to feature classes

Month	Median Distance to Natural Features	Median Distance to Anthropogenic features
1	410	791
2	162	865
3	104	322
4	983	98
5	443	161
6	596	431
7	558	1490
8	1034	834
9	**1527**	**2562**
10	254	396
11	**31**	**337**

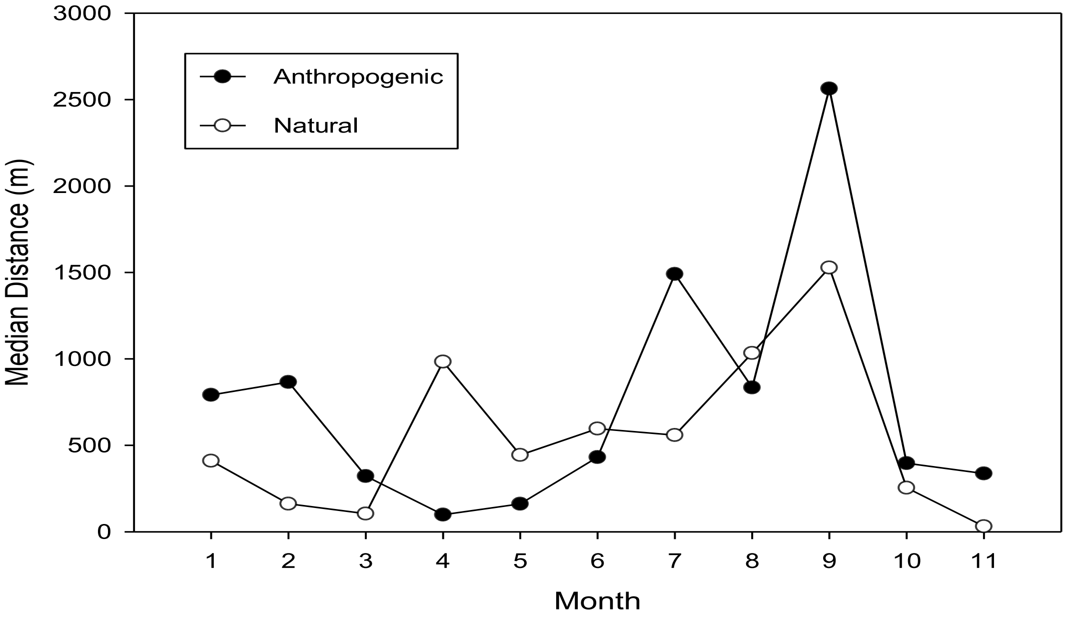


Figure 4.12. Line chart of monthly median distance to feature classes

Locations from pack wolves were compared against lone wolf locations, and their proximity to both feature classes (Table 4.10). Using a Mann-Whitney U test, no significant difference was found for proximity to natural features (P = 0.104) or anthropogenic features (P = 0.34). The tenfold (274 to 2706m) difference between pack and lone wolves to anthropogenic features, caused by wolf VHF8 primarily using a roadless area and a small sample size (n=12), while not significant, led to the removal of lone wolf data for comparison between feature classes.

Table 4.10. Median values of proximity to feature classes, Lone vs. Pack Wolves

Group	Median distance from natural features	Median distance from anthropogenic features
Pack	647	274
Lone	275	2706

Using only pack wolf data (n =52), a pairwise comparison of proximity to each feature class was conducted (Figure 4.13). Using a Wilcoxon test, it was determined that the difference in proximity between feature classes was not significantly different. (P= 0.469).

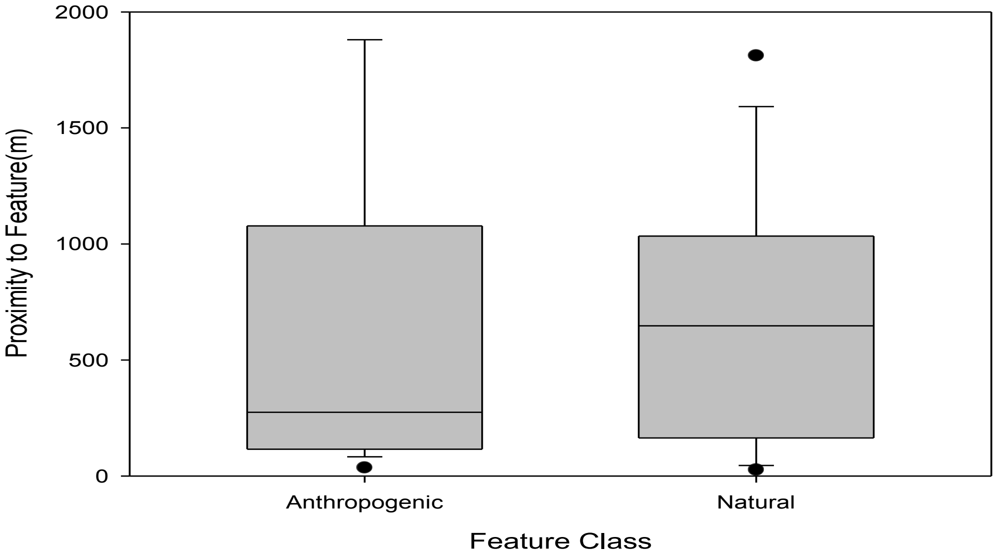


Figure 4.13. Boxplot of median wolf telemetry location proximity to feature classes.

GPS Telemetry

The GPS location comparisons of all wolf locations were compared with a Wilcoxon test (Alpha= 0.05) and showed that natural features (Median distance 163m) were significantly (P<0.001) nearer than anthropogenic features (Median distance 283m). Locations in the sedentary period and nomadic period were also significantly nearer to natural features (Figures 4.14 and 4.15; P <0.001 for each Wilcoxon test).

Table 4.11. Median values of speed and proximity to linear features between periods

Period	Speed (km/h)	Proximity to Natural Features (m)	Proximity to Anthropogenic features (m)
Sedentary	0.0950	116	272
Nomadic	0.0800	264	304
Average	0.0875	190	288

Movement rates were not significantly different between the sedentary and nomadic periods (P= 0.339).

