University of Alberta

Library Release Form

Name of Author: Nicole Ann McCutchen

Title of Thesis: Factors affecting caribou survival in northern Alberta: the role of wolves, moose, and linear features

Degree: Doctor of Philosophy

Year this Degree Granted: 2007

Signature

University of Alberta

Factors affecting caribou survival in northern Alberta: the role of wolves, moose, and linear features

by

Nicole Ann McCutchen

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

Doctor of Philosophy
in
Ecology and Environmental Biology

Department of Biological Sciences

Edmonton, Alberta
Spring 2007

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Factors affecting caribou survival in northern Alberta: the role of wolves, moose, and linear features** submitted by **Nicole Ann McCutchen** in partial fulfillment of the requirements for the degree of **Doctor of Philosophy in Ecology and Environmental Biology**.

Dr. Stan Boutin

Dr. Robert Hudson

Dr. Mark Lewis

Dr. Evelyn Merrill

Dr. Dennis Murray

Date: ________________________________

In memory of my grandpa, Leo Schuh
(September 6th, 1930 to February 16th, 2004)

Perhaps yellow isn’t such a bad color after all.

Abstract

The spatial segregation of woodland caribou (*Rangifer tarandus caribou*) from predators and alternative prey has been well documented and is often cited as necessary for the persistence of local herds. For example, boreal caribou in northern Alberta predominantly inhabit peatlands whereas moose (*Alces alces*) and wolves (*Canis lupus*) are more likely to be found in the surrounding uplands. Presumably, wolves focus on moose because they are larger and more abundant than caribou. However, recent declines in a number of herds suggest that the peatlands no longer provide refuge from wolf predation. I used grid-based computer simulation models to examine three mechanisms that may account for this change: (1) increased predator efficiency, in which wolf use of linear features mimics the functional response by increasing the probability of encountering moose and caribou; (2) increasing overlap between moose and caribou distributions, in which moose draw wolves into caribou range; and (3) an increase in the number of individual wolves hunting in caribou range, which may arise from the numeric effects of line use. Simulations indicated that: (1) the functional effects of line use depended on prey response to lines (i.e., degree of line avoidance), the probability of wolf use of lines, and species-specific prey densities. In general, there is potential for line use to increase wolf use of moose but not caribou; (2) the effects of overlap primarily depended on wolf hunting patterns and prey behavior. Caribou survival decreased with increasing overlap between moose and caribou, but only if wolves used "movement rules" (i.e., movement was not random) and if prey distributions were primarily random with respect to lines; and (3) caribou survival decreased with the number of individually hunting wolves, regardless of prey and predator behaviors. Furthermore, the functional effects of line use were extensive enough to facilitate a wolf numeric response. Overall, these results suggest that more predators in caribou range is the most rigorous explanation for the caribou declines and that this increase may result from line use "artificially" inflating wolf numbers. These findings are important for directing future empirical research and for guiding caribou management plans, which are often line-based. More effective management will likely require a combination of line, wolf, and moose control measures.

Acknowledgements

This thesis benefited tremendously from a number of people. My supervisor, Stan Boutin, was incredibly good at bringing things back to empirical reality and providing me with direction in terms of improving the overall context of the models. He is also exceptionally gifted at asking those hard questions that leave one stunned for a good five minutes or more but ultimately improve one's ability as a scientist. I would also like to thank my committee members, Mark Lewis and Robert Hudson, for one-on-one discussions that helped guided my thinking and prepared me for little things like candidacy exams.

Ainsley Sykes and Craig Aumann were invaluable for answering my multitude of stupid questions. I would also like to thank Craig Aumann and Fredrik Dalerum for reading draft #4 of this thesis. Their comments contributed significantly to the improvement of drafts #5 and #6. Thanks to all the members of Stan Clan, the diversity of which meant a lot of invigorating discussions on Friday afternoons. Caroline McParland, Kerri Charest, Heather Hinam, Jerry Filipski, and Richard Moses were other key individuals who contributed support morally, scientifically, or coffee-wise. Support from my non-human sources came in the form of Mr. Bub (who may be small but is all dog), the fat cats, the demon bird, Quest the amazingly fat palomino horse, and a number of places in Alberta that remain beautiful despite looming development. I must also thank my family, including my older brother, for reinforcing that biologists are meant to be outside whenever and wherever possible.

Personal and project support for this project was supplied by NSERC, ConocoPhilips, University of Alberta, NSERC-ILM Research Grant (under S. Boutin),

Canadian Circumpolar Institute, Northern Studies Training Program, and the Alberta Sport, Recreation, Parks, and Wildlife Foundation. The Bank of Mom and Dad also indirectly contributed to this project (and my university career in general), although rumor has it that this financial institution has now permanently closed my account. I will continue to pay you back with in depth (but maybe not always accurate) interpretation of all the neat things we see on the trail. I shall, as always, endeavor to be entertaining.

Alright Bub, I am done. Let’s go for a walk.

