University of Alberta

Spatial Dynamics of Wolves and Woodland Caribou in an Industrial Forest Landscape in West-Central Alberta

by

Lalenia Michele Neufeld ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the

requirements for the degree of Master of Science

in

Wildlife Ecology and Management
Department of Renewable Resources

Edmonton, Alberta

Spring, 2006

Library and
Archives Canada

Published Heritage
Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et
Archives Canada

Direction du
Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 0-494-13861-0
Our file Notre référence
ISBN: 0-494-13861-0

NOTICE:
The author has granted a non-exclusive license allowing Library and Archives Canada to reproduce, publish, archive, preserve, conserve, communicate to the public by telecommunication or on the Internet, loan, distribute and sell theses worldwide, for commercial or non-commercial purposes, in microform, paper, electronic and/or any other formats.

The author retains copyright ownership and moral rights in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

AVIS:
L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, publier, archiver, sauvegarder, conserver, transmettre au public par télécommunication ou par l'Internet, prêter, distribuer et vendre des thèses partout dans le monde, à des fins commerciales ou autres, sur support microforme, papier, électronique et/ou autres formats.

L'auteur conserve la propriété du droit d'auteur et des droits moraux qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Abstract

Woodland caribou (*Rangifer tarandus caribou*) populations are threatened in Canada. Wolves (*Canis lupus*) and anthropogenic industrial developments have been cited as proximate and ultimate causes for caribou decline, respectively. I used resource selection functions (RSFs) to assess selection patterns of wolves and caribou in relation to landscape features of the Little Smoky region in west-central Alberta; I also examined the potential for spatial and temporal overlap. In addition, I experimentally examined hypotheses related to predator-mobility and seismic line recovery via line-blocking. Both species exhibited seasonal variation in selection patterns, though in general caribou avoided, whereas wolves selected, human infrastructure. There was large potential for overlap between wolves and caribou, particularly during the spring. There was no evidence that line-blocking was an effective technique for reducing predator mobility. RSF models could be used in evaluating and implementing future conservation and management initiatives for the Little Smoky caribou region.

Acknowledgements

The completion of this work has not been without considerable support from several people and organisations. Fiona's office, wherever it might have been, was always open, inviting, and inspirational. Her perceptive comments and challenging questions have contributed to every endeavour of this degree. Thanks for instilling greater appreciations of conservation biology, academics, deadlines, writing, and how to balance absolutely everything in life (though, admittedly, I haven't perfected that one); I am grateful for the opportunity to have been part of the Schmiegelow research group. Additionally, my supervisory committee, Stan Boutin and Andy Derocher, offered constructive comments throughout my degree.

I was fortunate to have the invaluable support of Kim Lisgo, the "GPS collar expert of the province," without ever having to ask (and more recently, Simon Slater). The behind-the-scenes work of Kim and Simon was critical to successful captures, data sharing agreements, and clean GPS data. I am thankful to Kirby Smith and the rest of the West-Central Alberta Caribou Standing Committee for putting forth funds and providing the freedom to embark on this wolf-caribou thesis. Brian Coupal of the Caribou Range Restoration Project was critical to development and implementation of the line-blocking experiment and was the only one who truly appreciated seismic-line chatter. I also appreciate cooperation from local trappers Albert Steinwand and Lloyd Clark.

Saakje Hazenberg, Tobi Anaka, and Robbie Gordey were inspirations and the finest field assistants; thanks for the hard work, commitment, great dogs, and mutual loves of cheese, outdoors, and good books. I wish to thank Sophie Czetwertynski and Rolland Lemieux, without whom I wouldn't have increased *N* by 8. Rolland and Sophie were also responsible for transforming a rudimentary field camp into a five-star resort! Thanks Tony and Clay of Bighorn Helicopters for the professional caribou and wolf captures, especially for the occasions of "Layla, you owe us for this one." Thanks to the Devon and Burlington guys for deep fried turkey and new perspectives, in addition to an open invitation for help if needed.

Of all the dear friends I am fortunate to have made at the UofA, I must first acknowledge the support of Luc: thanks for letting me pull the "thesis card" over groceries and vacuuming, for reading drafts, and most importantly, for bringing motivations up when they sometimes fell down; I am waiting to give it back. Joanne Saher and Cam Aldridge never turned away an opportunity to help a fellow RSFer. Your contributions have been instrumental and I appreciate every long phone call and email. Thanks to the Schmiegelites lab group (Cindy, Kathy, Kim, Landon, Lee, Meg, Roger, Simon, Scott, Shannon, Shawn, Sophie, Theresa, and Tracy), with whom a phenomenal dynamic always existed, whether in swirling scientific banter or over scary Halloween movies; you guys have made the windowless office such a sunny place to be. Views of Nicky Koper, Mark Hebblewhite, and Meg Krawchuk on graduate life and statistical approaches shaped my outlook and analyses; thank you. John Acorn, I appreciate the opportunity to have assisted in teaching your wildlife class and all the quirky things you brought to life on the seventh floor. Campus Rec and the intramural program kept me in shape and clothed. And lastly, I can't possibly name fellow graduate students and others who've influenced my quality of life through adventures, sports teams, and friendship, but you know who you are.

My brother and sister have been helpful in sharing the graduate experience. Particularly Steph, your formatting expertise, treats, and flexible schedule have not gone unnoticed. Finally, thanks to my parents, who have encouraged that everything is possible and gave me the best appreciation for wild spaces through a life-long commitment to living in them. They've been a guiding influence throughout my life as a result of their personal sacrifices and have taught me everything I know about mechanics, hard work, appreciation for good food, and where to find clean air.

The following organisations provided funding, equipment and/or logistical support:

Alberta Conservation Association (Challenge Grants in Biodiversity)
Alberta Cooperative Conservation Research Unit (GPS collars and vehicle)
Alberta Sport, Park, Recreation, and Wildlife Foundation
Canadian Boreal Alberta Research Grants (Canadian Circumpolar Institute)
Environment Canada and World Wildlife Fund (Endangered Species Recovery Fund)
Rocky Mountain Elk Foundation Canada (Project Funding)
Alberta Newsprint Company (WCACSC; digital data)
Belcourt Contracting and North Aspect Contracting (line-blocking implementation)
Burlington Resources Incorporated (in-kind helicopter time)
Canadian Forest Products Ltd (WCACSC; digital data; funding through FRIP)
Devon Resources Canada (endless tanks of fuel)
Sustainable Resource Development (ATV)
West-Fraser Timber (WCACSC; digital data)
Weyerhaeuser Company (WCACSC; digital data)

Personal Funding:

Alberta Chapter of the Wildlife Society Post-Graduate Fund
Department of Renewable Resources Graduate Research Assistantship
Government of Alberta Graduate Student Scholarship
Margaret Brine Memorial Scholarship (Canadian Federation of University Women)
Mary Louise Imrie Graduate Student Award (Travel Grant)
Natural Sciences and Engineering Research Council (IPS with Canfor)
Orville Erickson Memorial Scholarship Fund
Province of Alberta Graduate Scholarship
Rocky Mountain Elk Foundation Yellowhead Chapter Scholarship

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1: Introduction

The Canadian boreal and southern mountain populations of woodland caribou (*Rangifer tarandus caribou*) are listed as Threatened in Canada (Thomas and Gray 2002). The southern mountain population consists of thirty local populations (also referred to as 'herds' in this thesis) from British Columbia (26) and Alberta (4). The boreal population includes local populations occurring from the Mackenzie Mountains in northwest Canada to southern Labrador in eastern Canada. Caribou have been extirpated from most of their historic southern reaches; for example, the Atlantic provinces and several northeastern states in the Great Lakes region. The southern-most woodland caribou herd remains in the Selkirk Mountains of Idaho, Washington and British Columbia (Thomas and Gray 2002). Population declines, in addition to contraction of historic caribou range and increased isolation, has contributed to formal listing and recovery planning within several provinces. To date, eight jurisdictions have completed at least draft Woodland Caribou Recovery Plans.

Woodland caribou may exploit nutrient-poor niches that other ungulates cannot (Thomas and Gray 2002). Although caribou will consume a variety of vascular plants, particularly in spring and summer, lichens comprise a significant portion of the diet (Thomas *et al.* 1996). As a result, caribou in mountain and foothills regions prefer dense stands of mature to old forests where lichens are abundant (Szkorupa 2002). In areas with predators, the *spatial separation hypothesis* predicts that caribou avoid predators via low densities (existing in small groups or individually) and refuge within contiguous tracts of forested habitat (Bergerud 1974; 1992, Bergerud and Elliot 1986, Bergerud and Page 1987, Seip 1992). By this theory, space is considered a critical environmental variable enabling woodland caribou to persist with predators and other ungulates (Bergerud *et al.* 1984, Bergerud 1988). Industrial development may alter habitat use patterns of caribou (*e.g.* through avoidance), and those of other ungulate and predator species (*e.g.* changes to forage availability), thereby compromising caribou anti-predator strategies. Quantifying these changes is important to caribou management.

As in other jurisdictions, woodland caribou in Alberta are sensitive to human development and infrastructure (*e.g.* Bradshaw *et al.* 1997, Stepaniuk 1997, James and

Stuart-Smith 2000, Smith *et al.* 2000, Oberg 2001, Dyer *et al.* 2001, Dyer *et al.* 2002). Industrial development may affect caribou though physical barriers to movement (Klein 1971), mortality from vehicle collisions and poaching (Johnson 1985), direct loss of habitat (Seip 1992, Brown *et al.* 2000), or through avoidance (Dyer 2002). Development also alters forest age, composition, and structure, resulting in an increase in suitable forage for moose and deer. Subsequent increases in cervid populations have the potential to influence predator-prey dynamics by supporting larger predator populations.

Declines in caribou populations across Canada were noted decades ago (Bergerud 1974), and specifically in west-central Alberta during the 1980s (Edmonds and Bloomfield 1984, Edmonds 1988). As of 2005, the Alberta Woodland Caribou Recovery Plan listed three herds in Alberta as being under immediate risk of extirpation: the Banff, Slave Lake, and Little Smoky. The Little Smoky herd, located in west-central Alberta, is the most rapidly declining herd in the province; from 1989-2000 the population declined 35% and between 1997- 2003 the adult female population declined 60% (Dzus 2001, Smith 2004). This local population (Figure 1-1) is the focal herd for the wolf and caribou analyses presented in the following chapters.

The Little Smoky range is included within portions of four Forest Management Agreements (Alberta Newsprint, Canadian Forest Products, Foothills Forest Products (E8 allocation – formerly managed by Weyerhaeuser Company), and West Fraser Timber Company). Intensive logging has primarily been restricted to the peripheries of the Little Smoky caribou range, though recent activities are encroaching on the core. Harvest plans and approaches to caribou management differ between companies; there is no definitive solution to balancing forest harvest with caribou habitat requirements and predator-prey interactions. However, forest managers generally agree that in any given area, management plans should consider local conditions that provide lichens, and habitats that are critical to calving and rutting (Cumming 1992). Meeting this need in the Little Smoky will require cooperation and discussion between the four FMA holders. However, in addition to forestry impacts, there is a very large oil and gas industrial presence in the region. There are approximately 3.5 linear kilometres of seismic line per square kilometre in the Little Smoky study area (Smith 2004). In addition, the Little Smoky has the highest road and pipeline density of any caribou range in Alberta and substantial industrial infrastructure (*e.g.* well site, compressor, processing plant, battery) facilities. At present, there is development pressure from all fronts leading to the core of the range and increases in allocations to industrial users within caribou range.

Accurate estimates of population sizes within Alberta are unavailable, but declining trends are apparent in 9 of 12 studied herds. Recent estimates of the Little Smoky herd suggest approximately 80 animals (46 females) are present (Smith 2004). While woodland caribou are not primary prey for predators, wolves are considered the primary cause for caribou mortality and decline in several systems (Bergerud and Elliot 1986, 1998; Edmonds 1988, 1998; Farnell and McDonald 1988, Seip 1991, 1992; Thomas 1995, Stuart-Smith *et al.*1997, Rettie and Messier 1998, James 1999). Although the contribution of wolf predation to declining caribou is not well understood, there appears to be wide agreement on the negative effects of increasing numbers of alternate prey (usually moose) on caribou (Bergerud 1974, 1988; Bergerud and Elliot 1986, 1998; Ferguson *et al.* 1988, Seip 1992, Racey *et al.* 1993, Cumming 1996, Cumming *et al.* 1996, Rettie and Messier 1998, Brown *et al.* 2000, Poole *et al.* 2000, Dzus 2001, Thomas and Gray 2002). Moose have a higher reproductive potential than caribou, and early seral stage forests may improve habitat quality sufficiently to greatly increase moose fecundity (Franszmann and Schwartz 1985, Thomas and Gray 2002). Direct competition between moose and caribou for food or other habitat requirements is thought to be weak, but they may share wolves as their main predator. Because caribou are least able of the two to withstand predation, caribou survival may be negatively related to moose abundance and proximity (Simkin 1965, Seip 1992).

Wolf-caribou interactions have been well studied in some environments, though research tends to focus on the winter months. In a local caribou population like the LS, where the importance of the summer season to adult and calf mortality is recognized (Smith 2004), research during the summer months is required. In addition, a lack of spring and summer wolf data precludes understanding of spatial and temporal relationships between wolves and caribou year-round (James 1999, Kuzyk 2002).

One approach to examining questions related to spatial and temporal overlap between two species is to quantify and relate habitat selection patterns. Resource selection functions (RSFs), which compare used landscape variables to those available, allow development of spatially explicit models to describe animal occurrence (Manly *et al.* 2002). There are a number of designs for RSFs, depending on the scale of selection (Johnson 1980, Thomas and Taylor 1990, Manly *et al.* 1993). Measurements can be made: 1) at the population level without identification of individual animals; 2) at the population level where individuals are identified, use is measured for each, and availability is measured at the population level; or 3) individuals are identified as in 2), but both used and available resources are sampled for each animal (Thomas and Taylor 1990). Each of these corresponds to a different order of selection (Johnson 1980); inferences from 1) and 2) are second order selection (selection of individual home ranges within the geographic range) and 3) results in conclusions about third order selection (selection of resources within the home range) (Wagner 2003). Pooling data among animals may constitute pseudo-replication (Hurlbert 1984) and could strongly affect results if individuals are unequally sampled (Garshelis 2000). Models based on individual selection sampled at the third order, but accounting for variation within individuals and/or packs, allow derivation of general conclusions about habitat selection in a given region.

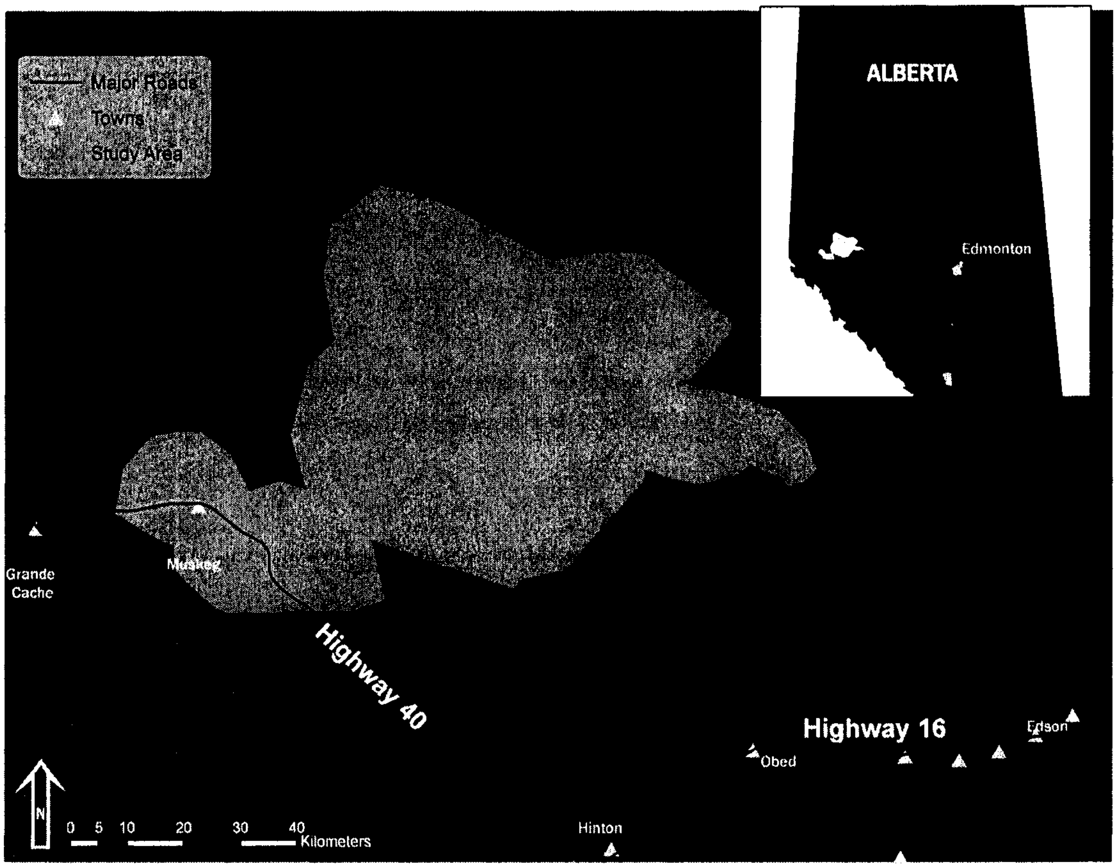
1. Thesis overview

I provide an analysis of year-round resource selection patterns of wolves and caribou in west-central Alberta. More specifically, I develop spatially explicit habitat models by examining the factors (natural and anthropogenic) leading to caribou and wolf habitat occupancy within the study area in west-central Alberta, Canada. To accomplish this goal, I use resource selection function methods for characterizing and predicting caribou- and wolf-habitat relationships (Manly *et al.* 1993, 2002; Boyce and McDonald 1999). In addition to providing practical information for management and conservation of woodland caribou in Alberta via spatial models, I examine questions relating to mitigation of the most ubiquitous industrial feature in the area: seismic lines.

Data chapters in this thesis are written in manuscript format. Consequently, there is some overlap in introductory and methodological descriptions between Chapters 2-4. In Chapter 2, data from wolves (13 individuals from 5 packs), are used to relate environmental variables to habitat use patterns across the study area. I develop an index of relative ungulate biomass based on pellet transect surveys for incorporation into wolf habitat selection models. I also employ random effects to account for multiple sampling within each pack and individual. In Chapter 3, I develop RSF models for woodland caribou of the Little Smoky herd and individuals that remain year-round in the adjacent A la Pêche winter range (all part of the Little Smoky study area defined here). I then analyze spatial overlap potential between wolves and caribou for three seasons in the Little Smoky study area. Seasons are defined based on wolf pack dynamics and behaviour, and for the purposes of this thesis, refer to time-frames within a year (*i.e.* spring, fall, winter) rather than different years. In Chapter 4, I describe the findings of an experiment designed to assess the efficacy of blocking seismic lines as a predator mobility management tool within caribou range. In Chapter 5, I summarise the findings of my work and discuss implications for resource practitioners working toward long-term caribou conservation in Alberta.

This thesis provides information regarding wolf and caribou response to industrial features and mitigation. To my knowledge, I have provided the first detailed year-round assessment of simultaneous habitat selection patterns and potential spatial-temporal overlap in boreal caribou regions. Results of this study are intended to inform future conservation and management approaches within the Little Smoky range and provide a comparative measure for future research in the area.

Figure 1-1: Study area in west-central Alberta, encompassing the Little Smoky caribou range and A la Pêche caribou winter range.



2. Literature Cited

Andison, D.W. 1998. Temporal patterns of age-class distributions on foothills landscapes in Alberta. Ecography **21**:543–550.

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

Bergerud, A.T. 1988. Caribou, wolves and man. Trends in Ecology & Evolution **3**:68-72.

Bergerud, A.T. 1992. Rareness as an antipredator strategy to reduce predation risk for moose and caribou. *In* Wildlife 2001: populations. *Eds.* D.R. McCullough and R.H. Barrett. Elsevier Science Publishers, Ltd., London. Pp. 1008–1021.

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., and J.P. Elliot. 1998. Wolf predation in a multiple-ungulate system in northern British Columbia. Canadian Journal of Zoology **76**:1551-1569.

Bergerud, A.T., and R.E. Page. 1987. Displacement and dispersion of parturient caribou at calving as an antipredator tactic. Canadian Journal of Zoology **65**:1597-1606.

Bergerud, A.T., R.D. Jakimchuk, and D.R. Carruthers. 1984. The buffalo of the North: caribou (*Rangifer tarandus*) and human developments. Arctic **37**:7-22.

Boyce, M.S., and L.L. Mcdonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology & Evolution. **14**:268-272.

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.

Brown, W.K., J.L. Kansas, and L.R. Linton. 2000. Predicting terrestrial lichen occurrence in the Redwillow Landscape Unit, northeastern British Columbia. Report prepared for Canadian Forest Products Ltd., Chetwynd, B.C. and HCK Forestry Ltd., Victoria, B.C.

Cumming, H. G. 1992. Woodland caribou - facts for forest managers. Forestry Chronicle **68**:481-489.

Cumming, H.G. 1996. Managing for caribou survival in a partitioned habitat. Rangifer **Special Issue No. 9**:171-179.

Cumming, H.G., D.B. Beange, and G. Lavoie. 1996. Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared predation risk. Rangifer **Special Issue No. 9**:81-94.

Dyer, S.J., J.P. O'Neill, S.M. Wasel, and S. Boutin. 2001. Avoidance of industrial development by woodland caribou. Journal of Wildlife Management **65**:531-542.

Dyer, S.J., J.P. O'Neill, S.M. Wasel, and S. Boutin. 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. Canadian Journal of Zoology **80:**839-845.

Dzus, E. 2001. Status of the woodland caribou (*Rangifer tarandus caribou*) in Alberta. Alberta Environment, Fisheries and Management Division, and Alberta Conservation Association, Wildlife Status Report No. 30, Edmonton, AB.

Edmonds, E.J. 1988. Population status, distribution and movements of woodland caribou in west-central Alberta. Canadian Journal of Zoology **66**:817-826.

Edmonds, E.J., and M. Bloomfield. 1984. A study of woodland caribou (*Rangifer tarandus caribou*) in west-central Alberta, 1979-1983. Alberta Energy and Natural Resources Fish and Wildlife Division.

Farnell, R., and J. McDonald. 1988. The demography of Yukon's Finlayson caribou herd, 1982-1987. Progress Report, Yukon Renewable Resources, Whitehorse, YT.

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

Franzmann, A.W., and C.C. Schwartz. 1985. Moose twinning rates: a possible population condition assessment. Journal of Wildlife Management **49**:394-396.

Garshelis, D.L. 2000. Delusions in habitat evaluation: Measuring use, selection, and importance. *In* Research Techniques in Animal Ecology, Controversies and Consequences. *Eds.* L. Boitani and T. K. Fuller. Columbia University Press, NY. Pp. 111-164.

Hulbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs **54**:187–211.

James, A.R.C. 1999. Effects of industrial development on the predator-prey relationship between wolves and caribou in northeastern Alberta. Ph.D. Thesis, University of Alberta, Edmonton, AB.

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

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

Johnson, D.R. 1985. Man-caused deaths of mountain caribou, *Rangifer tarandus,* in southeastern British Columbia. Canadian Field Naturalist **99**:542-544.

Klein, D.R. 1971. Reaction of reindeer to obstructions and disturbances. Science **173:**393-398.

Kuzyk, G.W. 2002. Wolf distribution and movements on caribou ranges in west-central Alberta. M.Sc. Thesis, University of Alberta, Edmonton, AB.

Manly, B.F.J. 1993. Comments on design and analysis of multiple-choice feeding-preference experiments. Oecologia **93**:149-152.

Manly, B.F.J., L.L. McDonald, D.L. Thomas, T.L. McDonald, W.P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Oberg, P.R. 2001. Responses of mountain caribou to linear features in a west-central Alberta landscape. M.Sc. Thesis, University of Alberta, Edmonton, AB.

Poole, K.G., D.C. Heard, and G. Mowat. 2000. Habitat use by woodland caribou near Takla Lake in Central British Columbia. Canadian Journal of Zoology **78**:1552-1561.

Racey, G.D., K. Abraham, W.R. Darby, H.R. Timmermann, and Q. Day. 1991. Can woodland caribou and the forest industry coexist: The Ontario scene. Rangifer **Special Issue No. 7**:108-115.

Rettie, W.J., and F. Messier. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. Canadian Journal of Zoology **76**:251-259.

Rhemtulla, J.M., 1999. Eighty years of change: The montane vegetation of Jasper National Park. M.Sc. Thesis, University of Alberta, Edmonton, AB.

Seip, D.R. 1991. Predation and caribou populations. Rangifer **Special Issue No.** 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.

Simkin, D.W. 1965. A preliminary report of the woodland caribou study in Ontario. Ontario Department of Lands and Forests. Res. Br. Sec. Rep.

Smith, K.G. 2004. Woodland caribou demography and persistence relative to landscape change in west central Alberta. M.Sc. Thesis, University of Alberta. Edmonton, AB.

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:**1433-1440.

Stepaniuk, D.W. 1997. Planning for woodland caribou winter habitat needs in west-Central Alberta. M.Sc. Thesis, University of Alberta, Edmonton, AB.

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

Szkorupa, T.D. 2001. Multi-scale habitat selection by mountain caribou in west-central Alberta. M.Sc. Thesis, University of Alberta, Edmonton, AB.

Tande, G.F. 1979. Fire history and vegetation pattern of coniferous forests in Jasper National Park, Alberta. Canadian Journal of Botany **57**:1912–1931.

Thomas, D.C. 1995. A review of wolf-caribou relationships and conservation implications in Canada. *In* Ecology and conservation of wolves in a changing world. *Eds.* L.N. Carbyn, S.H. Fritts, and D.R. Seip. Canadian Circumpolar Institute, Occasional Publication No. 35, Edmonton, AB. Pp. 261-273.

Thomas, D.C., and D.R. Gray. 2002. Update COSEWIC status report on the woodland caribou *Rangifer tarandus caribou* in Canada. *In* COSEWIC assessment and update status report on the Woodland Caribou *Rangifer tarandus caribou* in Canada. Ottawa, ON.

Thomas, D.C., E.J. Edmonds, and W.K. Brown. 1996. The diet of woodland caribou populations in west-central Alberta. Rangifer **Special Issue No. 9:** 337-342.

Thomas, D.L., and E.J. Taylor. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management **54**:322-330.

Wagner, R.O. 2003. Developing landscape-scaled habitat selection functions for forest wildlife from Land Sat data: judging black bear habitat quality in Louisiana. Ph.D. Thesis, Louisiana State University, Baton Rouge, LA.

Chapter 2: Year-Round Resource Selection by Wolves in the Little Smoky Caribou Region of West-Central Alberta

1. Introduction

The boreal Little Smoky caribou (*Rangifer tarandus caribou*) herd in west-central Alberta (WCA) is the most rapidly declining woodland caribou population in the province and has been identified by the Alberta Caribou Recovery Plan as one of three "under immediate risk of extirpation" (Alberta Caribou Recovery Team 2005). The Little Smoky caribou, unlike other herds in the region, do not migrate seasonally and remain year-round in an industrialised landscape (Edmonds 1988, Thomas and Gray 2002). Ultimate factors contributing to caribou decline include overall loss of habitat and reduction in the quality of remaining habitat through landscape change. In Alberta, a booming energy industry, high demand for petroleum products, and record-breaking prices have encouraged industrial development at an extraordinary pace. Woodland caribou are sensitive to industrial activities from expanding forest and energy sector development (Bradshaw *et al.* 1997, Smith *et al.* 2000, Dyer 2001). Direct and effective habitat loss, barrier effects, and shifts in species distributions and abundances from anthropogenic landscape change may ultimately affect caribou anti-predator and survival strategies partly through compromise of refuge habitats and limitation to population growth (Bergerud *et al.* 1983, Bergerud 1988, 1996; Seip 1992, Bergerud and Elliot 1998, James and Stuart-Smith 2000).

Predation by wolves (*Canis lupus*) is considered the main factor limiting woodland caribou populations and is purported as a significant cause of reduced caribou survivorship and resultant declines in several caribou herds across western Canada, including boreal Alberta (Bergerud *et al.* 1983, Bergerud 1988, Edmonds 1988, Dzus 2000, McLoughlin *et al.* 2003). Other predators, such as grizzly bears, black bears, coyotes, and cougars have been implicated in caribou decline in other regions (Zager *et al.* 1996, Young and McCabe 1997, Rettie and Messier 1998, Mosnier *et al.* 2003). However, while predators cause most deaths of forest-dwelling caribou, wolf predation is the immediate factor contributing to population declines in most locations and is thought to be significantly influenced by the effects of human developments (Thomas and Gray 2002). There is uncertainty, however, about the influence of anthropogenic landscape features on wolf resource selection and subsequent potential effects of landscape change on wolf, and ultimately caribou, populations. This is particularly true in areas where forests are highly fragmented, shaped mainly by industrial practices, and also during the summer months when data on wolves are more difficult to collect via traditional means.

Wolves have often been considered as habitat generalists (Mech 1970, Mladenoff *et al.* 1995), though newer information suggests they may respond strongly to particular landscape features (*e.g.* Ciucci *et al.* 2003). Wolves respond to landscape changes associated with industrial activities: in northern Alberta, wolves were located closer to linear corridors than random (James and Stuart-Smith 2000); wolf-killed moose were located farther from edges of young cutblocks than expected in south-eastern British Columbia (Kunkel and Pletscher 2000); den-sites were never located within 1.5-km of cleared land in central Ontario (Norris *et al.* 2002); and, scientists in central Europe and western Canada concluded that secondary roads, in addition to prey density, had significant influence on the movements of wolves within their territories (Ciucci *et al.* 2003, Whittington *et al.* 2004).

In addition, particular vegetation features may influence wolf resource selection within a territory. Research in west-central Alberta revealed that wolves used non-forested natural habitats (shrub/water) much more frequently than expected relative to their availability (Kuzyk *et al.* 2004). Similarly, wolves in north-western British Columbia selected shrubs and/or burned/disturbed habitats (Gustine 2005). In Jasper National Park, wolves selected low elevation, shallow slopes, southwest aspects, and areas within 25-m of roads (Whittington *et al.* 2005). At a coarser scale, when the landscape was delineated into two categories: 1) well-drained and 2) fen/bog complexes, a greater proportion of wolf locations occurred in well-drained habitat (James *et al.* 2004).

There are, however, inconsistent results: Kuzyk *et al.* (2004) found no evidence that wolves preferred or avoided forest cutblock edges. Mladenoff *et al.* (1995)

concluded that wolves avoid areas with higher densities of roads, whereas Merrill (2000) documented wolf territories in areas of unprecedented road densities (1.42-km/km^2). As well, Kunkel and Pletscher (2000) located wolf kill sites farther from edges of young cutblocks and small trees. Wolves are a broadly distributed and fecund species with the ability to persist under extreme circumstances (*e.g.* Wabakken *et al.* 2001), and their generalist patterns may enable rapid response to landscape change. As a result, wolves may exhibit variable patterns of resource selection across their worldwide distribution and it is valuable to explore local patterns of response.

Effective management of wildlife populations hinges partly on our understanding of environmental requirements in all seasons. Unfortunately, a clear picture of year-round wolf response to landscape variables is missing from most evaluations, as very few studies have considered resource use and selection in the summer period. Wolf pack structure varies substantially through seasons (Fuller *et al.* 2003) and presumably wolf affinity for, and response to, landscape variables may also vary. Examination of year-round resource selection is critical to clarifying the potential impact of wolf predation during the caribou calving and post-calving periods, when most caribou mortalities have been recorded in the study area (Chapter 3).

As a component of ongoing work in this region, I have collected comprehensive and concurrent year-round location information for wolves and caribou in boreal caribou ranges within Canada. In this chapter, I detail wolf response to landscape variables in an industrialised caribou region in Alberta using mixed-model resource selection functions (RSFs). Development of resource selection functions is one approach to describing patterns of space-use and environmental associations and while causation cannot be inferred from correlative RSFs, magnitude and sign of coefficients as well as strength of prediction can reveal responses to environmental components (Austin 2002). For systems where space is a critical variable in influencing the process of predation, RSFs provide a mechanism for predicting potential spatial and temporal overlap between focal species. In certain situations, RSFs can be a critical tool in conservation and management, because they allow for interpolated and predicted distributions based on current or future scenarios (Boyce *et al.* 2002). Thus, detailing patterns of wolf response to current landscape features, whether anthropogenic or natural, can provide resource practitioners opportunities to predict outcomes of future landscape change.

My specific objectives in this chapter were to: 1) identify wolf patterns of selection with respect to a suite of landscape variables (in three seasons), using resource selection functions within a mixed-model framework; 2) develop models from pellet transect data to inform an index of ungulate biomass across the range for inclusion in wolf habitat selection models; 3) predict findings of wolf selection to areas of caribou range with no wolf data; and 4) relate findings to current industrial development practices.

2. Study Area

This research was conducted in a 7350-km^2 region of the Little Smoky and A la Pêche caribou ranges in west-central Alberta (centred at 54° N, 118° W) (Figure 2-1). The boundaries of the study area were defined by 100% MCPs of wolf territories and caribou ranges in the Little Smoky region (Figure 2-2). The Little Smoky range is approximately midway between the towns of Fox Creek and Grande Cache; the A la Pêche range lies 20-km east of Grande Cache and the outer boundaries of the A la Pêche and Little Smoky are less than 10-km apart. The A la Pêche winter range is located to the southwest of the Little Smoky range.

The study area is classed into Upper Foothills and Sub-Alpine Natural Subregions (AEP 1992), and contains several major rivers, many small creeks, and a few lakes. Elevations range from 850- to 2270-m. The climate is subarctic, with short, wet summers and long, cold winters (Smith *et al.* 2000). Temperatures average 16°C in July and -13.5°C in December (Beckingham and Archibald 1996). The Foothills Region is well forested, and has been described in detail by Edmonds and Bloomfield (1984). Dry sites support primarily lodgepole pine (*Pinus contorta*) or lodgepole pine/black spruce (*Picea mariana*) forests. At higher elevations, mixed fir (*Abies* spp.), spruce (*Picea* spp.) and lodgepole pine forests dominate. Willow (*Salix* spp.) and birch (*Betula glandulosa*) meadows, interspersed with dry grassy benches, are found along some drainages.

The Berland and Simonette Rivers are located in the southern and north-western parts of the Little Smoky range, respectively; the range is bisected by the Little Smoky River. The A la Pêche range contains the Muskeg River and Little Smoky River headwaters, in addition to numerous small creeks. The Berland, Simonette, and Muskeg are fast-flowing, cold rivers whose flow is tied directly to mountain run-off. Contrastingly, the Little Smoky is turbid, slow-moving, and collects run-off from surrounding wetlands. The area surrounding the Little Smoky River consisted of bogs and peatlands, interspersed with upland areas.

Major land use activities include logging, extensive oil and gas exploration and development, non-motorized outdoor recreation (hiking, horse travel, camping, fishing), off-road vehicle use (snowmobile, all-terrain vehicles), recreational hunting, and commercial trapping (Brown and Hobson 1998). Additional ungulate and predator species share the study area, including moose (*Alces alces*), elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), grizzly bears (*Ursus arctos*), black bears (*U. americanus*), cougars (*Felis concolor*), lynx (*Lynx canadensis*), wolverine (*Gulo gulo*) and coyotes (*C. latrans*).

Access in the area exists in the form of all-weather and dry-weather resource roads, and rights-of-ways (ROWs) for pipelines, powerlines and seismic lines (Smith *et al.* 2000). Only gravelled resource roads exist in the Little Smoky range; however, a major highway (Highway 40) bisects the A la Pêche winter range. Major resource roads service small sections of the ranges and, at the time of this study there were no cross-range connecting roads.

3. Methods

3.1 Wolf location data

During five separate capture efforts from March 2003 to May 2004, 19 wolves (11 male; 8 female) from 5 packs were captured and collared (Table 2-1; Figure 2-2). Three of the 19 wolves (two females and one male) were recaptured and fitted with new radiocollars (one VHF, two GPS) during the study. Capture techniques included aerial net-gunning and foothold traps.

Bait sites were set out to assist initial identification of wolf packs in March 2003; a fixed-wing spotting plane was used to search the study area until wolves were located, then subsequently captures were conducted by a helicopter capture crew (Bighorn Helicopters). Wolves were captured by net-gun (shot from the helicopter) and physically restrained while fitted with collars and ear-tags. Consistent with previous captures (Kuzyk 2002), biometric measurements were taken on each captured wolf; blood and hair samples were also collected.

In total, 14 wolves were collared via helicopter net-gunning (including two recaptures). An additional eight wolves, including one recapture whose original radiocollar had stopped functioning, were captured during two 8-day ground-trapping efforts (September 2003; May 2004). Ground captures utilised modified Newhouse #4 traps (or modified Soft-Catch #3), equipped with several shock absorbers, rubber-pads, and long chain-drags to minimise injury. All traps were modified or designed by Rolland Lemieux (Mikin Incorporated, Québec), who also assisted with ground captures. Traps were placed in prime wolf travel areas, which had been previously identified through several weeks of reconnaissance in the study area. No major injuries to captured wolves were sustained with foothold traps, and in all but one case, wolves were handled by physical restraint without administering immobilizing drugs or sedatives. Where necessary, we administered 1 to 2-ml of 200 to 400-ml/mg of Telezol™.

Captured wolves were fitted with Lotek 2200 or 3300 GPS radiocollars (Lotek Engineering Systems, Newmarket, Ontario) with differential correction capabilities. These collars contained a remote data storage system; therefore, collection from the field was necessary to download data. Radiocollars were programmed to acquire locations at variable intervals, ranging from 15-minutes to 6-hours, depending on collar capabilities, battery life, and time of year. All locations with an HDOP (horizontal dilution of precision) greater than 12, indicating probable erroneous location accuracy, were removed prior to analysis (D'Eon and Delparte 2005). Three wolves, including one male recapture, were fitted with VHF collars to maintain contact with various packs.

3.2 Wolf season delineation

To account for variation in patterns of resource selection through time, I stratified wolf location data into three seasons based on behavioural habits of wolves in the study area and guided by known aspects of wolf pack biology: denning, rendezvous, and nomadic periods. During the denning period, the social centre of the pack is usually the pups (Jedrzejewski *et al.* 2001, Mech and Boitani 2003). Therefore, the denning season was characterized by return visits to a centrally-located den-site, a peak in daily-distance movements as compared to other seasons, and lack of rendezvous sites. The den period for wolves in this region was defined as being between 20 April and 30 June. Early in July of each year, wolves moved to rendezvous sites. Rendezvous sites were characterized by small, return looping movements to a new area that was not the den site, shorter daily movement distances, and frequent stops. Based on this definition, the rendezvous season was delineated as 1 July to 20 September. There was variation in the number of rendezvous sites (one site usually lasted for 1-3 weeks, with earlier sites existing for longer), but all packs illustrated the same patterns of movement once they left the den site. The looping pattern of movement was increasingly rare by mid-September, when young wolves presumably began to travel with the pack. This shift in pack behaviour commenced the nomadic season, which was characterized by lack of a central return-point, circular patterns of movement through the whole territory with little to no directional bias (aside from territory boundaries), and short daily movement distances.

The three wolf seasons also correspond to key periods for caribou: during the denning period, female caribou are in the final stages of pregnancy, giving birth in early June. During the spring and summer seasons (denning and rendezvous), young caribou calves are most vulnerable to predation. The rest of the rendezvous period coincides with increased calf growth, the snow-free summer when caribou forage intake is highly variable (Thomas *et al.* 1996), and the caribou calf-growth period. Winter, when caribou depend primarily on lichens and require specific forage areas high in lichen availability (Saher 2005), is represented by the nomadic season.

3.3 Nonlinear modelling

To reduce autocorrelation in location data and remove effects of multiple locations at kills, rendezvous sites, and dens, I used a nonlinear curve-fitting model and rates of movement to identify behaviour bouts for each wolf using two categories: fast and slow or stopped movement (Johnson *et al.* 2002). Historically, behaviours have been identified via broken-stick modelling, which uses log survivorship analysis to subjectively determine a break-point between two behaviours (Sibly *et al.* 1990). However, because points are not independent, objective fit of a broken-stick model is compromised (Sibly *et al.* 1990). Therefore, Sibly *et al.* (1990) introduced a Poisson method, accommodating two processes or behaviours, to increase objectivity in defining behaviours. Johnson *et al.* (2002) further adapted Sibly's (1990) method, employing movement rates to delineate activities. I used a similar non-linear modelling strategy to fit a $\log_e$ transformed frequency distribution to movement rates. The model was of the form:

$$y = \log(N_s \lambda_s e^{-\lambda sr} + N_f \lambda_f e^{-\lambda fr}) \qquad \text{(Equation 2.1)}$$

where y is the estimated number of wolf movements that occur during each discrete interval of movement rates; N is the number of slow and fast movements that occur at each rate interval; subscripts s and f refer to slow and fast movements; λ represents the probability that slow or fast movement occurs in the next interval; and r is the movement rate (Johnson *et al.* 2002). The bout criterion introduced by Sibly *et al.* (1990) was adapted for movement rates and calculated as a scale criterion, r_c, which represents the breakpoint value. Given starting points, the non-linear model derived estimated values, which were used to determine the inflection point scale criterion (r_c) of the $\log_e$ frequency distribution of wolf movement rates:

$$r_c = \frac{1}{(\lambda_s - \lambda_f)\log_e(\frac{N_s \lambda_s}{N_f \lambda_f})} \qquad \text{(Equation 2.2)}$$

I employed this technique, described in Johnson *et al.* (2002), to delineate two scales of movement behaviours in wolves. I examined a frequency histogram of $\log_e$

transformed movement rates between consecutive points to identify the initial estimated break-point (r_i). Linear regression on either side of the break-point provided estimates of initial model parameters (N_s, N_f, λ_s, λ_f) and the model was iterated to convergence. I calculated the scale criterion, and movement rates of wolves $<r_c$ were considered to be stopping points and were excluded from future analyses; rates $> r_c$ were considered to be movement points and were retained for RSF analyses. This was an effective way to reduce multiple locations at one site (*i.e.* den, kill, rendezvous, resting) and subsequent spatial autocorrelation in the data, however, the spatial distribution of wolf GPS points within wolf territories was not greatly affected. Wolves hunt while they travel (Peterson *et al.* 1984, Mech 1992) and examining RSF models using travel points allows examination of encounter potential with caribou (Chapter 3).

3.4 Resource Sampling

3.4.1 Ungulate models

Study design

I used pellet transect surveys (*e.g.* Chen *et al.* 1997) to create an index of ungulate biomass. For logistical reasons, the study area was initially delineated into five sections of approximately equal size with respect to major rivers. Within each section, the ground cover was stratified into 12 habitat feature classes (Table 2-2), which represented major vegetation and human infrastructure components that could influence ungulate distribution. Forest stands were surveyed based on the dominant species cover (>60%). Previous research has shown that ungulates may respond to the age of logdegpole pine stands (Pauley *et al.* 1993, Skzorupa 2002), the most prevalent conifer in the region; for this reason, pine-dominated stands were further delineated into three age categories. Within each section of the study area, I randomly chose three replicates of each cover type for surveying. It was necessary that the survey polygons of each stand type be large enough to encompass the survey track, approximately 1-km by 500-m (with some variation due to field measurement inaccuracies). Within a Geographic Information System (GIS), I selected a start-point for each polygon and calculated starting azimuths (Figure 2-3). Three replicates of each feature class (12) were sampled within sections (five) of the study area.

The survey was conducted by two field workers, commencing at the same point and proceeding in opposite directions. Each person walked a triangular path of 1.5-km in length, returning to the start point. Field personnel walked at a slow pace, recording all pellet groups or scat within a 1.5-m width (0.75-m on either side) along their direct path. Upon encountering a pellet grouping, species and approximate decay class (recent=1 to old=4) was noted, as well as visibility, habitat details, animal observations, and an approximate distance since the last pellet observation. Further information detailing crossings of roads, game trails, and notes on conventional, low-impact, and hand-cut seismic lines encountered was recorded.