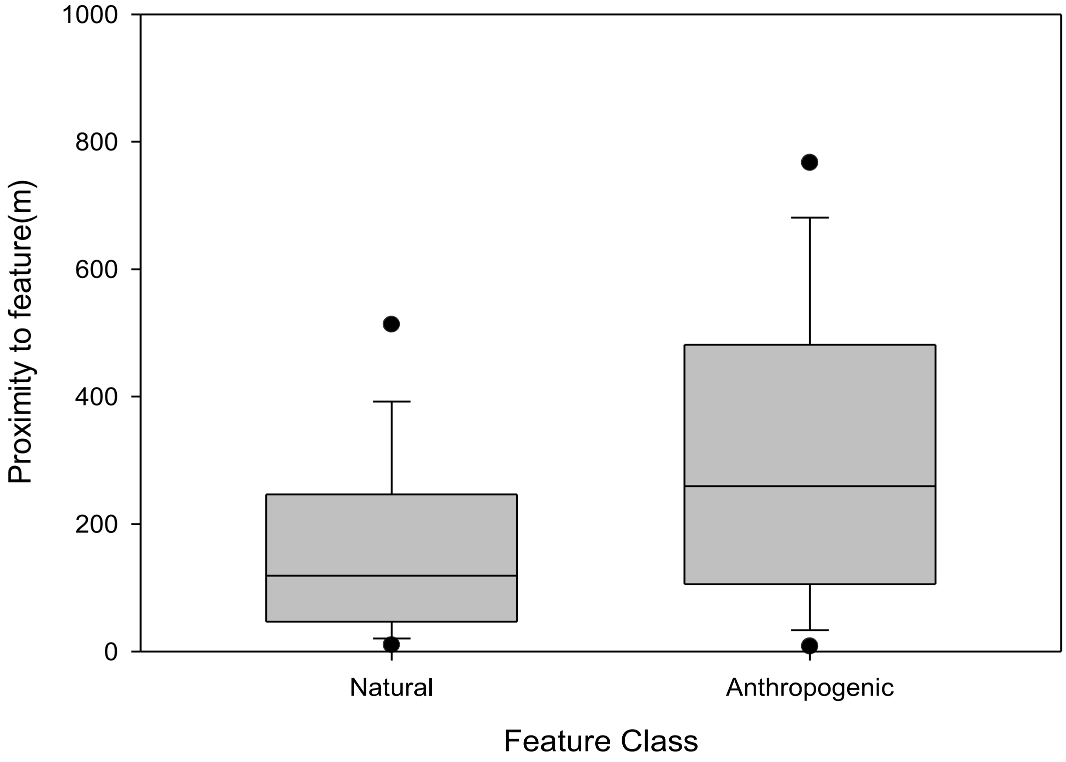


Figure 4.14. Boxplot of median telemetry location proximity to natural vs. anthropogenic features in the sedentary period

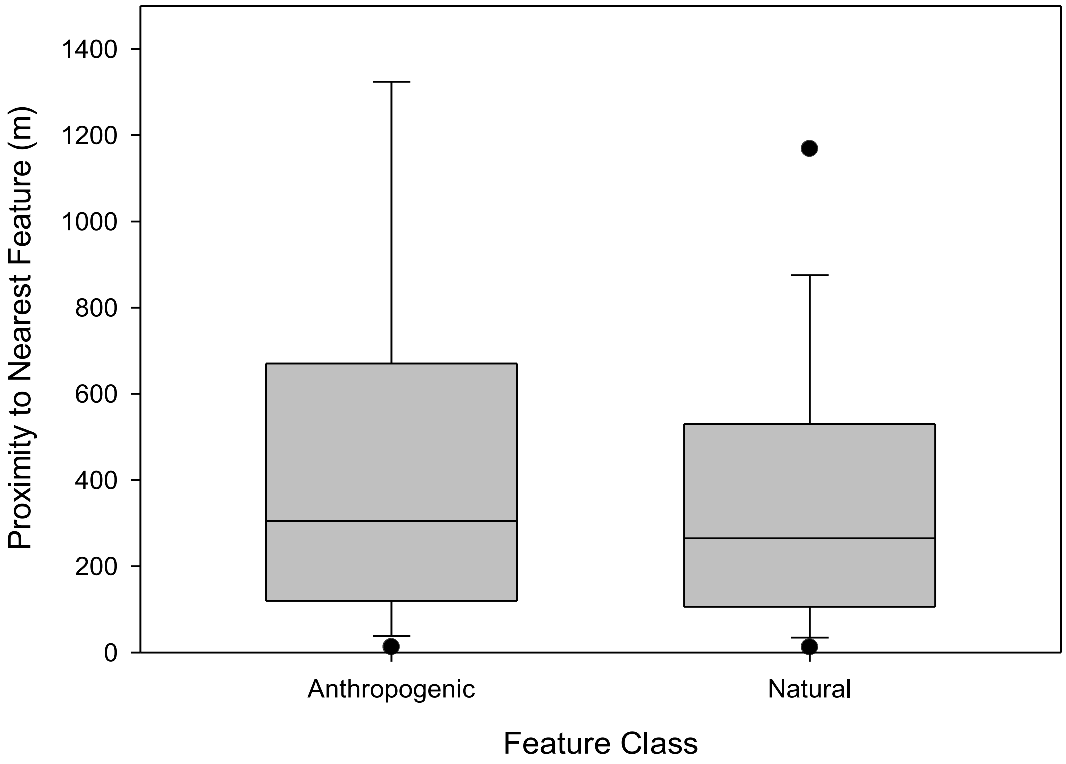


Figure 4.15. Boxplot of telemetry location proximity to natural vs. anthropogenic features in the nomadic period

Discussion

Corridor Survey

Track distributions occurred at the same proportions as expected, based on surveyed distances. While more extensive and frequently repeated surveys would provide a more detailed assessment of corridor use, the general assessment made indicates that both feature classes are used as they are available. This suggests that at a coarse level, wolves use features that help them, and rather than replacing natural corridors, anthropogenic features act to expand the existing travel network of wolves. The value of corridors to wolf hunting behaviour may be enhanced by density of functional corridors. While using corridors for travel while locating prey, locating tracks or scents depends on proximity (Mech, 1970). The further a landscape is fragmented by functional paths for wolves, the smaller the mean distance to features becomes. In modeling wolf predation risk, corridor proximity may be a useful tool in quantifying refuge habitat for prey species. Rather than considering the presence of anthropogenic corridors independently, the cumulative effect of expanding the existing travel network of rivers and natural edges should be considered as well.