Table of Contents

List of Tables

List of Figures

Chapter 1: Introduction

Prey use "enemy free space" to minimize their vulnerability to predators (Jeffries and Lawton 1984). Although enemy free space may be a function of behavioral and morphological adaptations, it quite literally may be the physical space that provides refuge from predation (Jeffries and Lawton 1984; McNair 1986; Sih *et al*. 1985; Sih 1987; Murphy 2004). Refuge use can affect more than just individual survival. Huffaker (1958) was one of the first to show that spatial refuges can stabilize predator-prey interactions because predators are unable to fully exploit the prey population (see McNair 1986; Sih 1987; Collings 1995; Ruxton 1995; Gonzalez-Olivares and Ramos-Jiliberto 2003; Srinivasu and Gayatri 2005 for more recent work on refuges and stability). The use of spatial refuges may also affect community structure by promoting habitat segregation among prey species (Jeffries and Lawton 1984; Mercurio *et al*. 1985; Kotler and Brown 1988; Martin 1996; Lingle 2002; Namgail *et al*. 2004). Use of refuge can mean little overlap with alternative prey, which minimizes the effects of "apparent competition" (i.e., the adverse affects of sharing a predator; Holt 1977; Holt 1984; Holt and Lawton 1994; also see Jeffries and Lawton 1984; Martin 1996; Lingle 2002). This effect is further enhanced if alternative prey have some attribute that deflects predation pressure away from refuge prey. For example, if alternative prey are easier to find, predators may spend little time in refuge prey habitat (Holt 1984).

The spatial segregation of woodland caribou (*Rangifer tarandus caribou*) from wolves (*Canis lupus*) and alternative prey species like moose (*Alces alces*) has been well documented in Canada (Bergerud 1985; 1988; Bergerud and Page 1987; Cumming *et al*. 1996; Ferguson *et al*. 1988; Bergerud *et al*. 1990; Seip 1992; Rettie and Messier 2000;

Schaefer *et al*. 2001; see Kojola *et al*. 2004 for a European example with wild Reindeer (*R. t. fennicus*)). Presumably, wolves focus on moose because moose are larger and more abundant than caribou (see Cumming *et al*. 1996 for an explicit depiction of this). Specific segregation strategies often depend on caribou ecotype (Thomas and Gray 2002). For example, mountain caribou in British Columbia and west-central Alberta migrate to higher elevations during the calving season, which reduces their encounters with valley-dwelling wolves and moose (Bergerud and Page 1987; Edmonds and Smith 1991; Seip 1992). Seasonal migrations are also evident in Ontario, where pregnant boreal caribou move to wolf- and moose-free islands in spring (Bergerud *et al*. 1990).

A year-round spacing strategy is used by the boreal caribou in northeastern Alberta and parts of west-central Alberta (Figure 1.1). These herds predominantly inhabit lichen-rich peatlands whereas wolves and moose are more likely to be found in the surrounding uplands (Edmonds 1988; Bradshaw *et al*. 1995; Stuart-Smith *et al*. 1997; James *et al*. 2004). Segregation appears to be a relatively successful anti-predator strategy. Wolf predation on caribou is largely incidental (i.e., caribou make up less than 1% of the wolf diet; James *et al*. 2004) and mortality locations in McLoughlin *et al*. (2005) suggest that predation pressure is lower for adult female caribou that "space away" from the uplands (sensu Bergerud 1988). However, peatlands do not provide an absolute refuge given that than half of adult female mortality is attributed to wolf predation (Stuart-Smith *et al*. 1997; James *et al*. 2004).

In fact, increased wolf use of adult caribou may explain why many of Alberta's herds are in decline (Dzus 2001; McLoughlin *et al*. 2003; Alberta Caribou Committee, *unpublished results*). This trend has led to the designation of caribou as provincially threatened (COSEWIC 2005). Female adult survival has high elasticity, meaning that a small change in adult survival can mean a large change in herd size (see Fancy *et al*. 1994 for an example with caribou; see Gaillard *et al*. 1998; 2000 for more general examples). Adult survival varies across herds in Alberta and there is some indication that declines are more likely or greater for herds with lower adult survival (based on data in Dunford 2003; McLoughlin *et al*. 2003; Neufeld 2006). Low adult survival has been linked to caribou declines elsewhere in Canada and is generally attributed to increased predation pressure (Schaeffer *et al*. 1999; Wittmer *et al*. 2005*a*). While it isn't clear why predation may be increasing for Alberta's caribou, the empirical and theoretical literature point to three hypotheses: (1) increased wolf mobility between uplands and peatlands via wolf use of linear features, (2) movement of moose, and consequently wolves, into caribou range, and (3) increased number of wolves hunting in caribou range (Holt 1977; 1984; Holt and Kotler 1987; Fuller 1989; James and Stuart-Smith 2000; James *et al*. 2004; D. Latham, *unpublished results*).