Because I was interested in arriving at an index of ungulate biomass in relation to habitat covariates (for inclusion in wolf habitat selection models), I made no attempt to implement distance-sampling to estimate ungulate abundance. I assumed that all scats were detectable within each transect's 1.5-m width and there was no attempt to survey beyond this distance.

Pellet transect surveys were conducted from 3 June to 3 August 2004. Due to time and visibility constraints due to vegetation growth, we were not able to complete the fifth section of the delineated study area.

Analysis

I developed a descriptive model of ungulate pellet-group count and created a spatial index of ungulate biomass. Because the main interest was biomass, and due to uncertainty in identifying caribou from deer pellets, I grouped counts of caribou and deer in analyses. Caribou and deer are relatively similar in mass (Franzmann and Schwartz 1997), and although their habitat requirements vary, caribou likely made up a very small proportion of the actual sample.

I used information theoretic techniques to define an appropriate equation linking ungulate pellet counts and landscape features. I modelled the number of pellet groupings per species group per transect as a response variable within a generalized linear model (GLM) to estimate spatial distribution and index of moose and deer/caribou (Hedley and Buckland 2004). The GLM formulation was expressed as:

$$E(n_i) = \exp\left[\ln(2l_i w) + \beta_0 + \sum_k \beta_k z_{ik}\right], \; i = 1,\ldots,T.$$

(Equation 2.3)

Each 3-km transect was considered a spatially independent "segment" (1...T); segments were of similar length, of consistent habitat type, and were a minimum of 1-km from segments in other habitat types. The length of the i^{th} segment is denoted by l_i and the number of pellet groupings detected by n_i, $i = 1, \ldots, T$. For each segment, I calculated a set of spatial environmental covariates, k, whose values in the i^{th} segment are denoted by z_{ik}. I entered the logarithm of the area of each transect, $\ln(2l_iw)$, as an offset in the linear predictor to adjust for small variation in transect lengths (Hedley and Buckland 2004). I specified a negative binomial error distribution to account for overdispersion in the data. The detection probability of observing a pellet group was assumed to be the same for all species groups within a transect.

Although I surveyed a small area per transect, each transect survey was selected to represent approximately 1-km² sampling units. Therefore, covariates and predictions were related to 1-km² resolution Alberta Vegetation Inventory (AVI) maps (Table 2-3). I used an information theoretic approach (Burnham and Anderson 2002) and based candidate models on processes such as foraging, movement, habitat avoidance, and predation risk to incorporate knowledge of ecological processes (Austin 2002). Candidate sets for each season and biomass class (moose in winter, moose in summer, deer/caribou in winter, and deer/caribou in summer) represented informed static models with biologically relevant covariates that described current ungulate pellet counts in the study area.

I used Aikaike's Information Criterion corrected for small sample size (AIC_c) to select the most parsimonious model. Model averaging was used to produce more robust estimates and strengthen inference because weights for the top model were less than 0.9 (Burnham and Anderson 2002). For model averaging, the influence of each variable was independently examined by summing the weights of models that contained the variable; covariates with large summed weights were added to the top model. Each covariate estimate in the final model was then standardized and averaged to give the adjusted coefficient estimate (Burnham and Anderson 2002). Averaged model coefficients for each species-season combination were entered into Equation 2.3 to estimate $E(n_i)$ – the count of expected moose or caribou/deer per 1-km^2 pixel. Predicted counts of respective species groups for the four maps were weighted by respective biomass values for moose and caribou/deer, then summed across seasons to create two relative biomass index maps. Maps were created for the summer and winter seasons, not specifically for wolf seasons identified earlier, as delineation into more decay classes was not practical.

3.4.2 Additional predictor variables for wolf models

In addition to ungulate biomass layers, I used a GIS to define 30 land cover, terrain, and human use layers. Four forest management agreements (FMAs) lie within the study area: Canadian Forest Products Ltd., Weyerhaeuser Company Ltd.[1], West-Fraser Timber Company Ltd.[2], and the Alberta Newsprint Company. I combined AVI data from each FMA holder to create 30-m pixel raster maps consistent with GPS error (D'Eon *et al.* 2002). Additional descriptions of anthropogenic features, such as roads, cutlines, well-sites, and facilities (compressors etc.), were acquired from IHS Energy. Digital elevation models and hydrological data were provided by the Government of Alberta. Slope, aspect, distance, density, and proportion values for various landscape attributes were calculated with the Spatial Analyst extension of ArcGIS 9.0 (Environmental Systems Research Institute, Redlands, California).

I developed a terrain ruggedness index (TRI) from 30-m digital elevation models, similar to Nellemann and Fry (1995). TRI was calculated using a 300-m circular moving window and the formula:

$$\text{TRI} = \frac{(\text{Aspect Variation} * \text{Average Slope})/(\text{Aspect Variation} + \text{Average Slope})}{100} \qquad \text{(Equation 2.4)}$$

where aspect variation was calculated from digital elevation models (Turner 1989). Two categorical variables, calculated from the AVI, were included in the variable set: *cover* and *wetness* (Table 2-4). I used an indicator contrast with the most prevalent class as the reference category ("forest" for *cover* and "mesic" for *wetness*). Additional predictor

---

[1] E8 allocation recently re-allocated to Foothills Forest Products Inc.

[2] Formerly Weldwood of Canada Ltd

variables considered in wolf models are described in Table 2-4. Due to rapidly changing landscape of the study area, I created time-stamped digital layers in 6-month increments.

3.5 Model building strategies and statistical methods

3.5.1 Variable selection

Sizeable GPS data sets and large log-likelihood values are known to inadequately penalize AIC calculations (Boyce *et al.* 2002). This shortcoming can result in selection of the global model over other candidates. In this case, I considered the bias too strong and selected model variables based on frequentist methods popularized by Hosmer and Lemeshow (1999, 2000). Each variable's influence was initially assessed in univariate analyses using $p < 0.25$ based on a Wald z-statistic as a cut-off for inclusion in the preliminary multivariate model. If two variables were correlated ($r > |0.7|$), I retained the variable with the lowest log-likelihood and smallest p-value (Nielsen *et al.* 2002, Saher 2005). I first assessed the full multivariate model, then dropped the least significant parameter and refit the reduced model. This process was repeated until all remaining parameters were significant at $\alpha = 0.05$ (Hosmer and Lemeshow 1999, Hosmer and Lemeshow 2000). I used variance inflation factors (VIF) to test for multicollinearity (Menard 1995). Variables that are orthogonal to each other (*i.e.* completely uncorrelated with each other) have tolerance and VIF values of 1. Variables that are very closely related have tolerance values closer to 0 which increases the variance inflation factor substantially. Where VIF scores for individual parameters were greater than 10 or mean scores for a given model were considerably larger than 1, erroneous variables were removed (Chatterjee *et al.* 2000). All analyses were conducted in STATA 9.1 (STATA Corp., College Station, Texas).

3.5.2 Modelling strategy

I developed resource selection functions (RSFs) for wolves in each season, using GPS points and uncorrelated explanatory variables. I chose to separate the 2 years of data from the Simonette pack, acknowledging the potential for year-to-year variation in selection.

Wolf location data for each season (restricted to those points categorized as moving) were classified as used points. For each wolf-season (*n*=37), I created a set of random available locations at a 1:1 ratio to each used point. In order to maintain consistency between the spatial autocorrelation of the used and available data and also to account for individual variation in movement patterns due to social status of wolves, I defined available data based on movement parameters defined by step angles and turn angles for each wolf-season. I drew available points randomly from distributions of step length and turn angle for each wolf-season. I used the ArcGIS extension Hawth's Tools (Research and Development version) (Beyer 2005) to assist in creating available points.

Used and available points were contrasted using an availability-use design with the following log-linear form:

$$w^*(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_K) \qquad \text{(Equation 2.5)}$$

where $w(x)$ represents the relative use function and β_i is the coefficient estimated from environmental predictors x_i (Manly 1993). Coefficients for the model were estimated using logistic regression with random effects.

3.5.3 Inclusion of random effects

Longitudinal data consisting of repeated observations on individuals over time can be considered hierarchical (Rabe-Hesketh and Skrondal 2005). In this case, the first hierarchical level was the observations (location points) and the second level was the individual (wolf). The individuals were also clustered within packs. Sociality in wolf packs leads to observations that are not independent and constitutes pseudoreplication (Hurlbert 1984). Also, repeated observations on the same subject taken over time (for example, GPS fixes at different points in time and/or space) may not be independent, resulting in residuals that may be correlated (Rabe-Hesketh *et al.* 2004a). Recent developments in multivariate statistics allow for incorporation of random effects to accommodate non-independence within groups. Using a generalised linear mixed model (GLMM), the residual correlations can be modelled by partitioning the total variation into a subject-specific random intercept (which remains constant over time) plus a residual (which varies over time) (Rabe-Hesketh *et al.* 2004a, Piepho *et al.* 2003). Inclusion of random effects can improve model fit substantially and change both the magnitude and direction of coefficients (Gillies *et al. in press*). Random effects enter models as either random intercepts (which allow the intercept of magnitude of the response to vary among groups) or random coefficients (which allow the effects of covariates to vary among groups).

I included two random intercepts in wolf logistic regression models (Breslow and Clayton 1993, Skrondal and Rabe-Hesketh 2004); I did not use random coefficients as their interpretation within an RSF is complicated and the techniques are still being developed. By introducing random intercepts, I was able to represent individual differences in the overall mean level of the response after controlling for covariates; the result was slightly modified coefficient values for covariates (Rabe Hesketh *et al.* 2004a). I used maximum likelihood via adaptive quadrature (integration) to estimate coefficient values as this method suitable for unbalanced and large sample sizes (Rabe-Hesketh *et al.* 2002, Rabe-Hesketh *et al.* 2004b, Rabe-Hesketh and Skrondal 2005).

I examined two-level (random effect for pack) models using *gllamm* and STATA's built-in GLMM function *xtlogit* (Gauss-Hermite quadrature), then analysed three-level (random effect for pack and individual) models with *gllamm* and both 8 and 12 integration points to assess coefficient stability. I chose to use the *gllamm* program to define models with random effects because it uses adaptive quadrature, estimates via maximum-likelihood, and allows three-level models.

RSFs were estimated for each season using Equation 2.5 and the adjusted beta coefficients and models were interpolated within the Spatial Analyst extension of ArcGIS 9.1. I standardized original RSF values, $w(x)$, by dividing by $(1+ w(x))$ to facilitate RSF classification. Standardized RSF maps were separated into ten equal-sized ordinal bins. Resultant maps provided a relative assessment of animal occurrence, ranging from a low value of 1 (low relative index of use) to a high value of 10 (high relative index of use).

3.5.4 Model validation and fit

Receiver operator characteristics are not appropriate for use-availability designs (Boyce *et al.* 2002). Therefore, I validated the top seasonal models using a 1:5 testing-to-training *k*-fold partitioning procedure (Fielding and Bell 1997). The data were randomly assigned to one of five groups and the model was trained iteratively on four groups, retaining the fifth for testing. Each model was validated by comparison with the ranked bins of the predicted RSF values using a Spearman rank correlation statistic. The average Spearman rank correlation statistic indicates the within-sample internal predictive ability of the model (Boyce *et al.* 2002). I also assessed model fit by using a McFadden's pseudo R-Squared, which measures the strength of association, and examined specificity and sensitivity of each model.

4. Results

4.1 Wolf location data

GPS collars were deployed on 20 wolves in five packs. Despite relatively frequent relocation surveys, six collars either stopped functioning or the wolves dispersed from the study area. In the first year, two Lotek GPS 2200 collars stopped transmitting; one detached GPS 2200 was discovered in a remote bog during transect surveys, near an old moose kill. Location data could not be recovered. Two Lotek GPS 3300 collars stopped functioning during the course of the study. One collar was recovered when wolf 41 was recaptured (data were not recoverable). An additional two GPS 3300 with drop-offs and wolf modifications also suddenly stopped transmitting. Both wolves were adults from well-established packs. Several reconnaissance flights throughout west-central Alberta have failed to locate the missing collars.

In addition to lost or malfunctioning collars, there were three presumed wolf mortalities over the course of the study (Table 2-1). An adult female of the Horse Creek pack died shortly following capture. A necropsy revealed an old injury and extensive damage to the diaphragm, presumably from an ungulate kick. The wolf was in compromised condition at the time of capture and the additional stress of helicopter pursuit and capture resulted in eventual asphyxiation. It is unknown what happened to a large male wolf in the Berland East pack. The VHF collar transmitted a mortality signal repeatedly from the same location but the animal could not be located in the deep snow cover. The collar stopped transmitting altogether by the next attempts to locate the wolf.

Wolf 33, from the Berland East pack, was located in a remote location and likely died from natural causes.

Data used in RSF analyses were thus derived from 13 wolves in five packs. Although five wolves were captured in the Buckbean pack, two GPS collars failed and two VHF collared animals dispersed north-west of the study area. Data from the Buckbean pack was thus retrieved for one adult female (Wolf 51). We were able to collect data on three wolves in the Horse Creek pack despite one non-functioning GPS collar and one mortality. Two wolf collars were deployed and recovered from the Muskeg pack, though both wolves dispersed near the end of the study; Wolf 48 was struck by a car near Leslieville, Alberta. We had the most success in the Simonette pack, where five wolf-years of data were recovered. In the Berland East pack, two wolf collars were deployed and recovered in 2003, but an additional GPS collar deployed in 2004 has not been recovered.

4.2 Non-linear modelling

Rates of movement used to distinguish behavioural states were relatively consistent across individuals and packs. The movement rate cut-off identified by non-linear modelling and used for each wolf ranged from 3.27-m/min to 6.09-m/min, substantially reducing the numbers of locations per individual used in subsequent analyses (Table 2-5).

4.3 Ungulate models

I estimated a spatial ungulate biomass index surface throughout the survey region from the observed transect data (Figure 2-4), excluding well-sites from the analysis as the scale of observation was not comparable to other transects. Transects conducted in well-sites were bounded by the cleared area; therefore, they were much smaller and more highly correlated than all other transects.

A total of 134 transects (survey distance of 335.7-km) were completed in four sections of the study area. Surveyors recorded 1194 moose and 342 caribou/deer pellet groupings of decay class 3 or 4 and 708 moose and 524 caribou/deer groupings of decay class 1 or 2. Elk (*n*=1230), wolves (*n*=295), bears (*n*=354), coyotes (*n*=205), unknown ungulates (*n*=1179), and small carnivores (*n*=88) were also recorded (Table 2-6). Bear, coyote, and wolf scats were found in disproportionately high quantities on seismic lines compared to other habitats (Table 2-6). Moose and caribou/deer pellets were most dense in non-forested and young pine habitats, respectively, though cutblocks >5, non-forested habitats, and well-sites also had high densities of pellet groupings. Although elk were locally abundant and have been documented as an important prey sources for some wolf packs, their distributions were localised and disjunct. It is known that elk are prevalent in certain watersheds in the study area and transects located near large elk populations contained large number of pellet groupings. In addition, elk are gregarious and would have to be modelled with a different technique. Therefore, I could not include elk in these analyses.

After screening for correlation, I retained 20 variables (Table 2-3) for candidate models; I developed 8 to 9 candidates for each species-season combination (Table 2-7). For predicting moose pellet count during the winter and summer seasons, percent pine, black spruce, coarse habitat cover (including categories for forest, grass, shrub, and bare ground), distance to well-sites, distance to roads, and distance to cutblock and/or proportion cutblock in a 1-km^2 area were predictors in the top models. However, for both seasons, models had sufficient uncertainty to warrant model averaging (Table 2-8). Top caribou/deer models differed in winter and summer. In summer, distance to cutblock, roads, and rivers, as well as percent pine, percent larch, and coarse ground cover were variables of the top model, for which the weight was 0.86. For winter, the top model included percent pine, percent larch, distance to rivers, coarse habitat categories, and age. No model had weights above 0.9 and all species-season models were averaged by adjusting coefficients and standard errors (Table 2-9). Final models were not intended to capture density or absolute abundance of ungulates in the study area, but were used to calculate a relative index of total ungulate biomass in relation to habitat covariates.

4.4 Wolf model building and validation

Although each stepwise procedure was initiated with the same set of variables, there was notable variation between seasonal models (Table 2-10). For example, distance to cutblock was not an important descriptor of variation in wolf resource use during the denning or rendezvous season, though it did enter the nomadic season model. The final seasonal models also differed in the number of explanatory variables: 12, 14, and 18 for the nomadic, rendezvous, and den models, respectively.

4.4.1 Denning season

The model derived to predict wolf occurrence during the denning season was of the form:

$$\begin{aligned} w^*(x) = \mathrm{Exp}[&-0.0056(\text{forest age}) + 0.127(\text{distance to pipelines}) - 0.129(\text{\% larch/1-km}^2) \\ &- 0.286(\text{\%pine/1-km}^2) + 2.835(\text{proportion cutblock/10-km}^2) - \\ &2.848(\text{proportion cutblock/1-km}^2) - 0.268(\text{\% black spruce/1-km}^2) - \\ &0.055(\text{seismic density/1-km}^2) + 0.00025(\text{seismic density/10-km}^2) - \\ &0.336(\text{\%white spruce/1-km}^2) + 0.738(\text{terrain ruggedness index}) + \\ &0.119(\text{distance to wells}) + 0.022(\text{distance to facilities}) - 0.844(\text{distance to} \\ &\text{water}) + 0.00004(\text{summer biomass index}) + 0.0571(\text{\%white spruce}) + \\ &0.954(\text{dry land}) + 0.466(\text{wet land}) + 0.511(\text{grass cover}) + 0.125(\text{bare ground}) - \\ &0.019(\text{shrub cover})]. \end{aligned}$$

The direction and magnitude of each coefficient is the primary factor describing selection or avoidance by wolves. However, ranges of covariates are also critical to understanding the degree of selection or avoidance: small coefficients (near zero) generally indicate that wolves select resources more proportionately to what is available, but the range of the covariate value is influential in the $w^*(x)$ model. Small values may be misleading if the covariate has a very large range. In general, larger coefficients may imply stronger selection, but are also dependent on the coefficient's range. The sign of the coefficient, describing the direction of response (negative versus positive), does not change with varying coefficient values.

During denning, wolves were farther from pipelines, wells, and facilities, associated with younger forest stands, and more likely to occur in areas with high proportions of cutblocks at the 10-km^2 scale but less likely to occur in areas of high cutblock density at the 1-km^2 scale (Figure 2-5), although the pattern of the latter is largely influenced by the skewed distribution of availability and should be interpreted with caution (there are very few areas where the proportion is large) (Figure 2-5). Wolves also responded positively to areas of greater terrain ruggedness (Figure 2-6). Interestingly, facilities – which tend to be very noisy and have higher levels of traffic – were avoided to a distance of 6-km, areas farther than 6-km from facilities were used substantially more than available (Figure 2-7).

The coefficient for seismic density at the 10-km^2 scale was small, likely due to the lack of a distinct pattern in use and availability across varying seismic densities (Figure 2-8). Wolves were associated with lower proportions of black spruce, lodgepole pine, larch, and white spruce at the 1-km^2 scale, but at the local (30-m) scale showed slight selection for sites with high proportions of white spruce. Finally, wolves were located closer to water than available points. The confidence intervals of total summer biomass (ungulate model), and bare ground and shrub in comparison to forested areas (reference category) overlapped zero, indicating that these variables were not important in explaining the variation in used and available sites.

Variances for the random effects were relatively small, but larger than for any other season (Table 2-11), indicating higher variation among wolves and packs during the denning season than other times of year. Variance between packs was larger than variance between individuals, suggesting that individuals within a pack are more similar while packs exhibit different patterns during denning.

The den model had good fit (Likelihood ratio-test X^2 *p*-values <0.0005, with McFadden's pseudo R-Square R^2= 0.23). *K*-fold cross validation resulted in a Spearman's ρ of 0.99 which indicated that the coefficients were robust and accurately predicted wolf use. The model was able to predict use (sensitivity) 71% of the time and available (specificity) 74% of the time. Overall, the proportion of used (1) and available (0) correctly classified by the model was 0.72.

4.4.2 Rendezvous season

The rendezvous season model used to interpolate the resource selection functions was of the form:

$$w^*(x) = \text{Exp}[-0.0048(\text{forest age}) - 0.072(\%\text{pine}/1\text{-km}^2) - 0.048(\%\text{ black spruce}/1\text{-km}^2) - 0.077(\text{seismic density }(\text{km}/1\text{-km}^2)) + 0.0002(\text{seismic density }(\text{km}/10\text{-km}^2)) - 1.456(\text{distance to seismic}) + 0.033(\text{distance to pipelines}) + 0.542(\text{terrain ruggedness index}) - 0.0002(\text{winter biomass index}) + 0.092(\text{distance to wells}) - 0.318(\text{distance to water}) + 0.069(\%\text{white spruce}) + 1.29(\text{dry land}) + 0.161(\text{wet land}) + 0.098(\text{grass cover}) - 0.204(\text{bare ground}) + 0.140(\text{shrub cover})].$$

During the rendezvous season, distance to seismic lines was one of the driving explanatory variables influencing the interpolated surface. Wolves were located closer to seismic lines than random (Figure 2-9), but did not respond strongly to the overall density of seismic lines across the territory. Wolves were farther from pipelines and wells than random, but closer to water. As in the denning season, wolves were positively associated with more rugged terrain (Figure 2-10), dry and wet areas as compared to mesic (moderately wet) areas, and grassy and shrubby areas in comparison to the reference category, forested areas. Wolves were negatively associated with bare ground in comparison to forested areas. Confidence intervals of the categories grass, bare ground, and shrub in comparison to forested areas (reference category) overlapped zero, indicating lack of contribution to explaining variation in used and available sites during the rendezvous season.

Relatively little variation was explained by random intercepts (Table 2-11) in the rendezvous model. Similar variance existed at the pack and individual level; in general, wolves across the study area exhibited relatively similar responses to landscape features.

The rendezvous model had the poorest fit (Likelihood ratio-test X^2 p-values <0.0005, and McFadden's pseudo R-Square $R^2 = 0.06$). K-fold cross validation resulted in a Spearman's ρ of 0.89 which indicated that the coefficients were robust and accurately predicted wolf use. The model was able to discern use (sensitivity) 52% of the time and available (specificity) 70% of the time. Overall, the proportion of used (1) and available (0) correctly classified by the model was 0.61.

4.4.3 Nomadic season

The final model derived from the stepwise procedure to explain the proportional probability of wolf resource use during the winter (nomadic) period took the form:

$$w^*(x) = \text{Exp}[-0.0067(\text{forest age}) + 0.0737\ (\%\ \text{deciduous cover}) + 0.0596(\text{distance to cutblock}) + 0.0318(\text{distance to facilities}) - 0.624(\text{distance to water}) + 0.0088(\%\text{white spruce}) + 1.9361(\text{proportion cutblock}/10\text{-km}^2) - 0.181(\text{distance to major rivers}) - 0.0778(\text{distance to roads}) - 0.1298(\%\ \text{black spruce}/\text{km}^2) + 0.5312(\text{dry land}) + 0.4429(\text{wet land}) + 0.7730(\text{grass cover}) + 0.4396(\text{bare ground}) + 0.3577(\text{shrub cover})].$$

Wolf occurrence in the winter was related to younger forests, overall more deciduous cover (though white spruce was a preferred conifer while areas with higher proportions of black spruce were negatively selected), closer to water and major rivers, more often in dry and wet areas as compared to the reference mesic (moderately wet) category, and positively associated with grassy, bare, and shrubby areas in comparison to forested areas. Selection coefficients were large for proportion cutblock within a 10-km^2 circular area, though smaller for distance to facilities (*e.g.* compressor stations), cutblocks, and roads.

More specifically, wolves used regions with larger proportions of cutblocks much more than available, while they used areas with lower proportions of cutblocks less than available (Figure 2-11 a). Areas where percent black spruce within 1-km^2 was very small were used disproportionately more in relation to what was available, for percent cover >20%, wolves were present less than available (Figure 2-11 b). Although areas within 1-km of a cutblock were readily available (50% of the landscape), nearly 70% of wolf locations were within this proximity from a cutblock (Figure 2-12 a). Similar to the response in the denning season, wolves avoided human facilities up to a distance of 3-km to 6-km (Figure 2-12 b). Confidence intervals for all variables did not overlap zero, indicating that each contributed to explaining variation in used and available sites.

This model accounted for two levels or random effects: wolf pack and individual, the inclusion of which slightly modified the coefficient values. However, little overall variation was explained with random intercepts (Table 2-11). Low variation at both levels (pack and individual) indicated that wolves across the study area were relatively similar in their responses to landscape features during the nomadic period.

The nomadic model had good fit (Likelihood ratio-test X^2 *p*-values <0.0005, and McFadden's pseudo R-Square R^2= 0.09). *K*-fold cross validation resulted in a Spearman's ρ of 0.96 which indicated that the coefficients were robust and accurately predicted wolf use. The model was able to predict use (sensitivity) 60% of the time and available (specificity) 70% of the time. Overall, the proportion of used (1) and available (0) correctly classified by the model was 0.65.

Relative index of use for each season predicted across the study area identified seasonal variation in likelihood of wolf occurrence (Figure 2-13). Locations along and around river valleys, those with higher densities of cutblocks, and linear features (roads, pipelines, and seismic lines in varying degrees across seasons) are detectable in each seasonal predictive surface. Within areas near the centre of the Little Smoky caribou range, there are locations where wolves are predicted to occur with higher likelihood, but overall suitability is lower than the peripheral parts of the study area.

5. Discussion

Wolf selection patterns were variable relative to landscape features in the industrialised Little Smoky landscape. I used resource selection functions and mixed models to quantify these responses and identify which variables were significant in describing habitat use by wolves during the denning, rendezvous, and nomadic seasons. I developed a spatial index of ungulate biomass in the region in an attempt to incorporate data on prey and mechanisms for observed selection patterns. Overall, wolves responded to a suite of landscape features, though they exhibited different seasonal patterns of selection. Human infrastructure and related variables were consistently among the most important explanatory covariates in describing patterns of wolf use. Distance to rivers and streams, terrain ruggedness, and coarse vegetation cover were also significant predictors of wolf use. Using parameter values from RSF models, I predicted resource selection function across core caribou areas where data were not collected on wolves (Figure 2-2; Figure 2-13). Predictive spatial models indicated that suitability for wolves was variable by season, and overall low in core caribou areas relative to portions of the study area within wolf territories. However, the models predicted that wolves in this area would select human infrastructure, particularly areas with higher densities of cutblocks and seismic lines during certain seasons.

5.1 Response to human infrastructure

Overall, wolves showed a clear positive response to cutblocks in all seasons, evidenced by a high index of use in RSF maps (Figure 2-13). Although a direct measurement of proportion-cutblock or distance-to-cutblock did not enter all models as a significant variable, there were additional surrogate variables that captured cutblock features and were additive in quantifying selection patterns. For example, the variable "cover" was a four-level categorical variable that defined habitat into coarse categories: forest, shrub, no cover, or grass. Within this coarse variable, cutblocks 5-20 years old were classified as shrubs because they were the dominant cover in the young blocks (Dyrness 1973). Most cutblocks (74%) were less than 15 years old (Figure 2-14) and a majority were younger than 20 years (94%). In addition to being classified as shrub, cutblocks were of young age classes (calculated from harvest date) and contained no dominant species for "% cover" calculations. Wolf use was associated with younger forests in all seasons, and shrub (in reference to forest) in the nomadic season (not significant in other seasons). This pattern is generally similar to that described by Kuzyk (2002); wolves preferred shrubs and water over other habitats. In addition, while not statistically significant, forest cutblocks were used proportionately more compared to forest and non-forest anthropogenic habitats (Kuzyk *et al.* 2004). Kuzyk (2002) categorised habitats differently than my analyses, but patterns of selection for shrub and cutblock were similar.

Resource selection maps also predicted relatively high probability of use of roads, pipelines, and well-sites. However, wolves did not explicitly select these attributes as represented by the distance-to coefficients. Similar to the effect noted with respect to cutblocks, predicted selection of these anthropogenic features was likely influenced by additional variables. Roads, pipelines, and rivers were also represented as grass-covered and bare habitat classes and contrasted directly to the reference category (forest), and wolves exhibited high selection coefficients for these features during the denning and nomadic seasons. Roads, pipelines, and well-sites were also classified as dry as parts of the wetness variable and this also influenced the observed predicted selection of roads and pipelines by wolves (see below for further discussion about wetness). In Jasper National Park, wolves selected areas within 25-m of roads and trails, while also showing a preference for low-use roads and trails compared to high-use sites (Whittington *et al.* 2005).

Effects of linear disturbances as a component of habitat selection analyses are difficult to quantify because of seismic line ubiquity. Nevertheless, seismic lines are thought to be a significant landscape feature for wolves. James (1999) deployed four GPS collars in northern Alberta packs to record wolf movements within one winter month; analyses were based on a small GPS data set. Using a similar GLM approach as mine to compare the distance of use and random points to linear corridors, James (1999) concluded that wolves were located closer to linear features than random points. In addition, average travel rates of wolves within 50-m of linear features were 2.8 times faster than rates in the forest (James and Stuart-Smith 2000). In contrast to James' (1999) work, no measures of seismic lines I quantified were significant in describing wolf resource use during the nomadic (winter) season. Most seismic lines collect more snow than surrounding forest because tree cover does not interrupt snowfall; deep snow cover consequently may influence the potential mobility benefits conferred by seismic lines. Discrepancies in results from James (1999) may be due to varying availability of linear corridors and natural corridors (such as rivers), or behavioural differences in wolf response to corridors. During the rendezvous season, wolves selected areas closer to seismic lines than available. When I examined this pattern further, it was the closest distance-category that was driving the trend (Figure 2-11). Wolves used areas within 50-

m of seismic lines more than random, while areas within 100-m and 200-m were used less than expected based on their availability. It is significant that this pattern was detectable, as 96% of the landscape is within 500-m of a seismic line and 91% is within 300-m. Seismic lines are so readily available that it is more difficult to find areas not close to a line, though elevated levels of wolf use compared to very high availability corroborates the importance of seismic lines during the rendezvous season. Distance-to-seismic was not selected as a significant variable during the denning period; however the influence of den site proximity to seismic lines and historic trails near den sites may have affected this result.

During the nomadic and denning season, wolves exhibited a very strong negative response to human facilities. Facilities included gas processing plants, batteries, compressor stations, gathering systems, and meter stations; all of which generally have noise-producing machinery and higher levels of human activity. A cut-off of approximately 6-km from facilities was apparent. Relatively few facilities exist and most are recent developments, but as oil and gas development spreads farther into caribou range facilities will become more common. Although wolves avoided areas near facilities, in other regions in the world wolves are tolerant of humans and infrastructure (*e.g.* Ciucci *et al.* 1997).

5.2 Other influential variables

Wetness was an influential variable in all wolf models. Dry and wet habitats were selected in comparison to the reference category (mesic) year-round. Dry habitats were selected more strongly than wet habitats, although during the winter season the coefficient values were similar (presumably because the effect of wet habitats is negated by frozen ground). Roads, major pipelines, lakes, and river shorelines were classified as dry areas. A curiosity in the RSF maps is the localised predicted high selection of lakes north of the Little Smoky River during the denning period (Figure 2-13). Although wolves did use these lake areas during the denning season, misclassification in the wetness variable likely influenced this result (lakes were classified as dry because of dry shorelines and their ability to exist as large, frozen openings for most of the year). Wet areas (including areas immediately adjacent to these lakes) also had a positive selection coefficient.

5.3 Ungulate biomass index

Ungulate biomass models were not influential in describing habitat selection by wolves. Ungulate-wolf relationships are much more complex than simplistic relative biomass estimations, such as those I developed. Factors such as weather conditions (Mech *et al.* 1971, 2001; Peterson 1977, Nelson and Mech 1986), ungulate vigilance and anti-predator tactics (Ims 1990, Nelson and Mech 1993, Schaefer 2000, Laundré *et al.* 2001, Hebblewhite and Pletscher 2002), preference among packs for prey types (Mech 1970, Fritts and Mech 1981, Carbyn 1983), varying capture success with prey density and vulnerability (Haber 1977, Nelson and Mech 1993), or individual prey health (Mech *et al.* 1998, Mech *et al.* 2001) were not considered, nor could they be accounted for in pellet transect surveys. I was also unable to quantify the localised and potentially influential contribution of elk to the biomass measure. These limitations may have contributed to an observed lack of selection of high potential prey areas by wolves.

Evaluating wolf response to ungulate biomass at a local scale may also not be appropriate. In this study, ungulate models were surveyed and interpolated across the study area at a 1-km^2 scale. However, wolves adjust to prey at a territory or pack scale: one-third of the variation in territory size can be explained by prey biomass and, when prey are scarce, boundaries shift or individuals seek opportunities elsewhere (Mech and Boitani 2003). In addition, wolves often hunt by travelling extensively and randomly encountering prey (Kelsall 1957, Peterson *et al.* 1984, Peterson and Ciucci 2003). It is impossible to know whether wolves, at any particular GPS point, are actively seeking out ungulates in predictable locations (Huggard 1993), or if they are using the area for other reasons (such as efficient travel, because of other pack members (den, rendezvous, or kill-site), or territory maintenance).

It is also possible that ungulate models did not predict well because of the transect methodology and AIC modelling technique resulting in an inaccurate index of biomass across the study area. Ungulates are difficult to census and models were not validated with independent data. Available aerial survey data were not suitable for validation due to low spatial overlap with the study area and because they were not conducted in the same year or seasons.

Despite the lack of significance of the modelled ungulate biomass index to resource selection by wolves, it is worth noting that ungulates and wolves responded similarly to several independent variables. In all four ungulate models, higher pellet counts were positively associated with shrub cover (Table 2-9). A greater number of moose pellet groupings were found in younger forest in summer, while wolves also selected younger forest during all seasons. Models for moose and summer caribou/deer counts were negatively associated with black spruce, which was also avoided by wolves. Finally, counts of moose pellets were negatively associated with a higher proportion of pine forest; likewise wolves selected against pine during the denning and rendezvous seasons. Cutlines, cutblocks, and shrubby non-forest areas were heavily used by moose (Table 2-6); these factors were also strong contributors to describing patterns of wolf habitat selection. Bear, coyote, and wolf scats were found in disproportionately high quantities on seismic lines compared to other habitats, suggesting that these features were utilised heavily by predators.

5.4 Variation between packs and individuals

Relatively little variation was explained through inclusion of random effects for packs and individuals in the logistic regression models. Wolves largely responded similarly to habitat metrics, and where variation did exist, it was greatest between packs. Although I noted individual variation in the GPS data (such as varying time-spent at den and rendezvous sites), presumably as a consequence of different social status of wolves in the same pack, statistical measurements of individual variation through mixed models were small. It was nevertheless appropriate to include random-intercepts in logistic regression models, calculate the subject-specific probabilities, and allow for adjusted coefficient values as a consequence of non-independence in the sample. Low levels of variance between packs and individuals, and high Spearman rank scores through *k*-fold cross-validation, suggest that these wolf RSF models could be suitable for application to surrounding areas of similar habitat structure; however, statistical evaluation with independent data would be necessary to determine this.

There were large differences between the two-level estimations using *gllamm* and *xtlogit* (Table 2-11). While *xtlogit* did not have a directional relation to *gllamm*, it produced much different results for each seasonal model. For the denning model, the pack-level variance was more than seven times greater when using xtlogit and during the rendezvous season, variation between packs was 0.027 with *gllamm* and 9.3×10^{-8} with *xtlogit* (Table 2-11). It is not clear why the *xtlogit* results are different to those generated using *gllamm*. The *xtlogit* procedure uses a different type of integration (Gauss-Hermite) and took only several minutes to run, compared to several hundred minutes using *gllamm*. The very quick computation of such large datasets with *xtlogit* is suspicious and the accuracy of the estimates is questionable. This is noteworthy because *xtlogit* is the built-in Stata mixed-model option.

5.5 Wolf habitat selection in caribou range

Within the core caribou areas, there were fewer areas that were predicted to have a high index of wolf use compared to portions within territories (Figure 2-13). The Little Smoky River region, which remains relatively undeveloped and is bordered by white spruce, is predicted to be the most attractive feature for wolves within the caribou range during the rendezvous period. Seismic lines are also predicted to be attractive features during this time, and the ubiquity of these features in caribou range increases the overall probability of use by wolves. In the nomadic period, the model predicts that wolves will frequent large wetland complexes and rugged terrain on the north side of the Little Smoky River; otherwise, wolves are predicted to occur only rarely in the rest of the caribou range. Finally, during the critical caribou calving period and wolf denning, the model predicts that wolves will be positively associated with human infrastructure and wetland complexes in the caribou range.

5.6 Analytical approach and limitations

In several cases, specific variables were important in only certain seasons. Distance to seismic lines was a significant explanatory variable during the rendezvous season, but only density measures appeared in other models. Variables that were measured at multiple scales were occasionally included within a single model at several scales: during the denning season, wolves selected for a greater proportion of cutblocks within a 10-km^2 area, but negatively selected for a greater proportion of cutblocks within a 1-km^2 area. During the rendezvous season, wolves selected positively for greater densities of seismic lines at the 10-km^2 scale, but negatively at the 1-km^2 scale. In addition, percent cover of spruce, at the 30-m and 1-km^2 scale, was a significant explanatory variable in the denning model. The variation in selection or avoidance at different scales indicates that future wolf studies should consider multiple scales when evaluating wolf patterns of habitat use.

A 1:1 ratio (used to available) was adequate for capturing the representative availability of each independent variable throughout the wolf territories (Figures 2-5 to 2-12). However, in some cases, 'available' measured with random points was different from 'available' within the wolf territories, though the match was relatively close and the bias non-directional.

One criticism of resource selection functions is the neglected influence of potentially important resources that are used in proportion to their availability, resulting in coefficient values near zero, indicating neither positive nor negative selection. Consider a territory with 50% lodgepole pine where 50% of wolf locations are found in pine, indicating no selection or avoidance. In this case, lodgepole pine may not enter the model as a significant variable, or have a coefficient value close to zero. In terms of predicting wolf distribution, it is thus difficult to account for highly-used areas that are not "selected" within a RSF model.

However, it is important to note that measures of multiple landscape characteristics within a GIS help offset this problem. Each 30-m pixel is characterised by several variables. Whereas a wolf may use pine in proportion to its availability, it may also use and 'select' additional variables within the pine forest; for example, areas closer to seismic lines or those with a higher proportion of cutblocks. Therefore, the landscape should be considered as a suite of interacting characteristics. Additionally, the scale of resource selection analysis may also not be appropriate for recognition of a very prevalent resource, such as pine or tree-cover. Within territories, wolves may not select pine; however, across a larger geographic extent the importance of tree-cover would likely contribute to explaining variation in used and available with respect to territory placement (*e.g.* Szkorupa 2002).

A related, but outstanding, question is whether measuring selection is adequate to describe wolf habitat use and related ecological parameters. For example, wolves using habitats in proportion to their availability still represent a potential predation risk to prey. Nevertheless, wolf response measured through positive or negative selection provides insight into how wolves may respond to changing landscapes and enables predictions to other areas which can be tested with additional data. Furthermore, measures of resource selection do not provide insight into mechanisms driving wolf habitat selection or use, but RSFs may help to generate new hypotheses.

6. Conclusions

Caribou research across the province has consistently identified the critical influence of human development to caribou persistence (Bradshaw 1994, Dyer 1999, Oberg 2001, Weclaw 2001, Smith 2004, Lessard 2005, Saher 2005), but research presented here is an initial step in establishing insight into the response of a primary predator to multiple human developments. Recognition that wolves selected human developments and young forests in the Little Smoky study area has implications for industrial managers.

Woodland caribou in the Little Smoky and A la Pêche winter range use space and habitat refuges as a primary predator avoidance strategy (Bergerud *et al.* 1984, Bergerud 1988). With current and encroaching industrial development, and selection of human development by wolves, caribou refuge areas are compromised and their anti-predator strategies may no longer be effective. However, an issue that remains unaddressed, despite several calls from the ecological community, is a thorough examination of the multi-predator/prey system that exists throughout caribou ranges in Alberta (*e.g.* James 1999, Kuzyk 2002, Smith 2004). Bear species in particular also respond favourably to young forests and human developments (Wielgus 2002, Nielsen 2005) and have been shown to be significant predators of caribou calves elsewhere (Young and McCabe 1997, Rettie and Messier 1998). Additionally, moose are assumed to be a dominant and driving prey species in west-central Alberta (Lessard 2005). A more thorough examination of these other predators and prey in caribou range in association with process-based or adaptive-management science may further our understanding of management scenarios and also provide a better understanding of the mechanism behind wolf habitat selection.

Table 2-1: **Capture methods, characteristics, and collar fate of collared wolves in west-central Alberta caribou ranges, 2003-2005.**

Wolf ID	Capture Date	Wolf Pack	Collar Type	Sex	Age	Colour	Caribou Herd	Capture Method	Fate (as of 01/01/2006)
W32	16-Mar-03	Simonette	GPS	Male	Adult	Black	LSM	Netgun	Unknown
W33	18-Mar-03	Berland East	GPS	Male	Adult	White	LSM	Netgun	Collar recovered; recollar
W33 - RECAP	18-Oct-03	Berland East	VHF	Male	Adult	White	LSM	Netgun	Collar not recovered; Dead
W34	18-Mar-03	Horse Ck	GPS	Male	Adult	Black	LSM	Netgun	Collar recovered
W35	19-Mar-03	Berland East	GPS	Male	Adult	Gray	LSM	Netgun	Collar recovered
W36	19-Mar-03	Simonette	GPS	Female	Adult	Black	LSM	Netgun	Collar recovered
W37	20-Mar-03	Simonette	GPS	Female	Adult	Gray	LSM	Netgun	Collar recovered; recollared
W37 - RECAP	21-Feb-04	Simonette	GPS	Female	Adult	Gray	LSM	Netgun	Collar recovered
W38	11-Sep-03	Buckbean	VHF	Female	Pup	Gray	LSM	Foothold	Active - dispersed northwest of Cutbank River
W39	11-Sep-03	Buckbean	VHF	Male	Pup	Gray	LSM	Foothold	Active – dispersed northwest of Cutbank River
W40	11-Sep-03	Buckbean	GPS	Male	Pup	Gray	LSM	Foothold	Unknown - likely malfunction
W41	07-Sep-03	Horse Ck	GPS	Female	Pup	Gray	LSM	Foothold	Collar recovered; recollared
W41 – RECAP	14-May-04	Horse Ck	GPS	Female	Yearling	Gray	LSM	Foothold	Collar recovered
W43	18-Feb-04	Muskeg	GPS	Male	Adult	Gray	ALP	Netgun	Collar recovered - dispersed to Cutbank River region
W44	18-Feb-04	Buckbean	GPS	Male	Adult	Gray	LSM	Netgun	Unknown
W45	20-Feb-04	Berland East	GPS	Male	Adult	Cream	LSM	Netgun	Unknown
W46	20-Feb-04	Simonette	GPS	Female	Adult	Black	LSM	Netgun	Collar recovered
W47	21-Feb-04	Simonette	GPS	Male	Adult	Black	LSM	Netgun	Collar recovered
W48	21-Feb-04	Muskeg	GPS	Male	Adult		ALP	Netgun	Collar recovered; Dispersed -hit by car and shot near Leslieville, Alberta
W49	14-May-04	Horse Ck	GPS	Female	Yearling	Gray	LSM	Foothold	Collar recovered
W50	13-May-04	Horse Ck	GPS	Female	Yearling	Gray	LSM	Foothold	Collar recovered
W51	14-May-04	Buckbean	GPS	Female	Adult	White	LSM	Foothold	Collar recovered

Table 2-2: Delineations of ground cover types and linear distance surveyed for ungulate pellet transects situated randomly throughout the Little Smoky study area in west-central Alberta. Surveys were conducted in the summer of 2004.

Categories	Kilometres Surveyed
Cutblock < five years in age	29.95
Cutblock > five years in age	33.22
Seismic line	33.97
Pipeline	29.04
Well site	11.61
Natural non-forest	28.04
Larch dominated (> 60%) stand	31.34
Black spruce dominated (> 60%) stand	35.39
White spruce dominated (> 60%) stand	25.04
Pine dominated (> 60%) stand, < 80 years in age	21.82
Pine dominated (> 60%) stand, 80 to 160 years in age	37.82
Pine dominated (> 60%) stand, >160 years in age	18.45

Table 2-3: Covariates used to develop ungulate biomass index models from pellet transects conducted in the Little Smoky study area of west-central Alberta during summer 2004. All variables were measured from the transect start point in a GIS with a minimum mapping unit of 1-km^2. 'Forest' was used as the reference category (indicator contrast) for comparisons within the 'cover' (grass, bare, shrub) variable.