Transect Survey

Comparison of species relationship to linear features associated wolves with potential travel corridors, and caribou avoiding corridors with the exception of lakes, which may also serve as escape habitat (Bergerud, 1985). Moose were associated with rivers and creeks, but not lakes, and all roads except highways (Class 1) and transmission lines. Overlap of selection was distinct between moose and wolves, which supports the assertion in chapter 3 that wolf distribution is related to moose, as the primary prey. Road features in the analysis area were largely associated with forestry operations, either leading to or within cut blocks (Manitoba Model Forest, 2005). Moose preference for deciduous shrubs found in early seral stages produced by logging (Potvin et al., 2005) likely drives their association to forestry roads. Wolves gain a double advantage in this regard, with prey distribution and travel corridors occurring simultaneously.

Caribou avoided features selected by moose or wolves, and were associated with features not selected by them, indicating a partition based selection.

Selection by caribou of landscapes associated with later seral stages (mature conifer stands, bogs; Schindler, 2006) and away from recently logged or burned areas (Schaefer and Mahoney, 2007; Schaefer and Pruitt, 1991) and major roads (Schindler et al. 2008) is reflected by the observed avoidance, and is likely related to the presence of moose. Since logging has been the primary driver of road and trail development in the study area, the two disturbances are generally related. The management of timber harvesting has directed the development of roads, and since 1995, this has included consideration for caribou habitat, through use of the ‘two thirds rule’ for maintaining high quality areas in the Owl-Flintstone range (Manitoba Model forest, 1995). Experimental harvesting to assess the potential of logging while maintaining caribou habitat (retention cut design) may prove effective at regulating moose distribution in caribou range, and thereby reduce wolf interest. Wolves will still travel through caribou range if it is practical, and may prey upon caribou as a matter of chance encounter (James and Stuart-Smith, 2000). The odds of encounter are minimized by spatial partitioning, however with expanded access, probabilities of encounter may increase, regardless of changes to moose distribution or density (James et al., 2004; McKenzie, 2012). Experimental design for habitat retention developed cut patterns that would minimize landscape impact on high quality, or soon to be high quality caribou habitat and also called for access control to the Owl Lake Range. Decommissioning practices are geared towards regulating human access, and involve removing road crossings, and substantial alterations to road structure within the first two kilometers of road (Tembec, 2009). However, these practices may not deter wolves, and following a reduction in human traffic, may become more valuable to predators (Whittington et al., 2005).

Moose, like caribou, depend on a disturbance regime to provide habitat, but on a much shorter cycle. While caribou habitat may not become viable for over fifty years (Schindler, 2006), moose habitat is usable in under ten years (Potvin et al., 2005; Courtois et al., 2002). Moose decline in the study area due to hunting and predation pressure has left the estimated population in 2010 at a quarter of the 2000 estimate (Manitoba Model Forest, 2011). The role of predation is thought to be more substantial than the human impact. While caribou predation can be minimized by landscape management to maintain spatial partitioning, moose distribution is highly correlated with wolf distribution, making separation infeasible. Moose and wolf populations also correlate, with moose populations being regulated by wolves, and wolves responding to declines in moose (Peterson, 1977; Bergerud, 1983; disputed by Boutin, 1992).

Transmission lines and Class 1 roads were rare on the landscape and mean distances to both actual and random points were over 7km away from either type. These features may be more relevant to wolf distribution where they are more strongly represented.

Telemetry Survey

Radio telemetry study showed that wolves in the Sand River pack in the study area did not show a preference for natural or anthropogenic features overall. Seasonal use comparison showed no significant difference in anthropogenic feature use between months, but found locations were significantly farther in the fall. All winter months showed locations closer to natural than anthropogenic features, while spring and summer locations were closer to anthropogenic features. Natural features such as rivers and lakes are available as corridors in the winter, owing to being frozen solid at this time. Wolves may switch to anthropogenic features in the spring and summer due to the impassability or ineffectiveness of natural features during the warmer months. While less effective as corridors, water features remain important as prey habitat, where moose seek sodium rich aquatic vegetation (Belvoski, 1978).

Lone wolves used much larger areas, and tended to be much farther from anthropogenic features, due to occupying largely roadless areas north of the study area. Satellite telemetry showed the preference of a dispersing wolf for natural features overall. Data were divided between two distinct periods, nomadic and sedentary, during which a preference for natural features was evident for both. The sedentary period, however, showed the distance to both feature classes to be reduced. Wolves may interpret natural features as posing lower risk of mortality, by avoiding human contact. While wolves can become quite aware of human activity patterns along roads, and act accordingly (Whittington et al., 2005), a lack of familiarity with features may lead a wolf to select the safer option, and utilize natural features in new landscapes or be less apt to travel on open routes at all. The decrease in distance from features between the nomadic and sedentary period may suggest a growing familiarity with a small landscape, or perhaps the influence of joining a local wolf or pack already acclimatized to the area. Fritts and Mech (1981) observed wolf dispersal and pack behaviours in Minnesota and indicated that lone wolves occasionally join packs, it is a rare event as existing wolf packs tend to be aggressive to other wolves. More often, a lone wolf will locate a vacant area, and then locate a mate thereby establishing the nucleus of a pack(Rothman and Mech, 1979).

Hypotheses

Wolves used natural and anthropogenic corridors equally, showing no preference or aversion to either type, so the null hypothesis is accepted. The role of anthropogenic corridors to be additive rather than compensatory to natural features and contributes to the overall movement network available to wolves.

Wolf distribution around linear corridors in the study area (radiotelemetry data) showed no significant difference between the distances to natural or anthropogenic features. Satellite telemetry from a lone dispersing wolf showed a preference for the use of natural corridors, in both the nomadic period, and the sedentary period. Locations from the sedentary period, while closer to natural features, were also closer to both feature types than in the nomadic period. The null hypothesis is accepted in part, where the wolf pack in the study area showed no feature preference, but not upheld to include dispersing wolf movement. The trend towards the preferential use of natural features in the nomadic period may indicate a level of unfamiliarity with the landscape, where natural features may be seen as a safer option without foreknowledge of the actual features. This trend is supported by the decreased median distances to features observed in the sedentary period, where the wolf may have become more familiar with local features.