The first two hypotheses are largely related to factors that directly increase wolf activity in peatlands. For example, if predator mobility between refuge and alternative prey patches is high, then refuges may provide little safety for resident prey because individual habitats essentially merge from the perception of the predator (Holt 1984). In Alberta, increased mobility may stem from wolf use of linear features (James and Stuart-Smith 2000). These features, which are predominantly seismic lines, vary from 0.7 to 3.5 km/km^2 in caribou range and can be as dense as 10 km/km^2 outside of caribou range (Dzus 2001; Schneider 2002; Lee and Boutin 2006; Neufeld 2006). Movement on lines is about three times faster than movement in the forest (James 1999). This should mean that line use increases the likelihood of wolf-caribou and wolf-moose encounters because wolves can move between uplands and peatlands more quickly (i.e., line use will increase predator efficiency). In fact, kill rate:line density relationships may mimic the functional relationships that are often evident between wolf kill rate and prey density (e.g., Messier 1994). Yet, this relationship is complicated by a number of factors. For example, caribou usually avoid linear features (i.e. use is less than expected within 250 m of a line; Dyer *et al*. 2001), which is a behavior that may negate line use because predator and prey never “cross paths”.

Predator activity may also increase in a refuge if it becomes more profitable. Increases in profitability may stem from the movement of alternative prey into the refuge prey habitat, followed by a shift in predator hunting activities (Holt and Kotler 1987). The consequence of this may be more incidental encounters between predators and refuge prey (Holt and Kotler 1987). Recent work in Alberta suggests that moose now occupy at least one caribou range, which may explain why wolf activity in the range has also increased (D. Latham, *unpublished results*). This shift is considered a change in moose distribution and not density (D. Latham, *personal communication*), although changes in moose density may be occurring in other caribou ranges; see below and Chapter 5). Of course, the effect of overlap may be enhanced by wolf use of lines, as wolves are more likely to be in peatlands and searching more efficiently at the same time.

The last hypothesis is more a function of the number of wolves hunting in peatlands. Increases in predator densities often stem from increases in the number of alternative prey (Holt 1977; 1984; Fuller 1989; Messier 1994). This can lead to predator “spillover” into a refuge and cause the reduction or extinction of refuge prey (i.e., Holt

1984; Jeffries and Lawton 1984). Increased predator density is an oft-cited cause of caribou declines and is usually linked to forestry operations which create good quality moose habitat (Bergerud and Elliott 1986; Seip 1992; Rettie and Messier 1998; Schaefer *et al*. 1999; Wittmer *et al*. 2005*ab*). In northeastern Alberta, "spillover" may be the numeric consequence of wolf use of lines, if line use does lead to more wolf kills. In west-central Alberta, where timber harvest within caribou ranges is more likely to occur (Dzus 2001), spillover may reflect a combination of wolf use of lines and increased moose density. Either way, there may now be more wolves making incidental forays into individual caribou ranges. Again, this effect may be furthered by wolf use of lines.

While logical, all of the above arguments remain speculative and are supported by little or no empirical data. The lack of data reflects the difficulty and expense of working in the wolf-caribou-moose system in Alberta. Caribou survival and calf recruitment are the only parameters that are regularly monitored across the province (Alberta Caribou Committee, *unpublished results*). Much of the information about moose and wolves is 20 years or older and/or limited to a specific caribou range (e.g., Fuller and Keith 1980; Hauge and Keith 1981; Bjorge and Gunson 1989; James and Stuart-Smith 2000; Kuzyk 2004; James *et al*. 2004; Osko *et al*. 2004; Lessard 2005; Neufeld 2006; D. Latham, *unpublished results*; but see Schneider and Wasel 2000 for more recent information on moose). Yet, hypothesis 1 would require a detailed investigation of wolf movements, prey-specific wolf kill rates, and prey survival across a range of line densities and caribou ranges. This type of data often requires the use of GPS or VHF collars, aerial monitoring, and back-tracking, all of which are expensive (e.g., a single GPS collar can cost more than $5000, based on a 2006 price list from Lotek Wireless). At the very least, hypotheses 2 and 3 would require detailed moose and/or wolf surveys across a large number of caribou ranges, although more detailed data on wolf and moose movements would make for better inferences. Of course, all these investigations are correlative in nature. A true test of the effect of each mechanism on caribou survival would require a large-scale manipulation of (1) line density and/or wolf use of lines; (2) moose distribution in and outside caribou range; and (3) wolf density and distribution in and outside of caribou range. Aside from the difficulty of performing these experiments on such a large scale, there are a number of land-use and ethical issues with manipulating line densities, line use, and prey and predator densities (e.g., Bergerud and Elliott 1986; Gasaway *et al*. 1983; 1992; Gunson 1992; Gunson *et al*. 1993).