Variable Code	Description	Type
age	Age of forest stand within 1-km^2	Linear
cover	Coarse ground-cover (forest, grass, no cover, shrub)	Categorical
dtcb	Distance to nearest cutblock	Linear
lt	Proportion larch in 30-m pixel	Linear
lt_1 km^2	Proportion of area within 1-km^2 that is larch	Linear
pipes	Distance to nearest pipeline	Linear
pl	Proportion lodgepole pine in 30-m pixel	Linear
pl_1km^2	Proportion of area within 1-km^2 that is lodgepole pine	Linear
propcb1k	Proportion of 1-km^2 area that is cutblock	Linear
propcb10k	Proportion of 10-km^2 area that is cutblock	Linear
rdsdt	Distance to nearest road	Linear
rivsdt	Distance to nearest river	Linear
sb	Proportion black spruce in 30-m pixel	Linear
sb_1 km^2	Proportion of area within 1-km^2 that is black spruce	Linear
seismic	Distance to nearest seismic line	Linear
sldens1k	Length of linear seismic line within 1-km^2	Linear
sldens10k	Length of linear seismic line within 10-km^2	Linear
sw	Proportion white spruce in 30-m pixel	Linear
sw_1 km^2	Proportion of area within 1-km^2 that is white spruce	Linear
wells	Distance to nearest well site	Linear

Table 2-4: Covariates used to develop wolf habitat selection models; all variables were measured at each used (GPS) and available (random) point within a GIS. Variables were measured at a minimum mapping unit of 30-m. Wolf data were collected from 2003-2005 in the Little Smoky study area.

Variable Code	Description	Type
age	Age of forest stand, where applicable	Linear
aw	Proportion trembling aspen at 30m scale	Linear
bw	Proportion white birch at 30m scale	Linear
conifer	Proportion conifer at 30m scale	Linear
cover	Coarse ground-cover (categories: forest, grass, no cover, shrub)	Categorical
decid	Proportion deciduous at 30m scale	Linear
dendt	Distance to den-site (km)	Linear
dtcb	Distance to nearest cutblock (km)	Linear
facilities	Distance to petroleum infrastructure (*e.g.* compressors) (km)	Linear
lt	Proportion larch at 30m scale	Linear
lt_1 km^2	Proportion of area within 1-km^2 that is larch	Linear
pipes	Distance to nearest pipeline (km)	Linear
pl	Proportion lodgepole pine at 30m scale	Linear
pl_1km^2	Proportion of area within 1-km^2 that is lodgepole pine	Linear
propcb1k	Proportion of 1-km^2 area that is cutblock	Linear
propcb10k	Proportion of 10-km^2 area that is cutblock	Linear
rdsdt	Distance to nearest road (km)	Linear
rivsdt	Distance to nearest river (km)	Linear
sb	Proportion black spruce at 30m scale	Linear
sb_1 km^2	Proportion of area within 1-km^2 that is black spruce	Linear
seismic	Distance to nearest seismic line (km)	Linear
sldens1	Length of linear seismic line within 1-km^2	Linear
sldens10	Length of linear seismic line within 10-km^2	Linear
sw	Proportion white spruce at 30m scale	Linear
sw_1 km^2	Proportion of area within 1-km^2 that is white spruce	Linear
totsumb	Index of ungulate biomass in summer	Linear
totwintb	Index of ungulate biomass in winter	Linear
triwhol	Terrain Ruggedness Index	Linear
wetness	Dry, mesic, or wet (based on AVI)	Categorical
waterdt	Distance to water source (including creeks and lakes) (km)	Linear
wells	Distance to nearest well site	Linear

Table 2-5: Number of GPS points excluded from analysis through non-linear modelling, per wolf per season. The scale criterion refers to the rate at which stopping and moving behaviours were delineated. Only moving points (M) were retained as 'use' points when modelling habitat selection; stopping (S) points were excluded. Wolf data were collected in the Little Smoky study area of west-central Alberta from 2003-2005.

Pack	Wolf ID	Scale Criterion (m/min)	Den		Rendezvous		Nomadic	
			S	M	S	M	S	M
Berland East	w33	4.21	1631	1152	282	217	122	61
Berland East	w35	3.27	227	195	n/a	n/a	215	127
Simonette	w36	5.29	428	289	150	104	51	22
Simonette	w37	4.48	1576	1259	375	26	143	76
Simonette	w3705	4.87	752	586	258	195	272	190
Simonette	w46	5.30	1413	765	801	424	376	179
Simonette	w47	4.86	1375	785	738	329	376	169
Muskeg	w43	5.61	1446	132	544	223	1157	279
Muskeg	w48	5.46	213	43	n/a	n/a	314	210
Horse Creek	w41	6.51	1630	390	1170	628	77	42
Horse Creek	w49	6.09	1595	443	1351	696	203	125
Horse Creek	w50	5.78	1457	487	1229	665	122	174
Buckbean	w51	5.07	1379	453	1086	667	162	98

Table 2-6: Density per lineal km (and count) of pellet groupings and scat for each species and habitat class surveyed. Data were collected during ungulate pellet transect surveys conducted in the Little Smoky study area in the summer of 2004.

Species	Cutblock < 5yrs	Cutblock >5 yrs	Cutline	Pipeline	Well-site	Non-forest	Larch dom.	Pine < 80 yrs	Pine 80-160	Pine > 160	Black spruce dom.	White spruce dom.
Moose	0.63 (19)	9.21 (306)	4.35 (148)	2.89 (84)	6.89 (80)	12.1 (340)	8.39 (263)	9.99 (218)	2.54 (96)	3.57 (66)	6.07 (215)	7.75 (194)
Caribou/ Deer	0.27 (8)	4.99 (166)	1.3 (44)	1.89 (55)	8.1 (94)	0.92 (26)	1.69 (53)	7.83 (171)	3.23 (122)	2.93 (54)	1.86 (66)	3.63 (91)
Elk	0	2.47 (82)	0.79 (27)	0.72 (21)	14.9 (173)	4.03 (113)	1.12 (35)	10.3 (225)	1.82 (69)	6.18 (114)	0.85 (30)	20.0 (501)
Wolf	0	0	5.00 (170)	0.34 (10)	0.34 (4)	0.18 (5)	0	0.92 (20)	0.26 (10)	0.54 (10)	0.71 (25)	1.80 (45)
Bear	0	0.90 (30)	5.12 (174)	2.27 (66)	0.86 (10)	0	0	0	0.63 (24)	1.30 (24)	0	1.44 (36)
Coyote	0	0	3.29 (112)	0.72 (21)	0.08 (1)	0	0.45 (14)	1.60 (35)	0.19 (7)	0.76 (14)	0	0
Small Carnivore	0	0	1.41 (48)	0.55 (16)	0	0	0	0	0	0	0.23 (8)	0.64 (16)
Unknown ungulate	0	1.62 (54)	1.59 (54)	1.86 (54)	0.60 (7)	2.25 (63)	3.73 (117)	22.7 (495)	3.09 (117)	2.93 (54)	2.29 (81)	3.60 (90)

Table 2-7: Candidate model sets for each species-season combination of ungulate biomass index models derived from pellet transect surveys. Surveys were conducted in the Little Smoky study area of west-central Alberta during summer 2004. Counts of elk and unidentified ungulates were not included in the analyses. See Table 2-2 for covariate codes.

MOOSE MODELS FOR SUMMER		
1	Global	age cover dtcb lt sb sw pipes pl propcb1k rdsdt rivsdt seismic sldens1k wells
2	Coarse Habitat	lt_1km^2 pl_1km^2 sb_1km^2 sw_1km^2 prpcb10k rivsdt slden10k
3	Shrub/Forage	age cover propcb1k rivsdt rdsdt dtcb wells
4	Summer	cover pl age rdsdt seismic
5	Cover Local	cover dtcb sb pl sw lt propcb1k
6	Cover Area	lt_1km^2 pl_1km^2 sb_1km^2 sw_1km^2 prpcb10k
7	Moose Biology	age cover dtcb pl_1km^2 sb_1km^2 rdsdt wells
8	Human	dtcb pipes propcb1k rdsdt slden1k seismic wells

DEER/CARIBOU MODELS FOR SUMMER		
1	Global	age cover dtcb lt_1km^2 pl_1km^2 sb_1km^2 sw_1km^2 pipes propcb1k rdsdt rivsdt seismic sldens1k wells
2	Coarse habitat	lt_1km^2 pl_1km^2 sb_1km^2 sw_1km^2 propcb10k rivsdt sldens10k
3	Forest	age dtcb lt_1km^2 pl_1km^2 sb_1km^2 sw_1km^2 propcb1km
4	Edges	dtcb pipes propcb1k rivsdt seismic sldens1k wells
5	Deer cover	age cover lt_1km^2 pl_1km^2
6	Local	cover lt pl sb sw
7	Edge + Cover	age cover dtcb pipes pl_1km^2 wells
8	Access	dtcb pipes propcb1k rdsdt seismic sldens1k wells
9	Access + Cover	cover dtcb lt_1km^2 pl_1km^2 rdsdt rivsdt sldens1k

MOOSE MODELS FOR WINTER		
1	Global	age cover dtcb lt_1km^2 pl_1km^2 sb_1km^2 sw_1km^2 pipes propcb1k rdsdt rivsdt seismic sldens1k
2	Coarse habitat	lt_1km^2 pl_1km^2 sb_1km^2 sw_1km^2 propcb10k rivsdt sldens10k
3	Shrub/Forage	age cover dtcb propcb1k rdsdt rivsdt wells
4	Winter	age cover dtcb pl_1km^2 sb_1km^2
5	Cover Local	cover dtcb lt pl sb sw propcb1k
6	Cover Area	lt_1km^2 pl_1km^2 sb_1km^2 sw_1km^2 propcb10k
7	Moose Biology	age cover pl_1km^2 sb_1km^2 propcb1k rdsdt wells
8	Human	dtcb pipes propcb1k rdsdt seismic sldens1k wells

DEER/CARIBOU MODELS FOR WINTER

1	Global	age cover dtcb lt_1km^2 pl_1km^2 sb_1km^2 sw_1km^2 pipes propcb1k rdsdt rivsdt seismic sldens1k wells
2	Coarse habitat	lt_1km^2 pl_1km^2 sb_1km^2 sw_1km^2 propcb10k rivsdt sldens10k
3	Forest	age dtcb lt_1km^2 pl_1km^2 sb_1km^2 sw_1km^2 propcb1km
4	Edges	dtcb pipes propcb1k rivsdt seismic sldens1k wells
5	Deer cover	age cover lt_1km^2 pl_1km^2 rivsdt
6	Local	cover lt pl sb sw
7	Edge + Cover	age cover dtcb pipes pl_1km^2 wells
8	Access	dtcb pipes propcb1k rdsdt seismic sldens1k wells
9	Access + Cover	cover dtcb lt_1km^2 pl_1km^2 rdsdt rivsdt sldens1k

Table 2-8: Ungulate candidate model weights, AIC_c values, and model selection outcomes for the Little Smoky study area in west-central Alberta in 2003-2004. Top models are shaded. Top models did not meet weight criteria of >0.9, thus all coefficients and standard errors were averaged to produce an adjusted model for each season.

MOOSE SUMMER	-LL*-1	K	AIC_c	ΔAIC_c	W_i	Model Order
Global	295.99	18	635.34	12.69	0.0012	5
Coarse Habitat	316.68	8	650.76	28.11	0.0000	8
Shrub/Forage	299.96	11	624.56	1.91	0.2733	2
Summer	305.64	9	631.04	8.40	0.0107	3
Cover Local	304.10	11	632.84	10.19	0.0044	4
Cover Area	317.11	6	647.02	24.37	0.0000	7
Moose Biology	299.00	11	622.65	0	0.7103	1
Human	314.97	8	647.33	24.68	0.0000	6
DEER-CARI SUMMER	-LL*-1	K	AIC_c	ΔAIC_c	W_i	Model Order
Global	266.84	18	577.03	10.54	0.0044	5
Coarse Habitat	276.90	8	571.20	4.71	0.0820	2
Forest	281.35	8	580.09	13.60	0.0010	7
Edges	281.70	8	580.80	14.31	0.0007	8
Deer Cover	277.73	8	572.86	6.36	0.0358	3
Local	278.56	9	576.88	10.39	0.0048	3
Edge + Cover	277.12	10	576.42	9.92	0.0060	4
Access	280.50	8	578.39	11.90	0.0022	7
Access + Cover	270.93	11	566.49	0.00	0.8631	1
MOOSE WINTER	-LL*-1	K	AIC_c	ΔAIC_c	W_i	Model Order
Global	345.74	18	734.84	7.78	0.0141	5
Coarse Habitat	374.16	8	765.72	38.67	0.0000	7
Shrub/Forage	353.26	11	731.16	4.11	0.0888	4
Winter	355.74	9	731.25	4.19	0.0850	3
Cover Local	352.96	11	730.56	3.51	0.1197	2
Cover Area	374.81	6	762.43	35.37	0.0000	6
Moose Biology	351.21	11	727.05	0.00	0.6924	1
Human	374.92	8	767.23	40.18	0.0000	8
DEER-CARI WINTER	-LL*-1	K	AIC_c	ΔAIC_c	W_i	Model Order
Global	232.72	18	508.80	13.97	0.0006	5
Coarse Habitat	245.25	8	507.90	13.07	0.0009	6
Forest	249.54	8	516.47	21.64	0.0000	9
Edges	246.45	8	510.30	15.47	0.0003	7
Deer Cover	237.53	9	494.83	0.00	0.6247	1
Local	239.51	9	498.79	3.96	0.0862	4
Edge + Cover	238.03	10	498.23	3.40	0.1140	3
Access	248.35	8	514.09	19.27	0.0000	8
Access + Cover	236.38	11	497.39	2.56	0.1734	2

Table 2-9: Averaged coefficient values and standard errors for the top ungulate models (all coefficients within each candidate set were averaged). Top averaged models were used to predict species-season counts of ungulates and were then interpolated into spatial ungulate biomass models. Data were collected across the Little Smoky study area in west-central Alberta during summer 2004. 'Forest' was used as the reference category (indicator contrast) for comparisons within the 'cover' (grass, bare, shrub) variable.

Variable Code	Moose Summer		Moose Winter		Deer-Caribou Summer		Deer-Caribou Winter	
	Coef.	S.E.	Coef.	S.E.	Coef.	S.E.	Coef.	S.E.
Pl_1km^2	-0.011	0.002	-0.078	0.002	0.070	0.003	0.040	0.002
Sb_1km^2	-0.085	7.25E-4	-0.010	0.003	-0.194	0.009	–	–
Cover (grass category)	-0.158	0.342	0.064	0.050	-0.180	0.115	0.743	0.142
Cover (bare ground category)	-1.496	0.502	-1.615	0.115	-1.110	0.249	-2.737	0.728
Cover (shrub category)	1.113	0.243	1.163	0.043	0.737	0.102	1.042	0.146
Age	-0.002	6.50E-6	3.52E-4	4.62E-6	–	–	-0.002	8.52E-6
Wells	0.248	7.50E-6	0.192	5.95E-6	–	–	–	–
Dtcb	0.087	1.80E-6	–	–	0.161	4.04E-6	–	–
Lt	–	–	0.087	0.002	–	–	–	–
Rdsdt	1.73	6.00E-10	0.018	3.63E-6	-0.202	5.15E-12	–	–
Prpocb	–	–	-0.298	0.306	–	–	–	–
Lt_1km^2	–	–	–	–	–	–	-0.171	0.011
Rivsdt	–	–	–	–	0.096	6.17E-6	0.0741	2.29E-6
Pipes	–	–	–	–	–	–	–	–
Sldens1k	–	–	–	–	-0.219	3.81E-10	–	–

Table 2-10: Explanatory variables included in stepwise regression variable selection for seasonal wolf models used to model wolf habitat selection across the Little Smoky study area in Alberta. GPS data were collected from 2003-2005.

Variable	Description	Den	Rendezvous	Nomadic
age	Age of forest stand, where applicable	$p < 0.000$	$p < 0.000$	$p < 0.000$
aw	Proportion trembling aspen at 30m scale	Dropped	Dropped	Dropped
bw	Proportion white birch at 30m scale	Dropped	Dropped	Dropped
conifer	Proportion conifer at 30m scale	Dropped	Dropped	Dropped
cover	Coarse ground-cover (forest, grass, no cover, shrub)	$p < 0.000$	$p = 0.008$	$p = 0.019$
decid	Proportion deciduous at 30m scale	Dropped	Dropped	$p < 0.000$
dendt	Distance to den-site	$p < 0.000$	$p < 0.000$	$p < 0.000$
dtcb	Distance to nearest cutblock	Dropped	Dropped	$p = 0.039$
facilities	Distance to petroleum infrastructure (*e.g.* compressors, batteries)	$p < 0.000$	Dropped	$p = 0.041$
lt	Proportion larch at 30m scale	Dropped	Dropped	Dropped
lt_1 km^2	Proportion of area within 1-km^2 that is larch	$p < 0.000$	Dropped	Dropped
pipes	Distance to nearest pipeline	$p < 0.000$	$p = 0.010$	Dropped
pl	Proportion lodgepole pine at 30m scale	Dropped	Dropped	Dropped
pl_1km^2	Proportion of area within 1-km^2 that is lodgepole pine	$p < 0.000$	$p < 0.000$	Dropped
propcb1k	Proportion of 1-km^2 area that is cutblock	$p < 0.000$	Dropped	Dropped
propcb10k	Proportion of 10-km^2 area that is cutblock	$p < 0.000$	Dropped	$p < 0.000$
rdsdt	Distance to nearest road	Dropped	Dropped	$p = 0.012$
rivsdt	Distance to nearest river	Dropped	Dropped	$p < 0.000$
sb	Proportion black spruce at 30m scale	Dropped	Dropped	Dropped
sb_1 km^2	Proportion of area within 1-km^2 that is black spruce	$p < 0.000$	$p = 0.002$	$p < 0.000$
seismic	Distance to nearest seismic line	Dropped	$p < 0.000$	Dropped
sldens1	Length of linear seismic line within 1-km^2	$p = 0.004$	$p < 0.000$	Dropped
sldens10	Length of linear seismic line within 10-km^2	$p < 0.000$	$p < 0.000$	Dropped
sw	Proportion white spruce at 30m scale	$p < 0.000$	$p < 0.000$	$p < 0.000$
sw_1 km^2	Proportion of area within 1-km^2 that is white spruce	$p < 0.000$	Dropped	Dropped
totsumb	Index of ungulate biomass in summer	$p < 0.000$	Dropped	Dropped
totwintb	Index of ungulate biomass in winter	n/a	$p = 0.002$	Dropped
triwhol	Terrain Ruggedness Index	$p < 0.000$	$p = 0.010$	Dropped
wetness	Dry, Mesic, or Wet (based on AVI)	$p = 0.004$	$p < 0.000$	Dropped
waterdt	Distance to any water source, including small creeks and lakes	$p < 0.000$	$p < 0.000$	$p < 0.000$
wells	Distance to nearest well site	$p < 0.000$	$p < 0.000$	Dropped

Table 2-11: Random effect variance and covariance for multi-level generalised linear mixed models estimated by two methods for the (a) denning, (b) rendezvous, and (c) nomadic seasons for wolf collar data collected from the Little Smoky study area in west-central Alberta in 2003-2004. Outputs from *gllamm* models estimated with 12 integration points were used for RSF development. *xtlogit* is the built-in STATA logistic GLMM standard, while *gllamm* is a user-developed program.

a)

Model	***gllamm*** 8 Integration Points (2 Level)	***gllamm*** 12 Integration Points (3 Level)	***xtlogit*** 8 Integration Points (2 Level)
Levels	Level 1: 13374 Level 2: 6 (pack)	Level 1: 13374 Level 2: 13 (wolf) Level 3: 6 (pack)	Level 1: 13374 Level 2: 6 (pack)
Variance	Level 2: 0.0765	Level 2: 0.0477 Level 3: 0.0906	Level 2: 0.584
Covariance	Level 2: 0.0309	Level 2: 0.0238 Level 3: 0.0460	Level 2: 0.0711
Time Conv.	91 minutes	2780 minutes	< 5 minutes

b)

Model	***gllamm*** 8 Integration Points (2 Level)	***gllamm*** 12 Integration Points (3 Level)	***xtlogit*** 8 Integration Points (2 Level)
Levels	Level 1: 8756 Level 2: 6 (pack)	Level 1: 8756 Level 2: 11 (wolf) Level 3: 6 (pack)	Level 1: 8756 Level 2: 6 (pack
Variance	Level 2: 0.0271	Level 2: 0.0044 Level 3: 0.0077	Level 2: 9.31 E-8
Covariance	Level 2: 0.021	Level 2: 0.0065 Level 3: 0.018	Level 2: 0.00009
Time Conv.	196 minutes	408 minutes	< 5 minutes

c)

Model	***gllamm*** 8 Integration Points (2 Level)	***gllamm*** 12 Integration Points (3 Level)	***xtlogit*** 8 Integration Points (2 Level)
Levels	Level 1: 3241 Level 2: 6 (pack)	Level 1: 3241 Level 2: 13 (wolf) Level 3: 6 (pack)	Level 1: 3241 Level 2: 6 (pack)
Variance	Level 2: 0.0019	Level 2: 1.03 E-12 Level 3: 0.0019	Level 2: 0.00056
Covariance	Level 2: 0.0095	Level 2: 3.21 E-7 Level 3: 0.0095	Level 2: 0.0029
Time Conv.	32 minutes	144 minutes	< 5 minutes

Figure 2-1: Study area in west-central Alberta where wolf habitat selection was examined. Four forest management agreement holders are present in the area in addition to substantial oil and gas activity.

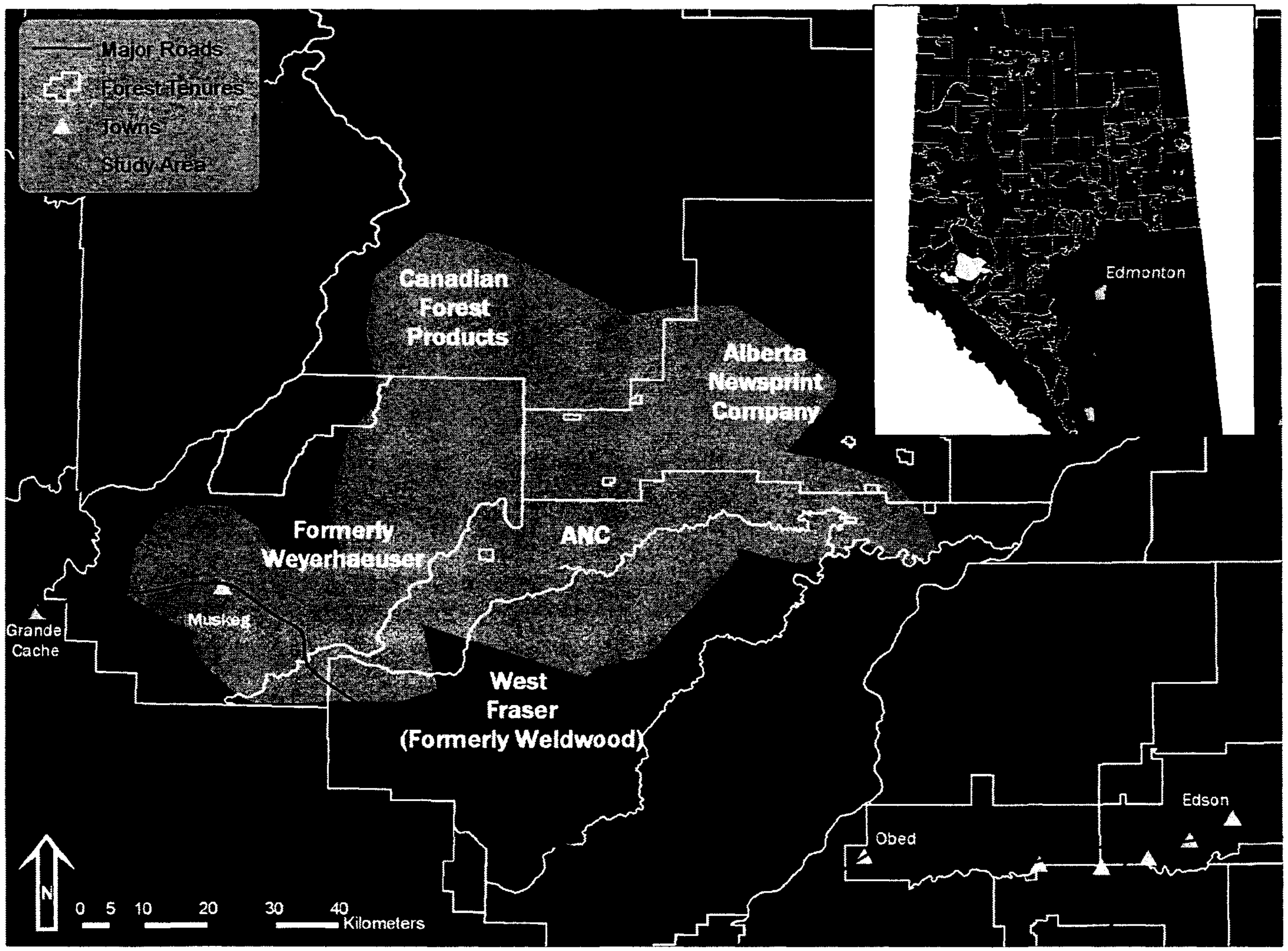


Figure 2-2: Delineation of study area in west-central Alberta into wolf pack territories and caribou ranges. Wolves were collared in the region from March 2003 to October 2005. Caribou monitoring has been ongoing since the 1980s with varying degrees of intensity.

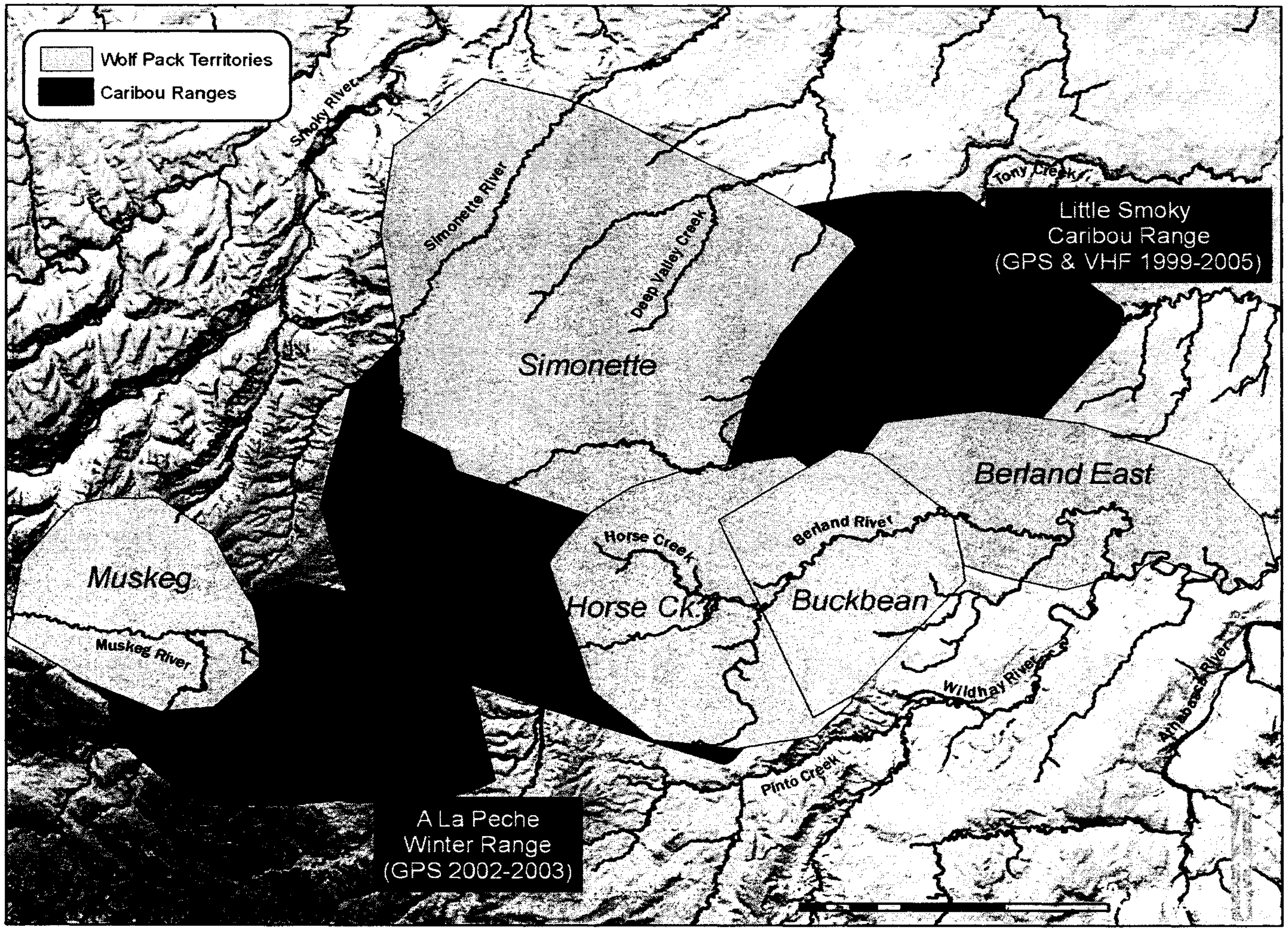


Figure 2-3: Example of transect study design. Random polygons of each landscape type were selected, start points were chosen, and transect paths identified. Two surveyors commenced transect at the centre point (denoted by UTM values) and each recorded pellet groupings within a 1.5-m diameter along the 1.5-km triangle. Three replicates of each habitat type were surveyed within four sections of the study area (335.7-km total surveyed transect length). Surveys were conducted in the Little Smoky study area in west-central Alberta.

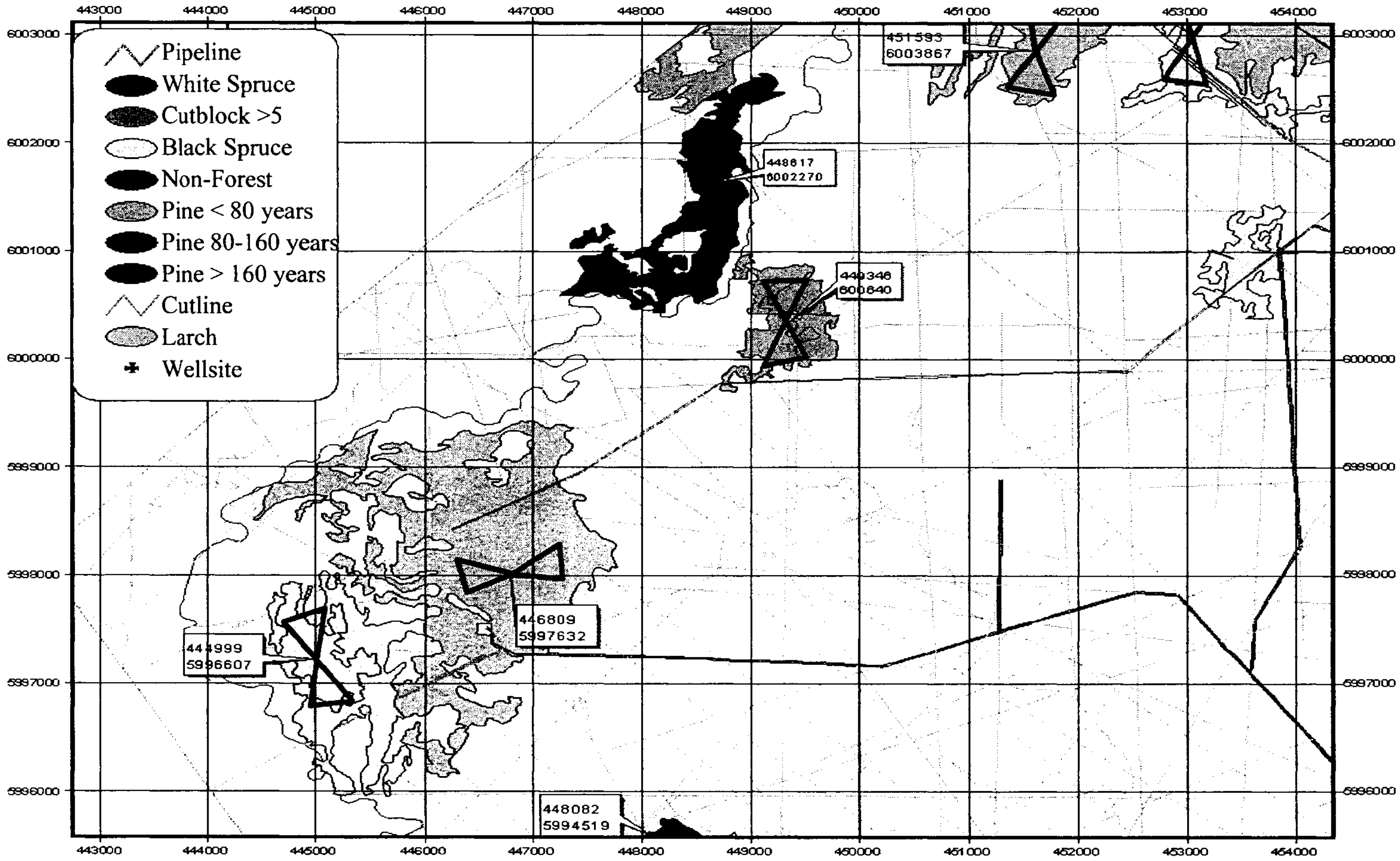


Figure 2-4: Predicted biomass index based on models developed from ungulate pellet transect surveys conducted across the Little Smoky study area in west-central Alberta. Surveys were done in the summer of 2004.

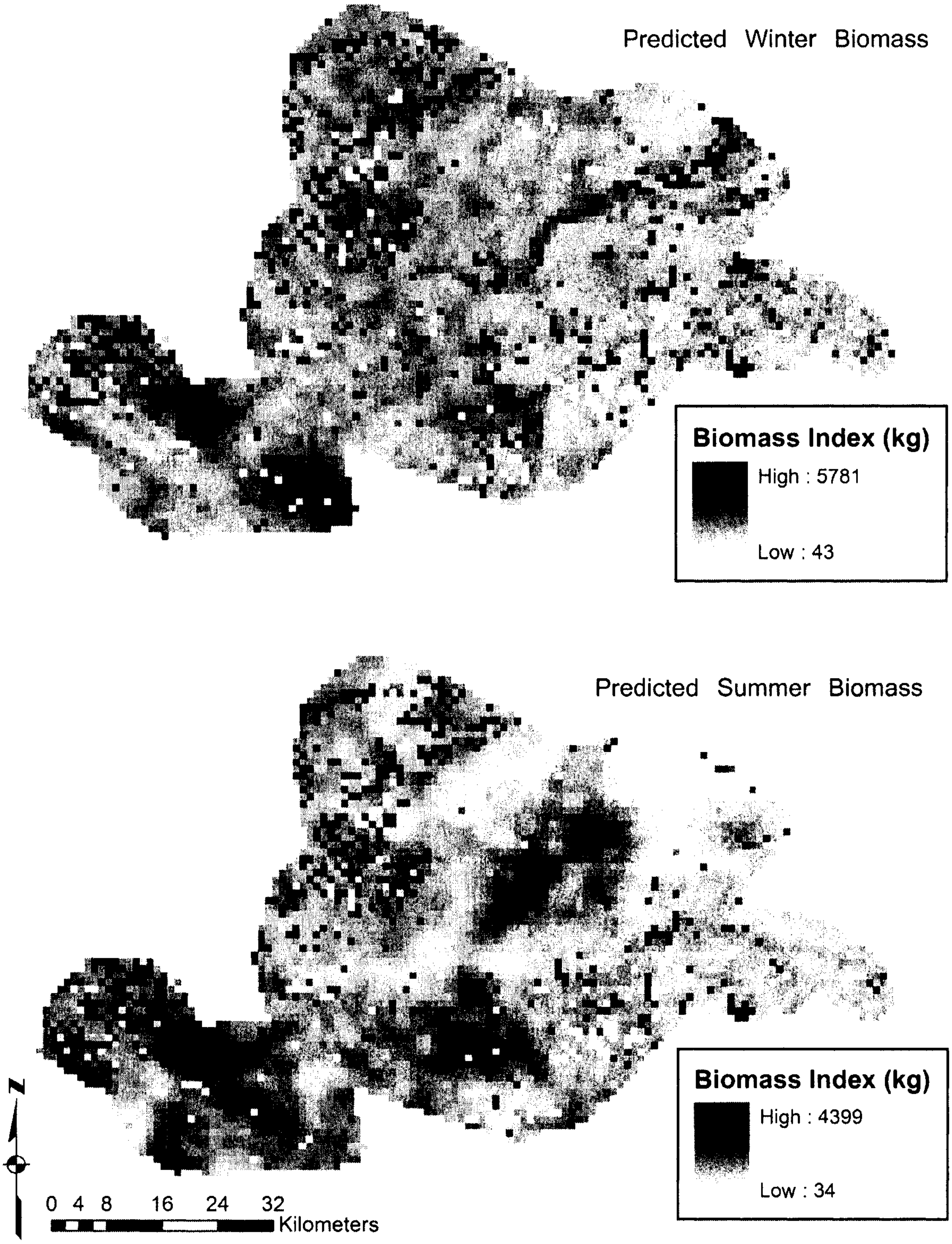


Figure 2-5: Proportions used and available measured during 2003-2005 for wolf response to proportion cutblock across the Little Smoky study area in west-central Alberta. Results are for two different scales a) 10-km2; and b) 1-km2 in the denning model. Two measures of availability are shown for comparison: "random points" quantified available for RSF models and "territories" is a measure of what was wholly available.

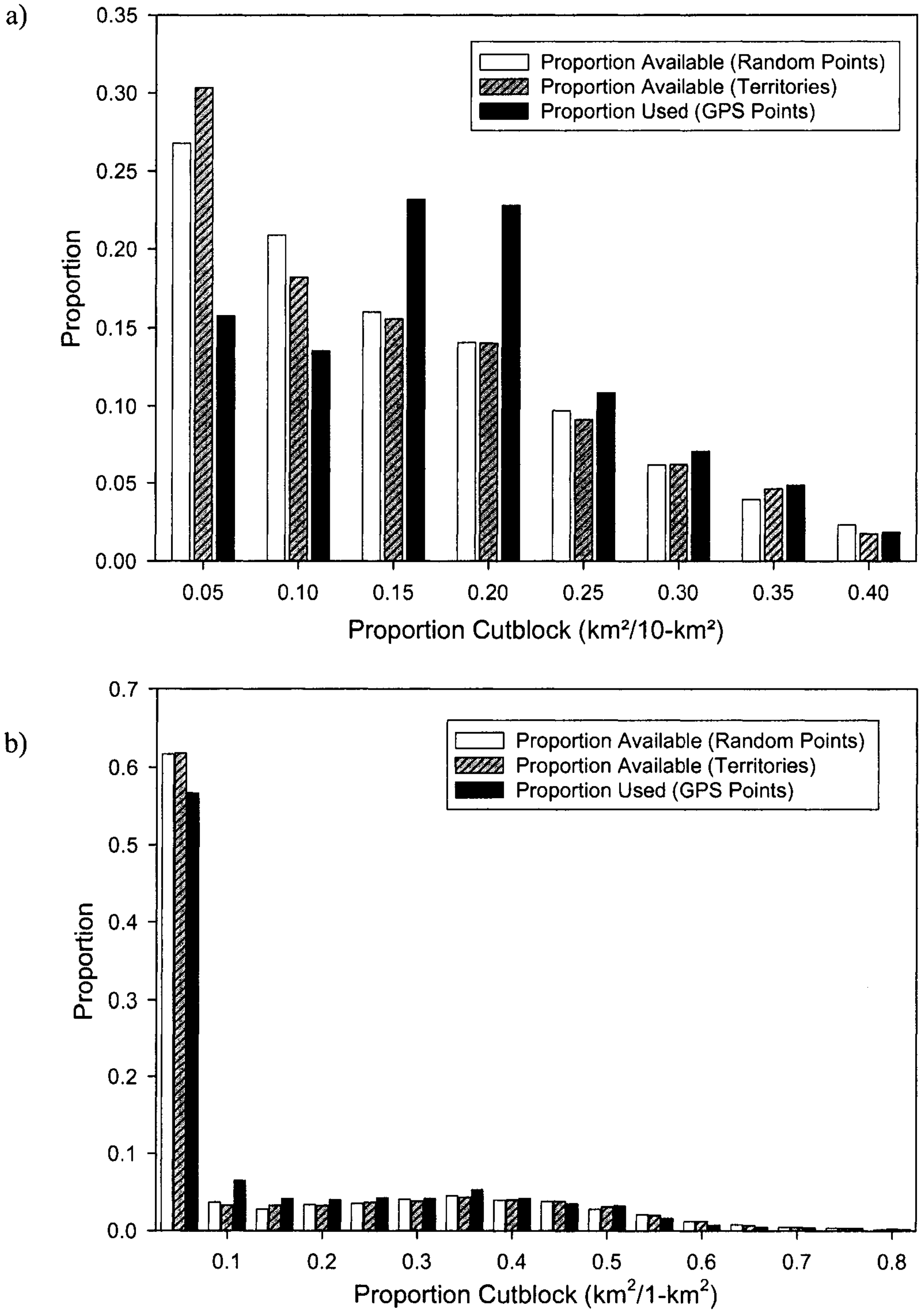


Figure 2-6: Proportions used and available measured during 2003-2005 for wolf response to terrain ruggedness across the Little Smoky study area in west-central Alberta during the denning season. Two measures of availability are shown for comparison: "random points" quantified available for RSF models and "territories" is a measure of what was wholly available.

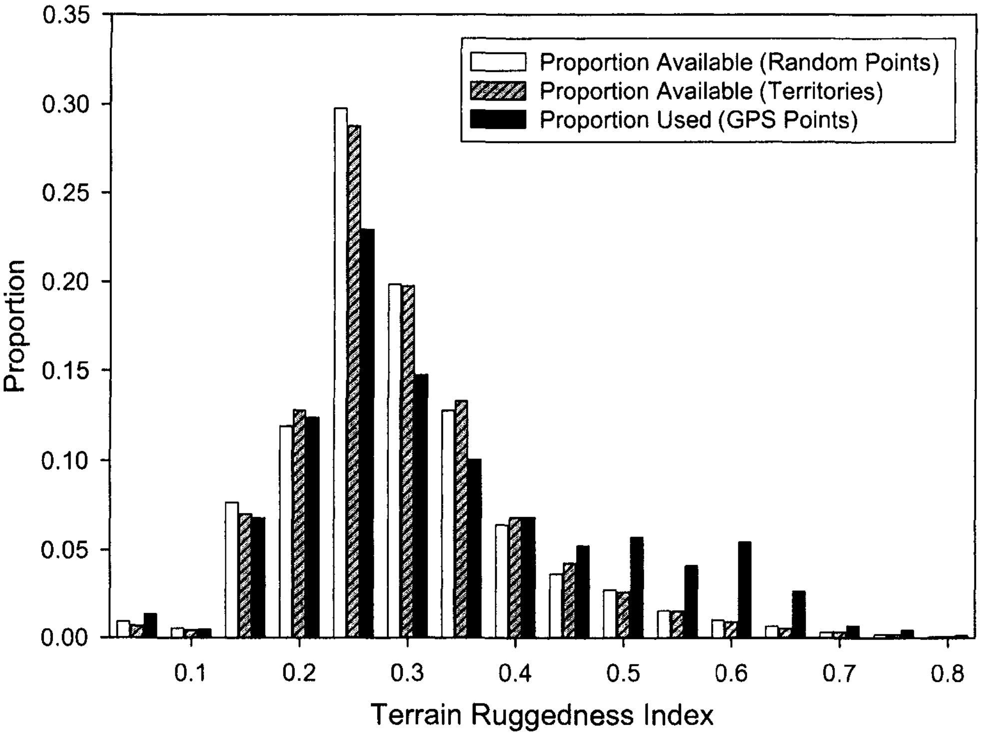


Figure 2-7: Proportions used and available measured during 2003-2005 for wolf response to facilities across the Little Smoky study area in west-central Alberta during the denning season. Two measures of availability are shown for comparison: "random points" quantified available for RSF models and "territories" is a measure of what was wholly available.