Wolves, caribou, and moose did not show uniform distribution to linear features, and wolves were typically closer to linear features than caribou. The alternative hypothesis is accepted, due to wolves selecting both natural and anthropogenic features (rivers, creeks and mid-sized roads). Caribou were either indifferent or negatively associated with linear features (rivers, creeks, and smaller roads), with the exception of lake features, which were significantly closer. Lake features are associated with escape habitat for caribou, and did not figure into wolf preferences for corridors.

Chapter 5: Conclusion

Summary

Species distribution and wolf diet

This study used transect-surveys and diet analysis to demonstrate spatial partitioning of moose and caribou, and what is assumed to be effectiveness in minimizing predation by wolves. Species track observations were converted to density surfaces and compared with linear regression to assess overlap between species. Scat samples were collected to assess the proportion of caribou in the local wolf diet.

Caribou remains were not observed in wolf scats, while moose remains occurred in 85% of samples. Distribution patterns show a strong pattern of spatial partitioning between caribou and moose (as in Cumming et al., 1996), more pronounced than caribou avoidance of wolves themselves, suggesting the possibility that caribou avoid moose in order to avoid wolves. The lack of apparent wolf predation on caribou suggests that this strategy is effective and that protection of caribou populations can be achieved by preserving this partitioning through landscape management.

Linear Corridors

Wolf travel along and around linear corridors was compared between natural and anthropogenic features using corridor surveys, GPS, and radio telemetry. Relative use of features between species were compared using systematic multispecies transect surveys. Wolves used natural and anthropogenic corridors equally, showing no preference or aversion to either. This was also observed in radiotelemetry of a wolf pack in the same area. Lone wolves showed greater affinity to natural features, possibly to avoid human encounters in unfamiliar territory.

Caribou showed different preferences than wolves and moose, which largely associated with the same features. Wolves and moose were associated with smaller roads (Class 2-4), and rivers and creeks, while caribou selected against roads, rivers and creeks, but selected lakes. Selection of features emphasised the observed spatial partitioning observed in the species density comparison.

Management Implications

Several major issues of management are coming into play in the study area. A vacuum of industrial operations, coupled with a serious decline in moose population, and the presence of an endangered caribou range will require considerable planning.

Until the closure of its mill in 2009, Tembec was the primary user of the landscape in the study area. As required by Manitoba Conservation, a twenty-year plan was developed to provide direction for operations on a long term basis. Cutting areas, access road construction and decommissioning plans were outlined, as well as monitoring and mitigation measures.

Following the closure and subsequent decommissioning and sale of the mill, Tembec has removed itself from the management of FML 1. This leaves a substantial void, as it had represented 95% of timber harvest in the license area (Tembec, 2009). While this means a substantial reduction in human impact on the landscape, the management burden rests entirely on government, First Nations, and local communities.

Forest regeneration and road management are no longer accommodated by resource managers, and an opportunity exists to reframe the long term plan for the ecosystem. Several options exist, from natural restoration and preservation of the area, to maintaining existing infrastructure for an anticipated return of large scale forest harvesting. In either case, the opportunity to make decisions based largely on managing a healthy population of all species without the caveat of economic development is presented. Landscape planning can establish rules for future industrial activity to proactively manage conflicts before they arise. In the short term, concerns about caribou, moose and wolves in the area need to be addressed.

Caribou

Management to date has allowed caribou to effectively partition themselves from moose, and thereby reduce predation risk from wolves as seen in Alberta (James and Stuart-Smith, 2000). In spite of the overlap of forestry interests and caribou habitat, simple management concepts, such as the ‘two thirds rule’ have provided adequate protection from predation (Manitoba Model Forest, 2005). Change in forest management and objectives of harvest following mill closure may reduce intersection of caribou habitat and logging interests, and more permanent establishment of protected landscapes for caribou should be considered to maintain the partitioning of moose and caribou (James et al., 2004). Permanent protection should be considered to preserve the southernmost caribou in Manitoba.

Moose

In the study area, and across the province, declining moose numbers have led Manitoba Conservation to respond with short term measures to protect moose populations from several vectors. Hunting seasons on moose have been closed, and a complete hunting ban has been put in place, with rights-based hunting included (Manitoba Model Forest, 2011). Communities support the closure to all hunting (Manitoba Model Forest, 2011), though illegal hunting remains a concern.

Wolf population reduction is also being pursued through local trapping efforts, where additional training and incentives (bounties) are being offered to trappers to reach a reduction goal of one hundred wolves (Manitoba Conservation, 2011). Supplemental wolf control is being considered pending the outcome of trapping efforts.

In addition to addressing moose numbers by regulating human and predator pressure, disease transmission is also being addressed by regulated hunting. Brain worm (*Parelaphostrongylus tenuis)* is carried by deer, and transmitted to moose and caribou via snails. White-tailed deer encroachment has been occurring for some time, as human alterations to the landscape such as highways create functional corridors for deer travel. To control disease transmission, additional opportunities have been provided to hunters to take deer in GHA 26.

All efforts in the short term to address moose mortality should be considered as a part of a longer term issue. Wolf control will not be effective if wolves repopulate rapidly, and hunting pressure will resume if a ban is lifted. Assessing the long term factors must be considered, including predation rates, appropriate hunting levels, and landscape factors that may exaggerate human- and wolf-related mortality.