However, these problems can be examined using computer simulation models, which are virtual representations of the system of interest. Manipulation of a model "world" can lead to insight and understanding of the system that may otherwise be difficult to study because of logistical, financial, or ethical reasons (Peck 2004). As such, models are valuable for providing direction for empirical data collection, experimental work, and management, even if knowledge of a system is poor (Starfield 1997; Cramer and Portier 2001; Schneider 2001; Stillman *et al*. 2001; West *et al*. 2003; Norris 2004; Peck 2004). The main goals of this thesis are to use simulation models to (1) determine how increased wolf mobility (Chapter 3), changes in moose distribution (Chapter 4), and an increase in wolf numbers (Chapter 5) affect caribou survival, and (2) recommend where future field and management work should be focused. The models are best described as behavior-based models, individually-orientated, or individually based movement models as they are built on the behavior and movement of individuals (e.g., Turchin 1998; Norris 2004; see Jones 1977; Turner *et al*. 1994; Berger *et al*. 1999; Railsback *et al*. 1999; South 1999; Zollner and Lima 1999; 2005; Cramer and Portier 2001; Stillman *et al*. 2001; West *et al*. 2003 for relevant examples). However, while models do focus on changes in caribou survival, they do not address other variables that are important for ungulate population dynamics (e.g., calf recruitment, Fancy *et al*. 1994; Gaillard *et al*. 1998; 2000). The decision to leave these other factors out stems mainly from the fact that they have either not been investigated (e.g., rates of immigration, emigration, or the role of male caribou) or they are even more poorly understood than adult survival (e.g., factors underlying calf survival and recruitment). As such, these models are not population-based and should not be confused with IBMS or IBPMs (i.e., Individual Based Models or Individual Based Population Models; Grimm 1999; DeAngelis and Mooij 2005; Grimm and Railsback 2005).

References

Berger, U., Wagner, G., and Wolff, W.F. 1999. Virtual biologists observe virtual grasshoppers: an assessment of different mobility parameters for the analysis of movement patterns. Ecological Modeling 115: 119-127.

Bergerud, A.T. 1985. Antipredator strategies of caribou: dispersion along shorelines. Canadian Journal of Zoology 63: 1324-1329.

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

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

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

Bergerud, A.T., Ferguson, R., and Butler, H.E. 1990. Spring migration and dispersion of woodland caribou at calving. Animal Behavior 39: 360-368.

Bjorge, R.R., and Gunson, J.R. 1989. Wolf, *Canis lupus*, population characteristics and prey relationships near Simonette River, Alberta. Canadian Field Naturalist 103: 327-334.

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

Collings, J.B. 1995. Bifurcation and stability analysis of a temperature-dependent mite predator-prey interaction-model incorporating a prey refuge. Bulletin of Mathematical Biology 57: 63-76.

Committee on the Status of Endangered Wildlife in Canada. 2005. Status of Woodland caribou (*Rangifer tarandus caribou*). Retrieved on Nov. 30th, 2005 at http://www.cosewic.gc.ca/eng/sct1/searchdetail_e.cfm.

Cumming, H.G., Beange, D.B., and Lavoie, G. 1996. Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared predation risk. Rangifer Special Issue 9: 81-94.

Cramer, P.C., and Portier, K.M. 2001. Modeling Florida panther movements in response to human attributes of the landscape and ecological settings. Ecological Modeling 140: 51-80.

DeAngelis, D.L., and Mooij, W.M. 2005. Individual-based modeling of ecological and evolutionary processes. Annual Review of Ecology and Systematics 36: 147-168.

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

Dzus, E. 2001. Status of the Woodland Caribou (*Rangifer tarandus caribou*) in Alberta. Alberta Environment, Fisheries and Wildlife Management Division, and Alberta Conservation Association, Wildlife Status Report No. 30, Edmonton, AB. 47 pp.

Edmonds, E.J., and Smith, K.G. 1991. Mountain caribou calf production survival, and calving and summer habitat use in west-central Alberta. Wildlife Research Series No. 4, Alberta Fish and Wildlife Division, Edmonton, AB. 16 pp.

Fancy, S.G., Whitten, K.R., and Russell, D.E. 1994. Demography of the Porcupine caribou herd, 1983-1992. Canadian Journal of Zoology 72: 840-846.

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

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

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

Gaillard, J.M., Festa-Bianchet, M., and Yoccoz, N.G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13: 58-63.

Gaillard, J.M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., and Toigo, C. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31: 367-393.

Gasaway, W.C., Boertje, R.D., Grangaard, D.V., Kelleyhouse, D.G., Stephenson, R.O., and Larsen, D.G. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs 120: 1-59.

Gasaway, W.C., Stephenson, R.O., Davis, J.L., Sheperd, P.E.K., and Burris, O.E. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs 84: 1-50.

Gonzalez-Olivares, E., and Ramos-Jiliberto, R. 2003. Dynamic consequences of prey refuges in a simple model system: more prey, fewer predators and enhanced stability. Ecological Modeling 166: 135-146.

Grimm, V. 1999. Ten years of individual-based modeling in ecology: what have we learned and what could we learn in the future? Ecological Modeling 115: 129-148.

Grimm, V., and Railsback, S.F. 2005. Individual-based modeling and ecology. Princeton University Press, Princeton, Princeton, USA, 428 pp.

Gunson, J.R. 1992. Historical and present management of wolves in Alberta. Wildlife Society Bulletin 20: 3003-339.