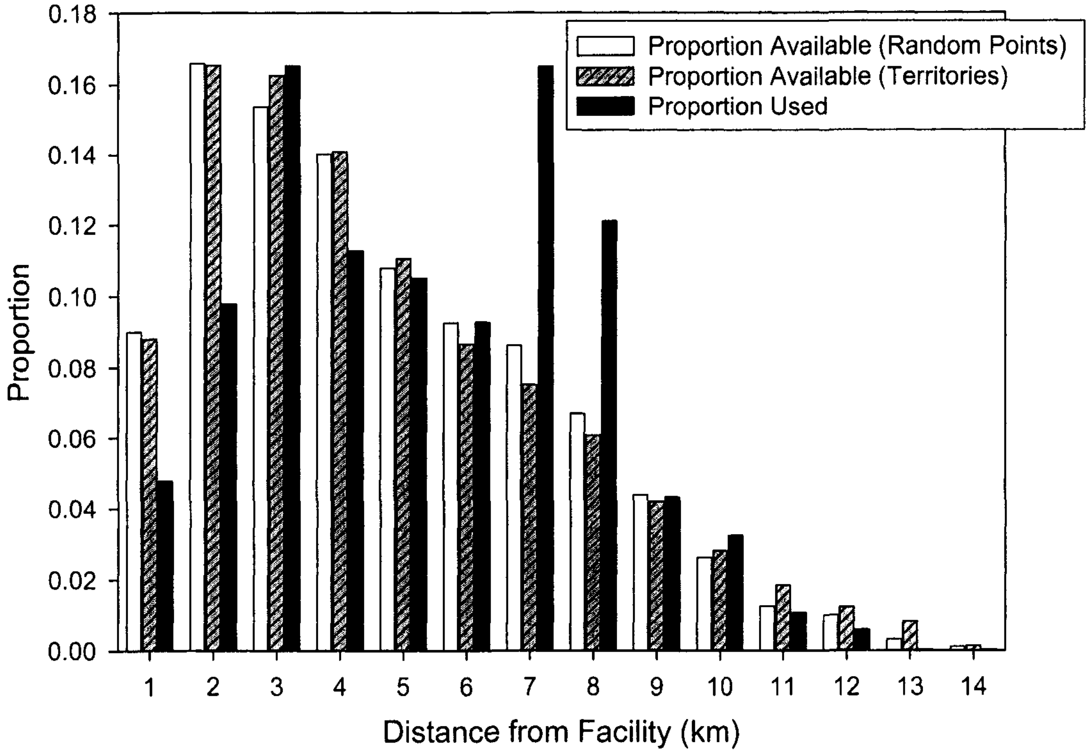


Figure 2-8: Proportions used and available measured during 2003-2005 for wolf response to density of seismic lines within a 10-km^2 area across the Little Smoky study area in west-central Alberta during the denning season.

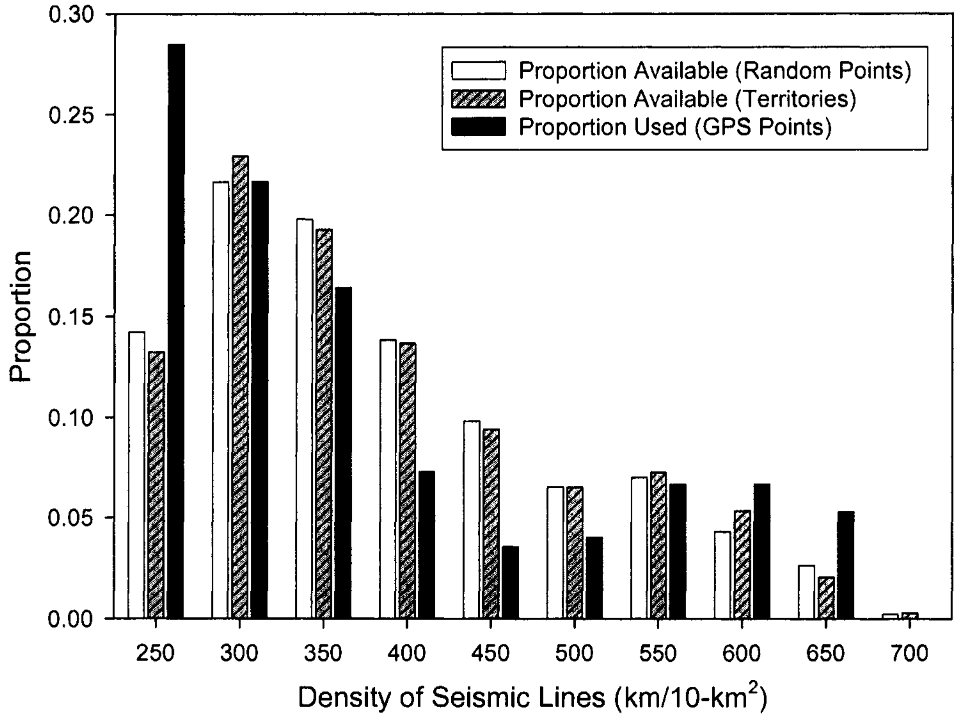


Figure 2-9: Proportions used and available measured during 2003-2005 for wolf response to proximity of seismic line across the Little Smoky study area in west-central Alberta during the rendezvous season.

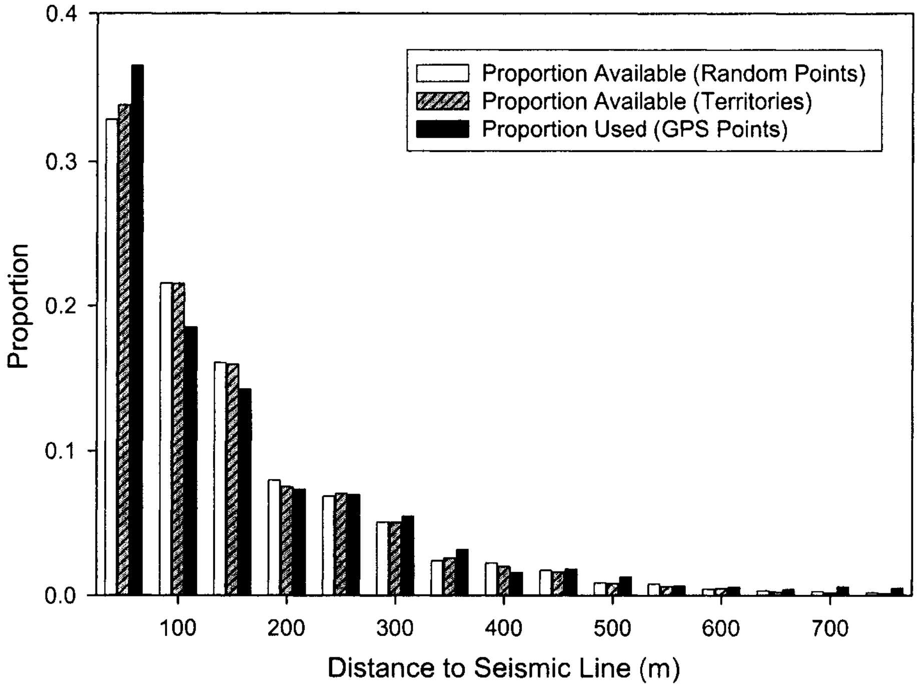


Figure 2-10: Proportions used and available measured during 2003-2005 for wolf response to terrain ruggedness index across the Little Smoky study area in west-central Alberta during the rendezvous season. Two measures of availability are shown for comparison: "random points" quantified available for RSF models and "territories" is a measure of what was wholly available.

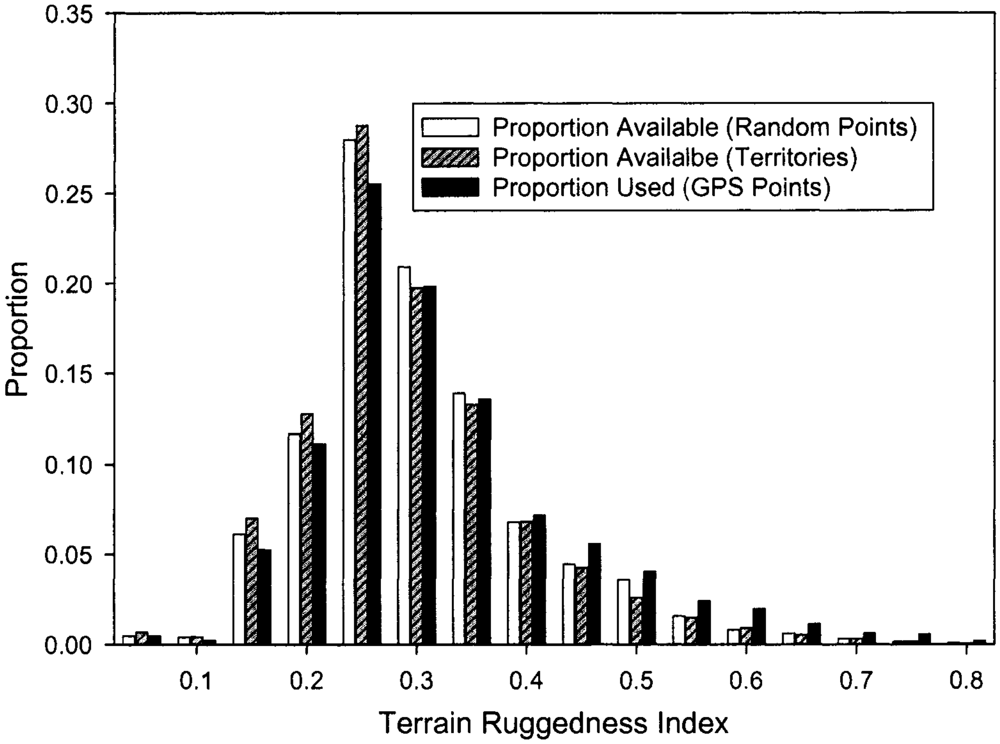


Figure 2-11: Proportions used and available measured during 2003-2005 of: a) proportion cutblock at 10-km2 scale; and b) proportion black spruce across the Little Smoky study area in west-central Alberta. Values are for influential variables in the nomadic model. Two measures of availability are shown for comparison.

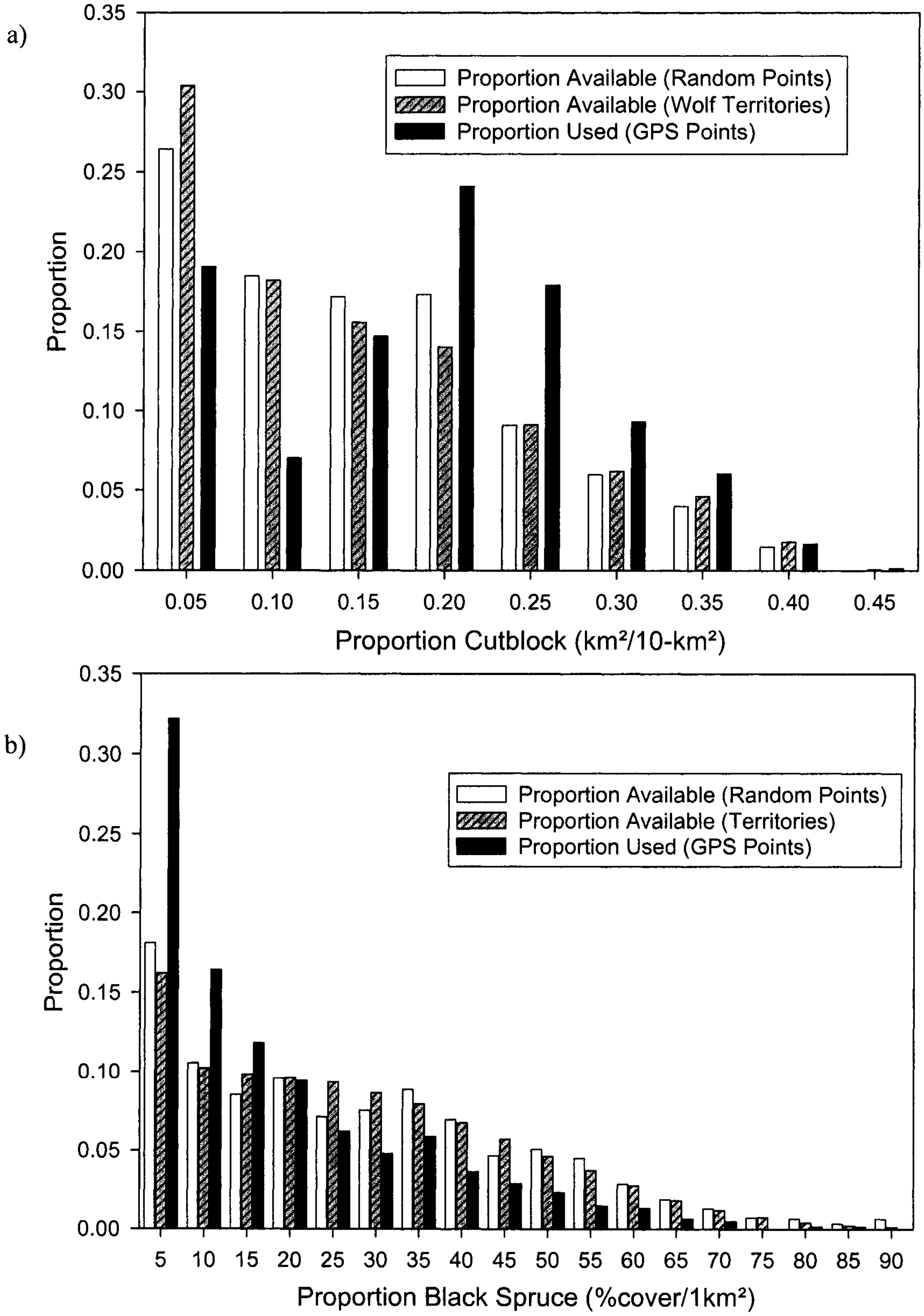


Figure 2-12: Proportions used and available measured during 2003-2005 for: a) distance to cutblock, and b) distance to facility across the Little Smoky study area in west-central Alberta. Results are for small coefficients in the nomadic model. Two measures of availability are shown for comparison.

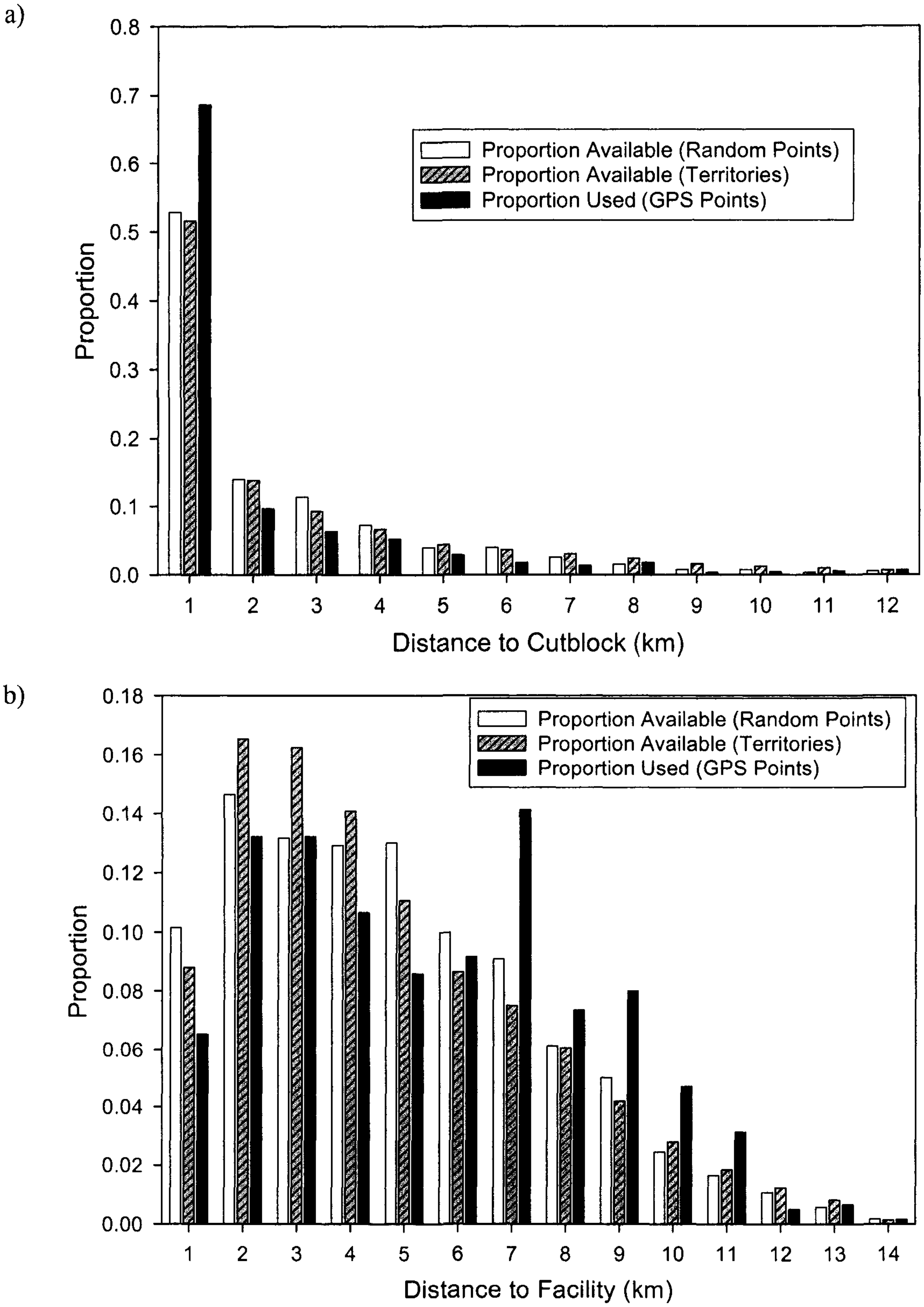


Figure 2-13: Relative index of use modelled for three time periods within the Little Smoky region study area. Dark areas represent higher index of use (relative probability of occurrence). Cutblocks occur primarily in the north and south parts of the study area (refer to Figure 2-14).

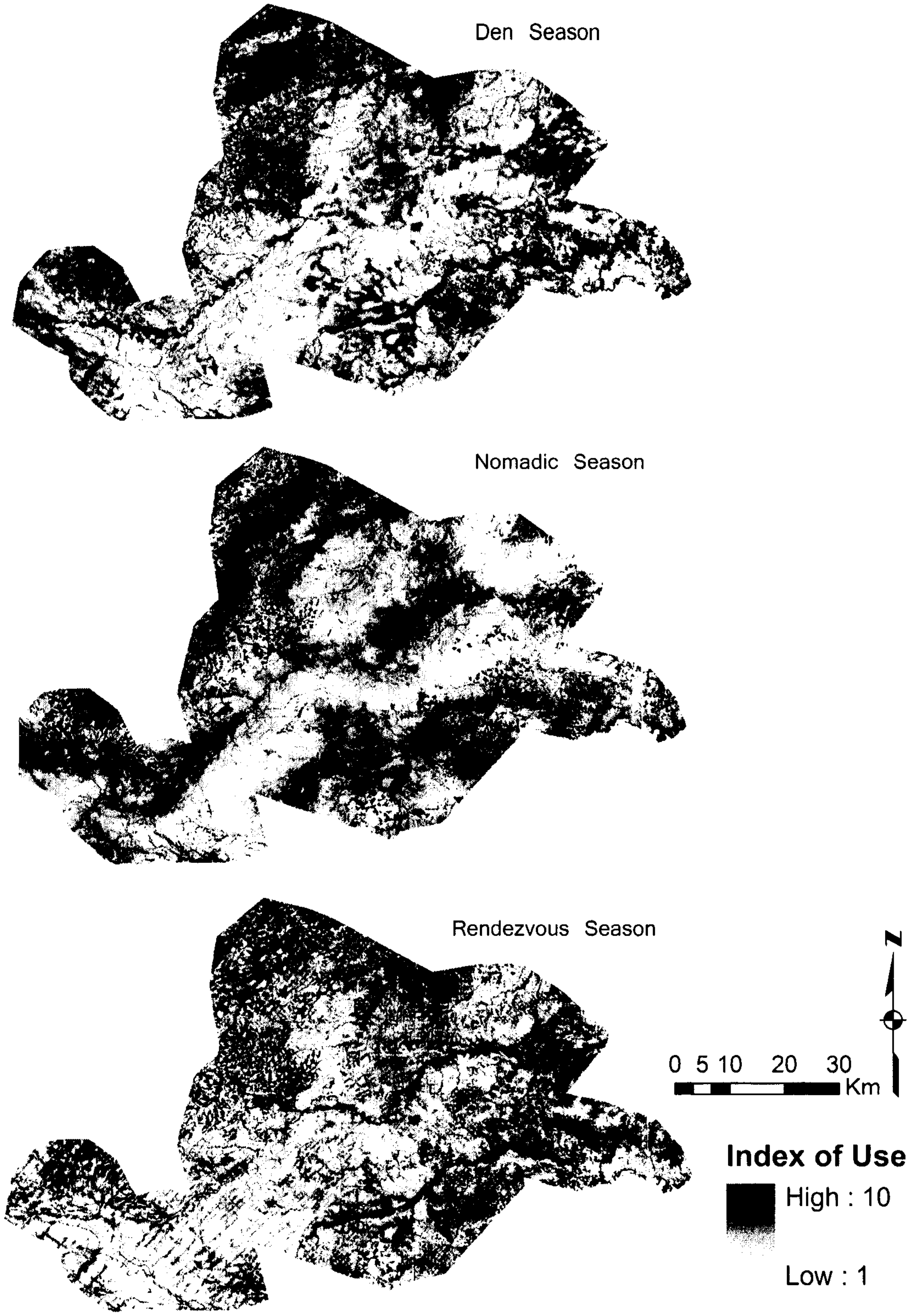
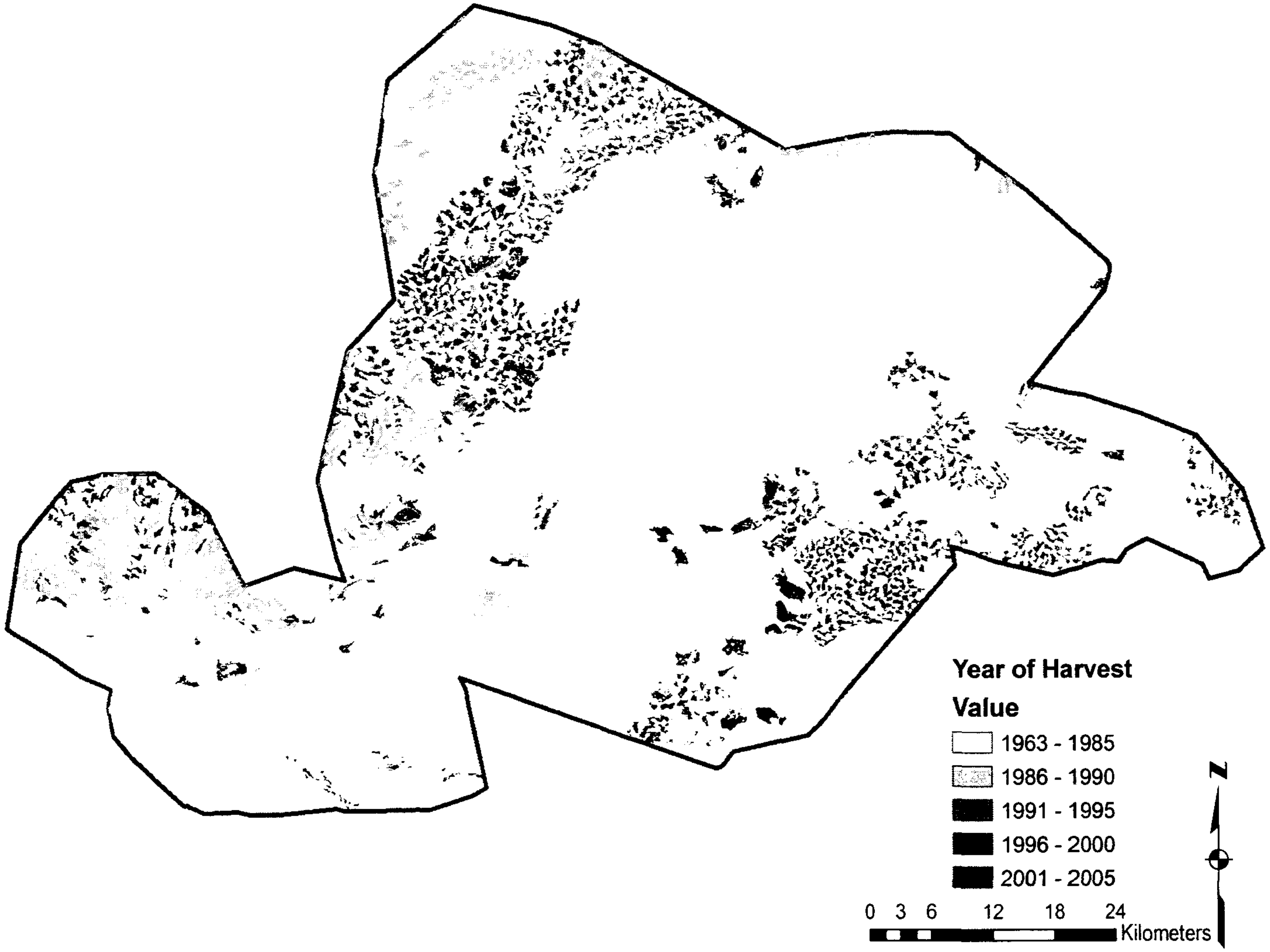


Figure 2-14: Pace of cutblock development across the Little Smoky study area in west-central Alberta from 1963-2005.



7. Literature Cited

Alberta Woodland Caribou Recovery Team. 2005. Alberta woodland caribou recovery plan 2004/05-2013/14. Alberta Sustainable Resource Development, Fish and Wildlife Division, Alberta Species at Risk Recovery Plan No. 4. Edmonton, AB.

Austin, M.P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecological Modelling **157**:101-118.

Beckingham, J.D., and J.H. Archibald. 1996. Field guide to ecosites of northern Alberta. Northern Forestry Centre, Edmonton, AB.

Bergerud, A.T. 1988. Caribou, wolves and man. Trends in Ecology & Evolution **3**:68-72.

Bergerud, A.T. 1996. Evolving perspectives on caribou population dynamics, have we got it right yet? Rangifer **Special Issue No. 9**:95–116.

Bergerud, A.T., and J.P. Elliot. 1998. Wolf predation in a multiple-ungulate system in northern British Columbia. Canadian Journal of Zoology **76**:1551-1569.

Bergerud, A.T., H.E. Butler, and D.R. Miller. 1983. Antipredator tactics of caribou: dispersion in mountains. Canadian Journal Zoology **62**:1566-1575.

Bergerud, A.T., R.D. Jakimchuk, and D.R. Carruthers. 1984. The buffalo of the North: caribou (*Rangifer tarandus*) and human developments. Arctic **37**:7-22.

Beyer, H. 2005. Hawth's Research and Development Tools, an extension for ArcGIS (ArcMap).

Boyce, M.S., P.R. Vernier, S.E. Nielsen, and F.K.A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling **157**:281-300.

Bradshaw, C.J.A. 1994. An assessment of the effects of petroleum exploration on woodland caribou (*Rangifer tarandus caribou*) in northeastern Alberta. M.Sc. Thesis, University of Alberta, Edmonton, AB.

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.

Breslow, N.E., and D.G. Clayton. 1993. Approximate inference in generalized linear mixed models. Journal of the American Statistical Association **88**:9-25.

Brown, W.K, and D.P. Hobson. 1998. Caribou in west-central Alberta – information review and synthesis. Prepared for The Research Subcommittee of the West-central Alberta Caribou Standing Committee. Terrestrial & Aquatic Environmental Managers Ltd., Calgary, AB.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodal inference: a practical information theoretic approach, 2nd edn. Springer-Verlag, New York, NY.

Carbyn, L.N. 1983. Wolf predation on elk in Riding Mountain National Park, Manitoba. Journal of Wildlife Management **47**:963-976.

Chatterjee, S., A.S. Hadi, and B. Price. 2000. Regression analysis by example. John Wiley and Sons, New York, NY.

Ciucci P., L. Boitani, and F. Francisci, and G. Andreoli. 1997. Home range, activity and movements of a wolf pack in central Italy. Journal of Zoology **243**:803-819.

Ciucci, P., M. Masi, and L. Boitani. 2003. Winter habitat and travel route selection by wolves in the northern Apennines, Italy. Ecography **26**:223-235.

D'Eon R.G., Serrouya R., Smith G., and Kochanny, C.O. GPS radiotelemetry error and bias in mountainous terrain. Wildlife Society Bulletin **30**:430-439.

Dyer, S.J., J.P. O'Neill, S.M. Wasel, and S. Boutin. 2001. Avoidance of industrial development by woodland caribou. Journal of Wildlife Management **65**:531-542.

Dyrness, C.T. 1973. Early stages of plant succession following logging and burning in the western Cascades of Oregon. Ecology **54**:57-69.

Dzus, E. 2001. Status of the woodland caribou (*Rangifer tarandus caribou*) in Alberta. Alberta Environment, Fisheries and Management Division, and Alberta Conservation Association, Wildlife Status Report No. 30, Edmonton, AB.

Edmonds, E.J. 1988. Population status, distribution and movements of woodland caribou in west-central Alberta. Canadian Journal of Zoology **66**:817-826.

Fielding, A.H., and J.F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation **24**:38-49.

Franzmann, A.W., and C.C. Schwartz. 1997. Ecology and management of the North American moose. Smithsonian Institute Press, Washington, DC.

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**. The Wildlife Society, Bethesda, MD.

Fuller, T.K., L.D. Mech, and J.F. Cochrane. 2003. Wolf population dynamics. Pages 161-91 *in* L.D. Mech and L. Boitani (eds). Wolves: behavior, ecology, and conservation. Univ. Chicago Press, Chicago, Ill., USA.

Gillies, C.S., M. Hebblewhite, S.E. Nielsen, M.A. Krawchuk, C.L. Aldridge, J.L. Frair, D.J. Saher, C.E. Stevens, and C.L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology, *in press*.

Gustine, D.D. 2005. Plasticity in selection strategies of woodland caribou (*Rangifer tarandus caribou*) during winter and calving. M.Sc. Thesis, University of Northern British Columbia, Prince George, BC.

Haber, G.C. 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. Ph.D. Thesis, University of British Columbia, Vancouver, BC.

Hebblewhite, M., and D.H. Pletscher. 2002. Effects of elk group size on predation by wolves. Canadian Journal of Zoology **80**:800-809.

Hedley S.L., and S.T. Buckland. 2004. Spatial models for line transect sampling. Journal of Agricultural, Biological, and Environmental Statistics **9**:181-199

Hosmer, D.W., and S. Lemeshow. 1999. Applied survival analysis: regression modeling of time to event data. John Wiley & Sons, New York, NY.

Hosmer, D.W., and S. Lemeshow. 2000. Applied logistic regression, 2nd ed. John Wiley & Sons, New York, NY.

Huggard, D.J. 1993. Prey selectivity of wolves in Banff National Park. I. Prey species. Canadian Journal of Zoology **71**:130-139.

Hulbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs **54**:187–211.

Ims, R.A. 1990. The ecology and evolution of reproductive synchrony. Trends in Ecology and Evolution **5**:135-140.

James, A.R.C. 1999. Effects of industrial development on the predator-prey relationship between wolves and caribou in northeastern Alberta. Ph.D. Thesis, University of Alberta, Edmonton, AB.

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

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**:799-809.

Jedrzejewski, W., K. Schmidt, J. Theuerkauf, B. Jedrzejewska, and H. Okarma. 2001. Daily movements and territory use by radio-collared wolves, *Canis lupus*, in Bialowieza Primeval Forest (Poland). Ecology **83**:1341-1356.

Johnson, C.J., K.L. Parker, D.C. Heard, and M.P. Gillingham. 2002. Movement parameters of ungulates and scale-specific responses to the environment. Journal of Animal Ecology **71**:225-235.

Kelsall, J.P. 1957. Continued barren-ground caribou studies. Canadian Wildlife Service, Wildlife Management Bulletin Series **12**.

Kunkel, K.E., and D.H. Pletscher. 2001. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. Canadian Journal of Zoology **78**:150-157.

Kuzyk, G.W., J. Kneteman, and F.K.A. Schmiegelow. 2004. Winter habitat use by wolves, *Canis lupus*, in relation to forest harvesting in west-central Alberta. Canadian Field Naturalist **118**:368-375.

Laundré, J.W., L. Hernández, and K.B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. Canadian Journal of Zoology **79**:1401-1409.

Lessard, R.B. 2005. Conservation of woodland caribou (*Rangifer tarandus caribou*) in west-central Alberta: a simulation analysis of multi-species predator-prey systems. Ph.D. Thesis, University of Alberta, Edmonton, AB.

Manly, B.F.J. 1993. Comments on design and analysis of multiple-choice feeding-preference experiments. Oecologia **93**:149-152.

McLoughlin, P.D., E. Dzus, B. Wynes, and S. Boutin. 2003. Declines in populations of woodland caribou. Journal of Wildlife Management **67**:755-761.

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

Mech, L.D. 1992. Daytime activity of wolves during winter in north-eastern Minnesota. Journal of Mammalogy **73**:570-571.

Mech, L.D., L.G. Adams, T.J. Meier, J.W. Burch, and B.W. Dale. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis, MN.

Mech L.D., and L. Boitani. 2003. Wolf social ecology. Pages 1-34 *in* L.D. Mech and L. Boitani (eds). Wolves: behavior, ecology, and conservation. Univ. Chicago Press, Chicago, Ill., USA.

Mech, L.D., L.D. Frenzel, Jr., and P.D. Karns. 1971. The effect of snow conditions on the ability of wolves to capture deer. Pages 51-59 *in* L.D. Mech and L.D. Frenzel, Jr. (eds). Ecological studies of the timber wolf in Minnesota. USDA Forest Service Research Paper NC-52. North Central Forest Experiment Station, St. Paul, MN.

Mech, L.D., D.W. Smith, L.M. Murphy, and D.R. McNulty. 2001. Winter severity and wolf predation on a formerly wolf-free elk herd. Journal of Wildlife Management **64**:998-1003

Menard, S. 1995. Applied logistic regression analysis. SAGE Publications, Thousand Oaks, CA.

Merrill, S.B. 2000. Road densities and gray wolf, *Canis lupus*, habitat suitability: an exception. Canadian Field Naturalist **30**:312-313.

Mladenoff, D.J., T.A. Sickley, R.G. Haight, and A.P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great-Lakes region. Conservation Biology **9**:279-294.

Nellemann, C., and G. Fry. 1995. Quantitative analysis of terrain ruggedness in reindeer winter grounds. Arctic **48**:172-176.

Nielsen, S.E. 2005. Habitat ecology, conservation, and projected population viability of grizzly bears (*Ursus arctos* L.) in west-central Alberta, Canada. Ph.D. Thesis, University of Alberta, Edmonton, AB.

Nielsen, S.E., M.S. Boyce, G.B. Stenhouse, and R.H.M. Munro. 2002. Modeling grizzly bear habitats in the Yellowhead Ecosystem of Alberta: Taking autocorrelation seriously. Ursus **13**:45-56.

Nelson, M.E., and L.D. Mech. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. Journal of Wildlife Management **50**:471-474.

Nelson, M.E., and L.D. Mech. 1993. Prey escaping wolves, *Canis lupus*, despite close proximity. Canadian Field Naturalist **107**:245-246.

Norris, D.R, M.T. Theberge, and J.B. Theberge. 2002. Forest composition around wolf (*Canis lupus*) dens in eastern Algonquin Provincial Park, Ontario. Canadian Journal of Zoology **80**:866-872.

Oberg, P.R. 2001. Responses of mountain caribou to linear features in a west-central Alberta landscape. M.Sc. Thesis, University of Alberta, Edmonton, AB.

Packard, J.P., and L.D. Mech. 1980. Population regulation in wolves. *In* Bio-social mechanisms of population regulation. Eds. M.N. Cohen, R.S. Malpass, and H.G. Klein. Yale University Press, New York, NY.

Pauley, G.R., J.M. Peek, and P. Zager. 1993. Predicting white-tailed deer habitat use in northern Idaho. Journal Of Wildlife Management **57**:904-913.

Peterson, R.O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. National Park Service Scientific Monograph Series **11**. Washington, DC.

Peterson, R.O., and P. Ciucci. 2003. The wolf as a carnivore. Pages 104-130 *in* L.D. Mech and L. Boitani (eds). Wolves: behavior, ecology, and conservation. Univ. Chicago Press, Chicago, Ill., USA.

Peterson, R.O., R.E. Page, and K.M. Dodge. 1984. Wolves, moose, and the allometry of population cycles. Science **224**:1350-1351.

Piepho, H.P., A. Buchse, and K. Emrich. 2003. A hitchhiker's guide to mixed models for randomized experiments. Journal of Agronomy and Crop Science **189**:310-322.

Rabe-Hesketh, S., A. Skrondal, and A. Pickles. 2004a. Generalized multilevel structural equation modelling. Psychometrika **69**:167-190.

Rabe-Hesketh, S., A. Skrondal, and A. Pickles. 2004b. GLLAMM manual. U.C. Berkeley Division of Biostatistics Working Paper Series. University of California, Berkeley, CA.

Rabe-Hesketh, S. and A. Skrondal. 2005. Multilevel and longitudinal modeling using STATA. STATA Press, College Station, TX.

Rabe-Hesketh, S., A. Skrondal, and A. Pickles. 2002. Reliable estimation of generalised linear mixed models using adaptive quadrature. The STATA Journal **2**:1-21.

Rettie, W.J., and F. Messier. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. Canadian Journal of Zoology **76**:251-259.

Saher, D.J. 2005. Woodland caribou habitat selection during winter and along migratory routes in west-central Alberta, M.Sc. Thesis, University of Alberta, Edmonton, AB.

Schaefer, C.L. 2000. Spatial and temporal variation in wintering elk abundance and composition, and wolf response on Yellowstone's Northern Range. M.Sc. Thesis, Michigan Technological University, Houghton, MI.

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.

Sibly, R.M., H.M.R. Nott, and D.J. Fletcher. 1990. Splitting behavior into bouts. Animal Behaviour **39**:63-69.

Skrondal, A., and S. Rabe-Hesketh. 2004. Generalized latent variable modeling: multilevel, longitudinal and structural equation models. Chapman & Hall/CRC, Boca Raton, FL.

Smith, K.G. 2004. Woodland caribou demography and persistence relative to landscape change in west central Alberta. M.Sc. Thesis, University of Alberta. Edmonton, AB.

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:**1433-1440.

Szkorupa, T.D. 2002. Multi-scale habitat selection by mountain caribou in west-central Alberta. M.Sc. Thesis, University of Alberta, Edmonton, AB.

Thomas, D.C., and D.R. Gray. 2002. Update COSEWIC status report on the woodland caribou *Rangifer tarandus caribou* in Canada. *In* COSEWIC assessment and update status report on the Woodland Caribou *Rangifer tarandus caribou* in Canada. Ottawa, ON.

Thomas, D.C., E.J. Edmonds, and W.K. Brown. 1996. The diet of woodland caribou populations in west-central Alberta. Rangifer **Special Issue No. 9:**337-342.

Turner, M.G., 1989. Landscape ecology: The effect of pattern on process. Annual Review of Ecology and Systematics **20**:171-197.

Wabakken P., H. Sand, O. Liberg, and A. Bjarvall. 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. Canadian Journal of Zoology **79**:710-725.

Weaver, J.L. 1994. Ecology of wolf predation amidst high ungulate diversity in Jasper National Park. Ph.D. Thesis, University of Montana, Missoula, MT.

Weclaw, P. 2001. Modeling the future of woodland caribou in northern Alberta. M.Sc. Thesis, University of Alberta, Edmonton, AB.

Whittington, J., C.C. St. Clair, and G. Mercer. 2004. Path tortuosity and the permeability of roads and trails to wolf movement. Ecology and Society **9**:4. <http://www.ecologyandsociety.org/vol9/iss1/art4>.

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

Wielgus R.B., P.R. Vernier, and T. Schivatcheva. 2002. Grizzly bear use of open, closed, and restricted forestry roads. Canadian Journal of Forest Research **32**:1597-1606

Young, D.D. Jr., and T.R. McCabe. 1997. Grizzly bear predation rates on caribou calves in northeastern Alaska. Journal of Wildlife Management **61**:1056-1066.

Zager, P., L.S. Mills, W. Wakkinen, and D. Tallmon. 1996. Woodland caribou: A conservation dilemma. <http://www.umich.edu/~esupdate/library/95.10-11/zager.html>.

Chapter 3: Caribou (*Rangifer tarandus caribou*) habitat selection and potential spatial and temporal overlap with wolves (*Canis lupus*)

1. Introduction

Boreal caribou in Canada show a trend of declining population numbers and area of occupancy, by amounts of up to 60% in Alberta (Thomas and Gray 2002). For this reason, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has listed boreal populations of woodland caribou throughout Canada as "Threatened" (Thomas and Gray 2002). In Alberta, past studies of woodland caribou indicate that populations are either stable or declining; no sustained population increases have been documented (Brown and Hobson 1998, Dzus 2001). Furthermore, recent updates of population trends in 12 monitored herds of woodland caribou in Alberta reveal that nine are in decline, three of which are facing immediate extirpation (Thomas and Gray 2002, Alberta Woodland Caribou Recovery Team 2005). The Little Smoky herd, located in the foothills of west-central Alberta, has experienced precipitous declines and exceptionally low recruitment in recent years; it is one of the most rapidly declining caribou populations in Alberta with a finite population growth rate of 0.883 (Dzus 2001, Thomas and Gray 2002, Alberta Woodland Caribou Recovery Team 2005). The Little Smoky caribou are of the boreal ecotype; they do not migrate seasonally, unlike other herds in the region (Edmonds 1988, Dzus 2001, Alberta Woodland Caribou Recovery Team 2005). Recently, some caribou from the adjacent A la Pêche range also do not migrate.

Woodland caribou are traditionally linked to old-growth forests where terrestrial lichens are abundant. In west-central Alberta, terrestrial lichens form the bulk of the caribou diet and high terrestrial lichen biomass is associated with open, pine-dominated forests greater than 80 years of age (Thomas *et al.* 1996, Szkorupa 2002). In northern Alberta systems, mean abundance of lichens in peatlands (bogs and fens) is lower than in non-peatland systems (Dunford 2003); high water tables in peatlands likely limit lichen production while drier pine and spruce stands can support greater lichen biomass

(Dunford 2003). Nevertheless, boreal caribou in north-eastern Alberta exhibit a year-round preference for bogs and fens with low to moderate tree cover, perhaps as a means of enhancing spatial separation from predators (Stuart-Smith *et al.* 1997, Brown *et al.* 1998). In contrast, observations of individual radio-collared caribou in the Little Smoky River area were predominantly in dry, upland lodgepole pine (51%), mixed conifer lodgepole pine/ black spruce (16%), and treed muskeg (13%) (Johnson 1980, Edmonds 1993). Other woodland caribou populations in west-central Alberta were also associated with dry pine areas (Edmonds 1988, Szkorupa 2002). Although Anderson (1999) documented use of upland areas by the Red Earth South and Athabasca West caribou populations, the percentage use of those areas were never above 25%. Therefore, in their combination of choice of habitat and non-migratory life-history strategy, the boreal caribou of west-central Alberta are unique.