Wolves

Largely seen as a problem, or factor in managing for other species, the wolf is equally at risk in the face of the loss of its primary prey. As indicated in Chapter 1, a pack of five wolves would be fed for a year on the population of the Owl-Flintstone caribou. Without moose, wolves would be forced to abandon the area, either before or after attempting to subsist on caribou. Because wolves also appear to be the primary agent of moose decline at the moment, managing wolves may be necessary for both their own sake, and the sake of the moose. Short-term approaches to the situation include population control, via shooting, bounties, and poisoning. While these approaches may stave off population crashes, longer-term factors should be addressed. Is wolf predation the best factor to control? Can hunting pressure be effectively regulated? Can landscape management reduce wolf hunting efficiency? These issues will determine how wolf management should proceed (Theberge and Gauthier, 1985; Noss et al., 1996). Wolves utilize habitat based largely on moose distribution, and predation is relatively unavoidable. Use of corridors appears to increase predation rates, and encounter rates (James and Stuart-Smith, 2000; McKenzie, 2012). The association between anthropogenic corridors and harvest areas essentially leads wolves straight to moose (Houle et al., 2009), so road management may prove to be an appropriate measure to regulate predation pressure. Decommissioning efforts geared towards wolves would likely require a more substantial investment. Human access is easily managed by controlling key access points. Wolves are already on the landscape, and do not require highway access. The value of corridors appears to be the formation of a network to increase chances of picking up a trail, scent, or visual observation while allowing rapid movement (McKenzie, 2012). Cumulative effects of corridor development should be considered (Houle et al., 2009), both as part of anthropogenic disturbance, and in the formation of combined travel networks with existing natural features. Disruption of networks at regular intervals or meeting points through aggressive revegetation could be an appropriate method to limit the appeal of corridors. Landscape familiarity can play a role, where wolves familiar with the existing networks may not be inhibited greatly by short breaks in travel routes. In concert with wolf control, this familiarity could be lost, and broken corridors with only limited revegetation efforts could render a network impractical to wolves.

Human access to the landscape should be monitored and regulated, as decommissioning activities can be counteracted and disrupted by relatively few eager individuals (Leavesley, pers. Comm.) which opens the door to further access.

Future Study

The issues identified with this exploratory study should be expanded upon, given the uncertain state in which the management of this area has been placed. Further study of linear corridors should be undertaken with longer-term measurement, and a wider array of variables considered. As the costs of aerial and satellite monitoring are high, the value of track surveys as indices to monitor population change, as well as distribution and habitat selection should be considered. Additional variables such as snow depth, human traffic, and corridor proximity could be included with feature density and prey distribution to effectively model potential wolf habitat, and identify areas of concern. Wolf population, and the causes and rates of wolf mortality (disease, vehicular, trapping, hunting) should be assessed, especially with the implementation of wolf bounties, to better assess the effectiveness of control practices. Experimental harvest, as well as experimental road management should be undertaken to identify effective decommissioning methods to regulate wolf movements.

To further assess the actual use of linear corridors, track surveys should be utilized on a more frequent basis, allowing comparison of use over time along the same feature, and more consistent comparison between features. To further assess selection of features, paired analysis of parallel features should be used, to demonstrate a choice between features that provide an equivalent route. The Sand River/Sand River Road and the Black River/Black River Road could provide suitable locations for such study. In conjunction with track surveys, fine scale (5 min interval) GPS tracking, as used by McKenzie et al., (2012), would also provide direct use data to assess speed, and frequency of feature use. Additionally, fine scale telemetry can be used year round, where track surveys become less practical outside of winter. Application of GPS tracking and further track surveys within caribou range could further determine whether wolves attempt to hunt or simply travel across caribou range. Human activity along all features should be closely assessed, as this is a primary variable in the use of features, and regulated recreational use may prove to be a valuable tool to control wolf movement on fragmented landscapes.

Outside the study area, GPS data from a dispersing wolf showed a preference for natural features, possibly as a response to unfamiliar landscapes. The role of unfamiliarity in wolf habitat selection could be further assessed using tracking data from relocated or recolonizing wolves. Year to year comparisons as wolves settle into an area could show increasing activity around anthropogenic features.

References Cited

Adams, L., Singer, F. and Dale, B. 1995. Caribou calf mortality in Denali National Park, Alaska. *Journal of Wildlife Management* 59:584-594.

Adorjan, A. S. and G. B. Kolenosky. 1969. A manual for the identification of hairs of selected Ontario mammals. Res. Rep. (Wildl.), Ont. Dep. Lands For 90:1–64.

Alexander, S.M., P.C. Paquet, T.B. Logan, and D. J. Saher. 2005. Snow-tracking versus radiotelemetry for predicting wolf-environment relationships in the Rocky Mountains of Canada. *Wildlife Society Bulletin* 33 (4): 1216-1224

Atwood, T. and Gese, E. 2010. Importance of resource selection and social behavior to partitioning of hostile space by sympatric canids. *Journal of Mammalogy* 9:490-499.

Banfield, AWF (Ed). 1974. *The mammals of Canada.* University of Toronto Press, Toronto. 438 pp.

Bannatyne, B.B. and J.T. Teller. 1984. Geology of Manitoba Before the Ice Age; *in* Teller J.T. (editor). Natural Heritage of Manitoba: Legacy of the Ice Age. ISBN 0-920704-14-X. Manitoba Museum of Man and Nature, and Manitoba Nature Magazine. Winnipeg, Manitoba.

Belant, J., Griffith, B., Zhang, Y., Follmann, E. and Adams, L. 2010. Population level resource selection by sympatric brown and American black bears in Alaska. *Polar Biology* 33:31-40.

Belovsky, G.E. 1978. Diet optimization in a generalist herbivore: the moose. *Theor. Popul. Biol.*14: 105-134

Berger, K., and Gese, E. M. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology* 76:1075–1085.

Bergerud, A. T. 1974. The decline of caribou in North America following settlement. *Journal of Wildlife Management* 38:757–770.

Bergerud, A. T., H. E. Butler, and D. R. Miller. 1984. Antipredator tactics of calving caribou: dispersion in mountains. *Canadian Journal of Zoology* 62:1566–1575.

Bergerud, A. 1985. Anti-predator strategies of caribou; dispersion along shorelines. *Canadian Journal of Zoology* 63:1324-1329.

Bergerud, A. T. and J. P. Elliot. 1986. Dynamics of caribou and wolves in northern British

Columbia. *Canadian Journal of Zoology* 64:1515–1529.