Gunson, J.R., Jalkotzy, M., Carbyn, L.N., and Roy, L.D. 1993. Predation. In Hoofed Mammals of Alberta. Edited by J.B. Stelfox. Lone Pine Publishing, Edmonton, Alberta. pp. 69-80.

Hauge, T.M., and Keith, L.B. 1981. Dynamics of moose populations in northeastern Alberta. Journal of Wildlife Management 45: 573-597.

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

Holt, R.D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. American Naturalist 124: 377-406.

Holt, R.D., and Kotler, B.P. 1987. Short-term apparent competition. American Naturalist 130: 412-430.

Holt, R.D., and Lawton, J.H. 1994. The ecological consequences of shared natural enemies. Annual Review of Ecology and Systematics 25: 495-520.

Huffaker, C.B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia 27: 343-383.

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

James, A.R.C., Boutin, S., Hebert, D.M., and Rippin, A.B. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. Journal of Wildlife Management 68: 799-809.

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

Jeffries, M.J. and Lawton, J.H. 1984. Enemy free space and the structure of ecological communities. Biological Journal of the Linnean Society 23: 269-286.

Jones, R.E. 1977. Movement patterns and egg distribution in cabbage butterflies. Journal of Animal Ecology 46: 195-212.

Kojola, I., Huitu, O., Toppinen, K., Heikura, K., Heikkinen, S., and Ronkainen, S. 2004. Predation on European wild forest reindeer (*Rangifer tarandus*) by wolves (*Canis lupus*) in Finland. Journal of Zoology 263: 229-235.

Kotler, B.P., and Brown, J.S. 1988. Environmental heterogeneity and the coexistence of desert rodents. Annual Review of Ecology and Systematics 19: 281-307.

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

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

Lee, P. and Boutin, S. 2006. Persistence and developmental transition of wide seismic lines in the western Boreal Plains of Canada. Journal of Environmental Management 78: 240-250.

Lingle, S. 2002. Coyote predation and habitat segregation of white-tailed deer and mule deer. Ecology 83: 2037-2048.

Martin, T.E. 1996. Fitness cost of resource overlap among coexisting bird species. Nature 380: 338-340.

McLoughlin, P.D., Dunford, J.S., Boutin, S. 2005. Relating predation mortality to broad-scale habitat selection. Journal of Animal Ecology 74: 701-707.

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

McNair, J.N. 1986. The effects of refuges on predator-prey interactions: a reconsideration. Theoretical Population Biology 29: 38-63.

Mecurio, K.S., Palmer, A.R., and Lowell, R.B. 1985. Predator-mediated microhabitat partitioning by two species of visually cryptic, intertidal limpets. Ecology 66: 1417-1425.

Messier, F. 1985. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. Canadian Journal of Zoology 63: 239-244

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology 75: 478-488.

Murphy, S.M. 2004. Enemy-free space maintains swallowtail butterfly host shift. Proceedings of the National Academy of Sciences 101: 18048-18052.

Namgail, T., Fox, J.L., and Bhatnagar, Y.V. 2004. Habitat segregation between sympatric Tibetan argali *Ovis ammon hodgsoni* and blue sheep *Pseudois nayaur* in the Indian Trans-Himalaya. Journal of Zoology London 262: 57-63.

Neufeld, L. 2006. Spatial dynamics of wolves and woodland caribou in an industrial forest landscape in west-central Alberta. M.Sc. Thesis, University of Alberta, Edmonton, AB.

Norris, K. 2004. Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. Journal of Applied Ecology 41: 413-426.

Osko, T.J., Hiltz, M.N., Hudson, R.J., and Wasel, S.M. 2004. Moose habitat preferences in response to changing availability. Journal of Wildlife Management 68: 576-584.

Peck, S.L. 2004. Simulation as experiment: a philosophical reassessment for biological modeling. Trends in Ecology and Evolution 19: 530-534.

Railsback, S.F., Lamberson, R.H., Harvey, B.C., and Duffy, W.E. 1999. Movement rules for individual-based models of stream fish. Ecological Modeling 123: 73-89.

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

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

Ruxton, G.D. 1995. Short-term refuge use and stability of predator-prey models. Theoretical Population Biology 47: 1-17.

Schaefer, J.A., Veitch, A.M., Harrington, F.H., Brown, W.K., Theberg, J.B., and Luttich, S.N. 1999. Demography of decline of the Red Wine Mountains caribou herd. Journal of Wildlife Management 63: 580-587.

Schaefer, J.A., Veitch, A.M., Harrington, F.H., Brown, W.K., Theberge, J.B., and Luttich, S.N. 2001. Fuzzy structure and spatial dynamics of a declining woodland caribou population. Oecologia 126: 507-514.

Schneider, M.F. 2001. Habitat loss, fragmentation and predator impact: spatial implications for prey conservation Journal of Applied Ecology 38: 720-735.

Schneider, R.S. 2002. Alternative futures: Alberta’s boreal forest and the crossroads. Federation of Alberta Naturalists, Edmonton, Alberta, 152 pp.