Industrial activity, wolf (*Canis lupus*) predation, and increases in other ungulate populations have been identified as major contributors to declining caribou numbers in ranges across Canada (Thomas and Gray 2002). In Alberta, there are many overlapping industrial activities in caribou ranges, including timber harvesting, oil and gas development, and coal mining (Hervieux 1996). The Little Smoky study area, the focus of this research, contains the entire range of the Little Smoky caribou herd and the winter range of the A la Pêche herd, which occurs to the southwest of the Little Smoky range; this area falls within portions of four Forest Management Agreement Areas (Alberta Newsprint Company, Canadian Forest Products, Foothills Forest Products (formerly Weyerhaeuser Company), and West Fraser). To date, forest harvesting has occurred primarily on the peripheries of the Little Smoky study area, though the region is fully allocated for future logging. In addition, the foothills region has the largest relative number of conventional oil and gas deposits in Alberta (ERCB 1992) and many land parcels have been leased under the mineral sales program in the foothills (Hervieux 1996, Dzus 2001). Oil and gas exploration relies heavily on seismic technology to locate deposits, generally requiring linear corridors for machinery access. The Little Smoky study area has experienced high levels of industrial "footprint"; specifically the Little Smoky caribou range has seven times the linear disturbance and two times the cutblock density as other ranges in west-central Alberta (Smith 2004). Development in the region has been rapid: intensive and overlapping industrial work was prevalent in 48% of the Little Smoky range as of 1999-2000 and by winter of 2000-2001, up to 54% of the Little Smoky range area had similar proposals for industrial development (Dzus 2001). In 2004, a record number of applications (44 000) were received by the Energy and Utilities Board for Alberta, related largely to hydrocarbon industrial development. Over 24 000 oil and gas well applications were approved across the province; the number of allocations continues to increase. Forest harvesting is on-going in the region, though some companies have postponed further harvest within caribou ranges while recovery planning takes place.

Consequences to woodland caribou living year-round in a rapidly developing landscape include: physical barriers to movement (Klein 1971), mortality from vehicle collisions and poaching (Johnson 1985), direct loss of habitat (Seip 1992, Brown *et al.* 2000), effective habitat loss through displacement and avoidance (Whitten and Cameron 1983, James and Stuart-Smith 2000), barrier effects (Dyer 2002), and changes in predator-prey relationships (Edmonds and Bloomfield 1984, Bradshaw *et al.* 1995, Rettie and Messier 1998, James and Stuart-Smith 2000, Kunkel and Pletscher 2000). In addition to stresses on woodland caribou populations caused by habitat fragmentation and loss from industrial activities, caribou are subject to significant levels of predation by wolves (Bergerud 1983, 1988; Edmonds 1988, Rettie and Messier 1998). It has been hypothesised that caribou avoid predators through *spatial separation* – the selection of habitats where primary prey and their predators are less likely to occur (Bergerud and Page 1987, Seip 1992). Spatial separation is thought to be a critical anti-predator strategy; however, industrial development may alter this relationship, thereby influencing caribou-predator interactions (Bergerud 1988).

Industrialised landscapes may lead to increases in regenerating early-seral stage forests and enhanced forage conditions, notably for moose (*Alces alces*) and deer (*Odocoileus* spp.). Increases in available prey for wolves may affect caribou populations through predator-mediated apparent competition, where a positive numeric response occurs between the primary prey and its predator (Holt 1977). Under apparent competition, higher numbers of wolves and moose could result in exploitation of traditional caribou refuges, resulting in increased predation rates on caribou (*e.g.* Seip

1992). This has been documented in Ontario, where moose immigration brought higher wolf densities that changed conditions for caribou (Cumming *et al.* 1996). Predators that depend on a primary prey species may extirpate secondary species within the same landscape (Sinclair *et al.* 1998). However, while predators cause most deaths of forest-dwelling caribou and predation is cited as the immediate factor contributing to caribou decline, it is thought to be significantly influenced by the effect of human developments and increasing populations of other ungulates (Thomas and Gray 2002).

Caribou habitat selection patterns have been detailed for ranges across Canada (Rettie and Messier 2000, Apps 2001, Szkorupa 2002, Mahoney and Virgil 2003, Johnson *et al.* 2004a, Gustine 2005, Saher 2005). However, few studies have incorporated predator and/or primary prey data in habitat selection assessments, including the collection and evaluation of high-quality, concurrent GPS data on boreal caribou and wolves in an industrial forest. With continued development, increasing pressures to reverse declining trends in caribou populations, and recent implementation of controversial management options such as predator control, a thorough examination of caribou and wolf habitat selection is warranted.

In this chapter, I develop models to explore selection of resources by caribou in west-central Alberta, year-round and by season, as variation is likely to occur seasonally (Boyce *et al.* 2002). I also examine potential spatial overlap between caribou and wolves by comparing predicted indices of use between caribou and wolves across three seasons. My specific objectives are to: 1) quantify caribou habitat selection in relation to measures of ungulate biomass, wolf habitat selection, and anthropogenic and natural features; 2) identify seasonal differences in habitat selection by caribou; 3) describe potential spatial-temporal overlap between wolves and caribou; and, 4) identify habitat features that influence overlap potential. I focus predominantly on the Little Smoky herd, but also include data from non-migratory caribou of the adjacent A la Pêche herd.

2. Study Area

The Little Smoky range and A la Pêche winter range are located in the eastern foothills of the Canadian Rocky Mountains in west-central Alberta (54° 05' 00", 117 ° 55' 00"; Figure 3-1). Within the study area, a total of 231-km^2 (3% of the larger study area) has been harvested since 1985. In addition, 10 928-km of seismic lines, 780-km of roads, and 666 well sites existed in the 3768-km^2 (Figure 3-2). Before 1950, a 100-year cycle of stand-replacing fires was the primary natural disturbance in this region (Andison 1998). Since the 1950s, forest harvesting and fire suppression strategies have resulted in fire reduction throughout west-central Alberta (Andison 1998, Rhemtulla 1999).

Major land use activities include logging, extensive oil and gas exploration and development, non-motorized outdoor recreation (*e.g.* hiking, horse travel, camping, fishing), off-road vehicle use (*e.g.* snowmobile, all-terrain vehicles), recreational hunting, and commercial trapping (Brown and Hobson 1998). Access in the area exists in the form of all-weather and dry-weather resource roads, and rights-of-ways for pipelines, powerlines and seismic lines (Smith *et al.* 2000). Gravelled resource roads service small sections of the Little Smoky range. At the time of this study, there were no cross-range connecting roads. A two-lane highway bisects the A la Pêche winter range.

The area is classed into Upper Foothills and Sub-Alpine Natural Subregions (AEP 1992), and contains several major rivers, many small creeks, and a few lakes. Elevations range from 1000- to 1700-m, and the climate was subarctic, with short, wet summers and long, cold winters (Smith *et al.* 2000). Temperatures average 16°C in July and -13.5°C in December (Beckingham and Archibald 1996). The Foothills Region is well forested, and has been described in detail by Edmonds and Bloomfield (1984). Dry sites support primarily lodgepole pine (*Pinus contorta*) or lodgepole pine and black spruce (*Picea mariana*) forests. At higher elevations, mixed fir (*Abies* spp.), spruce (*Picea* spp.) and lodgepole pine forest dominate. Willow (*Salix* spp.) and birch (*Betula glandulosa*) meadows, interspersed with dry grassy benches, are found along some drainages. Aspen (*Populus tremuloides*) occurs in small amounts through the study area, usually on south-facing well-drained slopes.

3. Methods

3.1 Caribou location data

From 2002 to 2005, we captured and collared 20 female adult caribou from the Little Smoky and A la Pêche caribou herds using aerial net-gunning capture techniques. Captures protocols were approved by the University of Alberta's Faculty of Agriculture, Forestry and Home Economics Animal Policy and Welfare Committee (Protocol No. 2003-29D). Caribou were fitted with Lotek GPS collars (Lotek Engineering Systems, Newmarket, Ontario), programmed to acquire locations every 4 hours. Collars were remotely dropped and collected from the field. Caribou locations were imported into a geographic information system (GIS). All locations with an HDOP (horizontal dilution of precision) greater than 12, indicating probable erroneous location accuracy, were removed prior to analysis (D'Eon and Delparte 2005). Locations were used to delineate 100% minimum convex polygon (MCP) home ranges (Mohr 1947). Caribou home ranges were used to identify "available" locations for each individual using a random point-generator from the Hawth's Tools extension in ArcGIS 9.1 (Beyer 2005). Sampling intensities for available locations within MCP home ranges were equal to the average location intensity of GPS data across all caribou: 4.5 points per km^2.

To account for variation in habitat use through time (Schooley 1994) and to enable comparisons with selection patterns of wolves, I stratified caribou location data into three seasons, based on wolf behaviour and caribou biology. The first season, denning, was defined as the period during which individual wolves within a pack travelled more independently and exhibited clear association with a den site (April 20-June 30). This season corresponded with caribou calving (typically late May to early June). The second season, rendezvous, was characterised by wolf movement to and from a common area that was not the den site (July 1 – September 20). During this season, caribou calves are particularly vulnerable to predation from bears (Young and McCabe 1997, Nielsen 2004) and wolves (Stuart-Smith *et al.* 1997). The third season, nomadic, was defined as September 21 to April 19. During this period, wolves travelled as a pack and did not regularly return to a common area. Caribou rut during the beginning of the nomadic season. The nomadic season encompasses winter, when the wet areas are frozen and the ground is snow-covered. Winter is considered the most limiting time with respect to availability of lichens and is also the time of the year when most industrial development occurs in the study area, due to access limitations.

3.2 Modelling strategy and variable selection

I compared seasonal GPS radio-telemetry locations with random or available locations to identify the influence of a suite of variables on caribou habitat selection. Analyses were evaluated at the third-order level (home-range) following a 'design III' approach, where individuals were identified, and both used and available resources were sampled for each animal (Johnson 1980, Thomas and Taylor 1990). For each season, I calculated a resource selection function across all caribou using the following model structure from Manly *et al.* (2002):

$$w^*(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_K) \qquad \text{(Equation 3-1)}$$

where $w^*(x)$ represents the resource selection function and β is the coefficient estimated from environmental predictors x_i. Logistic regression was used to estimate the β values in STATA 9.1 (STATA Corp., College Station, Texas). I specified the robust cluster option to calculate variance around the estimated coefficient using the Huber-White sandwich estimator (White 1980). 'Caribou' (*i.e.* individuals) was specified as the cluster, and estimators assumed that observations were independent across clusters, but not necessarily within clusters.

Linear predictor variables (Table 3.1) were screened for collinearity through use of Pearson's correlations (r) and variance inflation functions (VIF). All variables with correlations $r > |0.65|$, individual VIF scores >10, or a mean VIF score considerably larger than 1 were assumed to be collinear. I assessed each variable's influence in univariate analyses, using $p < 0.25$ based on a Wald z-statistic as a cut-off for inclusion in the preliminary multivariate model. Following initial removal of variables that were not significant, I assessed the full multivariate model, dropping the least significant parameter (largest p-value) and refitting the reduced model. This process was repeated until all remaining parameters were significant at $\alpha = 0.05$ (Hosmer and Lemeshow 1999, Hosmer and Lemeshow 2000).

3.3 Model validation

I validated the top seasonal models using a 1:5 testing-to-training *k*-fold partitioning procedure (Fielding and Bell 1997, Boyce *et al.* 2002). I evaluated the predictive performance of the final model by comparing map predictions to frequency of within-sample independent testing data (caribou use locations). A total of 10 quantile bins were generated based on a histogram of predicted caribou occurrence and then ranked from low relative probability of occurrence to high relative probability of occurrence (1-10 respectively). Model performance was measured with a Spearman rank correlation (r_s), which assessed the relationship between the bin rank and the observed number of telemetry locations per bin. The model was considered to have good predictive capabilities if r_s was positive and significant at $\alpha = 0.05$.

3.4 Resource sampling

Multiple variables were used to quantify the study area, generally categorised as indices of predator and prey, industrial footprint parameters, and landscape structure descriptors. An index of ungulate biomass, created by modelling counts of pellets located along transects (see Chapter 2), was incorporated into caribou selection models. Models also included an index of wolf use to account for the predicted seasonal presence of wolves throughout the caribou range. I also assessed caribou response to industrial variables, such as distance to anthropogenic features (roads, cutblocks, facilities) and density of cutblocks and seismic lines. Finally, I included landscape structure variables, such as an index of terrain ruggedness, age of forest, canopy closure, proportion of dominant species at varying scales, and distance to natural features (Table 3-1). Two categorical variables, calculated from the Alberta Vegetation Inventory for the study area, were included in the variable set: *cover* and *wetness* (Table 2-4). I used an indicator contrast with the most prevalent class as the reference category ("forest" for *cover* and "mesic" for *wetness*). For more detail about how predictor variables were calculated or created see Chapter 2. All data layers were time-stamped to ensure an accurate reflection of landscape attributes during the time of collar data collection.

3.5 Spatial overlap potential

As predicted by the *spatial separation hypothesis*, minimisation of spatial and temporal overlap with wolves is thought to be a critical component of caribou survival strategy (Bergerud 1974, Bergerud *et al.* 1984, Bergerud and Elliot 1986, Bergerud and Page 1987, Seip 1991, 1992). I used predictive maps of wolf habitat selection from previous analyses (Chapter 2), with a binned relative index of use ranging from 1-10, to compare overlap potential between wolves and caribou. Habitat selection maps for the two species were combined in a GIS to highlight the spatial distribution of potential separation and overlap between them. Values closer to zero indicate higher predicted overlap, as both wolves and caribou were exhibiting little variation in selection of that area. Values closer to -10 indicate high suitability for caribou but not wolves; conversely, values closer to 10 indicate high suitability for wolves but not caribou. I also examined potential for separation across the landscape and for overlap only in areas that caribou were predicted to highly select (caribou RSF value ≥ 7).

To statistically test whether caribou and wolves were negatively correlated, as would be predicted by the 'spatial separation' hypothesis, I placed 5 random points per km^2 of caribou range and recorded RSF values for each species and season. I used a Spearman rank correlation statistic to assess spatial overlap potential at each random point throughout the study area, within each season ($\alpha = 0.05$). I controlled for wolf and caribou simultaneous avoidance by identifying cases where selection values of 1-4 were equal for each species; records that were low and equal were removed from the database.

4. Results

4.1 Caribou location data

A total of 41 569 locations were recovered from 20 caribou: 16 individuals from the Little Smoky and 4 from the A la Pêche herd. Over the course of the study, one caribou from the Little Smoky herd made repeat visits to the A la Pêche range during the spring and summer. Caribou F543, an adult female of the Little Smoky herd, left the Little Smoky range in late June 2003 and returned in mid-July (Figure 3-3). Similarly, in

2004, F543 left the Little Smoky range on 4 June 2004 and returned on 26 June 2004 (Figure 3-4). Caribou F543 was not observed with a calf in either of 2003 and 2004 surveys. During movements to and from the A la Pêche range, F543 generally used areas with higher RSF values, including the aforementioned between-range areas (Figures 3-3, 3-4). Movement between herds is rare in this area: Smith (2004) reported that with more than 700 radio-tracking caribou-years in west-central Alberta, only one instance of temporary interchange was documented.

4.2 Caribou model building and validation

Variable selection procedures were initiated with the same set of variables for each seasonal model (Table 3-1). Correlations among independent variables changed with season, depending on GPS location points. During the denning and rendezvous seasons, proportion of larch at 30-m was correlated with proportion larch at 1-km (r=0.74 and r=0.73, respectively), and distance to cutblock was correlated with proportion cutblock at 10-km (r=0.67). In addition, age was correlated with proportion conifer (r=0.65) and pine at 30-m was correlated with pine at 1-km (r=0.65) during the rendezvous season. For the nomadic season, proportion larch at 30-m was correlated with proportion larch at 1-km (r=0.72) and wetness was correlated with proportion black spruce (r=0.66). No further evidence of collinearity was evident using VIF tests.

Inclusion of sandwich estimators to adjust standard errors had considerable effect on the significance values at α=0.05 (Table 3-2). The inference for these coefficients is not strong and they were not significant contributors to explaining variation in habitat selection models as a result of inflated standard errors. Caribou response to habitat metrics varied across seasons (*e.g.* Figure 3-5).

4.3 Model predictions for wolf denning/caribou calving season

Industrial features were predictors of caribou habitat selection patterns during the wolf denning/caribou calving period. Caribou avoided young forests and selected against areas with greater proportions of recent cutblocks, though 95% confidence intervals (CI) of the latter overlapped zero (Table 3-2). For seismic variables, caribou strongly selected against proximity to seismic and avoided areas with high densities of seismic lines at the

1-km scale. There was significant, but weak, selection for areas with high densities of seismic lines at the 10-km scale. Caribou selected areas farther from well sites than available. Pipelines were selected against, but the relationship was weak because of inflated standard errors.

Caribou associated positively to increasing age of forest stands, showing a preference for older stands (Table 3-2). Aspen stands and coniferous forest as a whole were both negatively selected. Caribou exhibited positive selection for larch (also for pine and black spruce, though with high standard error), but responded negatively to white spruce. Caribou were located farther from main rivers than available and selected wet areas in comparison to mesic areas. They also preferred grass covered locations over forested locations. Ungulate biomass index did not enter the model as a significant variable. Caribou appeared to select areas with a higher predicted index of wolf use than available, though standard errors were large.

4.4 Model predictions for rendezvous/caribou calf-growth season

During the rendezvous season, caribou responded to features in a similar way to the denning season: caribou weakly selected areas closer to cutblocks and facilities, but they also used areas closer to pipelines, although confidence intervals for the latter two overlapped zero due to inflated standard errors (Table 3-2). Caribou negatively selected areas with high proportions of cutblocks at the 1-km scale and were located farther from roads than available, though again, CIs for both overlapped zero. Areas in close proximity to seismic lines were selected against, but caribou were associated with areas that had a higher density of seismic lines at the 10-km scale. Caribou locations were recorded in areas closer to well sites than available, but negatively associated with areas of high well site density. However, the seismic density variable and well site measurements were not statistically significant in the robust cluster model.

Caribou displayed unambiguous avoidance of areas with a high proportion of aspen, white and black spruce at the 30-m scale, in addition to pine, black spruce, and white spruce at the 1-km scale, although only measures at the 30-m scale were statistically significant. Caribou selected areas with dense canopy closure and areas farther from streams and major rivers.

Caribou selected wet and dry areas in comparison to mesic habitats, and also preferred grass, shrub, and wet muskeg areas in comparison to forested regions. Caribou avoided bare areas, which were generally newly created anthropogenic habitats, though confidence intervals overlapped zero. Ungulate biomass did not contribute significantly to explaining caribou occurrence. Caribou were negatively associated with areas that had a higher predicted index of wolf use than available.

4.5 Model predictions for nomadic/winter season

During the nomadic season, areas farther from facilities, pipelines, seismic lines, and roads were selected by caribou. Areas with larger proportions of cutblocks, lower densities of well sites, and higher seismic line densities at the 1-km scale were also negatively selected, though CIs overlapped zero. Caribou selected locations closer to well sites, with a larger proportion cutblock and density of seismic lines at the 10-km scale, although confidence intervals overlapped zero for all variables.

During this season, caribou selected younger forests and those with more open canopies. Although caribou still avoided areas with high proportions of aspen, there was an overall selection of coniferous forests. Caribou avoided locally abundant pine (30-m), but showed strong selection for pine, black spruce, and larch at the 1-km scale, though only measures at the 1-km scale were significant. Similar to other seasons, caribou selected against white spruce, significantly at the 30-m and not significantly at the 1-km scales. During winter, caribou preferred less rugged locations and those farther from rivers, though CIs overlapped zero. Caribou presence was negatively associated with higher levels of ungulate biomass, yet positively associated with predicted wolf presence, though neither was significant within the robust cluster model for the nomadic season.

Several variables were significant in all seasonal models, illustrating year-round importance and variation in predicting caribou occurrence (Figure 3-5). Nevertheless, although caribou responded similarly across the season to many variables, the spatially predicted index of use surface demonstrates substantial variation across seasons (Figure 3-6).

4.6 Model validation

Five k-fold partitions with 10 bins for validation in each season yielded significant Spearman's ρ values at $\alpha = 0.05$ (critical value=0.648). The den and rendezvous season models validated perfectly over each k-fold run, resulting in a ρ of 1.0. The nomadic was also significant with $\rho = 0.995$. Significant values indicate that the models were predictive of within-sample caribou occurrence and overall performed well. The model is predicting the relative probability of occurrence of caribou on the landscape.

4.7 Spatial overlap potential

Wolves and caribou appear to occupy different habitats although there is potential for spatial separation; in general, wolves are likely to occur without caribou along major drainages, while caribou are likely to exist in regions without wolves in various patches throughout the study area (Figures 3-7, 3-8). Likelihood of spatial overlap in areas that are most likely to be selected by caribou was largest during the denning season, compared to the rendezvous and nomadic seasons, while overlap with wolves is least likely to occur during the rendezvous season (Figures 3-9, 3-10). Correlative analyses corroborate this finding: Spearman's ρ was negative and significant for the rendezvous and nomadic seasons (ρ = -0. 4146 and -0.2024, respectively), but positive and significant for the denning season ($\rho = 0.200$). Examining separation potential categorically by season, more than 45% of the study area is predicted to have high spatial overlap during all seasons, though during the denning season specifically, there is overlap potential of up to 65% (Figure 3-11).

5. Discussion

Caribou habitat selection patterns have been documented across several ranges in Canada, although detailed, simultaneous examination of caribou and their primary predator is rare. Identifying year-round habitat selection patterns of woodland caribou in relation to wolf habitat selection, distribution of primary prey, and industrial development variables is a key step in advancing understanding of caribou response to highly industrialised landscapes. In the Little Smoky area, a great majority of the landscape has been affected by resource development. As well, much of the area is allocated for future resource development and increasing numbers of permits are granted each year. Consequently, there is urgency to identify contributing factors to caribou habitat selection patterns and potential spatial overlap with wolves to inform management decisions specific to west-central Alberta. Resource selection functions provide a statistically-sound approach to developing quantitative models that describe habitat selection patterns. I used comprehensive and simultaneous wolf and caribou location data to examine year-round caribou response to landscape variables. I examined how caribou responded to multiple landscape metrics within various seasons (as defined by previous wolf analyses). I also quantified caribou response to indices of ungulate biomass and wolf use. Finally, I identified spatial overlap potential between caribou and wolves.

5.1 Response to anthropogenic features

Overall, caribou responded significantly to a suite of landscape features, with some seasonal variation in selection patterns. Human infrastructure and landscape alteration covariates were consistently significant variables describing patterns of caribou use. There was strong evidence that caribou avoided areas closer to seismic lines, as demonstrated by positive coefficients for distance to seismic lines and negative coefficients for increasing densities of seismic lines. Caribou showed the strongest response to seismic lines during seasons without snow cover.

Seismic lines have been implicated in altering caribou habitat use patterns in other areas. Caribou avoidance of linear features was documented by Dyer *et al.* (2001) in northern Alberta, where maximum avoidance distances of 250-m were reported for roads and seismic lines. Oberg (2001) concluded that roads in west-central Alberta were avoided to a distance of 500-m, but there was no definitive evidence that seismic lines were avoided by mountain caribou. Sample sizes for RSF analyses in this chapter were substantially larger than those used by Oberg (2001) and therefore provided more statistical power to detect the effect of seismic lines.

Similar to their avoidance of seismic lines, caribou also weakly selected areas farther from pipelines in all seasons and farther from roads in the rendezvous and nomadic seasons, although confidence intervals for these variables overlapped zero.

Avoidance of large linear features by caribou is a well-documented phenomenon: Smith and Cameron (1983) reported that female caribou with calves avoided the Trans-Alaska pipeline and haul road in Alaska, Mercer *et al.* (1985) reported that caribou in Newfoundland centered their activity at maximum possible distances from roads, and Villmo (1975) noted that domestic reindeer avoided passing under power lines in Sweden. In terms of non-linear human disturbances, caribou strongly selected areas farther from well sites, but only during the denning season. During the rendezvous and nomadic seasons, caribou generally selected areas closer to well sites, although confidence intervals overlapped zero for the rendezvous model and coefficients were small for both seasons. Dyer (1999) also documented ambiguous results for well site avoidance, noting that there was no consistent evidence of avoidance during summer and fall. In Dyer's (1999) study area, avoidance was generally greatest during spring, consistent with results from the Little Smoky region. Well sites vary in their remoteness, human activity level, infrastructure density, and noise production. Any, or all, of these factors could have influenced the likelihood of caribou selecting regions adjacent to well sites.

Caribou response to cutblocks was consistent over the seasons, but not all metrics were negatively selected. During the den and rendezvous periods, caribou selected areas closer to cutblocks, but year-round, avoided areas with a large proportion of cutblock at the 1-km scale. This result illustrates the importance of measuring variables at multiple scales and by differing approaches. Nevertheless, it is also difficult to interpret. One explanation is that distribution of forest harvesting has affected selection coefficients: harvesting has occurred in select areas of the range, concentrated in the northwest and south regions. These areas may have traditionally been a significant part of the caribou range and therefore individuals are still using remaining habitat in areas closer to cutblocks. When compared to central parts of the range, where cutblocks are scarce, caribou may appear to be selecting areas near cutblocks when in fact this is due primarily to concentrated harvesting activities in preferred portions of the caribou range. However, caribou clearly exhibit strong, year-round negative selection for areas with high densities of cutblocks at the 1-km^2 scale.

Several studies have highlighted the negative impacts of human landscape alterations on Alberta woodland caribou distribution, movement, and persistence (Dyer 1999, Oberg 2001, Smith 2004, Lessard 2005). Corroborating evidence from these RSF analyses on caribou from the highly industrialised Little Smoky region further confirms the potential for direct and functional habitat loss within industrialised regions of caribou ranges. Functional habitat loss may occur as an outcome of avoidance behaviour; for example, caribou in northeastern Alberta avoided up to potentially 44% of their habitat due to negative response to industrial features (Dyer 1999). Functional habitat loss mediated through avoidance of industrial features may have a number of potential consequences for woodland caribou. In areas of intensive industrial use, woodland caribou may be functionally restricted from accessing historical parts of their range, resulting in further range contractions. Additionally, displacement could lead to use of less-suitable habitat and have demographic consequences as a result of decreased spatial separation (Darby and Duquette 1986). However, I made no attempt to relate habitat selection to demographic parameters, nor have I explicitly evaluated the mechanisms driving caribou response to various landscape features.

5.2 Response to natural features

Inclusion of dominant tree species cover variables revealed that proportion larch within 1-km^2 was a significant predictor of caribou occurrence during winter and spring. During the rendezvous season, caribou did not select any particular dominant species stands, and in fact, showed slight avoidance for locations with larger proportions of dominant conifer stands (increasing homogeneity). In west-central Alberta, terrestrial lichens – a key winter diet component for caribou (Bjorge 1984, Thomas *et al.* 1996, Rettie *et al.* 1997) – are most abundant in older semi-open lodgepole pine stands (Szkorupa 2002). As expected, caribou selected locations with a greater proportion of pine forests at the 1-km^2 scale during the nomadic season. Interestingly, caribou selected against high proportions of pine at the local (30-m) scale, although the CIs for this coefficient overlapped zero. Although high lichen densities are often associated with upland lodgepole pine, they do not necessarily relate exclusively to stands predominantly of pine. In the Narraway range northwest of the Little Smoky, Saher (2005) discovered that *Cladina mitis* occurrence (a key lichen species for caribou) was related to forests with lower proportions of white spruce and larch and greater proportions of black spruce. In the Little Smoky region, mixed pine and black spruce stands are common. The selection of pine at a larger scale may be a reflection of lichen distribution, where lichens occur in dry, mixed stands predominantly comprised of pine at the 1-km scale, but not necessarily the local, 30-m scale. Evidence from northern BC supports this assertion: pine-lichen woodlands used by caribou were often adjacent to wetlands and black spruce patches, or mixed stands of black spruce and pine (Johnson *et al.* 2004b). Errors in mapping at the 30-m scale may have also contributed to disparities in selection at the two scales.

Finally, white spruce and large rivers were negatively selected at all scales during all seasons. White spruce in the Little Smoky study area is generally restricted to river valleys. Not only are terrestrial lichens negatively associated with white spruce (Saher 2005), but both rivers and white spruce were positively selected by wolves (Chapter 2). Not surprisingly, caribou also strongly avoided aspen dominated stands in all seasons, although these areas are not common in the range and are also restricted to south-facing slopes of major drainages. Aspen stands generally support other cervid species and have very low lichen availability.

RSF maps created for the Little Smoky region predicted high probabilities of caribou occurrence in locations where caribou have not historically been known to occur. In particular, between the Little Smoky and winter A la Pêche ranges a large area exists with a high predicted index of use, most pronounced during the nomadic season (Figure 3-6). Although some of the area is used by caribou in the A la Pêche herd, the majority of it is not. The area of high predicted use between ranges may have arisen due to failure to incorporate additional critical factors in predicting caribou occurrence (such as lichen), or perhaps because certain important landscape metrics in this region were not adequately measured (for example, intensity of road use by humans). The consequence of either would be poor predictive ability of the model beyond boundaries of highly used areas within the caribou ranges examined here. In contrast, the area might be excellent caribou habitat that does not support caribou for behavioural reasons. Although woodland caribou are do not often occur in large, gregarious groups, they frequently are observed in small groups. The effects of presence of conspecifics for formation of small groups and mating opportunities might serve to keep caribou within the bounds of their herd's range. F543, during between-range movements, did appear to spend more time in areas with a higher predicted index of use (Figure 3-3).

5.3 Caribou response to ungulate biomass and wolf habitat selection

Caribou did not respond strongly to measures of ungulate biomass or wolf relative indices-of-use in the resource selection models. The ungulate index was not an important predictor for the den season model, and was not consistently selected in the nomadic and rendezvous seasons. In addition, coefficients for the ungulate biomass index were small and confidence intervals overlapped zero, thus the variable was not informative in describing habitat selection. Areas with predicted higher wolf use were selected during the den and nomadic seasons, though only in the den model was the coefficient significantly different from zero. During the rendezvous season, caribou negatively selected areas with high predicted wolf occurrence, suggesting lower spatial overlap. When potential spatial overlap across the study area was explicitly examined, wolves and caribou were predicted to have the greatest overlap during the denning season; positive correlations between wolves and caribou corroborated this, indicating that similar habitat types were being selected by both species. Most caribou mortalities of collared animals in the Little Smoky region have occurred during the spring and summer: of 14 confirmed mortalities since 1999, seven were during the den season and another three were in either the den or rendezvous seasons. Additionally, over a 10 year monitoring period in northeastern Alberta, 79% of adult female caribou mortalities occurred during the snowless period (McLoughlin *et al.* 2003). A recent simulation study using caribou data from this region concluded that caribou populations decline as a result of increasing spatial overlap with wolves (Lessard 2005).

5.4 Potential for spatial and temporal overlap

Although wolf packs were not collared throughout the Little Smoky region, the models identified locations across the study area that were most likely to be selected by wolves. If, as assumed by wolf-caribou overlap analyses, the range was saturated by wolves (*i.e.* that additional packs exist in the interstitial regions between documented wolf packs), overlap potential between caribou and wolves was predicted to be significant year-round. However, I could not directly evaluate the mechanisms behind this pattern. Suggestions from previous work indicate that spatial separation between wolves and caribou is compromised as a result of increased moose and deer populations (Seip 1992, Seip and Cichowski 1996, Poole *et al.* 2000, Kuzyk 2002). Subsequent increases in densities of wolves, through a numerical response, create the potential for increased caribou-wolf encounters.

I found that wolves and caribou generally selected opposite covariates, indicating inherent selection differences between the two species: wolves selected younger forests, while caribou usually selected older forest; wolves strongly favoured areas close to rivers and white spruce dominated stands, while caribou avoided these areas; wolves never showed selection for larch or black spruce stands, while caribou generally preferred them. Caribou avoided areas near seismic lines in all seasons, but wolves responded positively to seismic line proximity in the rendezvous season (Chapter 2). Variables associated with cutblocks described wolf occurrence; for example, shrub presence, forest age, and distance to roads, in addition to distance to and proportion cutblock covariates were all significant predictors. Wolves were predicted to select regions with many cutblocks, while caribou avoided areas with high densities of cutblocks at the 1-km scale. At a larger scale, however, cutblock density was not a significant predictor in caribou models, although wolves selected locations with higher densities. This resulted in an increased potential in overlap over parts of the study area with several cutblocks at the 10-km^2 scale.

Despite several disparities in selection patterns, potential spatial overlap between caribou and wolves was substantial year-round, suggesting that caribou were unable to spatially separate from wolves. The ability for caribou to separate from wolves in the past, in addition to causes of the present predicted high spatial overlap, cannot be determined from my analyses. However, the role of human infrastructure variables in shaping patterns of caribou and wolf habitat selection and influence to spatial refuges should be considered a primary factor in future analyses of spatial and temporal overlap and development of management plans for the region.

6. Management Implications

Considering the rate of expansion of the oil and gas industry in Alberta and complete allocation of most caribou ranges to forestry companies, there is a clear need to address the relationship between expanding industrial operations and declining caribou herds in Alberta. In these analyses, I have provided a first step toward evaluating habitat constraints and concerns by highlighting caribou response to various landscape attributes and examining the potential for spatial and temporal overlap with wolves. Two key findings may be of importance to managers: 1) within the Little Smoky study area, caribou avoided some aspects of human infrastructure; and 2) spatial and temporal overlap potential between caribou and wolves was large year-round.

6.1 Caribou avoidance of human infrastructure

Results from this work are supportive of minimising and recovering linear developments where possible. While implementing less invasive techniques in future developments (*e.g.* low-impact and heli-portal seismic, remotely operated infrastructure) is an important initial step in reducing habitat loss and fragmentation, it does not address existing, extensive developments in the Little Smoky region. Recovering seismic lines and future linear disturbances, including existing lines that are re-used, could be within the mandate of each industrial operator. However, while habitat restoration may alter caribou avoidance patterns, there is a need to assess the effectiveness of recovery techniques in relation to caribou response. Resource selection maps from these analyses may be used to locate key areas for hypothesis testing of experimental techniques related to habitat restoration and subsequent caribou response.

Caribou avoided young forests and areas with high proportion of cutblock at the 1-km^2 scale, though proportion cutblock at a larger scale was not a significant predictive variable. Visually, areas with higher cutblock density were predicted to have large overlap potential between caribou and wolves. Cutblocks situated closely to each other have the effect of reducing the overall forest age at a larger scale and increasing proportion cutblock; in addition, local productivity for other ungulates will likely increase while suitability for lichens will likely decrease (Coxson and Marsh 2001). Pace and density of harvest in caribou range should be a critical factor in planning cutblocks in caribou range; however, during the recovery phase, cessation of forest harvest may be necessary for caribou recovery.

6.2 Spatial and temporal overlap

Managing wolf-caribou spatial and temporal overlap and encounter rate is an extremely challenging endeavour. Although one answer may be to locally eliminate predator species and potentially effect an immediate, short-term increase in caribou numbers through increased recruitment and survival, this alone cannot provide a permanent solution to caribou decline (Kuzyk 2002, Weclaw and Hudson 2004, Alberta Woodland Caribou Recovery Team 2005, Lessard 2005). Findings from my research support recommendations by the Alberta Caribou Recovery Plan, which states, "to avoid herd extirpation, predator management and possibly management of other prey species will be required to improve caribou herd trend and affect [sic] a caribou population increase … Predator control must be predicated on land management and habitat restoration procedures (appropriate for caribou recovery) being in place, or under development" (Alberta Woodland Caribou Recovery Team 2005).

Results illustrate that overlap is substantial year-round, though the role of industrial development in influencing this overlap cannot be overlooked. For example, spatial overlap was predicted to be high in areas with large numbers of cutblocks, suggesting that density and distribution of cutblocks within caribou range has implications for increasing shared caribou and wolf habitats and should be considered strongly in future management plans. The models presented here, in conjunction with previous evaluations of wolf habitat selection, could be applied to future evaluation of potential management scenarios with respect to caribou and wolf spatial overlap potential.

Table 3-1: Independent variables included in variable selection for seasonal caribou models describing habitat selection from 2002-2004 in the Little Smoky study area of west-central Alberta. I used three methods to determine variable inclusion: 1) univariate analyses on all variables; variables were included if $p < 0.25$, 2) collinearity analyses with Pearson's correlation ($r < |0.65|$) and variance inflation factor diagnostics, and 3) stepwise regression.

Variable Code	Description	Variable Range
age	Age of forest stand, where applicable	**0-315**
aw	Proportion trembling aspen at 30m scale	**0-10**
canopy	Percentage canopy cover at 30m scale	**0-100**
conifer	Proportion conifer at 30m scale	**0-10**
cover	Coarse ground-cover (forest, grass, no cover, shrub)	**0 or 1**
dtcb	Distance to nearest cutblock	**0-13**
facilities	Distance to nearest petroleum-sector facility	**0-16**
lt	Proportion larch at 30m scale	**0-10**
lt_1km	Proportion of area within 1-km^2 that is larch	**0-10**
pipesdt	Distance to nearest pipeline	**0-9**
pl	Proportion lodgepole pine at 30m scale	**0-10**
pl_1km	Proportion of area within 1-km^2 that is lodgepole pine	**0-10**
propcb1k	Proportion of 1-km^2 area that is cutblock	**0-1**
propcb10k	Proportion of 10-km^2 area that is cutblock	**0-1**
rdsdt	Distance to nearest road	**0-10**
rivsdt	Distance to nearest river	**0-8.6**
sb	Proportion black spruce at 30m scale	**0-10**
sb_1km	Proportion of area within 1-km^2 that is black spruce	**0-10**
seismic	Distance to nearest seismic line	**0-1.5**
sldens1	Length of linear seismic line within 1-km^2	**0-12**
sldens10	Length of linear seismic line within 10-km^2	**0-599**
sw	Proportion white spruce at 30m scale	**0-10**
sw_1km	Proportion of area within 1-km^2 that is white spruce	**0-10**
tri	Terrain Ruggedness Index	**0-1**
ungulates	Ungulate Biomass Index (Ch. 2)	**0-2300**
wetness	Dry, Mesic, or Wet (based on AVI)	**0 or 1**
waterdt	Distance to any water source, including small creeks	**0-2.4**
wellden	Density of wells within 1-km^2	**0-11**
wolf RSF	Predicted occurrence of wolves	**0-10**
wellsdt	Distance to nearest well site	**0-9.8**

Table 3-2: Estimated coefficients for the best models describing caribou habitat selection in the Little Smoky study area for three seasons (denning, rendezvous, and nomadic) over 2002-2004. Robust clusters (Huber-White sandwich estimators) were specified to adjust standard errors in account of correlation within individual caribou. Gray-shaded cells represent significant ($p < 0.05$) variables after standard errors were adjusted. Light shaded variables are marginally significant ($0.05 > p < 0.10$). 'Forest' and 'mesic' were used as the reference categories (indicator contrast) for comparisons within the 'cover' (grass, bare, shrub, water) and 'wetness' (dry, wet) variables.

Variable	Denning		Rendezvous		Nomadic	
	Coefficient	S.E.	Coefficient	S.E.	Coefficient	S.E.
age	.00578	.00194	.00585	.00157	-.00300	.000993
aspen	-.760	.320	-1.21	.306	-.590	.175
canopy	-.00289	.00362	.00372	.00284	-.00639	.00185
conifer	-.0421	.0207	–	–	.0466	.0156
grass	.652	.277	.879	.332	-.170	.169
bare	.0713	.239	-.254	.312	-.756	.269
shrub	.227	.200	.458	.267	.110	.112
water	.499	.335	.655	.268	-1.14	.254
dtcb	-.0530	.0385	-.170	.0537	.0389	.0487
facilties	-.0660	.0521	-.00600	.0744	.0692	.0337
lt	–	–	–	–	–	–
lt_1km	.150	.0628	–	–	.185	.0660
propcb1k	-.274	.173	-.585	.689	-.484	.254
propcb10k	–	–	–	–	–	–
pipesdt	.0504	.0399	.0534	.0437	.0551	.0282
pl	.0285	.0243	–	–	-.0135	.0213
pl_1km	–	–	-.0978	.0759	.172	.0659
rivsdt	.124	.0515	.186	.0578	.0103	.0575
rdsdt	–	–	.0224	.0829	.0228	.0513
sb	–	–	-.0484	.0224	–	–
sb_1km	.0356	.0590	-.0192	.105	.225	.0732
seismic	1.52	.295	1.47	.298	.830	.219
slden1km	-.100	.0503	–	–	-.0242	.0408
slden10k	.00439	.00174	.00262	.00222	.000112	.000131
sw	–	–	-.0935	.0152	-.0444	.0144
sw_1km	-.670	.277	-.498	.320	-.132	.0922
tri	.555	.568	.116	.000181	-.302	.334
waterdt	.146	.273	1.04	.233	–	–
wellsdt	.263	.0855	-.0392	.0920	-.0862	.0713
wellsden	–	–	-.243	.194	-.0856	.0703
dry	.575	.406	.470	.228	-.530	.192
wet	.589	.214	.630	.251	-.134	.141
wolf RSF	.0365	.0255	-.0928	.0271	.00418	.00398
ungulates	–	–	.000152	.000181	-.0000376	.000164

Figure 3-1: Individual home ranges for caribou used in RSF and spatial overlap analyses. Available points were calculated within each home range and contrasted to caribou GPS locations. Data were collected from the Little Smoky and A la Pêche caribou herds in west-central Alberta between 2002 and 2004.

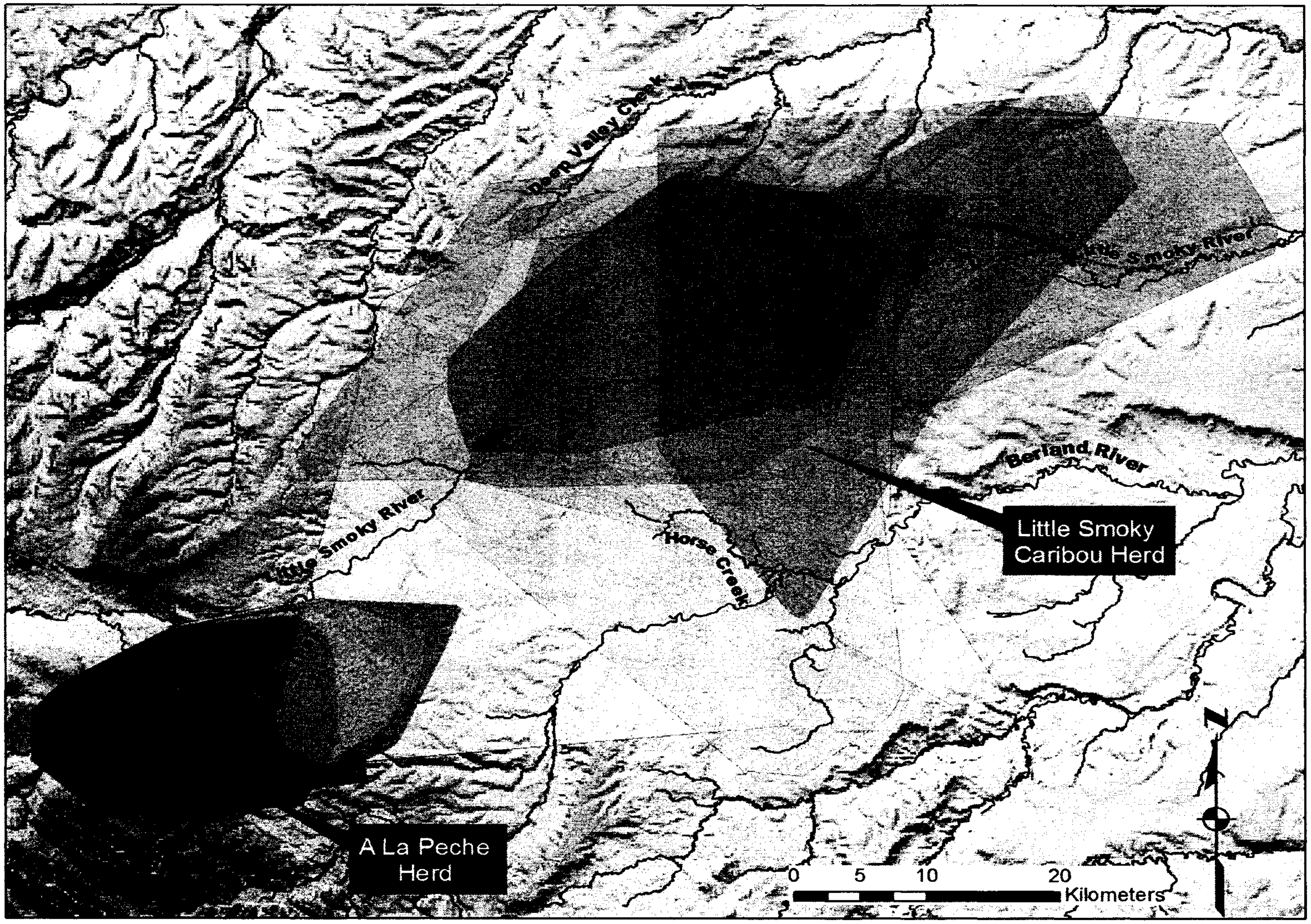


Figure 3-2: Seismic lines and well sites (triangles) in the study area, as defined by caribou home ranges within the Little Smoky and A la Pêche herds of west-central Alberta from 2002-2004. Seismic lines are not to scale. Additional infrastructure, including pipelines, roads, powerlines, and cutblocks, are not included in this map.