Bergerud, A.T., S. Ferguson, and H.E. Butler. 1990. Spring migration and dispersion of woodland caribou at calving. *Animal Behaviour*. 39(2): 360-368

Bradshaw, C. J. A., S. Boutin, and D. M. Hebert. 1997. Effects of petroleum exploration on woodland caribou in northeastern Alberta. *Journal of Wildlife Management* 61:1127–1133.

Bradshaw, C. J. A., S. Boutin, and D. M. Hebert. 1998. Energetic implications of disturbance caused by petroleum exploration to woodland caribou. *Canadian Journal of Zoology* 76:1319–1324

Brown, W., Huot, J., Lamothe, P., Luttich, S., Pare, M., St-Martin, G. and Theberge, J. 1986. The distribution and movement patterns of four woodland caribou herds in Quebec and Labrador. *Rangifer Spc Iss* 1:43-49.

Caraco, T. 1983. White-crowned Sparrows (Zonotricha leucophrys): foraging preferences in a risky environment. *Behav. Ecol. Sociobiol.*

Carbyn, L.N. 1980. *Ecology and Management of Wolves in Riding Mountain National Park, Manitoba*. Canadian Wildlife service, Edmonton, Canada.

Carbyn, L. and Trottier, T. 1988. Descriptions of wolf attacks on bison calves in Wood Buffalo National Park. *Arctic* 41:297-302.

Carbyn, L., Oosenbrug, S. and Anions, D. 1993. Wolves, bison and the dynamics related to the Peace-Athabasca Delta in Canada's Wood Buffalo National Park. Canadian Circumpolar Institute, Edmonton, Alberta.

Charnov, E.L., and G.H. Orians. 1973. Optimal Foraging.: some theoretical explorations. Unpublished Manuscript,

Chase, J. and Leibold, M. 2003. Ecological Niches: Linking classical and contemporary approaches. Chicago: University of Chicago Press.

Cooley, H., Robinson, H., Wielgus, R. and Lambert, C. 2008. Cougar prey selection in a white-tailed deer and mule deer community. *Journal of Wildlife Management* 72:99-106.

Courtois, R., and J-P. Oullette. 2007. Modeling the impact of moose and wolf management on persistence of woodland caribou. *Alces*. 43: 13-27

Cumming, H.G. and D.B. Beange. 1993. Survival of woodland caribou in commercial forests of northern Ontario. *The Forestry Chronicle* 69(5): 579-588

Cumming, H.G. and Beange, D.B. 1987. Dispersion and movements of woodland caribou near Lake Nipigon, Ontario. *Journal of Wildlife Management* 51:69-79.

Cumming, H.G., D.B. Beange, and G. Lavioe. 1996. Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared prédation risk. *Rangifer*. 16(4): 81-94

Darby,W.R. 1979. Seasonal movements, habitat utilization, and population ecology of woodland caribou (Rangifer tarandus caribou Gmelin) in the Wallace-Aikens Lake region of southeastern Manitoba Msc Thesis, University of Manitoba. 205 pp.

Derocher, A.E., O. Wiig, and G. Bangjord. 2000. Predation of Svalbard reindeer by polar bears. *Polar Biology*. 10: 675-678

Dukas, R. and C.W. Clark. 1995. Searching for cryptic prey: a dynamic model. *Ecology* 76: 1320-1326

Environment Canada. 2000. Climate Normals and Averages, Bissett, MB. http://www.climate.weatheroffice.gc.ca/climate_normals/index_e.html

Ferguson, S., Bergerud, A. and Ferguson, R. 1988. Predation risk and habitat selection in the persistence of a remnant caribou population. *Oecologia* 76:236-245.

Ferguson, S. and Elkie, P. 2005. Use of lake areas in winter by woodland caribou. *Northeastern Naturalist* 12:45-66.

Forman, R.T.T. and L.E. Alexander. 1998. Roads and their major ecological effects. *Annual Review in Ecology and Systematics*. 8:629-644.

Fortin, J., Farley, S., Rode, K. and Robbins, C. 2007. Dietary and spatial overlap between sympatric ursids relative to salmon use. *Ursus* 18:19-29.

Fritts, S., Bangs, E., Fontaine, J., Johnson, M., Phillips, M., Koch, E., and Gunson, J. 1997. Planning and implementing a reintroduction of wolves to Yellowstone National Park and Central Idaho. *Restoration Ecology* 5:7-27.

Fritts, S.H., and L.D. Mech. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. *Wildlife Monographs*. 80:1-79

Fuller, T. 1989. Population dynamics of wolves in north-central Minnesota. *Wildlife Monograph* 105:1-41.

Fuller, T.K. and Keith, L.B. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. *Journal of Wildlife Management*. 44(3): 583-602

Gese, E.M., and L.D. Mech. 1991. Dispersal of wolves (Canis lupus) in northeastern Minnesota, 1969-1989. *Can. J. Zool.* 69(12): 2946-2955

Gray, D. 1970. The killing of a bull muskox by a single wolf. *Arctic* 23:197-199.

Gray, D. R. 1987. The muskoxen of Polar Bear Pass. Fitzhenry and Whiteside, Markham, Ontario, Canada.

Grinnell, J. 1917. The niche-relationships of the California Thrasher. *The Auk* 34:427-433.

Gustine, D., Parker, K., Lay, R., Gillingham, M. and Heard, D. 2006. Interpreting resource selection at different scales for woodland caribou in winter. *Journal of Wildlife Management* 70:1601-1614.

Hirai, T. 1998. *An evaluation of woodland caribou (Rangifer tarandus caribou) calving habitat in the Wabowden area, Manitoba*. University of Manitoba, Natural Resources Institute practicum, Winnipeg, Manitoba. 119pp.

Holmes, W. 1991. Predator risk affects foraging behaviour of **pikas**: observational and experimental evidence. *Animal Behaviour*. 42(1): 111-119

Holt, R.D. And B.P. Kotler. 1987. Short-term apparent competition. The American Naturalist. 130(3): 412-430

James, A.R.C., S. Boutin, D.M. Hebert, and A.B. Rippin. 2004. Spatial Separation of Caribou from Moose and Its Relation to Predation by Wolves. *Journal of Wildlife Management* 68(4):799-809

James, A. R., and A. K. Stuart-Smith. 2000. Distribution of caribou and wolves in relation to linear corridors. *Journal of Wildlife Management* 64:154–159.