Schneider, R.S., and Wasel, S. 2000. The effect of human settlement on the density of moose in northern Alberta. Journal of Wildlife Management 64: 513-520.

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.

Sih, A. 1987. Prey refuges and predator-prey stability. Theoretical population biology 31: 1-12.

Sih, A., Crowley, P., McPeek, M., PetrankaJ., and Strohmeier, K. 1985. Predation, competition, and prey communities: a review of field experiments. Annual Review of Ecology and Systematics 16: 269-311.

South, A. 1999. Extrapolating from individual movement behaviour to population spacing patterns in a ranging mammal. Ecological Modeling 117: 343-360.

Srinivasu, P.D.N., and Gayatri, I.L. 2005. Influence of prey reserve capacity on predator-prey dynamics. Ecological Modeling 181: 191-202.

Starfield, A.M. 1997. A pragmatic approach to modeling for wildlife management. Journal of Wildlife Management 61: 261-270.

Stillman, R.A., Goss-Custard, J.D., West, A.D., Le V. Dit Durell, S.E.A., McGrorty, S., Caldow, W.G., Norris, K.J., Johnstone, I.G., Ens, B.J., Van der Meer, J., and Triplet, P. 2001. Predicting shorebird mortality and population size under different regimes of shellfishery management. Journal of Applied Ecology 38: 857-868.

Stuart-Smith, A.K., Bradshaw, C.J.A., Boutin, S., Hebert, D.M., and Rippin, A.B. 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. Committee on the Status of Endangered Wildlife in Canada. Ottawa. 1-98 pp.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Inc., Massachusetts.

Turner, M.G., Wu, Y., Wallace, L.L., Romme, W.H., and Brenkert, A. 1994. Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. Ecological Applications 4: 472-496.

West, A.D., Goss-Custard, J.D., McGrorty, S., Stillman, R.A., le V. dit Durrell, S.E.A., Stewart, B., Walker, P., Palmer, D.W., and Coates, P.J. 2003. The Burry shellfishery and oystercatchers: using a behaviour-based model to advise on shellfishery management policy. Marine Ecology Progress Series 248: 279-292.

Wittmer, H.U., McLellan, B.N., Seip, D.R., Young, J.A., Kinley, T.A., Watts, G.S., and Hamilton, D. 2005*a*. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. Canadian Journal of Zoology 83: 407-418.

Wittmer, H.U., Sinclair, A.R.E., and McLellan, B.N. 2005*b*. The role of predation in the decline and extirpation of woodland caribou. Oecologia 144: 257-267.

Zollner, P.A., and Lima, S.L. 1999. Search strategies for landscape-level interpatch movements. Ecology 80: 1019-1030.

Zollner, P.A., and Lima, S.L. 2005. Behavioral tradeoffs when dispersing across a patchy landscape. Oikos 108: 219-230.

Figure 1.1. Ranges of boreal caribou examined in this study, including WSAR, west side of the Athabasca River, ESAR, east side of the Athabasca River, and CLAWR, Cold Lake Air Weapons Range. The hatched line approximates the historical southern limit of woodland caribou range. This figure was modified with permission from McLoughlin, P.D., Paetkau, D., Duda, M., and Boutin, S. 2004. Genetic diversity and relatedness of boreal caribou populations in western Canada. Biological Conservation 118: 593–598.

Chapter 2: Model formulation and assessment

Model Objectives

The main objective of this study was to design a series of models that assessed how wolf kill rates, caribou survival, and moose survival were affected by (1) increased wolf mobility via wolf use of linear features; (2) movement of moose into caribou range; and (3) an increase in the number of predators hunting in caribou and moose range. A secondary objective was to determine how these relationships were affected by wolf behavior (i.e., movement strategies and degree of line use) and prey behavior (i.e., prey response to linear features).

Models documented wolf-caribou and wolf-moose interactions in a single wolf territory in winter. To address my study objectives, baseline territories were programmed to accommodate (1) the addition of linear features to the wolf territory (e.g., from territories with no linear features to territories with up to 5 km/km^2 of linear features); (2) changes in moose distributions such that an increasing proportion of caribou range was occupied by moose; and (3) an increase in the number of wolves hunting in the territory. Models were run for a "year" and yielded annual rates of wolf kills, moose survival, and caribou survival. However, models did not track changes in population size and thus were not population-level models.

Approach: Grid-based models

I used a grid-based modeling approach to address my study objectives. Grid-based models are rule-based computer simulations that include, but are not restricted to, cellular automata (Tischendorf 1997; Dieckmann *et al*. 2000; Wissel 2000; Vuilleumier and Metzger 2006). They are spatially explicit, which means that they are amenable to studying animal movement (Tischendorf 1997; Dieckmann *et al*. 2000; Gardner and Gustafson 2004; Moustakas *et al*. 2006; Vuilleumier and Metzger 2006). Grids are made up of equal sized cells that are coded to reflect certain ecological states (e.g., number of individuals, habitat type, etc.). Movement rules are based on logic arguments written up in a computer programming language (e.g., Basic, C++, Fortran, etc.).