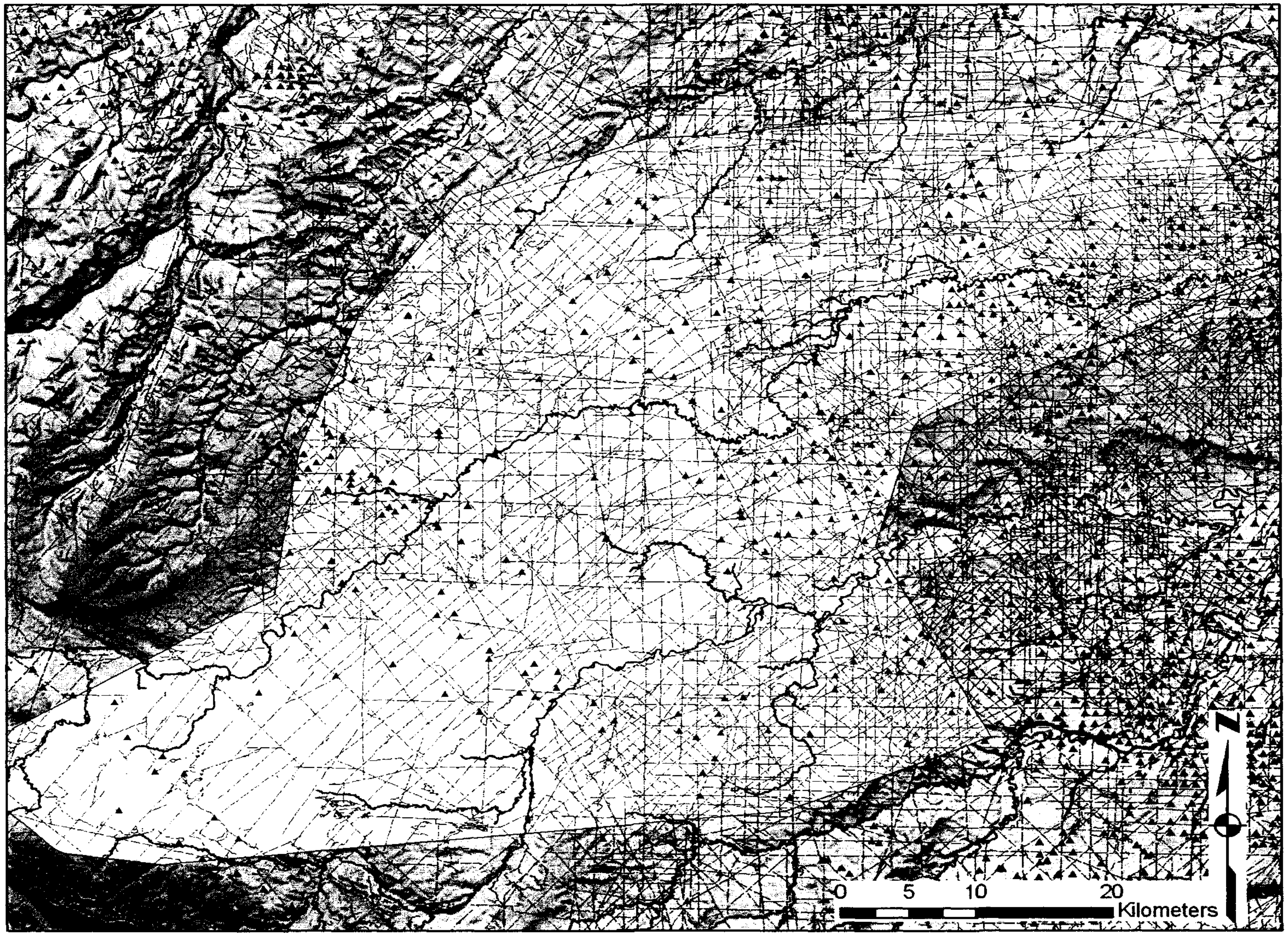
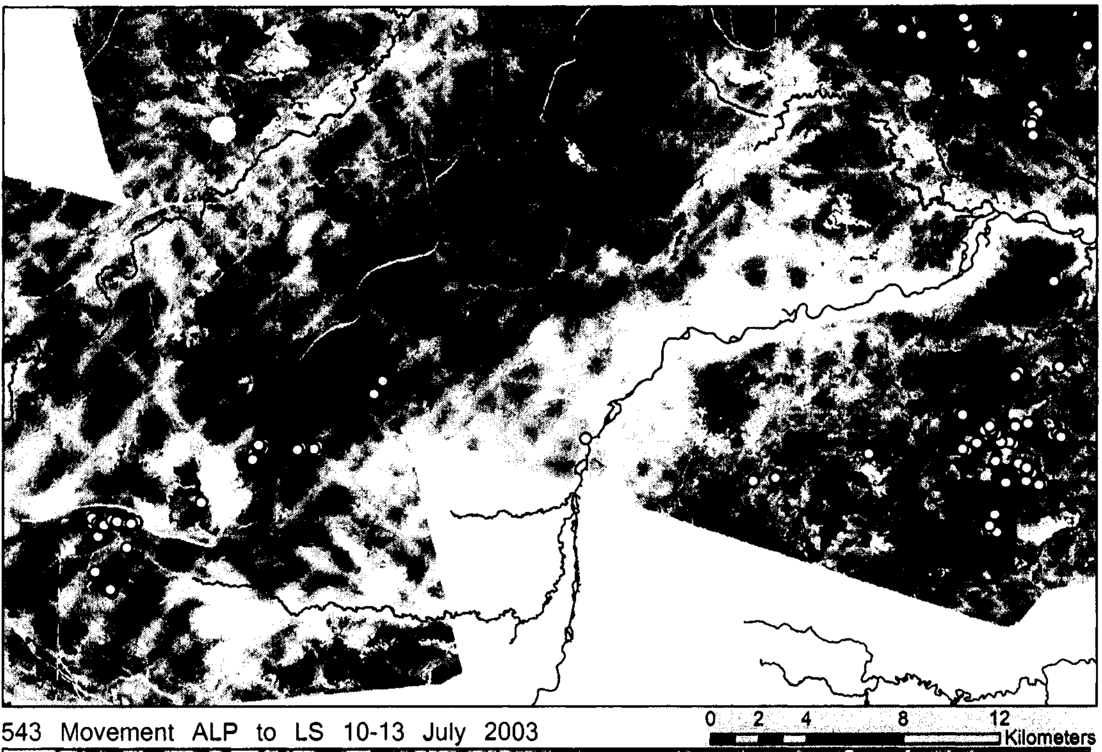


Figure 3-3: Caribou F543 movement from the Little Smoky range to the A la Pêche range in west-central Alberta during the summer of 2003. Caribou F543 selected areas predicted to be more highly used (darker) by the RSF surfaces. White gaps represent areas of no data.

F543 Movement LS to ALP 22-26 June 2003



F543 Movement ALP to LS 10-13 July 2003

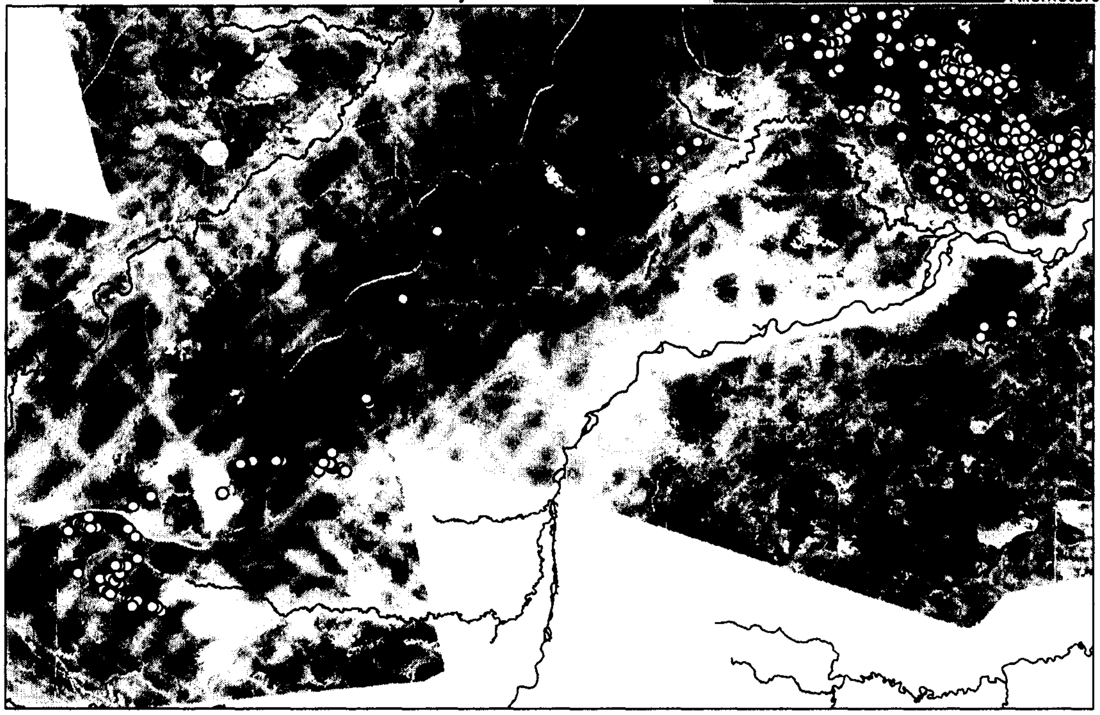


Figure 3-4: Caribou F543 movement to and from the A la Pêche range in west-central Alberta during the den season in 2004.

F543 Movement LS to ALP Return
04 - 26 June 2004

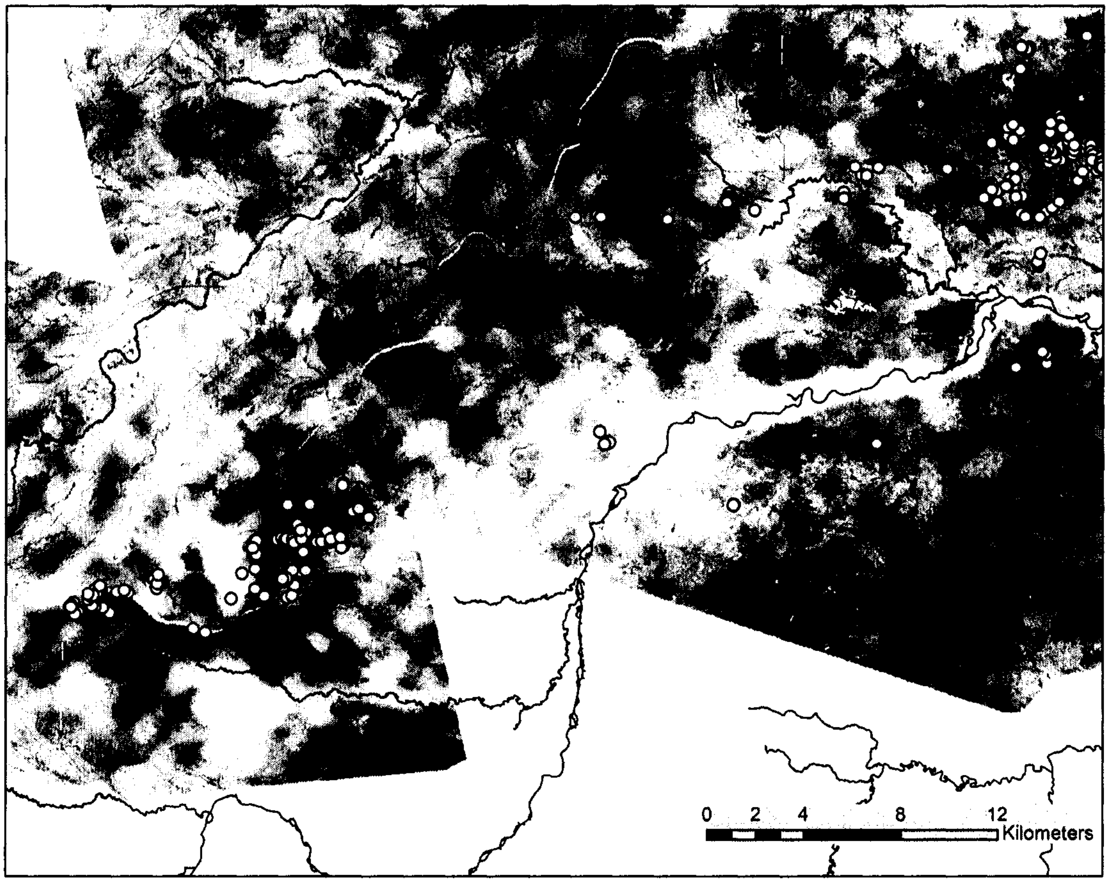


Figure 3-5: Estimated coefficients for several year-round variables from a west-central Alberta caribou RSF over three seasons. Positive coefficients correspond to selection, while negative values correspond to avoidance. Variables included were: distance to nearest seismic line (dtseismic), proportion cutblock within 1-km^2 (prpcb1k), proportion white spruce within 1-km^2 (sw_1km), distance to nearest river (dtriver), and value from the wolf RSF models (wolf RSF). 'Water', a categorical variable, was assessed against the reference category 'forest'. Positive distance-to variables refer to selection for areas farther from a particular feature. Error bars reflect adjusted standard errors by Huber-White sandwich estimators. Refer to Table 3-1 for a full description of covariate codes.

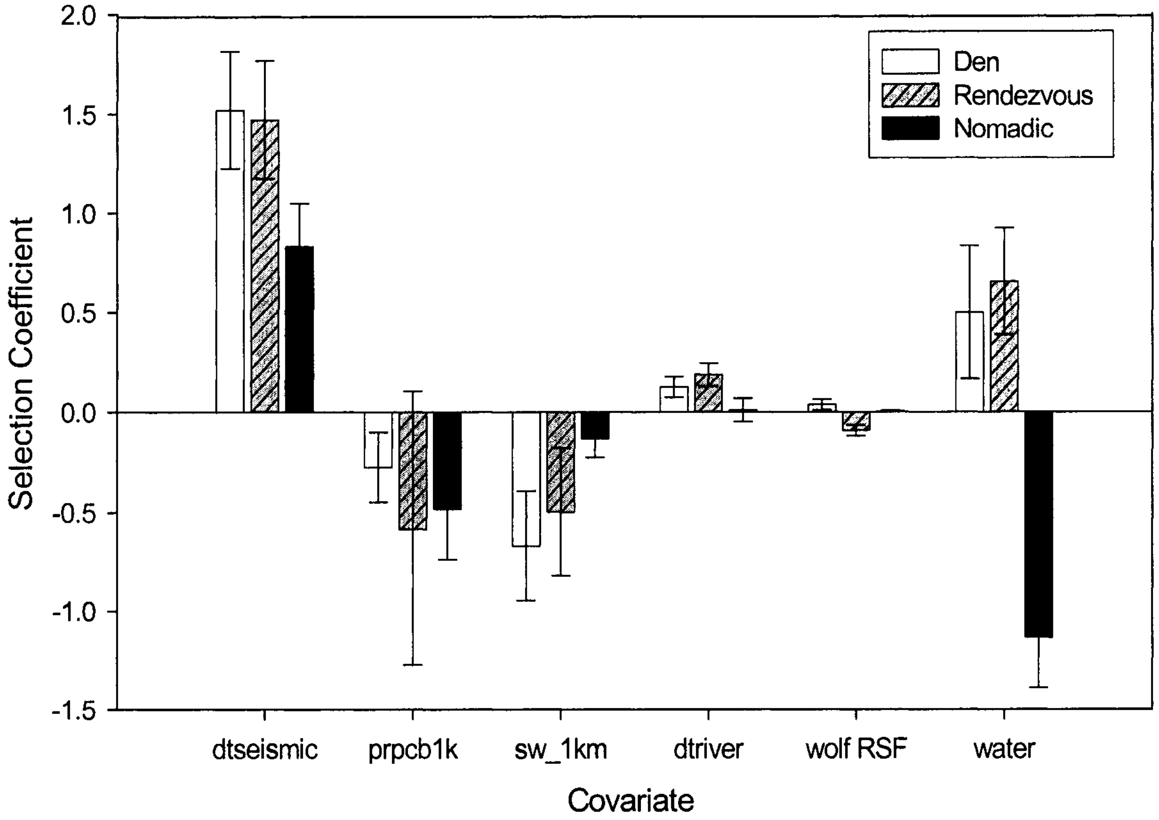


Figure 3-6: Relative index of predicted caribou use in the Little Smoky study area over three seasons. Caribou GPS data were collected in the Little Smoky and A la Pêche caribou ranges of west-central Alberta from 2002-2004.

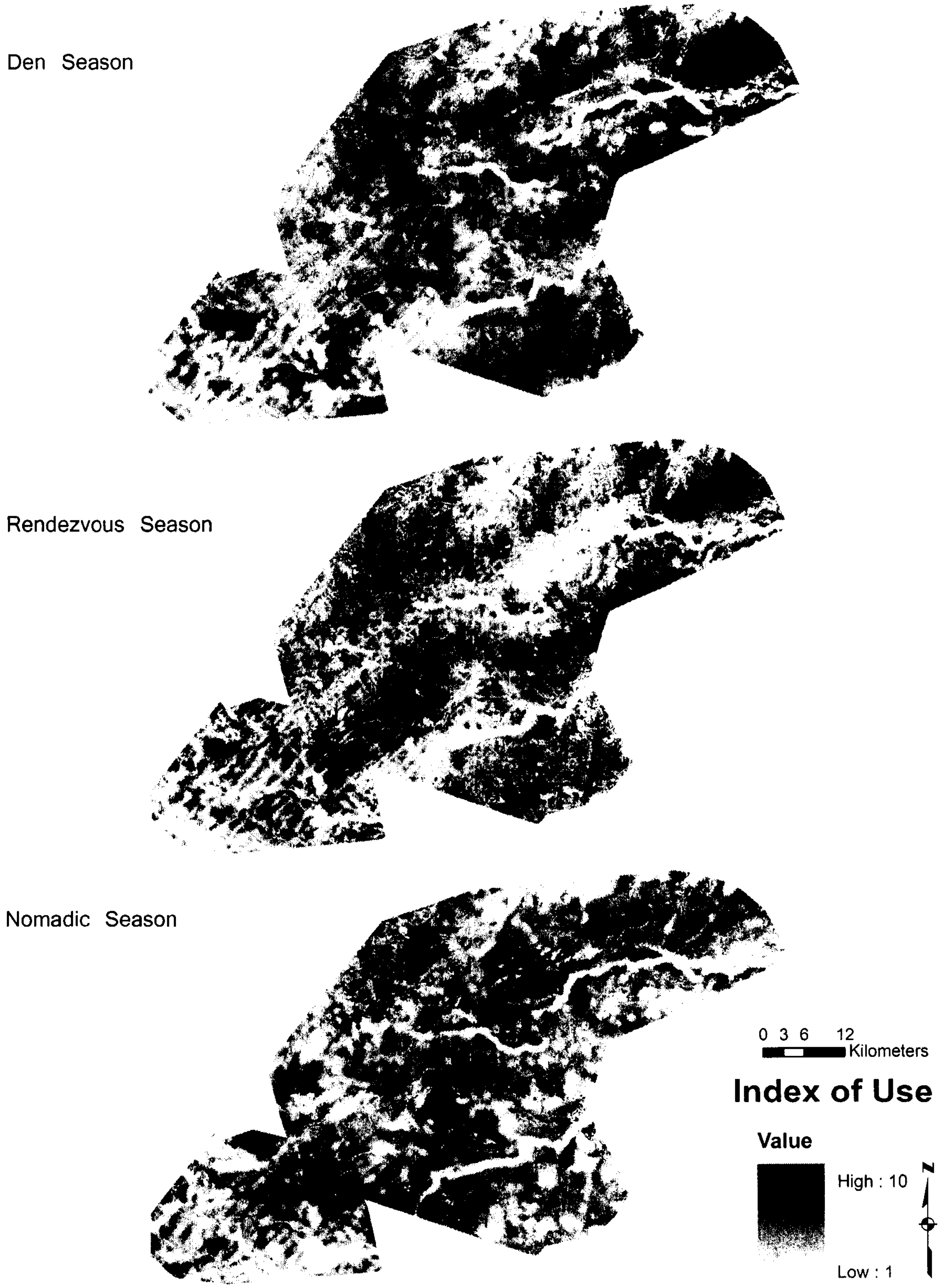


Figure 3-7: Spatial separation potential between wolves and caribou in the Little Smoky study area of west-central Alberta. Caribou have a higher relative probability of occurrence without wolves present in red areas, while wolves are predicted to occur without caribou in blue areas. Beige regions correspond to areas of predicted simultaneous selection, or non-selection, by both species.

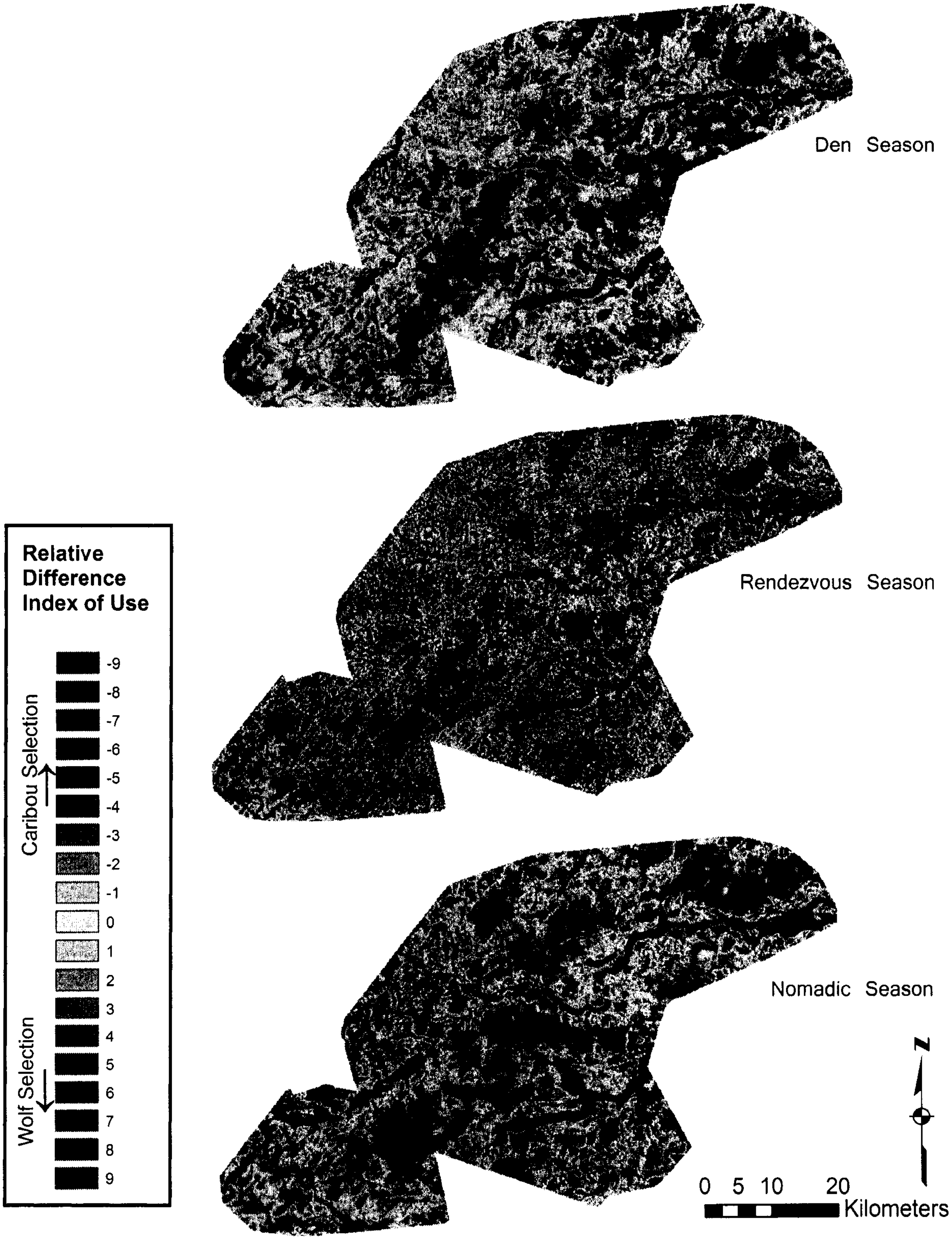


Figure 3-8: Difference in predicted index of use models for wolves and caribou in the Little Smoky and A la Pêche winter caribou ranges of west-central Alberta for the denning, rendezvous, and nomadic seasons. Positive values indicate areas more suitable for wolves with little to no caribou selection, while large negative values highlight areas selected by caribou with little to no wolf selection. Areas closer to zero indicate higher levels of co-occurrence between caribou and wolves.

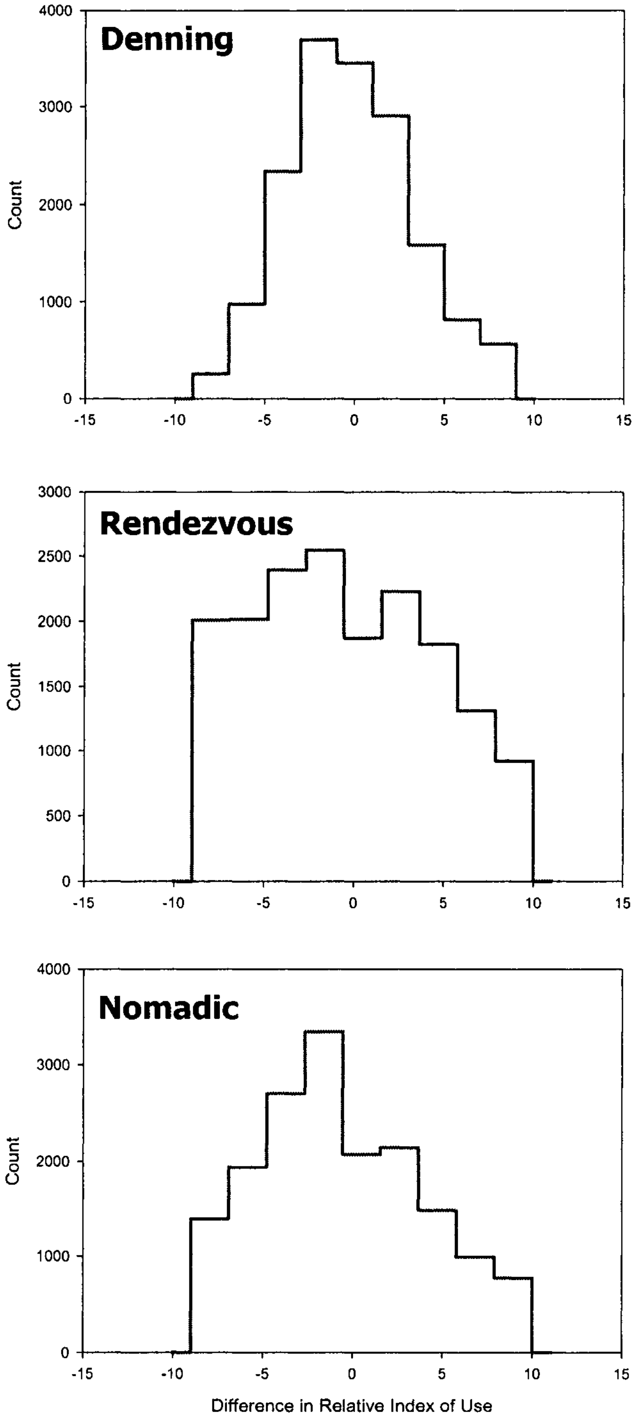


Figure 3-9: Spatial overlap potential between wolves and caribou in areas most likely to be selected by caribou within the Little Smoky study area of west-central Alberta. Wolves and caribou are predicted to overlap in areas that are red (0), while caribou are not predicted to overlap with wolves in blue areas (9). Black regions correspond to areas that caribou are not likely to select.

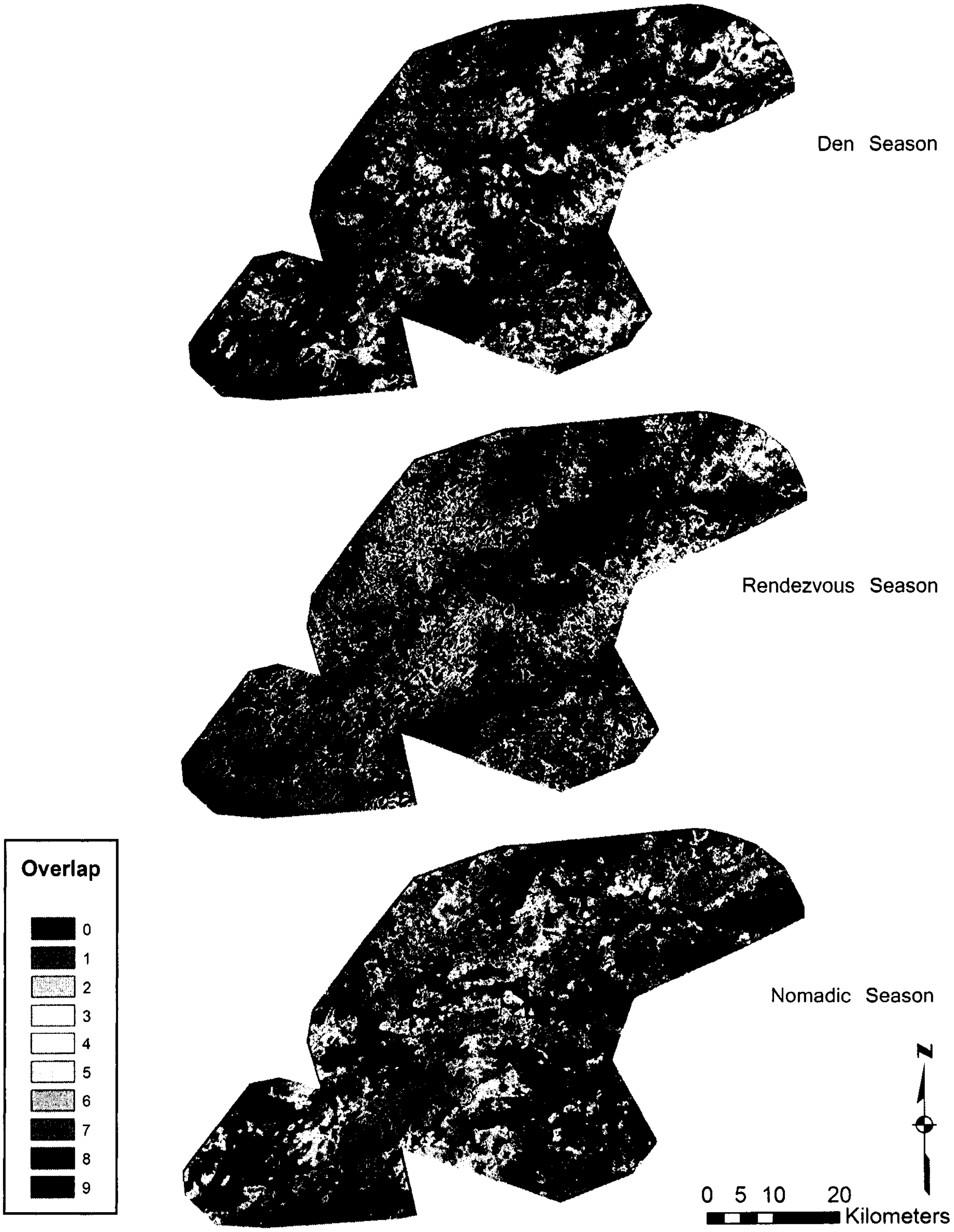


Figure 3-10: Absolute difference in predicted index of use models for wolves and caribou in areas selected by caribou. Data were collected in the Little Smoky study area of west-central Alberta during the denning, rendezvous, and nomadic seasons. Small values represent higher potential spatial overlap between wolves and caribou, while larger values are representative of increased spatial separation potential.

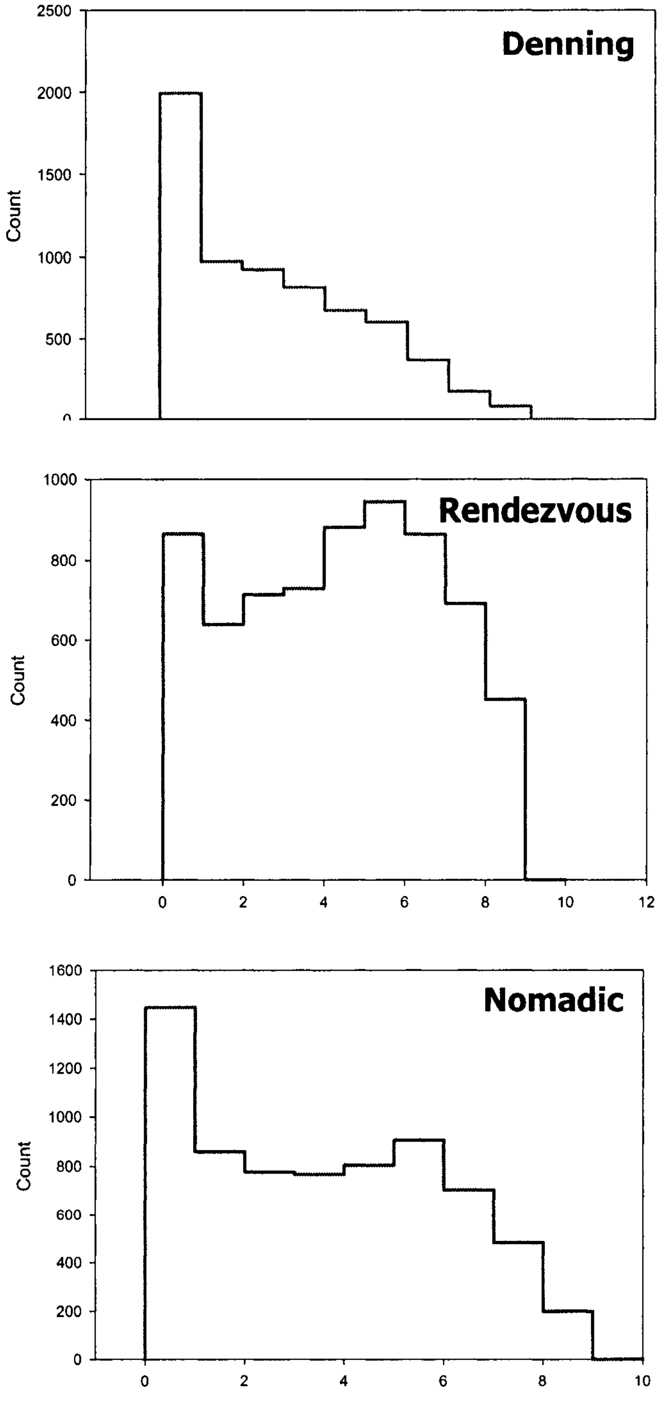
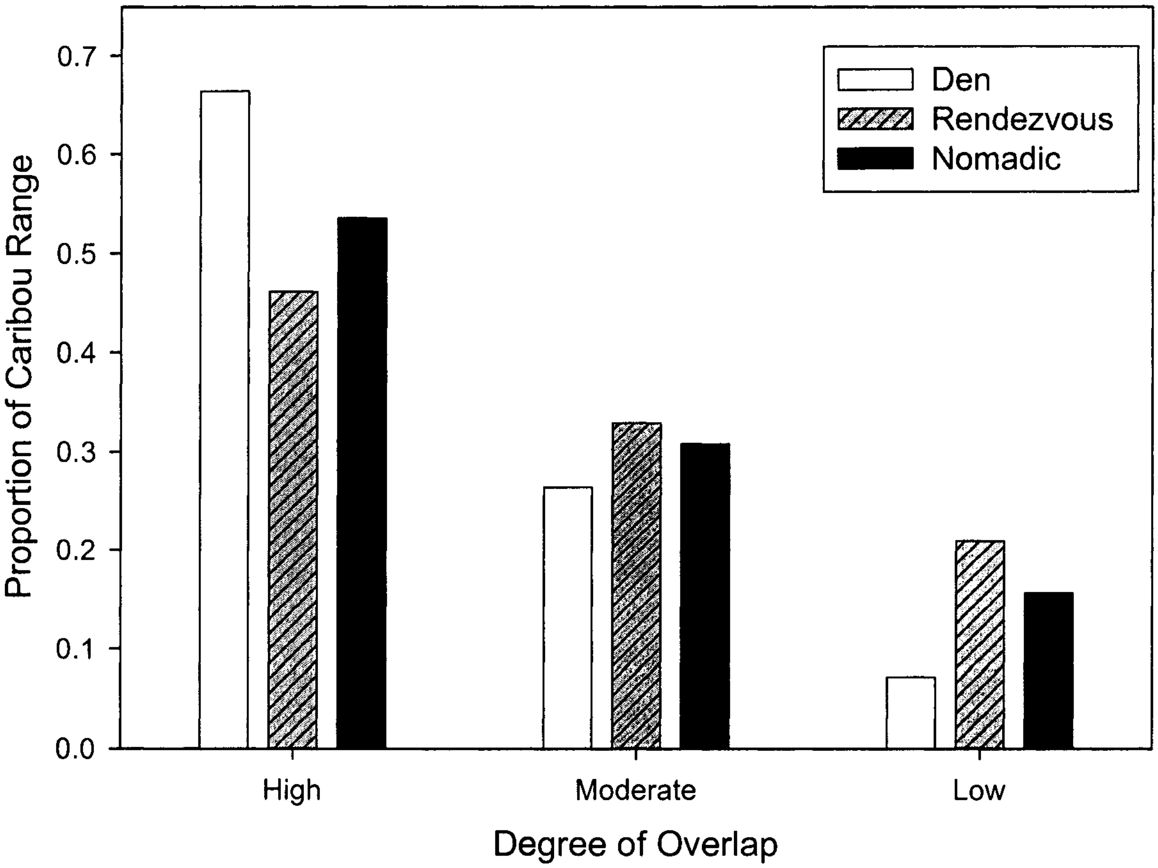


Figure 3-11: Proportion of the Little Smoky and A la Pêche winter caribou ranges of west-central Alberta in which potential overlap between caribou and wolves is high, moderate, or low. A much higher degree of overlap occurs in the den season, while the rendezvous season has the greatest potential for separation. However, overlap is substantial year-round.



7. Literature Cited

AEP (Alberta Environmental Protection). 1994. Natural regions of Alberta. Alberta Environmental Protection, Edmonton, AB. Available at http://www3.gov.ab.ca/srd/forests/fmd/timber/map4.html

Alberta Woodland Caribou Recovery Team. 2005. Alberta woodland caribou recovery plan 2004/05-2013/14. Alberta Sustainable Resource Development, Fish and Wildlife Division, Alberta Species at Risk Recovery Plan No. 4. Edmonton, AB.

Anderson, R.B. 1999. Peatland habitat use and selection by woodland caribou (*Rangifer tarandus caribou*) in northern Alberta. M.Sc. Thesis, University of Alberta. Edmonton, AB.

Andison, D.W. 1998. Temporal patterns of age-class distributions on foothills landscapes in Alberta. Ecography **21**:543–550.

Apps, C.D., B.N. McLellan, T.A. Kinley, and J.P. Flaa. 2001. Scale-dependent habitat selection by mountain caribou, Columbia Mountains, British Columbia. Journal of Wildlife Management **65**:65-77.

Beckingham, J.D., and J.H. Archibald. 1996. Field guide to ecosites of northern Alberta. Northern Forestry Centre, Edmonton, AB.

Bergerud, A. T. 1974. Decline of caribou in North America following settlement. Journal of Widlife Management **38**:757-770.

Bergerud, A.T. 1988. Caribou, wolves and man. Trends in Ecology & Evolution **3**:68-72.

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

Bergerud, A.T., and J.P. Elliott. 1986. Dynamics of caribou and wolves in northern British Columbia. Canadian Journal of Zoology **64:** 1515-1529.

Bergerud, A.T., and R.E. Page. 1987. Displacement and dispersion of parturient caribou at calving as an antipredator tactic. Canadian Journal of Zoology **65**:1597-1606.

Beyer, H., 2005. Hawth's Tools, an extension for ArcGIS (ArcMap). Available at: http://spatialecology.com/

Bjorge, R.R. 1984. Winter habitat use by woodland caribou in west-central Alberta, with implications for management. *In* Fish and Wildlife Relationships in Oldgrowth Forests, Proceedings of a Symposium held in Juneau, Alaska, 1982. Eds. W. R. Meehan, T. R. Merrel, and T. A. Hanley. American Institute of Fisheries Research Biology, Morehead City, NC. Pp. 335–342.

Boyce, M.S., P.R. Vernier, S.E. Nielsen, and F.K.A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling **157:**281-300.

Bradshaw, C.J.A., D.M. Hebert, A.B. Rippin, and S. Boutin. 1995. Winter peatland habitat selection by woodland caribou in northeastern Alberta. Canadian Journal of Zoology **73:**1567-1574.

Brown, W. K., and D.P. Hobson. 1998. Caribou in west-central Alberta – information review and synthesis. Prepared for The Research Subcommittee of the West-central Alberta Caribou Standing Committee. Terrestrial & Aquatic Environmental Managers Ltd., Calgary, AB.

Brown, W.K. 1998. Integrating woodland caribou needs and forestry: perspectives of Alberta's forest industry. Rangifer **Special Issue No. 10:**213-219.

Coxson, D.S., and J. Marsh. 2001. Lichen chronosequences (postfire and postharvest) in lodgepole pine (*Pinus contorta*) forests of northern interior British Columbia. Canadian Journal of Botany **79:**1449-1464.

Cumming, H.G. 1996. Managing for caribou survival in a partitioned habitat. Rangifer **Special Issue No. 9:**171-179.

Cumming, H.G., D.B. Beange, and G. Lavoie. 1996. Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared predation risk. Rangifer **Special Issue No. 9:**81-94.

Darby, W.R., and L.S. Duquette. 1986. Woodland caribou in northern Ontario, Canada. Rangifer **Special Issue No. 1**:87-93.

D'Eon, R.G., and D. Delparte. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. Journal of Applied Ecology **42**:383-388.

Dunford, J.S. 2003. Woodland caribou-wildfire relationships in northern Alberta. M.Sc. Thesis, University of Alberta, Edmonton, AB.

Dyer, S.J., J.P. O'Neill, S.M. Wasel, and S. Boutin. 2001. Avoidance of industrial development by woodland caribou. Journal of Wildlife Management **65:**531-542.

Dyer, S.J., J.P. O'Neill, S.M. Wasel, and S. Boutin. 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. Canadian Journal of Zoology **80:**839-845.

Dzus, E. 2001. Status of the woodland caribou (*Rangifer tarandus caribou*) in Alberta. Alberta Environment, Fisheries and Management Division, and Alberta Conservation Association, Wildlife Status Report No. 30, Edmonton, AB.

Edmonds, E.J. 1988. Population status, distribution and movements of woodland caribou in west-central Alberta. Canadian Journal of Zoology **66**:817-826.