Jenkins, K. and Wright, R. 1988. Resource portioning and competition among cervids in the Northern Rocky Mountains. *Journal of Applied Ecology* 25:11-24.

Keith, L. B. 1983. Population dynamics of wolves. Pages 66-77 in L. N. Carbyn, ed. Wolves in Canada and Alaska. Can. Wildl. Serv. Rep. Ser. 45.

Kelsall, J.P. 1968. The migratory barren-ground caribou of Canada. Queen's Printer, Ottawa. 339 pp.

Kitchen, A. M., Gese, E. M. and Schauster, E. R. 1999. Resource partitioning between coyotes and swift foxes: space, time, and diet. *Canadian Journal of Zoology* 77:1645–1656.

Krebs, J.R., A. Kacelnik, and P. Taylor. 1978. test of optimal sampling by great tits. *Nature*. 275: 27-31

Kunkel, K. and Pletscher, D. 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. *Canadian Journal of Zoology* 78:150-157.

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

Lent, P. 1974. Mother-infant relationships in ungulates. In Geist, V. and Walther, F. (Eds.) The Behaviour of Ungulates and its Relation to Management. I.U.C.N., Morges, Volume 1, pp. 14-55.

Lesmerises, F., C. Dussault, and M. St-Laurent. 2011. Wolf habitat selection is shaped by human activities in a highly managed boreal forest. *Forest Ecology and Management.* 276: 125-131

Lima S.L. 1987. Vigilance while feeding and its relation to the risk of predation. *J. Theor. Biol. 24:303-316*

Lima, S.L. and L.M. Dill. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68: 619-640

MacArthur, R.H., and E.R. Pianka. 1966. On optimal use of a patchy environment. *Am. Nat.* 100: 603-609

MacNulty, D., Smith, D., Mech, D., Vucetich, J. and Packer, C. 2012. Nonlinear effects of group size on the success of wolves hunting elk. *Behavioral Ecology* 23:75-82.

Manitoba Conservation. 2005. *Manitoba Conservation Forest Practices Guidebook: Forestry Road Management*. Winnipeg, MB. 33p.

Manitoba Conservation. 2006. *Manitoba's Conservation and Recovery Strategy for Boreal Woodland Caribou (Rangifer tarandus caribou*). Manitoba Conservation 38 p. 786-7101

Manitoba Endangered Species Act. 1990. C.S.S.M. c. E111, 7 p.

Manitoba Model Forest. 2011. *Moose News.* Committee for Moose Management publication. 2 pp.

Mech, L.D. 1970. *The wolf: the ecology and behavior of an endangered species*. Natural History Press, Doubleday Publishing Co., New York

Mech, D. 1998. Estimated cost of maintaining a recovered wolf population in agricultural regions of Minnesota. *Wildlife Society Bulletin* 26:617-622.

Mech, L. D. and Boitani, L. 2003. Wolves. Behaviour, ecology, and conservation. University of Chicago Press.

Mech, D. and Nelson, M. 1986. Mortality of white-tailed deer in northeastern Minnesota. *Journal of Wildlife* Management 50:691-698.

Mech, D. and Peterson, R. O. 2003. Wolf-prey relations, p. 131–157. In: L. D. Mech and L. Boitani (eds.). Wolves: behavior, ecology, and conservation. Univ. of Chicago Press, Chicago, Illinois.

Mech, L.D. 2010. What is the taxonomic identity of Minnesota wolves? *Can. J. Zool*. 88: 129-138

Mech, L.D., and W.J. Paul. 2008. Wolf body mass cline across Minnesota: related to taxonomy? *Can. J. Zool* 86(8): 933-936

Messier, F. 1985. Social organization, spatial distribution, and population density of wolves in relation to moose density. *Canadian Journal of Zoology*, 63, 1068-1077.

Murie, O.J. and M. Elbroch. 2005. *Peterson field guide to animal tracks*. Houghton Mifflin, New York 432 pp.

Noss, R. F., Quigley, H. B., Hornocker, M. G., Merrill, T. and Paquet, P. C. (1996), Conservation Biology and Carnivore Conservation in the Rocky Mountains. Conservation Biology, 10: 949–963.

Paquet, P. C. 1991. Winter spatial relationships of wolves and coyotes in Riding Mountain National Park, Manitoba. *Journal of Mammalogy* 72:397–401.

Paquet, P. C. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. *Journal of Mammalogy* 73:337–343.

Peterson, R. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. National Park Service Scientific Monograph, Series 11. Washington D.C. 210pp.

Peterson, R. and Ciucci, P. 2003. The wolf as a carnivore. In: Boitani, L. Wolves: Behavior, Ecology and Conservation. Chicago: University of Chicago Press.

Pimlott, D.H. 1967. Wolf predation and ungulate populations. *Amer. Zool*. 7(2): 267-278

Post, E., Boving, P. Pedersen, C. and MacArthur, M. 2003. Synchrony between caribou calving and plant phenology in depredated and non-depredated populations. *Canadian Journal of Zoology* 81:1709-1714.

Reed, J.E., R.J. Baker, W.B. Ballard, and B.T. Kelly. 2004. Differentiating Mexican gray wolf and coyote scats using DNA analysis. *Wildlife Society Bulletin* 32(3):685-692

Rempel, R.S., P.C. Elkie, A.R. Rodgers, and M.J. Gluck. 1997. Timber Management and natural disturbance effects on moose habitat: Landscape evaluation. *Journal of Wildlife Management*. 61(2): 517-524

Rettie, J.W., and F. Messier. 1997. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography*. 23(4): 466-478

Roed, K.H., M.A.D. Ferguson, M. Crete, and T.A. Bergerud. 1991. Genetic variation in transferring as a predictor of differentiation in evolution of caribou in eastern Canada. *Rangifer*. 11(2): 65-74

Schaefer, J.A. 1988. Fire and woodland caribou(Rangifer tarandus caribou): an evaluation of range in southeastern Manitoba. Msc. Thesis, University of Manitoba, Winnipeg. 145 pp.