I chose grid-based models over more sophisticated techniques because they are easily adapted to unique ecological systems even if data describing such systems is sparse (e.g., Wissel 2000). For example, Individual Based Models would be ideal to study how increased predation pressure affects long term population dynamics of caribou (see Grimm 1999; DeAngelis and Mooij 2005; Grimm and Railsback 2005 for examples of population level IBMS or IBPMs). However, the detailed data required to build such a model is lacking for this system. While key parameters could be estimated or guessed at, in the end, the model would be severely restricted by uncertainty in model inputs. Grid based models can also be designed by a novice programmer, meaning that the novice programmer has full control of the model and has an intuitive understanding of how the model works. This is essential for identifying program bugs, troubleshooting, and interpreting unexpected model results. Moreover, grid-based modeling approaches do not require an advanced study of mathematics as they are built on logic rules and not mathematical relationships.

The largest draw-back to using a grid-based approach is its computational intensity, which means that sacrifices must be made in terms of the resolution, complexity, and extent of the models (e.g., Tischendorf 1997; Vuilleumier and Metzger 2006). For example, a GIS modeling approach would more accurately depict the size of linear features relative to other features of the territory (e.g., Tischendorf 1997). However, sensitivity analyses suggest that resolution and extent did not affect model results (see below for details).

Parameters

Most of the parameters in the models were based on empirical data gleaned from the literature (Table 2.1.). Moreover, all parameters were solely or partly based on studies conducted in Alberta (e.g., Fuller and Keith 1980; Hauge and Keith 1981). The pattern of wolf movement in northern Alberta was the only parameter for which little or no data existed. As such, wolf movement was based on a series of "rules" (see below for details).

Model description

Wolf territory size

The size of each territory (or grid) was set at "625 km^2", which is about the size of a pack's winter territory in northern Alberta (Fuller and Keith 1980; Bjorge and Gunson 1989) (Figure 2.1.). Cells within the grid were 1 km x 1 km, yielding a total of 625 cells (i.e., 25 cells x 25 cells). The 1 km x 1 km cell size was chosen because it is within the range of reported wolf detection radiuses (i.e., the distance from which they can detect prey – be it visually, acoustically, tracking, or through scent; Mech 1981). Grid boundaries were reflecting (Berec 2002), thereby representing territorial boundaries.

Peatland and upland patches within the territory

Roughly half (325 out of 625 cells) of the grid was designated as upland while the other half was designated as peatland. Peatland and uplands were each represented by a single large patch.

Cell types

Cells in the "territories" were either "forest-only cells" or "forest cells with lines". The only territory with 100% forest-only cells was the 0 km/km^2 territory (i.e., the territory free of linear features). A total of twelve different territories were constructed to represent a linear feature density range of 0 to 5 km/km^2 (i.e., 0, 0.0625, 0.125, 0.25, 0.375, 0.5, 0.75, 1, 2, 3, 4, 5 km/km^2). This is within the range of densities observed in the peatlands and uplands across Alberta (e.g., Bayne *et al*. 2005; Lee and Boutin 2006). I used a random number generator to randomly assign lines to boundary cells (i.e., the top row running north-south and the left edge running east-west). Lines started from a boundary cell and either moved south (a north-south line) or west (an east-west line) (Figure 2.1.). There were 2 to 5 lines per cell, which accounted for prey avoidance buffers (e.g., a 250 m buffer zone around 2 lines spaced 500 m apart would mean that the cell was completely avoided by prey; see Dyer *et al*. 2001). This arrangement also ensured that some cells would be "line free" even in 5 km/km^2 territory. The initial configuration of lines was fixed. However, configurations did vary from one line density to the next (i.e., line configurations at 2 km/km^2 were not built on the 1 km/km^2 configuration).

Wolves, moose, and caribou within the territory

Each territory was populated by 1 wolf pack (comprised of 6 wolves), 25 caribou ($0.04/km^2$), and 150 moose ($0.24/km^2$). Wolf pack size was based on Fuller and Keith (1980) and Bjorge and Gunson (1989). Caribou density was averaged from data in Fuller and Keith (1981; $0.03/km^2$), Edmonds (1988; $0.01/km^2$), Stuart-Smith *et al*. (1997; 0.04-$0.12/km^2$), and James *et al*. (2004; $0.08/km^2$). Moose density was based on data in Schneider and Wasel (2000), which showed that moose are about twice as abundant in northwest than northeast Alberta (e.g., 0.24 vs 0.48 moose/km2). As such, baseline models reflect a northeastern Alberta scenario. For simplicity, other species of predators and prey were excluded from the models (e.g., bears (*Ursus americanus*), coyotes (*Canis latrans*), and deer (*Odocoileus* sp.) (but see Chapters 4 and 5 for more discussion of how these animals may affect caribou survival).

Start position

At the beginning of each simulation (i.e., $t = 1$), the pack was randomly assigned to one upland cell (i.e., of the 325 upland cells available, one was randomly picked with the aid of a random number generator).