Edmonds, E.J., and M. Bloomfield. 1984. A study of woodland caribou (*Rangifer tarandus caribou*) in west-central Alberta, 1979-1983. Alberta Energy and Natural Resources Fish and Wildlife Division.

Edmonds, E.J. 1993. Winter distribution of woodland caribou in the Little Smoky River area, November 1992 to March 1993. Alberta Fish and Wildlife Division, Edson, AB.

Energy Resources Conservation Board (ERCB). 1992. Report 92-A: ultimate potential and supply of natural gas in Alberta. Energy Resources Conservation Board, Calgary, AB.

Fielding, A.H., and J.F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation **24**:38-49.

Gustine, D.D. 2005. Plasticity in selection strategies of woodland caribou (*Rangifer tarandus caribou*) during winter and calving. MSc Thesis, University of Northern British Columbia, Prince George, BC.

Hervieux, D., J. Edmonds, R. Bonar, and J. McCammon. 1996. Successful and unsuccessful attempts to resolve caribou management and timber harvesting issues in west central Alberta. Rangifer **Special Issue No. 9:**185-191.

Holt, R.D. 1977. Predation, apparent competition and the structure of prey communities. Journal of Theoretical Biology **12**:197-229.

Hosmer, D.W., and S. Lemeshow. 1999. Applied survival analysis: regression modeling of time to event data. John Wiley & Sons, New York, NY.

Hosmer, D.W., and S. Lemeshow. 2000. Applied logistic regression, 2nd edn. John Wiley & Sons, New York, NY.

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

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

Johnson, C.J., K.L. Parker, D.C. Heard, and D.R. Seip. 2004a. Movements, foraging habits, and habitat use strategies of northern woodland caribou during winter: Implications for forest practices in British Columbia. BC Journal of Ecosystems and Management **5**:22–35.

Johnson, C.J., D.R. Seip, and M.S. Boyce. 2004b. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. Journal of Applied Ecology **41**:238-251.

Klein, D.R. 1971. Reaction of reindeer to obstructions and disturbances. Science **173:**393-398.

Kunkel, K.E., and D.H. Pletscher. 2001. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. Canadian Journal of Zoology **78:**150-157.

Kuzyk, G.W. 2002. Wolf distribution and movements on caribou ranges in west-central Alberta. M.Sc. Thesis, University of Alberta, Edmonton, AB.

Lessard, R.B. 2005. Conservation of woodland caribou (Rangifer tarandus caribou) in west-central Alberta: a simulation analysis of multi-species predator-prey systems. Ph.D. Thesis, University of Alberta, Edmonton, AB.

Manly, B.F.J., L.L. McDonald, D.L. Thomas, T.L. McDonald, and W.P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edn. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Mahoney, S.P., and J.A. Virgl. 2003. Habitat selection and demography of a nonmigratory woodland caribou population in Newfoundland. Canadian Journal of Zoology **81**:321-334.

McLoughlin, P. D., E. Dzus, B. Wynes, and S. Boutin. 2003. Declines in populations of woodland caribou. Journal of Wildlife Management **67**:755-761.

Mercer E., S. Mahoney, K. Curnew, and C. Finlay. 1985. Distribution and abundance of insular Newfoundland caribou and the effects of human activities. *In* Proceedings of the Second North American Caribou Workshop. Eds. T.C. Meredith and A.M. Martell. McGill Subarctic Research Paper No. 40, Montreal, PQ. Pp 16-32.

Mohr, C.O. 1947. Table of equivalent populations of North American mammals. American Midland Naturalist **37:**223-249.

Nielsen, S.E. 2005. Habitat ecology, conservation, and projected population viability of grizzly bears (*Ursus arctos* L.) in west-central Alberta, Canada. Ph.D. Thesis, University of Alberta, Edmonton, AB.

Oberg, P.R. 2001. Responses of mountain caribou to linear features in a west-central Alberta landscape. M.Sc. Thesis, University of Alberta, Edmonton, AB.

Rettie, W.J., and F. Messier. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. Canadian Journal of Zoology **76**:251-259.

Rettie, W.J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography **23**:466-478.

Rettie, W.J., J.W. Sheard, and F. Messier. 1997. Identification and description of forested vegetation communities available to woodland caribou: relating wildlife habitat to forest cover data. Forest Ecology and Management **93**:245-260.

Rhemtulla, J.M. 1999. Eighty years of change: The montane vegetation of Jasper National Park. M.Sc. Thesis, University of Alberta, Edmonton, AB.

Schooley, R.L. 1994. Annual variation in habitat selection - patterns concealed by pooled data. Journal of Wildlife Management **58**:367-374.

Saher, D.J. 2005. Woodland caribou habitat selection during winter and along migratory routes in West-Central Alberta, M.Sc. Thesis, University of Alberta, Edmonton, AB.

Seip, D.R. 1991. Predation and caribou populations. Rangifer **Special Issue No. 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.

Sinclair, A.R.E., R.P. Pech, C.R. Dickman, D. Hik, P. Mahon, and A.E. Newsome. 1998. Predicting effects of predation on conservation of endangered prey. Conservation Biology **12**:564-575.

Smith, K.G. 2004. Woodland caribou demography and persistence relative to landscape change in west central Alberta. M.Sc. Thesis, University of Alberta. Edmonton, AB.

Smith, W.T., and R.D. Cameron. 1983. Responses of caribou to industrial development on Alaska's Arctic Slope. Acta Zoologica Fennica **175**:43-45.

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

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

Szkorupa, T.D. 2001. Multi-scale habitat selection by mountain caribou in west-central Alberta. M.Sc. Thesis, University of Alberta, Edmonton, AB.

Thomas, D.C., and D.R Gray. 2002. Update COSEWIC status report on the woodland caribou *Rangifer tarandus caribou* in Canada. *In* COSEWIC assessment and update status report on the Woodland Caribou *Rangifer tarandus caribou* in Canada. Ottawa, ON.

Thomas, D.L., and E.J. Taylor. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management **54**:322-330.

Thomas, D.C., E.J. Edmonds, and W.K. Brown. 1996. The diet of woodland caribou populations in west-central Alberta. Rangifer **Special Issue No. 9:**337-342.

Villmo, L. 1975. Plenary Session: potential impact of accelerated northern development on caribou and reindeer populations and ecology – the Scandinavian viewpoint. Proceedings of the First International Reindeer/Caribou Symposium, Fairbanks, Alaska, 1972. Biology Paper University of Alaska, Special Report No. 1. West Central Alberta Caribou Standing Committee.

Weclaw, P., and R. J. Hudson. 2004. Simulation of conservation and management of woodland caribou. Ecological Modelling **177**: 75 – 94.

White, H. 1980. A heteroskedasticity-consistent covariance matrix estimator and a direct test for heteroskedasticity. Econometrica **48**:817–838.

Whitten, K.R., and R.D. Cameron. 1983. Movements of collared caribou, *Rangifer tarandus*, in relation to petroleum development on the Arctic Slope of Alaska. Canadian Field Naturalist **97**:143-146.

Young, D.D. Jr., and T.R. McCabe. 1997. Grizzly bear predation rates on caribou calves in northeastern Alaska. Journal of Wildlife Management **61**:1056-1066.

Chapter 4: Experimental approaches to controlling wolf (*Canis lupus*) movements in highly modified forests

1. Introduction

Exploration and development of oil and gas reserves in boreal Canada is altering the structure of forested landscapes. In Alberta, where the majority of Canada's oil and gas deposits lie, exploration activities since the 1950s have generated 1.5 million-km of seismic lines, which are generally 5- to 8-m wide and cleared of all vegetation at the time of establishment (Alberta Environmental Protection 1998). Seismic lines are created as access pathways for seismic exploration equipment, facilitating identification of subsurface hydrocarbon reserves. In general, regeneration of forest vegetation on seismic lines occurs slowly or not at all due to compaction from machinery, re-visitation by seismic crews, competition from non-native species, recreational use of lines, and insufficient light penetration (Revel *et al.* 1984, Osko and MacFarlane 1999). In some forest types, seismic lines persist relatively unchanged for decades.

There is evidence that linear corridors in forested landscapes influence wildlife movements and distributions (Jalkotzy 1997, James 1999). In areas without extensive human activity, linear features may reduce energetic demands of movement, creating attractive travel corridors for wide-ranging predators (Musiani *et al.* 1998). For example, wolves in northern Alberta selected areas near seismic lines and moved more quickly along these linear features than through the forest (James 1999). In Jasper National Park, wolves used linear features as travel routes and selected areas near human-made linear infrastructure (Whittington *et al.* 2005). Within the Little Smoky region in west-central Alberta, wolves selected areas closer to seismic lines than available during the rendezvous season (1 July to 20 September) (Chapter 2). Linear corridors may also affect wolf-prey dynamics through increased predator efficiency and higher encounter and kill rates (James and Stuart-Smith 2000).

Implications of increased predator mobility in fragmented landscapes are relevant for woodland caribou (*Rangifer tarandus caribou*), a threatened species in Canada, whose anti-predator strategy is to spatially separate and occupy habitats where coexisting ungulate species and their predators are rare (Bergerud 1974, 1992; Bergerud and Elliot 1986, Bergerud and Page 1987, Bergerud 1990, Seip 1992). Declines in boreal woodland caribou in Alberta due to landscape change (Stuart-Smith *et al.* 1997) have led to concerns that the presence of linear corridors may be compromising woodland caribou survival strategies via increased encounter rates with, and subsequent predation by, wolves: James and Stuart-Smith (2000) demonstrated that wolf-killed caribou were located closer to linear features than random; Kinley and Apps (2001) concluded that mountain caribou mortality was higher in areas with more young forest, higher road density, and a higher fragmentation index; and in west-central Alberta, Smith (2004) noted a negative correlation between adult female survival and road and cutblock density. In landscape simulation trials, encounter rates alone have been shown to strongly influence persistence of caribou, even when spatial overlap between wolves and caribou is relatively low (Lessard 2005).

In cases where habitat has been significantly altered, wolves may reduce or even eliminate caribou populations (Thomas and Gray 2002). Particularly in small populations, changes in predation pressure on caribou may have significant effects on population dynamics and local herd persistence (James and Stuart-Smith 2000). Recent modelling analyses from west-central Alberta, using empirical demographic parameter estimates from the west-central region, suggest that if seismic lines are facilitating wolf movement and increasing encounter rates between wolves and caribou, small populations will continue to decline and eventually succumb to high predation levels (Lessard 2005).

The Little Smoky caribou herd has experienced precipitous declines and exceptionally low recruitment in recent years; it is the most rapidly declining herd in Alberta (Dzus 2001, Thomas and Gray 2002). The Little Smoky range is highly influenced by industrial development, with more than 3500-m/km^2 of linear features and 5.5-ha/km^2 of cutblocks (Smith 2004). Potential increases in wolf efficiency and consequences of higher encounter rates have created pressure to mitigate the effects of industrial development on caribou decline. In 2001, the Boreal Caribou Committee identified restoration of seismic lines as a key research priority (BCC 2001). The Caribou Range Restoration Project (CRRP) was formed as a result, with a goal of implementing and examining mitigation techniques for linear disturbances in caribou ranges.

There are several methods proposed for seismic line mitigation in caribou ranges (CRRP 2005). I was interested in testing hypotheses related to influencing wolf mobility on linear features and assessing the efficacy of seismic line-blocking as a tool to limit predator-mobility. This direct technique requires physical alteration of seismic lines over a short time-frame, as opposed to recovering the original vegetation structure which necessitates thorough examination of site conditions and advanced planning for longer-term change. Possible line-blocking methods, which are hypothesised to reduce predator mobility on linear corridors, include mounding (redistributing soil into large mounds and depressions), rollback of woody debris (covering line with downed trees and organic material), tree-felling (deliberately felling trees over line), fences (erecting fences across lines), or fladry (hanging free-flowing ribbons, see Musiani and Visalberghi 2001). In cooperation with the Caribou Range Restoration Project, I chose to implement tree-felling, which requires less specialised equipment than mounding and simpler site requirements than rollback. Furthermore, no research exists on the technique, but it has been proposed as an effective deterrent to predators (see CRRP 2005 for more details). An assumption underlying hypotheses of influencing predator mobility is that wolves use seismic lines as effective means of travelling within their territories. Analyses in northern Alberta, while conducted in an area where linear corridor densities were three times lower than the area in which the line-blocking experiment was implemented, have reported elevated wolf use of linear corridors (James 1999). However, these analyses were based on 353 points over a short time-frame in the late winter; recent improvements in GPS capabilities, changes in seismic line density, and ability to examine patterns year-round warrant exploratory re-examination of wolf use of seismic lines.

Within one wolf territory overlapping the Little Smoky caribou range, I designed an experiment to examine the effectiveness of tree-felling in reducing wolf-use of linear developments. While most wolf movement and habitat-use studies have been conducted in the winter months when snow-tracking can provide supplemental data on wolf behaviours, I examined wolf use of linear features during the summer months, when caribou mortality rates are higher (details in Chapter 3) and seismic lines are predicted to be selected by wolves. I also used remote cameras to examine the response of other large mammals in the region to line-blocking by tree-felling. Finally, I explored an underlying assumption of hypotheses related to seismic line-blocking as a wolf-mobility tool: wolves select seismic lines for movement paths. My specific objectives were to: 1) assess wolf response to line-blocked sites versus controls; 2) quantify rates-of-use of other large mammals using seismic lines; and 3) examine wolf use of seismic lines in the Simonette territory. Based on the hypothesis that line-blocking will influence animal use of linear corridors, I tested the following predictions: 1) wolves will not be located in sites where seismic lines have been blocked, but will occur in control areas; 2) rates-of-use of linear corridors, as measured by remote cameras, will be higher outside of blocked areas than inside, but no difference between outside and inside will occur in the controls.

2. Study Area

The line-blocking experiment was implemented in high wolf-use areas within the Simonette wolf pack's territory. At the time of the study, the territory of the Simonette pack overlapped the Little Smoky caribou range, which is located east of Grande Cache, Alberta, Canada (Figure 4-1). The area contains several major rivers, many small creeks, and few lakes. Elevations range from 850- to 1500-m, and the climate is subarctic with short, wet summers and long, cold winters (Smith *et al.* 2000).

The Rocky Mountain Foothills region is well-forested, and has been described in detail by Edmonds and Bloomfield (1984). Dry sites support primarily lodgepole pine (*Pinus contorta*) or lodgepole pine and black spruce (*Picea mariana*) forests interspersed with Douglas fir (*Pseudotsuga menziesii*). Rare patches of aspen (*Populus tremuloides*) are located on south-facing, well-drained slopes. Willow (*Salix* spp.) and birch (*Betula glandulosa*) meadows, interspersed with dry grassy benches, are found along the drainages. As well, white spruce (*Picea glauca*) is largely restricted to riparian areas. Lowland areas were dominated by a mixture of larch (*Larix laricina*) and black spruce and made up substantial portion of the range.

Major land use activities include logging, oil and gas exploration and development, off-road vehicle use (*e.g.* snowmobile, all-terrain vehicles), recreational hunting, and commercial trapping (Brown and Hobson 1998). Access in the area exists in the form of all-weather and dry-weather resource roads, and rights-of-way for pipelines, power lines and seismic lines (Smith *et al.* 2000). The Simonette pack's range was bisected by Deep Valley Creek, to the east of which there were low levels of forest harvesting.

3. Methods

3.1 Study Design

Unlike past research assessing wolf use of linear features, I did not use individual seismic lines as the experimental unit (*e.g.* James 1999). Considering errors in acquiring GPS fixes (Frair *et al.* 2004) and the high density of linear features in the study area, I felt that objectively and accurately assigning GPS location points to seismic lines would be challenging and potentially biased. Instead, I conducted power analyses based on previous location data from the Simonette wolf pack to guide the choice of number of sites, site size, site shape, and distribution and location of sites. I chose to implement square experimental units (500-m x 500-m), which represented the best trade-off between probability of observing use with GPS data and financial cost of treatment.

Sites were randomly placed within areas of high wolf-use as defined by kernel home range estimates and assigned to one of two treatments: control or block. By choosing areas that had a high probability of wolf-use, I was more likely to detect effects on wolves where they existed. I stratified the design based on presence of cutblocks, informed by past analyses that suggested wolf affinity for cutblocks (Kuzyk 2002): treatments were equally distributed between areas with high harvest intensity and little to no harvest intensity. In total, I identified *a priori* 44 treatment areas and 44 controls.

3.2 Field methods

Blocked sites were treated with tree-felling, where a hypothesised impediment to movement was created by felling adjacent coniferous trees across seismic lines. At each site, two or three trees were felled across each seismic line every 10- to 15-m. All seismic lines that entered a 500-m^2 site were blocked for 200-m the site's edge toward the centre (Figure 4-2). For example, if a site was traversed by two seismic lines, four blockages of 200-m each were created. A large portion of each line within a site was treated, depending on the line's angle and location within a site (*e.g.* Figure 4-2a). All sites were treated in April 2004, before the wolf denning period. Controls and blocks were surveyed by helicopter to ensure criteria of both site types were met and to confirm GPS coordinates of blockages.

Wolves were captured as part of a larger, on-going research program in the Little Smoky caribou range. Three GPS-3300 collars were deployed on wolves of the Simonette Pack (Lotek Wireless, Newmarket, Ontario, Canada). Collars collected detailed location data over the summer and fall of 2004. Data were collected on a variable schedule, which maximised the trade-off between number of location points and available battery life. The majority of the data were collected in 30 minute or 1 hour intervals.

In addition to GPS collars, I monitored 16 of the sites with remote infrared cameras. I used infrared-triggered, commercially made Trailmaster TM-1500,TM-1550 (Goodson and Associates Inc., Lenexa, Kansas) and DeerCam (DeerCam, Park Falls, Wisconsin) active camera trap units that consisted of a 35mm weather-resistant camera, an infrared transmitter, and (for the TM cameras) a receiver. Cameras were triggered when the infrared beam was broken by a passing animal. Camera units were attached to secure trees on either side of the linear feature so that the beam was set at a height of approximately 0.25-m. Cameras were set to be active 24 hours per day and stations were neither baited nor scented. After initial placement, cameras were checked over a three day period every 12-15 days. Care was taken to minimize scent left at camera sites. Two cameras were placed on one seismic line at each site (Figure 4-2). Cameras were approximately 500-m apart from each other: one at the exterior of the blocked sites and one at the interior. Cameras monitored sites from mid-May to late-September 2004.

Data were prepared in ArcGIS 9.0 (Environmental Systems Research Institute, Redlands, California) and then transferred to STATA 8.2 (StataCorp LP, College Station, Texas) for statistical analyses.

3.3 Statistical analyses

GPS data

I was interested in differences between treatments; therefore, I included only GPS location points that fell within the boundaries of control and blocked sites. I used two approaches to explore GPS location data: 1) analysis of median use of all sites within each treatment, as identified by number of GPS locations, and 2) logistic regression of wolf presence, identified by presence of one or more GPS location(s) in the site.

Data were differentially corrected with base-station data. I removed all GPS locations with a PDOP of >12, indicating poor precision. Although PDOP is not always a good measurement of precision, there is a consistent trend among studies where higher PDOP values equate to higher location error (D'Eon and Delparte 2005). In some cases, accuracy can be substantially increased by imposing a PDOP limit (D'Eon and Delparte 2005).

I compared the number of GPS locations in control sites to the number of locations in blocked sites. I used all data that fell within either blocks or controls and then screened for independence: if wolves were travelling together, or if an individual used a site during consecutive locations, data were grouped and one independent visit was recorded. Data were non-normally distributed and did not meet the assumptions of an independent test of mean, thus I used a Wilcoxon-Mann-Whitney non-parametric test (Zar 1999).

Subsequently, I used a binary response variable within a logistic regression to model the probability that a site would be used or not used and ascertain the importance of treatment in predicting wolf use of a site as:

$$P_{use} = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n)} \qquad \text{Equation 4.1}$$

where P_{use} is the probability of using a site, β_0 is the regression constant and $\beta_1 .. \beta_n$ are coefficients estimated for variables $x_1 ... x_n$ (Hosmer and Lemeshow 2000).

Initially, wolf presence was modelled as a function of treatment alone. However, while the study design attempted to control for variation in habitat, wolf response to line-blocking could have been influenced by other metrics within the sites, independent of treatment. Thus, in subsequent models, I incorporated several habitat and environmental variables in an attempt to explain and further understand wolf presence as measured by GPS locations (Table 4-1). As one of the explanatory variables, I included an index of wolf use (wolf resource selection function from Chapter 2) for the denning season, which was correlated with the index during the rendezvous season. Because the majority of wolf GPS points were collected during the denning season, I retained the denning RSF as an estimate of wolf habitat selection. In addition to including a coarse measure of ungulate biomass (see Chapter 2) in the logistic models, I explored relationships between wolf presence (GPS locations) and ungulate presence using data from remote cameras.

Camera data

Remote cameras were not wolf-specific and photographed multiple other species travelling along seismic lines. As individuals of these species were un-marked, I defined independent observations based on time-between-photos: each observation was assumed independent unless an individual animal was observed several times within 1-5 minutes, which then equalled one observation. Also, because most sites were infrequently used, I was able to distinguish some individuals (in addition to consecutive locations within minutes), because of markings, presence of antlers, and colour. Where individuals were observed using a line multiple times over a longer time frame (*e.g.* days), the animal was assumed to have left and returned to the site and, in these circumstances, each observation constituted independent use. I modelled the total number of animal observations (count) as the response variable by which to identify the effects of the treatment.

Cameras were intended to monitor effects of blocking at an individual animal level, before and after encounter of a line-block. At control sites, I expected that an individual would be observed sequentially at the interior and exterior (or vice versa) camera as the animal travelled along the line. If tree-felling influenced movement, these consecutive recordings of an individual animal would not occur. However, due to circumstances of weather (heavy rain breaking the infra-red beam), interference by animals, and logistical challenges (*e.g.* dead batteries, infrequent checks), both cameras at a site were rarely simultaneously operational and it was not possible to analyse observation data at an individual level. Rather, I analysed animal observations within treatment types (control or block) as two separate tests with different predictions. At blocked sites, I expected to observe more animals (of each species) at exterior as compared to interior camera locations. At control sites, I predicted that the number of animals observed at exterior and interior camera locations would not differ as animals would not be deterred from using the seismic line.

The count of observations, fit to a negative binomial regression model to account for overdispersion in the response variable, was modelled as a function of two independent variables: 1) camera location (inside versus outside the treatment); and 2) five levels of species, grouped within similar taxonomic levels where data were limited (bear, deer, moose, woodland caribou, and wolf). For the categorical species-level variable, I used indicator coding and selected as a reference category the most prevalent class (*e.g.* Nielsen 2005). For these analyses, the reference category was "moose", and all other species observations were compared in relation to "moose". I accounted for factors that might influence the outcome of the analyses through inclusion of additional terms in the regression model. For example, each camera was operational for a different number of hours because of weather, animal interference, or dead batteries; therefore I entered an exposure time variable which reflected the amount of time that seismic lines were monitored for each camera location. I accounted for lack of independence within each site by specifying the robust cluster option to calculate variance through a Huber-White sandwich estimator (White 1980, Nielsen *et al.* 2002). Sandwich estimators assume that observations are independent across sites, but not necessarily independent within sites (Hardin and Hilbe 2001, Long and Freese 2003). Initial examination of treatment effects were examined with regression and followed with a Wald test to examine potential species*treatment interactions.

Wolf use of seismic lines

A key assumption in blocking seismic lines is that wolves utilise these features regularly for travelling through their territory. Following James (1999), I compared the proportion of GPS points within 50-m increments of seismic lines to what was available across the Simonette pack's territory, as defined by minimum convex polygons of individuals within the pack. I examined this pattern seasonally, based on seasons defined in Chapter 2.

In addition to examining proximity of GPS points, I also explored the use of lines by calculating the overall proportion of *movement paths* that existed within 50-m of a seismic line (*e.g.* Figure 4-3). Movement paths were created by joining GPS points and seismic lines were buffered by 50-m on each side. I expected that a large proportion of wolf movement paths would be located within this 50-m buffer if wolves were using seismic lines. Furthermore, I expected that wolves travelling along seismic lines would exhibit a greater proportion of long movement paths within the 50-m buffer, whereas wolves crossing seismic lines would exhibit a greater proportion of small movement paths within the 50-m buffer.

Although straight-line distances between GPS points do not provide an exact representation of a wolf path, they approximate the most direct potential path between two GPS points. Inter-fix times of 15- or 30-minutes have been used in previous research on wolf movements (Musiani *et al.* 1998, Jedrzejewski *et al.* 2001). Data from this experiment had a median inter-fix time of 59 minutes. Although shorter inter-fix times would better describe overall wolf movements patterns, I was interested in examining the proportion travel time within 50-m of lines and the number of short (*i.e.* crossing) *versus* long (*i.e.* along) distances travelled within 50-m of a seismic line.

4. Results

Six blocked sites were not implemented according to my experimental design or were affected by human-use during the study. In addition, the helicopter survey flight revealed that four control sites were located in areas inconsistent with the original criteria. As a result, a total of 38 blocked sites and 40 control sites were retained for analyses.

4.1 GPS data

Three GPS collars deployed on wolves in the Simonette Pack returned 8648 location points over the course of the line-blocking study (late April to mid-October). Wolves were located 177 times (~2% of all locations) within the boundaries of either control (99) or blocked (78) sites. Overall, 45% of sites were used (35 of 78). Once locations were screened for independence (*i.e.* consecutive locations for the same animal or animals travelling together were removed), wolves were located 37 times in blocked sites and 47 times in control sites. Although an overall pattern of more GPS locations in control areas was apparent, tests of median did not detect a significant difference between blocked and control sites (z=0.87, p=0.384).

Among the 35 sites that were used, 15 were blocked and 20 were controls (Figure 4-4). Similarly, of the 43 sites that were not used, 23 were treated with line-blocking and 20 were controls. Although wolves used controls more than blocks, the difference was not significantly different from equal use of controls and blocks (p=0.25, one-sided binomial test). Furthermore, within a logistic regression, treatment was not a significant predictor of use and wolves were no more or less likely to use a control site in the simple model including only site type (p=0.351, log-likelihood = -53.2).

Variables in Table 4-1 were added to the logistic model to quantify the influence of habitat and environmental parameters in predicting wolf presence. Although the overall model fit improved (log-likelihood -45.2), treatment remained a non-significant predictor of wolf presence at blocked versus control sites (p=0.611). Significant predictors included distance to den (p=0.047), index of wolf use during denning (p=0.037), and terrain ruggedness index (p=0.032). The ungulate biomass index was not a significant predictor of wolf use of sites (p=0.977), nor were any of the additional habitat metrics (Table 4-2). Standard errors were substantial for the terrain ruggedness index and the relative index of wolf use (Table 4-2). This is likely related to small sample sizes and the declining reliability of estimates when there are few cases for each observed combination of independent variables.

Akaike's information criterion (AIC) was used to compare which of the two logistic models (treatment only *versus* treatment + habitat) best explained wolf use (Burnham and Anderson 2002). The AIC value for the full model was 108.42 and for the simple model, 110.43. Models that differ by $\leq$ 2 AIC points are not differentiated statistically (Burnham and Anderson 2002); therefore the addition of habitat variables did not improve the predictive capability of the model.

Seismic line use

Wolves in the Simonette pack used areas within 50-m of seismic lines in proportion to their availability over the course of the study (Figure 4-5, first set of bars). However, when I removed the effect of the den-site by deleting GPS points in the denning area, wolves used seismic lines slightly more than available. During the rendezvous season, wolves used areas within 50-m of seismic lines substantially more than available, indicating a strong seasonal effect (Figure 4-5).

Movement path (connected GPS points) analyses revealed that an average of 30% of all wolf movement paths were within 50-m of seismic lines. However, the majority of these movements were very short, indicating that wolves crossed seismic lines substantially more than they travelled along lines (Figure 4-6). This pattern was consistent during various seasons and across individuals.

4.2 Camera data

Control and blocked sites were monitored for 219 914 hours and 190 642 hours, respectively. Observations from one interior blocked camera location were not included, because the camera was not placed properly in the field. I used data from 7 interior control, 8 exterior control, 8 exterior block, and 8 interior block camera placements.

Remote cameras recorded 47 bears (53% black bear; 47% grizzly), 102 deer (73% white-tailed deer), 109 moose, 36 woodland caribou, and 16 wolves. The overall observation frequency for control sites was 0.73 observations per 1000 hours, and for blocked sites 0.78 observations per 1000 hours. Some sites were visited more than others, though the total number of observations corrected for exposure time across all sites did not vary substantially (Table 4-3). Across treatments, there was variation in frequency of observation for species groups, with moose and deer making up the majority of observations (Table 4-4).

Controls

The negative binomial regression indicated that, for all species combined, there was no difference in the number of observations per 1000 hours at exterior camera locations compared to interior camera locations ($p=0.813$). There were also no significant species*treatment interactions (Table 4.5), indicating that all individual species and groups were equally likely to be observed at either interior or exterior camera locations.

For individual species analysis, response by wolves was excluded from the analysis due to very low sample sizes (n=5) in control sites. There was no significant difference in rate-of-observation for moose, bears, deer, or caribou (Table 4.4).

Blocks

Wolves were observed more frequently at the exterior camera location. The wolf*treatment interaction was marginally significant (p=0.063); had the sample size (n=11) been larger I would have had greater power to detect a statistically-significant difference in wolf-use. Although no other observed effects were significant at the α = 0.05 level, there were variations in species response and trends. Number of observations per 1000 hours for moose was as predicted in response to the line-blocking: moose were observed more often at the exterior camera location compared to the interior (Table 4.4). Bears exhibited a similar but weaker pattern, and there were no differences for caribou observations. Deer exhibited an opposite response: they were observed more frequently at the interior camera locations compared to the exterior.

4.3 Camera and GPS data

Although prey availability as measured by a biomass index was not a significant variable in the logistic model, I further examined potential relationships between ungulate distributions and wolf GPS locations using data from remote cameras. There was no correlation between number of wolf observations as indicated by GPS location points and high rate of ungulate observation by remote camera (Table 4-6).

5. Discussion

Seismic lines have been linked to increased predator access and efficiency resulting in higher potential encounter rates with caribou. Little research is available to inform recent mitigation proposals for linear features in caribou ranges. Increasing pressures to manage predation on caribou by manipulating predator mobility on linear features was the impetus to conduct this experiment. I used previously garnered wolf data and a statistical protocol to guide implementation and design of a line-blocking experiment in one wolf pack's territory. I found no statistical evidence to suggest that the line-blocking resulted in reductions in wolf use or movement through experimentally treated areas. However, while not statistically significant, there were patterns of more wolf GPS locations in control sites than blocked sites and higher rates-of-observation outside of blocks than inside.

A critical issue in measuring the success of the line-blocking treatment was correct identification of wolf use of sites, which was essential to subsequently attributing treatment differences to variation in wolf use. There are three major issues with regard to this: 1) quality of GPS location data and pack dynamics; 2) densities of seismic lines in the study region and costs of implementation; and 3) scale, replication and design.

1) Quality of GPS location data and pack dynamics

Based on power analyses conducted before implementation, I expected to locate wolves in greater than 45% of the sites, as was found in this study. Nevertheless, sample sizes of independent wolf locations were adequate for statistical analyses. While a greater sample size would have increased statistical power, GPS collars were programmed to optimise the trade-off between resolution and battery life, thus occasional use of some sites was likely missed. In addition, three GPS-collared individuals within a pack of 7-8 adults during summer, when pack cohesiveness is low, may have been inadequate to represent movement patterns of the entire pack. Remote camera photos were predominantly of wolves without GPS collars.

I focussed the experiment in areas of high wolf use identified from past GPS data. However, wolves have clustered and spatially autocorrelated distributions that are influenced heavily by kill-site, denning, and rendezvous locations, which may vary from year to year. Indeed, the Simonette pack territory shifted slightly from 2003 to 2004. The Simonette wolves maintained the same denning area as 2003, although they expanded the northern parts of their range substantially. The study was designed with 2003 location data (in addition to limited, supplementary data from previous studies in the area), and though there was no way to predict the range shift, it may have contributed to the overall low number of wolf observations in the experimental sites.

An important qualifier to interpretation of GPS data is that wolf use of a site did not necessarily imply that wolves were using linear features for travel. Use simply indicated that wolves either traversed blockages or travelled into a site without the use of linear features. Wolves generally travel along existing game trails, shorelines, ridges, or other terrain that is easily traversed (Mech and Boitani 2004), any of which may have been present in experimental sites. Nevertheless, there is no reason to believe that the influence would differ between controls and treatments and therefore was not a factor in this experiment.

2) Densities of seismic lines in the study region and costs of implementation

Given that approximately 5 680 km of linear features exist in the Simonette wolf territory, it was financially and logistically constraining to block a significant proportion of lines within the study area: the estimated cost to block 15% of the territory was $850 000 (Brian Coupal, personal communication). Therefore, although predation on caribou by wolves is a pressing issue in this region, it is exceedingly difficult to isolate the effects of seismic lines and analyse the significance of blocking in this highly dissected area.

3) Scale, replication and design

This study was designed to detect an effect where one may have existed, but it is possible that wolves responded to a different scale than that chosen here. Sites of 25-ha (500-m x 500-m sites) in size and blocks of 200-m in extent were a trade-off between statistical requirements and logistical considerations. Resources were available for a preliminary experiment within only one wolf pack's territory (no replication); therefore, it is problematic to extrapolate findings to other wolf packs in the area due to potential variation between packs.

I identified areas of high use using kernel density estimators. Kernels may be influenced by year-to-year variation, such as changes in kill-site locations, shifts in wolf territories, or movement of denning and rendezvous areas. For areas where prior wolf information is not available, wolf RSF (index-of-use), terrain ruggedness, and distance to den-site (significant variables in the logistic model) could better inform future study designs.

Wolf use of seismic lines

A major assumption in developing this experiment was that wolves regularly used seismic lines in the Little Smoky region. Based on RSF models, wolves selected areas closer to seismic lines during the rendezvous period; we also recorded a large number of wolf scats on seismic lines compared to other habitats during transect surveys (Chapter 2). However, during the time-frame of the line-blocking study, there was inadequate evidence to suggest that seismic lines were key routes for overall wolf movement within the Simonette territory. Over the year, wolves used areas close to seismic lines less than they were available, and only a very small proportion of wolf movement paths were along seismic lines. However, when seismic lines were examined with respect to seasonal variation in wolf pack behaviour, different patterns emerged. Removing the effect of the den-site revealed that wolves, while away from the den site, selected areas within 50-m of seismic lines more than available, but used areas within 100-m of lines in proportion to their availability (0.49 available to 0.50 used). During the rendezvous season, wolves used areas closer to seismic lines more than available at both the 50-m and 100-m distance categories. Nevertheless, results from the two measures of wolf use of seismic lines are ambiguous. Although wolves were located closer to seismic lines than available, movement paths of wolves crossed seismic lines more frequently than they followed seismic lines (Figure 4-6). This pattern did not change with season. However, better understanding of wolf movements in relation to seismic lines may have been garnered with more frequent GPS fixes. A median inter-fix time of 59 minutes was likely insufficient to capture short-term movements, particularly in a territory with several thousand kilometres of seismic lines. While lack of tortuosity in coarse wolf travel patterns (Mech 1995, Jedrzejewski *et al.* 2001) implies that greater than 15-minute inter-fix distances could adequately represent wolf movements, there have been suggestions that wolves may travel only short distances on trails (Whittington *et al.* 2004). With shorter inter-fix time, the distribution in Figure 4-6 may shift to the right, indicating longer consecutive movements within 50-m of a seismic line. Nevertheless, quantifying wolf use of seismic lines remains an outstanding issue; data collected for this study are adequate for exploratory purposes, but the concept requires further investigation and should be thoroughly examined prior to large-scale implementation of experimental mitigation techniques.

The overwhelming availability of linear features in the Little Smoky region was likely a significant factor influencing wolf use of seismic lines. Approximately 50% of the Simonette territory is within 100-m of a seismic line, resulting in substantial densities of linear features through most of the territory. There is clearly evidence to suggest that during the rendezvous season, areas near seismic lines are associated with higher wolf presence, but given the high density of seismic lines in the region it is difficult to know whether "closer than available" is an adequate measure of use. A more thorough understanding of how and when wolves are using seismic lines is necessary before efforts are solely focussed on linear feature mitigation.

6. Management Implications and Future Study

Line-blocking by tree-felling is a newly proposed approach to mitigating the negative effects of linear disturbances in the boreal forest. This study is the first to examine the potential efficacy of line-blocking on use of linear features by wolves and, to a smaller extent, other boreal mammals. I found no evidence that line-blocking is an effective mitigation technique for wolf use of linear features.

Line-blocking is an expensive and challenging mitigation technique, and if considered a step in restoring the integrity of caribou habitat in degraded ranges, it requires much greater substantiation before being applied on more than a pilot basis. Line-blocking is heavily dependent on suitable habitat. Within the Little Smoky range, problems were frequently encountered in areas of low tree density, of low-height stands, or in transition zones. Furthermore, even if effective, line-blocking is a short-term tool. Needles and branches die or are broken off fallen trees and trunks sink into moss and biodegrade, thereby reopening the line over a period of time.

Longer-term habitat restoration efforts are necessary to reduce multiple negative effects of linear features, including habitat loss, habitat fragmentation, potentially enhanced predator mobility, and human access. Future studies and management initiatives should be integrated in an adaptive management framework, where hypotheses are clearly outlined, key uncertainties identified, and experiments designed to distinguish between alternatives: which combination of lines, what length of blocking, in which habitat type and at what scale, or in combination with which other mitigation techniques, is most effective? I found no conclusive evidence that wolves avoided areas where line-blocking was present and have provided an initial step in assessing the efficacy of this mitigation technique. If line-blocking is to be further implemented, studies regarding wolves and linear features in this region should focus primarily on the rendezvous period (fall), when seismic lines are predicted to be of greater interest to wolves. To date, most studies have been conducted during the winter, when additional snow-tracking data can be included (James 1999, Whittington 2005). A focussed time-frame would also enable collection of higher-resolution GPS data, which is necessary to examine the outstanding issue of how and when wolves move along linear features. Significant wolf use of linear features is a critical assumption behind mitigation of predator-mobility on seismic lines and is imperative to identifying future directions with mitigation work.

Finally, we have a very poor understanding of other predators in the region. Forty-seven instances of seismic line use by bears were recorded during the study. Bears are significant predators of young caribou in other regions (Rettie and Messier 1998, Jenkins and Bartel 2005), but we currently have limited information about bear resource selection and predation in caribou ranges in west-central Alberta.

Table 4-1: Variables known to influence wolf movement or habitat use that were included in an assessment of wolf presence and absence in relation to a seismic line manipulation experiment in west-central Alberta. Wolf presence was identified by GPS locations within either blocked (trees felled across seismic line) or control sites.

Variable Name	Rationale
Treatment	Experimental line-blocking implementation
Proximity to road	Evidence of both avoidance and selection: Mladenoff (1995), Thurber *et al.* (1994), Whittington (2005)
Proximity to den	Evidence of decreased prey vulnerability away from core of wolf territory (Mech 1994)
Proximity to cutblock	More wolf use in areas with cutblocks: Kuzyk (2002)
Proximity to river	Affinity for areas near rivers (Mech and Boitani 2003)
Index of use during the denning	Probability of wolf occurrence from April 20-June 20. RSF values for the denning season are correlated with those for the rendezvous season (0.77).
Ungulate biomass index	Ungulates are the most important prey for wolves
Terrain ruggedness index	Significant variable for describing wolf selection during the denning and rendezvous seasons (Chapter 2)

Table 4-2: Variables and significance levels for a logistic model contrasting wolf presence and absence within experimental sites of a seismic line blocking experiment in west-central Alberta. The model incorporated habitat variables, in addition to site-type, in order to examine wolf response to a seismic line mitigation technique: line-blocking.

Variable Name	Coefficient	Standard Error	*p*-value of coefficient
Treatment	-0.2784	0.5472	0.611
Proximity to road (km)	-0.1898	0.2925	0.516
Proximity to den (km)	-0.0803	0.1081	0.047
Proximity to cutblock (km)	-0.186	0.0937	0.457
Proximity to river (km)	1.6607	1.1872	0.162
Index of use	7.5598	3.6215	0.037
Ungulate biomass index	0.00003	0.0012	0.977
Terrain ruggedness index	5.6348	2.6559	0.032

Table 4-3: Rate of observation per 1000 hours for each site monitored by remote camera during a seismic line blocking experiment in west-central Alberta. Blocks represent areas where seismic lines were blocked by tree-felling.

Site Name (B=block; C= control)	Number of Observations	Hours	Rate per 1000 hours
1 – B	37	23520	1.57
10 – B	12	51040	0.24
12 – C	39	39984	0.98
15 – C	10	6072	1.65
17 – C	12	51336	0.23
25 – B	31	29304	1.06
26 – B	20	26496	0.75
27 – C	8	6672	1.20
30 – C	15	13920	1.08
34 – C	35	31934	1.10
35 – B	18	12506	1.44
37 – B	16	10704	1.49
38 –B	16	12338	1.30
4 – B	16	24734	0.65
7 – C	23	36348	0.63
9 – C	34	33648	1.01

Table 4-4: Average rate of observation per 1000 hours for each species group and treatment type during a seismic line blocking experiment in west-central Alberta, summer 2004. Control E refers to camera locations on the outside of a control site, while Control I refers to a location on the same seismic line, but inside the control site. Block E refers to a camera location outside of a treated (blocked site, while Block I refers to the interior location on the same seismic line.

Treat	Bear	Deer	Moose	Caribou	Wolf
Control E	0.12	0.20	0.29	0.02	0.04
Control I	0.10	0.33	0.29	0.07	0.00
Block E	0.13	0.19	0.27	0.13	0.09
Block I	0.10	0.30	0.19	0.14	0.01

Table 4-5: Variables and significance levels in negative binomial regression model for controls and blocks in a seismic line blocking experiment in west-central Alberta during summer 2004. The reference category was "moose". All interactions were examined with a Wald test. Wolves were omitted from the control analyses due to insufficient data. They were included in block analyses though sample sizes were small (*n*=11).

Treatment Type	Variable Name	*p*-value of coefficient
Control	Moose*Treat	0.733
Control	Bear*Treat	0.735
Control	Deer*Treat	0.823
Control	Caribou*Treat	0.198
Block	Moose*Treat	0.312
Block	Bear*Treat	0.729
Block	Deer*Treat	0.102
Block	Caribou*Treat	0.701
Block	Wolf*Treat	0.063

Table 4-6: Comparison of prey data obtained from remote cameras (number of ungulate observations per 1000 hrs) and sites most used by wolves, based on GPS location data, within sites created for a seismic line blocking experiment in west-central Alberta from May to October 2004.

Site Name	Ungulates per 1000 hours	Site Name	Count (GPS locations)	Site Name	Count (Independent GPS locations)
30c	1.84	2c	43	38c	9
15	1.49	20c	25	20c	8
38	1.43	9	12	40c	5
34c	1.31	38c	11	2c	5
9	1.26	40c	10	18c	4
37c	1.13	13c	9	26c	4

Figure 4-1: Study area for seismic line blocking experiment design in west-central Alberta. Simonette Territory refers to the home-range of the Simonette wolf pack, as defined by multiple GPS collars in the pack. The line-blocking study was monitored from May to October 2004.