Schaefer, J.A., and W.O. Pruitt Jr. 1991. Fire and woodland caribou in southeastern Manitoba. *Wildlife Monographs.* 116:3-39

Schaefer, J.A. And S.P. Mahoney. 2007. Effects of progressiver clearcut logging on Newfoundland Caribou. *Journal of Wildlife Management*. 71(6): 1753-1757

Schindler, D. 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*. Masters thesis, University of Manitoba, Winnipeg, Manitoba. 165 p.

Seip, D.R. 1991 Predation and caribou populations. *Rangifer, Special Issue*. 7, 46-52.

Seip, D.R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology* 70:1494–1503.

Seip, D.R., and Cichowski, D.B. 1996. Population ecology of caribou in British Columbia. *Rangifer Spec. Issue*, 9: 73–80.

Severinghaus, C. and Cheatum, E. 1956. Life and times of the white-tailed deer. Pages 57-186 In Taylor, W. (Ed.) The deer of North America. Stackpole Company, Harrisburg, Pa. and the Wildlife Management Institute, Washington DC.

Shoesmith, M. and Storey, D. 1977. Movements and associated behavior of woodland caribou in Central Manitoba. Proc. Int. Congr. Game Biology 13:51-64.

Sih, A., and J.J. Krupa. 1992. Predation risk, food deprivation, and non-random mating by size in the stream water strider. *Behav. Ecol. Socibiol.* 31(1): 51-56

Smith, K. G., E. J. Ficht, D. Hobson, T. C. Sorensen, and D. Hervieux. 2000. Winter distribution of woodland caribou in relation to clear-cut logging in west-central Alberta. *Canadian Journal of Zoology* 78:1493–1440.

Soberon, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* 10:1115-1123.

Soberon, J., Jimenez, R., Golubov, J. and Koleff, P. 2007. Assessing completeness of biodiversity databases at different spatial scales. *Ecography* 30:152-160.

Species At Risk Act. 2003. R.S.C., 2002, c. 29

Stephens, D.W., and J.R. Krebs. 1986. *Foraging Theory*. Princeton University Press, Princeton. 247 pp.

Stewart, A. K., Bradshaw, C., Boutin, S., Hebert, D. and Rippin, A. 1997. Woodland caribou relative to landscape patterns in northeastern Alberta. *Journal of Wildlife Management* 61:622-633.

Stewart, K., Bowyer, R., Dick, B., Johnson, B. and Kie, J. 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. *Population Ecology* 143:85-93.

Stewart, K., Bowyer, R., Kie, J., Dick, B. and Ben-David, M. 2003. Niche partitioning among mule deer, elk, and cattle: Do stable isotopes reflect dietary niche? *Ecoscience* 10:297-302.

Stewart, K., Bowyer, R., Kie, J., Cimon, N. and Johnson, B. 2002. Temperospatial distributions of elk, mule deer and cattle: Resource partitioning and competitive displacement. *Journal of Mammalogy 83:229-244.*

Sweitzer, R.A. 1996. Predation or Starvation: Consequences of Foraging Decisions by Porcupines (Erethizon dorsatum). *Journal of Mammalogy* 77(4): 1068-1077

Telfer, E.S. And J.P. Kelsall. 1984. Adaptation of some large north american mammals for survival in snow. *Ecology*. 65(6): 1828-1834

Thiel, R. P. 1985. Relationship between road densities and wolf habitat suitability in Wisconsin. *American Midland Naturalist* 113:404–407.

Thurber, J. and Peterson, R. 1993. Effects of population density and pack size on the foraging ecology of gray wolves. *Journal of Mammalogy* 74:879-889.

Thurber, J.M., R.O. Peterson, T.D. Drummer, and T.A. Thomasma. 1994. Gray wolf response to refuge boundaries and roads in Alaska. *Wildlife Society Bulletin* 22:61-68

Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs* 57:189-214.

Torstenson, W., Mosley, J., Brewer, T., Tess, M. and Knight, J. 2006. Elk, mule deer, and cattle foraging relationships on foothill and mountain rangeland. *Rangeland Ecology and Management* 59:80-87.

Trites, A.W. and R. Joy. 2005. Dietary analysis from fecal samples: how many scats are enough? *J. Mamm*. 86(4): 704-712

Van Ballenberghe, V., Erickson, A. and Byman, D. 1975. Ecology of the Timber Wolf in Northeastern Minnesota. *Wildlife Monographs* 43:3-43

Voigt, D.R., G.B. Kolenosky, and D.H. Pimlott. 1976. Changes in summer food of wolves in central Ontario. *Journal of Wildlife Management*. 40(4): 663-668

Vors, L.S., J.A. Shaefer, B.A. Pond, A.R. Rodgers, and B.R. Patterson. 2007. Woodland caribou extirpation and anthropogenic landscape disturbance in Ontario. *Journal of Wildlife Management* 71(4):1249-1256b

Whittington, Jesse, Colleen Cassady St. Clair, and George Mercer. 2005. Spatial responses of wolves to roads and trails in mountain valleys. Ecological Applications 15:543–553

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

Wilson P.J.; Grewal S.; McFadden T.; Chambers R.C.; White B.N. 2003. Mitochondrial DNA extracted from eastern North American wolves killed in the 1800s is not of gray wolf origin. *Can. J. Zool.* 81(5): 936-940

Wilson, P.J., Grewal, S., Lawford, I.D., Heal, J.N.M., Granacki, A.G., Pennock, D., Theberge, J.B., Theberge, M.T., Voigt, D.R., Waddell. 2000. DNA profiles of the eastern Canadian wolf and the red wolf provide evidence for a common evolutionary history independent of the gray wolf. *Canadian J. Zool.* 78: 2156-2166.

Wilson PJ, Grewal SK, Mallory FF, White BN. 2009. Genetic characterization of hybrid wolves across Ontario. *J Hered.* 100: S80–S89

Wolff J.O. And T. Van Horn. 2003. Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. *Can. J. Zool*. 81: 266-271

Yahner, R. 1982. Avian use of vertical strata and plantings in farmstead shelterbelts. *Journal of Wildlife Managemen*t 46:50-60.

Young, S. and Goldman, E. 1944. The wolves of North America: Part I: Their history, life habits, economic status, and control, Parts 1-2. The American Wildlife Institute.