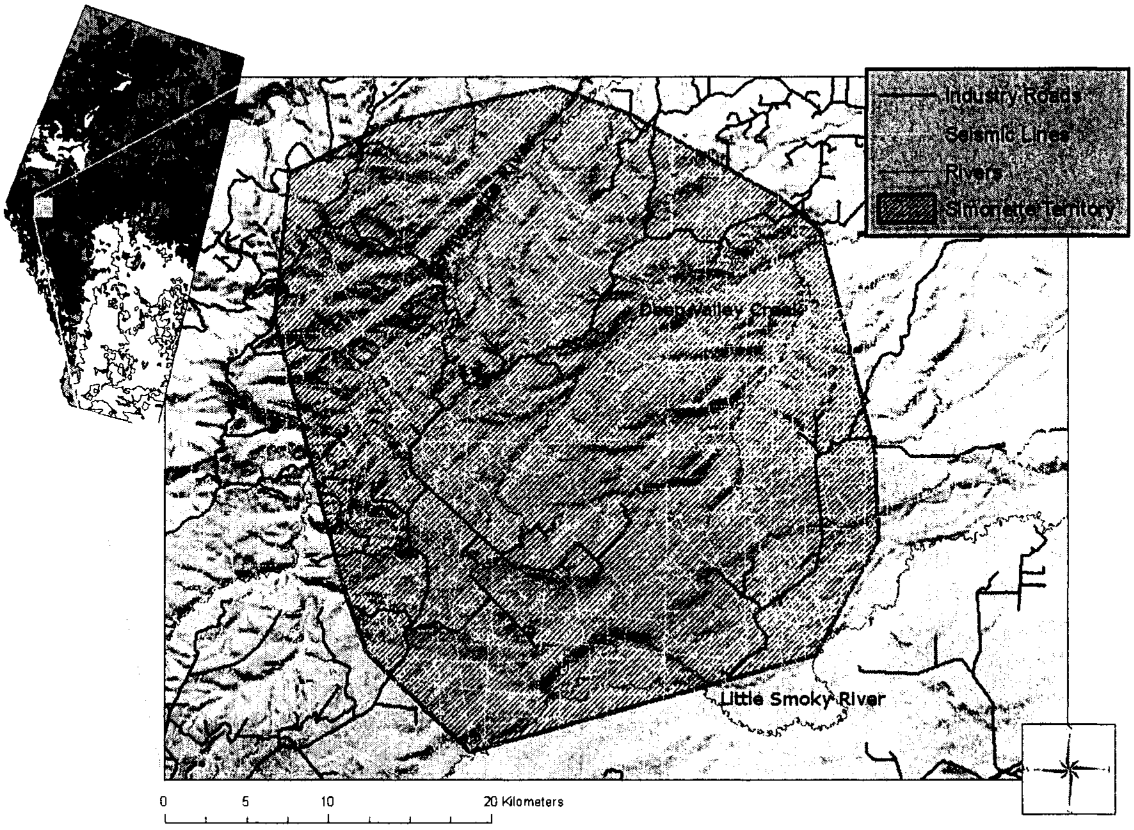


Figure 4-2: Design protocol for a seismic line blocking experiment in west-central Alberta, monitored from May to October 2004. (a) Blocked treatment, with remote camera. Seismic lines (black) were blocked (striped) from the point of entrance into a 500-m x 500-m site (box) toward the centre for a length of 200-m. Blocks were similar to the photo shown. Approximate camera locations are denoted by stars, where one was placed on the interior of the site and one on the exterior. (b) Layout of experiment within high-use areas of the Simonette pack's territory (defined by kernel home range estimators) in west-central Alberta.

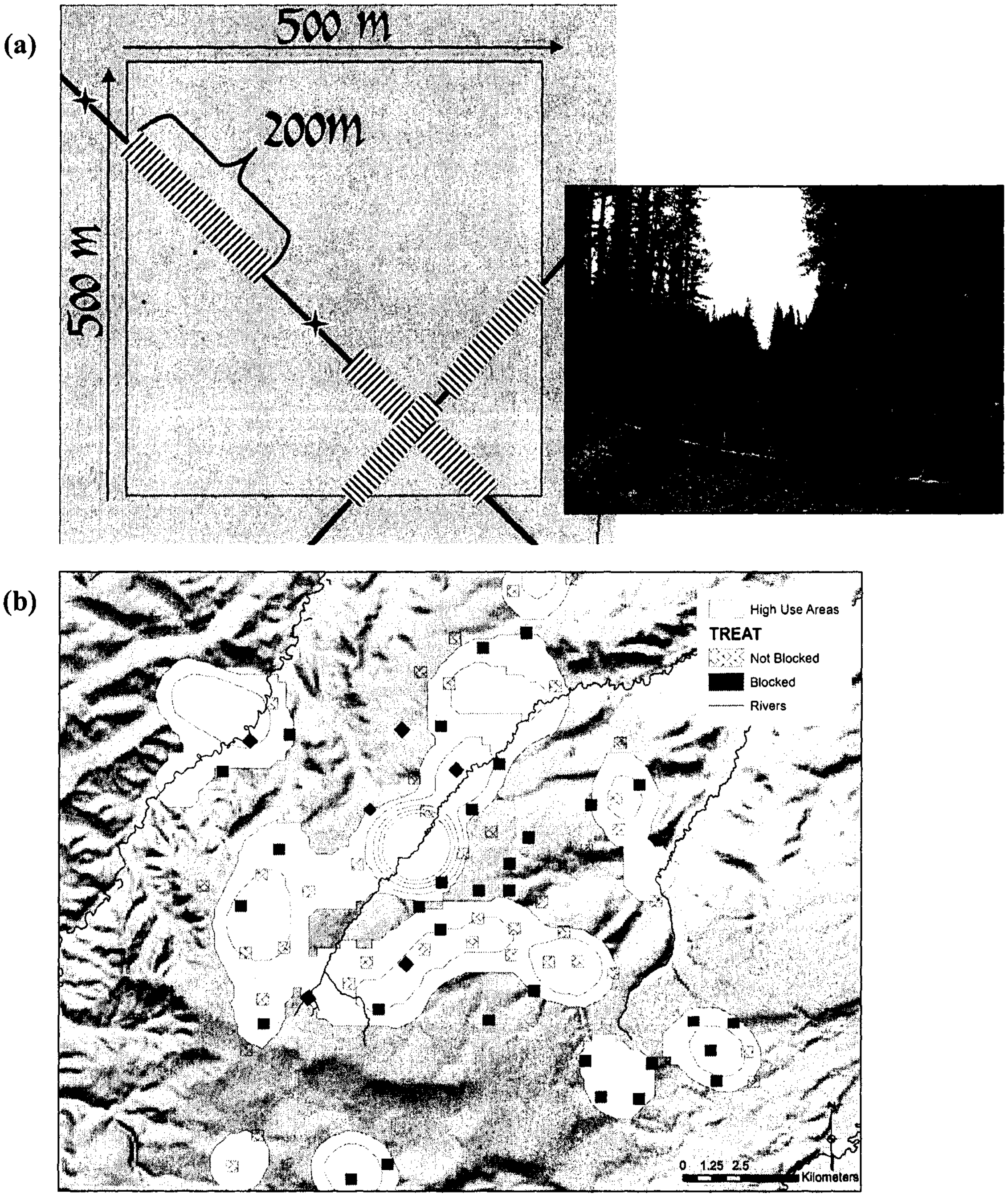


Figure 4-3: Exploratory analysis of wolf movements within 50-m of a seismic line in west-central Alberta. Wolf movement paths were created by joining GPS points with a median inter-fix time of 59 minutes (movement paths represented by thin lines). Seismic lines were buffered by 50-m on each side and distances of wolf movement paths within the buffer were examined in wolf seismic line use analyses.

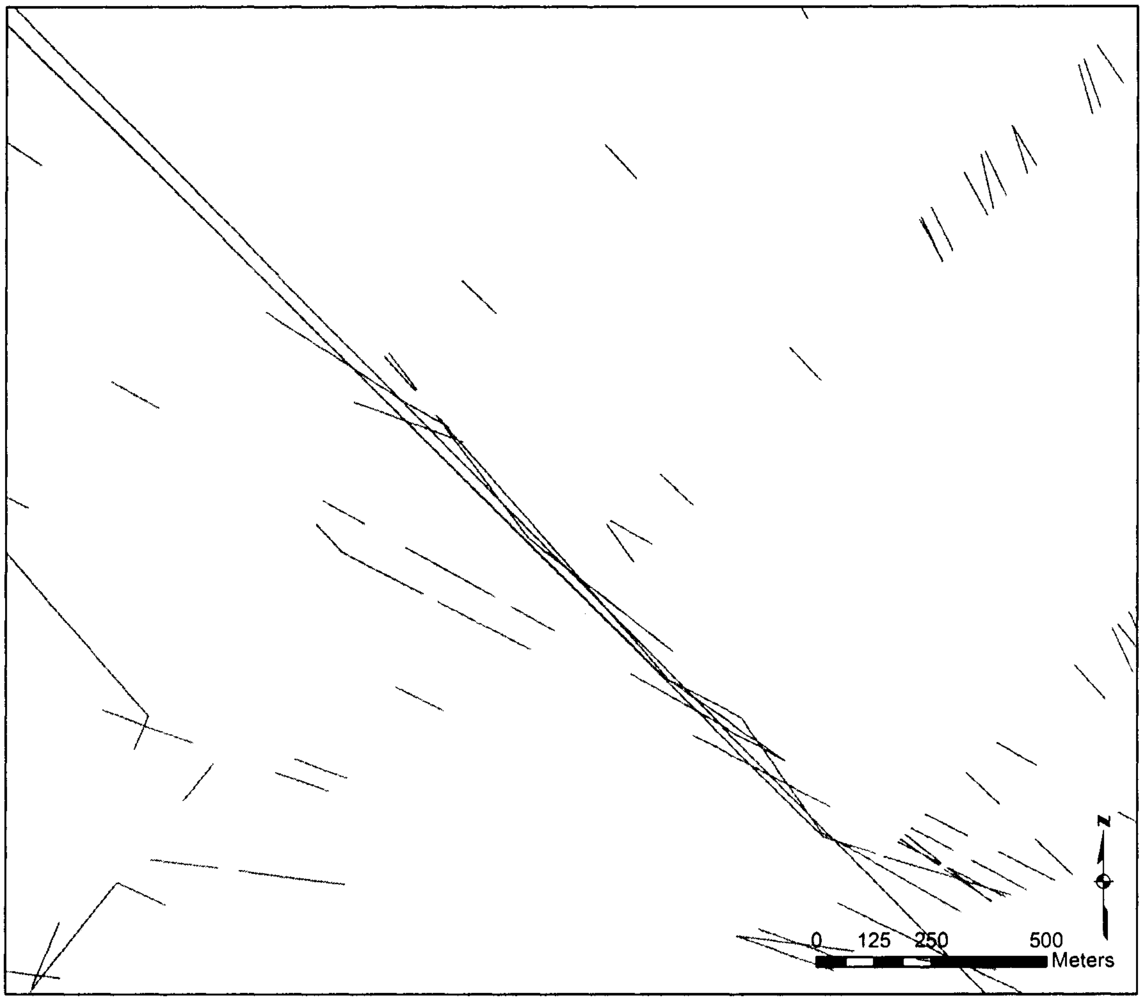


Figure 4-4: Comparison of used and unused sites within an experimental seismic line blocking study in west-central Alberta (May to October 2004). In blocked treatments, trees were felled across seismic lines to create a hypothesised impediment, while in control sites, seismic lines remained unchanged. Less than one-half of all sites were used, but fewer blocked sites were used than control sites. There was no statistical preference for controls over blocked sites.

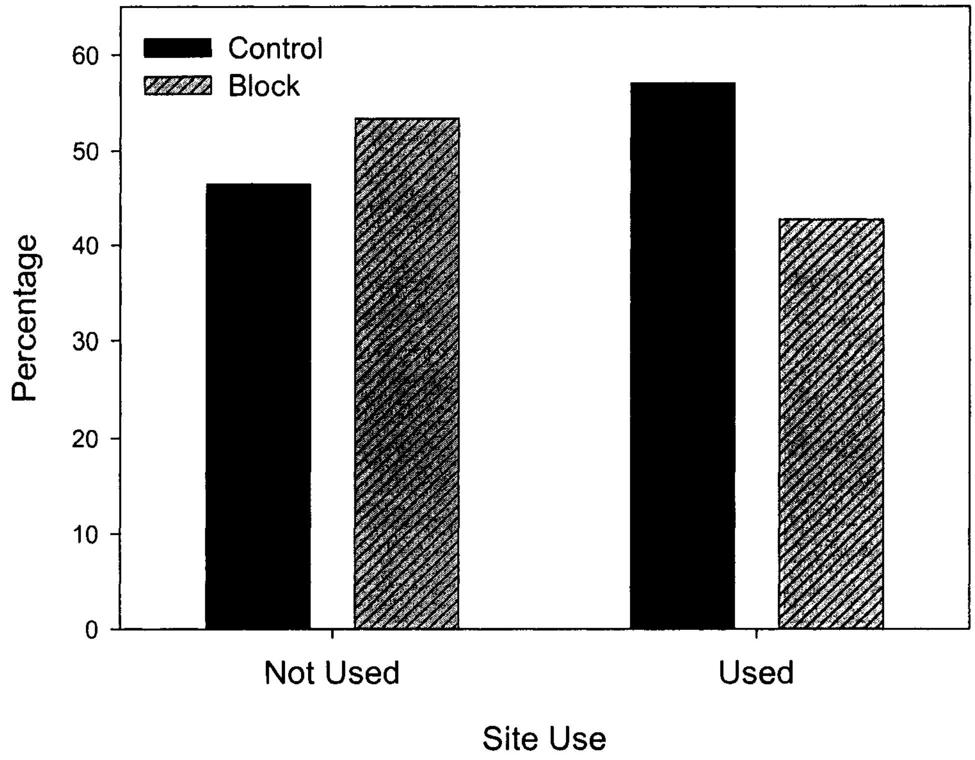


Figure 4-5: Proportion used and available of areas within 50-m of a seismic line within the Simonette wolf pack territory in west-central Alberta. 'Available' was measured across the pack's territory, while 'use' was informed from GPS locations from three wolves of the Simonette pack. 'No den-site' refers to removal of GPS locations at the den-site to account for the den's large effect. The rendezvous season was defined as 1 July to 20 September.

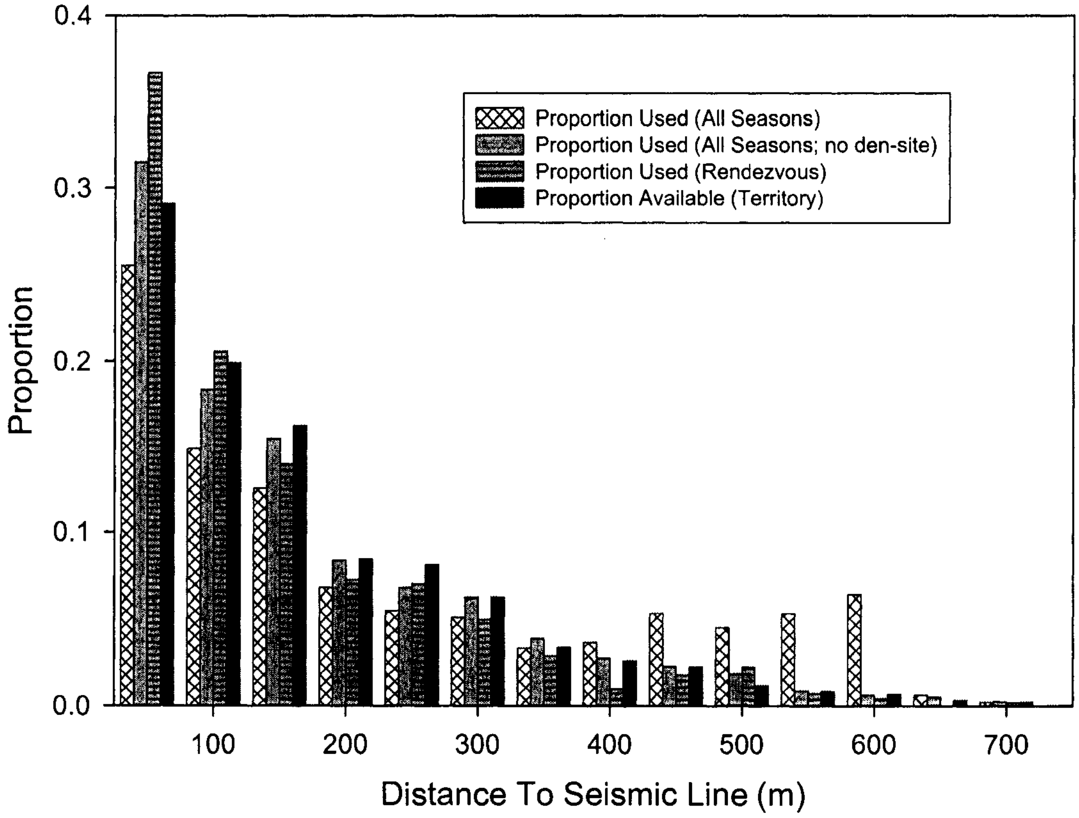
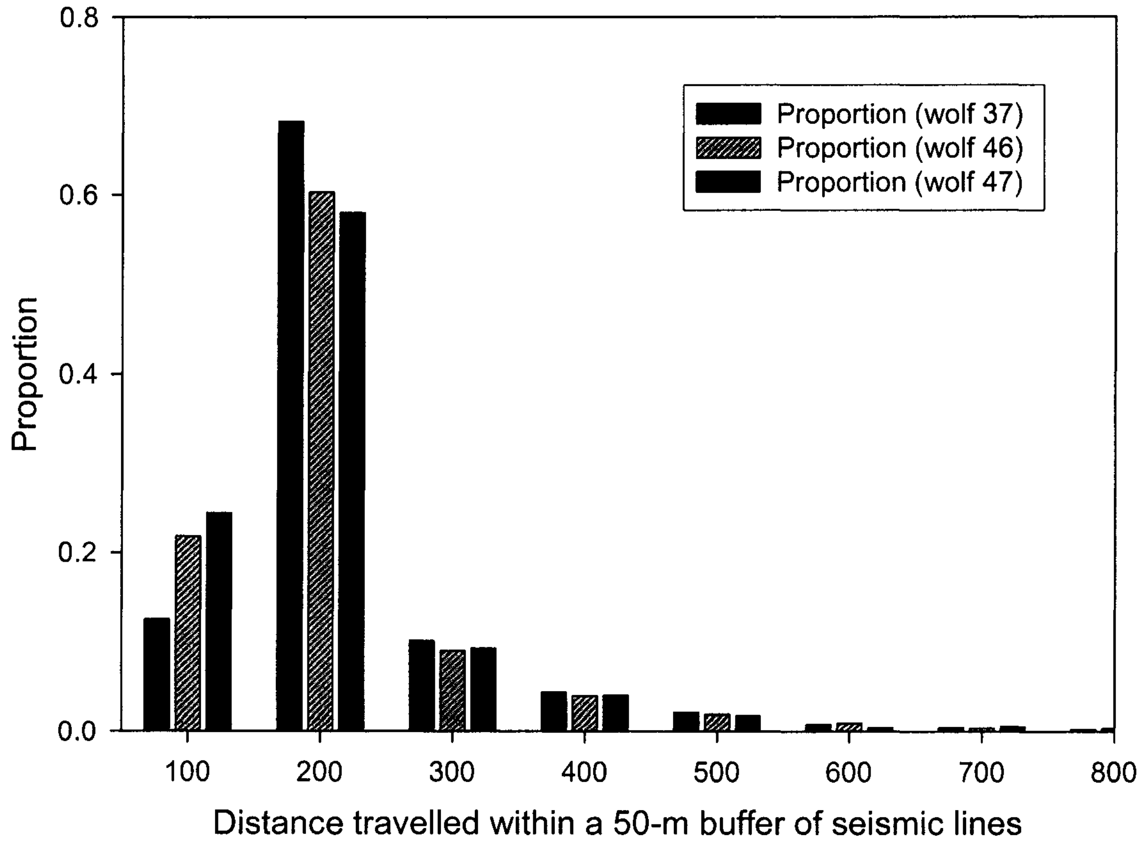


Figure 4-6: Proportion of time spent travelling by each wolf of the Simonette pack in relation to distances travelled, measured as straight-line distances between GPS points, within 50-m of seismic lines. Seismic line crossing resulted in distances of 100–200 metres (bin 200) as seismic line buffers were 100-m. Travelling along seismic lines resulted in larger distances travelled (bins 300+). Wolves were collared in west-central Alberta from May to October 2004.



7. Literature Cited

Alberta Environmental Protection. 1998. The boreal forest natural region of Alberta. Alberta Environmental Protection, Edmonton, AB.

Bergerud, A.T. 1990. Rareness as an antipredator strategy to reduce predation risk for moose and caribou. *In* Transactions of the 14th Conference of the International Union of Game Biologists. Ed. S. Myrberget.

Boreal Caribou Committee. 2001. Strategic plan and industrial guidelines for boreal caribou ranges in northern Alberta. Edmonton, AB.

Brown, W.K., and D.P. Hobson. 1998. Caribou in west-central Alberta – information review and synthesis. Prep. for: The Research Subcommittee of the West-central Alberta Caribou Standing Committee, Grande Prairie, AB.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodal inference: a practical information theoretic approach, 2nd edn. Springer-Verlag, New York, NY.

Caribou Range Restoration Project. 2005. Caribou Range Restoration Project: Guidelines for planning and implementation. Grande Prairie, AB.

D'Eon, R.G., and D. Delparte. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. Journal of Applied Ecology **42**:383-388.

Dzus, E. 2001. Status of the woodland caribou (*Rangifer tarandus caribou*) in Alberta. Alberta Environment, Fisheries and Management Division, and Alberta Conservation Association, Wildlife Status Report No. 30, Edmonton, AB.

Edmonds, E.J., and M. Bloomfield. 1984. A study of woodland caribou (*Rangifer tarandus caribou*) in west-central Alberta, 1979-1983. Alberta Energy and Natural Resources Fish and Wildlife Division.

Frair, J.L., S.E. Nielsen, E.H. Merrill, S.R. Lele, M.S. Boyce, R.H.M. Munro, G.B. Stenhouse, and H.L. Beyer. 2004. Removing GPS collar bias in habitat selection studies. Journal of Applied Ecology **41**:201-212.

Hardin, J., and J. Hilbe. 2001. Generalized linear models and extensions. Stata Press, College Station, TX.

Hosmer, D.W., and S. Lemeshow. 2000. Applied logistic regression, 2nd edn. John Wiley & Sons, New York, NY.

Jalkotzy, M.G., P.I. Ross, and M.D. Nasserden. 1997. The effects of linear developments on wildlife: A review of selected scientific literature. Prepared for the Canadian Association of Petroleum Producers. Arc Wildlife Services Ltd., Calgary, AB.

James, A.R.C. 1999. Effects of industrial development on the predator-prey relationship between wolves and caribou in northeastern Alberta. Ph.D. Thesis, University of Alberta, Edmonton, AB.

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

Jedrzejewski, W., K. Schmidt, J. Theuerkauf, B. Jedrzejewska, and H. Okarma. 2001. Daily movements and territory use by radio-collared wolves, *Canis lupus*, in Bialowieza Primeval Forest (Poland). Ecology **83**:1341-1356.

Jenkins, K.J., and N.L. Barten. 2005. Demography and decline of the Mentasta caribou herd in Alaska. Canadian Journal of Zoology **83**:1174-1188.

Kinley, T.A., and C.D. Apps. 2001. Mortality patterns in a subpopulation of endangered mountain caribou. Wildlife Society Bulletin 29:158-164.

Kuzyk, G.W. 2002. Wolf distribution and movements on caribou ranges in west-central Alberta. M.Sc. Thesis, University of Alberta, Edmonton, AB.

Lessard, R.B. 2005. Conservation of woodland caribou (*Rangifer tarandus caribou*) in west-central Alberta: a simulation analysis of multi-species predator-prey systems. Ph.D. Thesis, University of Alberta, Edmonton, AB.

Long, J.S., and J. Freese. 2003. Regression models for categorical dependent variables using Stata. Revised edition. Stata Press, College Station, TX.

Mech, L.D. 1994. Buffer zones of territories of gray wolves as regions of intraspecific strife. Journal of Mammalogy **75:**199-202.

Mech, L.D. 1995. Summer movements and behaviour of an arctic wolf, *Canis lupus*, pack without pups. Canadian Field Naturalist **109**:437-75.

Mech, L.D., and L. Boitani. 2003. Wolves: behavior, ecology, and conservation. Univ. Chicago Press, Chicago, Ill.

Mladenoff, D.J., T.A. Sickley, R.G. Haight, and A.P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great-Lakes region. Conservation Biology **9**:279-294.

Musiani M, and E. Visalberghi. 2001. Effectiveness of fladry on wolves in captivity. Wildlife Society Bulletin **29**:91-98.

Musiani, M., H. Okarma, and W. Jedrezejewski. 1998. Speed and actual distances travelled by radiocollared wolves in Bialowieza Primeval Forest (Poland). Acta Theriologica **43:**409-416.

Nielsen, S.E. 2005. Habitat ecology, conservation, and projected population viability of grizzly bears (*Ursus arctos* L.) in west-central Alberta, Canada. Ph.D. Thesis, University of Alberta, Edmonton, AB.

Nielsen, S.E., Boyce, M.S., Stenhouse, G.B., and Munro, R.H.M., 2002. Modeling grizzly bear habitats in the Yellowhead Ecosystem of Alberta: Taking autocorrelation seriously. Ursus **13**:45-56.

Osko, T.J., and A.K. MacFarlane. 2001. Natural reforestation rates on seismic lines and wellsites in comparison to natural burns or logged sites. Alberta-Pacific Forest Ind., Boyle, AB, Canada.

Rettie, W.J., and F. Messier. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. Canadian Journal of Zoology **76**:251-259.

Revel, R.D., T.D. Dougherty, and D.J. Downing. 1984. Forest growth and revegetation along seismic lines. University of Calgary Press, Calgary, AB.

Smith, K.G. 2004. Woodland caribou demography and persistence relative to landscape change in west central Alberta. M.Sc. Thesis, University of Alberta. Edmonton, AB.

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**:1433-1440.

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

Thomas, D.C., and D.R Gray. 2002. Update COSEWIC status report on the woodland caribou *Rangifer tarandus caribou* in Canada. *In* COSEWIC assessment and update status report on the Woodland Caribou *Rangifer tarandus caribou* in Canada. Ottawa, ON.

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

White, H. 1980. A heteroskedasticity-consistent covariance matrix estimator and a direct test for heteroskedasticity. Econometrica **48**:817-838.

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

Zar, J.H. 1999. Biostatistical analysis. Prentice-Hall, Upper Saddle River, NJ.

Chapter 5: Synthesis and Management Implications

1. Synopsis

In this thesis I attempted to address research gaps regarding woodland caribou and wolf ecology; specifically, spatial and temporal habitat selection, using resource selection functions (RSFs). I developed year-round spatially explicit models defining habitat selection for caribou and wolves which, at the simplest level, illustrate wolf affinity for industrial features concomitant with caribou avoidance of similar features. Models were developed for three seasons, defined primarily by wolf-pack dynamics but coincidental with caribou biology: 1) denning/caribou calving (10 April – 30 June); 2) rendezvous/caribou calf growth and development (1 July – 20 September); and 3) nomadic/winter forage period (21 September – 19 April). Based on selection patterns of wolves and caribou within the caribou range, there is substantial spatial overlap potential throughout the year, most notably during the denning season.

2. Interpreting and applying RSF results

Resource selection functions offer one method for examining animal response to landscape features. A drawback of the RSF approach is that patterns of selection cannot be related to habitat quality and population processes. Although I have identified habitats that caribou select, I have no measure of quality at these sites. Caribou may be selecting ecological traps: habitats that are of lower quality for processes like reproduction or survival, which may ultimately result in negative growth rates and extinction (Battin 2004). Resource selection functions remain valuable in that they are spatially explicit, predictive, and quantify response to multiple landscape variables simultaneously. As such, they can be an important first step in conservation planning (Boyce *et al.* 2002) and here provided an assessment of important attributes of areas utilized by caribou and wolves. Managers could use the maps generated from RSFs when considering development permits, companies could consider them when designing Caribou Protection

Plans, stakeholders might apply the maps to conservation planning in the region, and restoration agencies could prioritise key locations for habitat enhancement. In the following discussion, I highlight the key findings from my work.

In the Little Smoky region, resource selection functions identified a positive response by wolves to human features. Areas with cutblocks less than 15 years in age, as measured by several variables, were strongly selected and linear features were significant in describing wolf habitat selection in some seasonal models. Areas with larger proportions of cutblocks at the 10-km^2 scale were selected, as were younger forests during all seasons. Although the mechanisms underlying selection of cutblock regions were not quantified, Chapter 2 presented preliminary information indicating greater use of these habitats by moose: wolves selected younger forests, while data from pellet transect counts showed that young pine and cutblocks (5-20 years in age) were most heavily used by moose (Table 2-5). Although in need of further investigation, I infer that regenerating human features (such as cutblocks) result in higher predictability of prey resources.

Wolves were more often crossing linear features than travelling along them. However, wolves selected areas closer to seismic lines than available during the rendezvous (fall) period. Linear features did not figure prominently in the winter and spring models, although given their ubiquity and possibility that wolves may be using seismic lines in proportion to their availability, it is difficult to quantify the effect seismic lines have on wolf mobility. Other anthropogenic features, as measured by grass-covered and dry areas, were selected in relation to forested areas during all seasons.

Indications that wolves selected anthropogenic features were countered by opposite results for caribou. Year-round, caribou exhibited negative responses to most anthropogenic variables, particularly to seismic lines. There was unequivocal evidence illustrating a negative response by caribou to close linear feature proximity: caribou strongly selected areas farther from seismic lines than available in all seasons. It is notable that despite caribou avoidance of linear features, overlap potential between wolves and caribou was considerable during all seasons, indicating that avoidance behaviour may not be sufficient to preclude overlap. Although high levels of spatial and temporal overlap are not only a result of industrial development, the contributing role of industrial development in altering the wolf-caribou spatial dynamic cannot be ignored. Without knowing the mechanism behind caribou avoidance, it is challenging to identify implications for managers. Caribou might avoid seismic lines for a number of reasons, including open canopy cover and overall unwillingness to venture toward open areas, association with predators, and poor forage availability.

Uncovering the reasons for avoidance of human developments will require creative and well-identified experimental science within caribou range coupled with a better understanding of caribou behaviour. Nevertheless, there is a clear need for cooperation, transparency, and long-term planning among forest and petroleum tenure holders in the region. Industrial development plans developed in isolation may potentially negate conservation efforts made in overlapping or adjacent areas and undermine the best intentions of industrial operators in the region.

3. Current management protocols for caribou ranges

In response to declining populations and guidelines for industrial development in caribou ranges within Alberta (*e.g.* WCACSC 1996, BCC 2001), Alberta Sustainable Resource Development and representatives from the oil and natural gas industry developed "Oil and Gas Access best practices in the West Central Caribou Range" (Alberta Department of Energy 2003), which supplements an earlier directive, IL 1991-17 (Alberta Department of Energy 1991). Information Letter 1991-17, "Procedural Guide for Oil and Gas Activity in Caribou Range" states that "petroleum and natural gas exploration and development activities can occur on caribou range provided that the integrity of the habitat is maintained to support its use by caribou." While oil and gas developments occur year-round, increased accessibility during frozen-ground conditions focuses work in the winter; under the 1991-17 guidelines, operators are asked to respect an "early-out" policy, which aims to reduce disturbance to caribou during the late-winter and caribou calving period. There are also width restrictions on linear corridors and encouragement to coordinate development with other industries and existing infrastructure. Although implementation of best practices does attempt to mitigate potential impacts of industrial development, there may be a level at which development surpasses a threshold for caribou. That is, even if every industrial player is acknowledging and implementing best practices, the sheer quantity of activity compromises caribou persistence. For example, implementing a best practice of reusing corridors for future development purposes (seismic lines, pipeline, or roads) does not address avoidance responses or functional habitat loss. Establishment of thresholds has been identified as a management option in caribou ranges; however, the efficacy of this idea requires further examination (Anderson 1999, Dyer 1999, Adamczewski *et al.* 2003). A true best practice might be to examine alternate solutions to development within the Little Smoky caribou range, such as remote, roadless entry or re-routing pipelines to the exterior of the range. In addition, although IL 2003-23 supports the Caribou Range Restoration Project (CRRP), which exists for the purpose of recovering linear disturbance, the CRRP may not be able to keep pace with the geographic and temporal scale of industrial projects. Short- and long-term recovery of seismic lines, including old lines, should be priorities within the mandate of each operator's Caribou Protection Plan (the goal of which is to identify program activities and discuss measures to mitigate long-term effects by managing short-term impacts). Finally, a relevant concern highlighted by Schaefer (2005) is the danger of an extinction debt (Tilman *et al.* 1994) in the Little Smoky range, referring to continued negative effects and decline as a result of past activities, regardless of best practices, mitigation, and recovery efforts.

The Strategic Plan and Industrial Guidelines for Boreal Caribou Regions (BCC 2001) frame future development work within an adaptive management framework. The concept of adaptive management is a learning-by-doing approach that embraces uncertainty, where feedback from research trials is explicitly incorporated into subsequent decisions. Employment of this approach in caribou range requires formulation of testable hypotheses regarding ways to mitigate industrial development based on literature review, modelling exercises, and expert opinion, to ultimately reduce the likelihood of caribou extirpation. The approach necessitates replication, controls, and close monitoring in order to adapt the experimental strategies as necessary. Conservation and restoration are management actions that could be immediately applied to the Little Smoky caribou region at a scale appropriate for caribou. Conservation (a reduction in the rate and number of developments) would require volunteer postponement or relinquishment of development permits or agreements in portions of the range, as well as a moratorium on allocation of new permits. Restoration (minimising the effects of specific developments) and other practical management actions could follow a number of techniques identified by the Caribou Range Restoration Project (briefly discussed in Chapter 4). Implementing scientifically rigorous best practices for caribou ranges requires a credible, strong hypothesis-based management approach, concomitant monitoring program, and industrial willingness to refine scientific assumptions in an adaptive management framework.

4. Managing caribou decline – the Alberta scenario

The question of how to reduce further caribou population declines is critical. Addressing wolf predation through predator control programs will likely contribute to lower caribou mortality in the short-term. However, controlling wolves is a costly endeavour and does not present a long-term solution to declining populations, particularly with respect to the effect of other predators. In addition, reducing wolf densities has implications for the social dynamics of packs that are largely unknown. A review by the National Research Council (1997) concluded that predator reduction might hasten the recovery of prey, but an increase in prey density was demonstrated in only three of eleven case studies. More recently, Hayes *et al.* (2003) found that while wolf predation was limiting caribou recruitment, there was no evidence that adult female survival of caribou improved after wolf reductions. Wolf control is unlikely to result in sustained increases in prey populations unless a very high proportion of resident wolves are killed annually over a large area for at least 4 years (National Research Council 1997); broad-scale control of wolves was not recommended by Hayes *et al.* (2003). Wolf control is a controversial approach to managing the proximate cause of a threatened species. The solution for caribou conservation is recognition that habitat fragmentation and loss via forestry and oil and gas development indirectly threaten the long-term viability of woodland caribou populations in Alberta. Failure to address the ultimate causes will likely result in continued province-wide declines of caribou and require drastic conservation measures to sustain low populations in industrialised regions.

Given unprecedented levels of industrial development in caribou ranges throughout Alberta, in addition to current trends and future population projections (Smith 2004, Weclaw and Hudson 2004, Lessard 2005), it is unlikely that all caribou herds will persist without drastic intervention and/or serious changes in regulations to industrial users. The Little Smoky represents one of Alberta's first encounters with the potential large-scale extirpation of a sensitive and culturally significant ungulate species. After several decades of recording declines in the Little Smoky population, Albertans might ask, "at what economic, societal, and biological cost will caribou herds be maintained?" Alberta is obligated and committed to caribou conservation as a signatory to several national and provincial biodiversity agreements, wherein it has committed to maintaining viable populations of woodland caribou within the province (see Smith 2004 for an overview). As part of its commitments, Alberta recently released a Woodland Caribou Recovery Plan. The Recovery Plan recommends development of range teams for geographic areas of the province, moratoria on industrial development for herds in immediate risk of extirpation, and ensuring that land use guidelines designed for caribou conservation are effective and applied to all caribou ranges. The Alberta government endorsed all components of the plan except the development moratorium.

The precautionary principle, a guiding axiom for conservation biology, states that lack of scientific evidence should not preclude measures to minimize threats to losses in biodiversity. However, in the case of woodland caribou, it has not been a lack of scientific evidence that has stalled conservation initiatives. Despite substantial consensus-reaching research, commitments by the province to national and provincial agreements, and recent recommendations by the Recovery Team, there has been a conspicuous failure to act decisively on recommendations. Ultimately, questions surrounding the management and conservation of woodland caribou are as much ethical and economical as they are scientific. Any decision requires compromise and balance on all sides. Current regulations imposed on industry are not requiring sufficient compromise on its part.

Specific to the Little Smoky and A la Pêche winter range, my results are in agreement with the specific management recommendations put forth by Smith (2004). Particularly relevant for the Little Smoky and A la Pêche winter range, the ANC main haul road (Berland Resources Road) and the Smoky Mainline should continue to remain disjunct to avoid creation of a main thoroughfare through the ranges of both herds. The west-central region also contains other sensitive species at risk from changing environments, such as the grizzly bear (Nielsen *et al.* 2005). Future conservation programs should apply a holistic approach to managing wildlife for continued persistence of sensitive and threatened animals within Alberta's forests, including caribou.

5. Limitations and future research

Despite the general trends and implications of my work highlighted here, there are also a number of limitations. Not all packs in the study area were collared and we do not have information about wolf densities in the core caribou areas. Wolf packs are known to situate their territories based on overall prey biomass and not strictly on selected habitats (Mech and Boitani 2003). Although we marked the Buckbean pack near the centre of the Little Smoky caribou range, all collared wolves in that pack either dispersed or experienced collar failure. Other packs overlapped the caribou range considerably, but there were notable regions in the study area without wolf data. I therefore used data from surrounding areas to interpolate occurrence. Wolves likely exist in areas along the Little Smoky River, but we do not have information regarding specific packs: past research in the area (Kuzyk 2002) identified wolves along the western portion of the river. Interpolated RSF maps may identify areas that are "good" for wolves, but it does not necessarily mean that wolves occur there, nor does it provide any information regarding wolf densities. However, in-sample validation and variation explained through inclusion of a random effect for individuals revealed that wolf response was similar across packs within the study area: therefore, we can infer that should wolves be present in areas without collared animals, they would select areas predicted by the RSF model. Monitoring of wolves continues in the range and it would be interesting to examine whether future wolf response is consistent with model predictions. This could also be examined using data collected in 2000 and 2001 from other packs in the area. Additionally, continued monitoring of caribou in the Little Smoky and non-migratory caribou from the A la Pêche provide opportunities to assess changes in selection patterns with continued habitat change. For example, GPS data for caribou were collected prior to construction of a cross-range pipeline and new large-scale cutblocks in the southern range; range-wide effects of these significant changes are currently unknown.

I have provided an assessment of caribou response to current levels of industrial development in the Little Smoky caribou range and adjacent A la Pêche range. However, although the response is generally consistent with past research, the underlying mechanisms can only be inferred. Sampling at finer scales might identify factors driving larger-scale habitat selection. More detailed sampling should include examinations of critical factors neglected in the research presented herein, such as food resources. Fine scale variables could then be included in larger scale models, to increase their predictive capabilities. In addition, finer scale sampling of caribou response to industrial features would provide insight into caribou behavioural patterns and mechanisms of avoidance. These questions would be best approached from an experimental context including areas without substantial industrial development; for example, as part of a multi-herd assessment. Restoration of industrial features is challenging without an understanding of which aspect to reclaim. If canopy closure is a critical variable, it should be the restoration priority. Experimental treatments with alternate and competing hypotheses within a research context, in addition to fine scale sampling of caribou (whether via tracking in winter or higher resolution GPS data) would be a first step in addressing these questions. A multi-herd approach that takes advantage of long-term monitoring programs throughout the province would provide insight into boreal caribou population response in light of various levels of industrial development, habitat restoration, or predator management (*e.g.* Wittmer 2004).

Wolf response to seismic lines must also be clarified. James (1999) provided initial work linking seismic lines to wolf travel efficiency, but sample sizes were small. Unquestionably, seismic lines are used by wolves, but we do not currently know to what degree. I have presented findings that show wolves are located closer to seismic lines than available, but have made no effort to quantify wolf movement or use of other travel corridors, such as game trails. Understanding the implications of seismic lines for wolf travel and efficiency in all seasons would facilitate focussed restoration efforts and inform Caribou Protection Plans for industrial partners.

Inclusion of mixed models improved model fit for wolves; preliminary work with caribou data indicated similar results. The use of random effects and modelling variation within hierarchical data sets are new and promising techniques. I employed random intercepts in this work, but there are additional statistical approaches that could provide better insight to animal response. Using random effects, I was able to partition the variance and attribute it to individual and pack levels, therefore identifying the influences of pooling data at those levels. I discovered low variance between packs and individuals within packs. However, use of a random coefficient, although sometimes challenging to interpret, would permit examination of a specific covariate across space or levels. That is, the between-pack effects could have been identified for covariates of interest. For example, entering density of seismic lines as a random coefficient would provide between-pack response to density of seismic lines. However, random coefficients are statistically complicated and use of more than one random coefficient is not recommended.

Finally, I was unable to adequately quantify habitat selection patterns of additional predators and prey in the caribou range, which would be beneficial particularly for bears and moose. Although exploratory research suggests that higher densities of moose and deer will result in further caribou decline (Lessard 2005), the study lacked accurate estimates of moose and deer densities. Particularly under management scenarios of actively reduced moose and wolf densities, it is imperative to continue monitoring caribou, moose, and wolf response. Ideally, management scenarios should be couched within an adaptive management context, where competing hypotheses and assumptions are identified, actions implemented to reduce uncertainties, and investments in monitoring recognized as key components of the adaptive loop. Most importantly, the results of such a process should feedback to inform future management decisions.

6. Literature Cited

Adamczewski, J.Z., R.F. Florkiewicz, and V. Loewen. 2003. Habitat management in the Yukon winter range of the Litte Rancheria caribou herd. Department of the Environment, Government of the Yukon, Whitehorse, YT.

Alberta Department of Energy. 1991. Information Letter 1991-17: Procedural guide for oil and gas activity on caribou range. Edmonton, AB.

Alberta Department of Energy. 2003. Information Letter 2003-23: Oil and gas access best practices in the west-central caribou range. Edmonton, AB.

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

Boreal Caribou Committee. 2001. Strategic plan and industrial guidelines for boreal caribou ranges in northern Alberta. Edmonton, AB.

Boyce, M.S., P.R. Vernier, S.E. Nielsen, and F.K.A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling **157:** 281-300.

Hayes, R.D., R. Farnell, R.M.P. Ward, J. Carey, M. Dehn, G.W. Kuzyk, A.M. Baer, C.L. Gardner, and M. O'Donoghue. 2003. Experimental reduction of wolves in the Yukon: ungulate responses and management implications. Wildlife Monographs **67**.

James, A.R.C. 1999. Effects of industrial development on the predator-prey relationship between wolves and caribou in northeastern Alberta. Ph.D. Thesis, University of Alberta. Edmonton, AB.

Kuzyk, G. W. 2002. Wolf distribution and movements on caribou ranges in west-central Alberta. M.Sc. Thesis, University of Alberta.

Lessard, R.B. 2005. Conservation of woodland caribou (Rangifer tarandus caribou) in west-central Alberta: a simulation analysis of multi-species predator-prey systems. Ph.D. Thesis, University of Alberta, Edmonton, AB.

Mech, L.D., and L. Boitani. 2003. Wolves: behavior, ecology, and conservation. Univ. Chicago Press, Chicago, Ill.

National Research Council. 1997. Wolves, bears, and their prey in Alaska: Biological and social challenges in wildlife management. National Academy Press, Washington, D.C.

Schaefer, J. 2005. A review of Alberta's draft recovery plan for woodland caribou. Sierra Club of Canada, Ottawa, ON.

Smith, K.G. 2004. Woodland caribou demography and persistence relative to landscape change in west central Alberta. M.Sc. Thesis, University of Alberta. Edmonton, AB.

Tilman, D., R.M. May, C.L. Lehman, and M.A. Nowak. 1994. Habitat destruction and the extinction debt. Nature **371**:65-66.

Weclaw, P., and R. J. Hudson. 2004. Simulation of conservation and management of woodland caribou. Ecological Modelling **177**: 75 – 94.

West-central Alberta Caribou Standing Committee. 1996. 1996/1997 Operating guidelines for industry activity in caribou ranges in west central Alberta. Edmonton, AB.