Wolf movement

Wolf movement was essentially what “drove” the models, but was also the least understood parameter. While a fair amount of work has been conducted on the fine scale temporal and spatial patterns that contribute to wolf capture success (e.g., Mech 1981; Potvin *et al*. 1988; Huggard 1993; Thurber and Peterson 1993; Kunkel *et al*. 1999; 2004; Jedrzejewski *et al*. 2000; 2002; Kunkel and Pletscher 2000; 2001), much less is known about how wolves move more generally in their territories. There is some suggestion that daily movement is relatively straight (Bascompte and Vila 1997; review by Mech and Boitani 2003), whereas movement over a longer time scale follows a circular or rotational pattern (Mech 1981; Jedrzejewski *et al*. 2001; Mech and Boitani 2003). For example, a Polish study found that wolves returned to a central area within their territory every six days (Jedrzejewski *et al*. 2001). However, other work, and particularly that done in northern Alberta, suggests that wolves do not move in a recognizable pattern (Fuller and Keith 1980; Mech 1981).

This means that wolf movement may be variable and reflect local pack conditions. For example, prey density in Jedrzejewski *et al*. (2001) was at least 10 times greater than that in Fuller and Keith (1980). As such, the movement in Jedrzejewski *et al*. (2001) may be a response to behavioral prey depression, in which wolf presence decreases capture success because of prey avoidance behaviors (Jedrzejewski *et al*. 2001; Mech and Boitani 2003; Bergmann *et al*. 2006). Jedrzejewski *et al*. (2001)'s rotation schedule may be similar to a "giving-up rule" (i.e., Iwasa *et al*. 1981; McNair 1982; Green 1984), in which a pack leaves one area of their territory after so much time/distance traveled has passed since their last kill. This should minimize the amount of time a pack spends in an unprofitable part of their territory. Conversely, the low prey density in Fuller and Keith (1980) may preclude the need for rotational movement as behavioral prey depression is not as likely.

In terms of the models, the real issue is not how wolves move per se, but rather if different movement patterns yield different rates of hunting success (e.g., Lima and Zollner 1996; Zollner and Lima 1999; Lima 2002). Such differences could have a large impact on model results and interpretation. Based on sensitivity analyses designed to asses this (see below), I ran simulations in which the pack moved randomly and in which the pack used a 45 km^2 giving up rule (i.e., the movement patterns that yielded the lowest and highest rates of prey survival and kills). Random movement was based on a random number generator, in which there was an equal probability (i.e., 12.5%) of moving N, NE, E, SE, S, SW, W, or NW (i.e., an 8 cell rule). A "give-up" resulted in movement in the opposite direction, although not necessarily along the same path. For example, if the pack was moving east, then a "give-up" would involve moving south, north, west, southwest, or northwest after 45 km^2 of travel with no kill. Area searched was used instead of time because of difficulties with tracking a variable time step (i.e., when territories with lines were considered, time was variable, depending on forest or line travel; see below for details). However, a giving-up areas of 45 km^2 was equivalent to 15 d of search in a territory with no lines. Search distance instead of time has also been used as an estimate of search effort in empirical studies (e.g., Kunkel and Pletscher 2004).

If the pack was giving-up, it would move from peatland to upland habitat or from upland to peatland habitat (depending on where they were when they "decided" to give-up). Note that the pack did not automatically "jump" to the alternate habitat; rather, movement was based on sequential steps towards the alternative habitat. There was a 75% chance that they would move in an easterly/westerly direction and a 25% chance that they would move north or south. These values were arbitrarily selected, though the intention was to mimic Bascompte and Vila's (1997) finding that daily wolf movement is relatively straight. Moreover, varying these values had little effect on model results (see below). Before a "give-up" rule kicked in, the pack moved randomly. A give-up reverted back to random movement once a kill was made but otherwise resulted in the pack moving pack and forth between peatlands and uplands in a non-random fashion.

Travel time/day

Models assumed that the pack traveled ~35% of the day or 9 h/d for the period of one year (i.e., 1 time step was equal to 1 h, 9 time steps were equal to a day, and 3285 time steps were equal to a year). Travel time was based on Fuller and Keith (1980; 22%, Alberta study), Mech (1981; 30-34%; 1992; 28%), Peterson *et al*. (1984; 50% winter, 29% summer), and Theuerkauf *et al*. (2003; 45%).

Wolf use of lines

Line use depended on the probability of the pack using a line, if the pack encountered a line. Data from James (1999) indicates that ~26% of wolf GPS locations were on or near a line. Average line density in this study was 1.3 km/km^2, which likely meant that line use was not limited by line encounter rates (i.e., a pack would encounter at least 1 line per every km^2 of random travel). As such, I interpreted James' (1999) data to mean that there was a 25% chance that a pack used a line, if the pack was in a cell with lines. This was verified in the models (i.e., approximately 25% of travel time was on lines in a 1 km/km^2 territory). As line density increased, percent time on lines also increased (*unpublished results*).

The probability of using an individual line was independent of the number of other lines in the cell. For example, in a cell with 2 lines, there would be a 25% chance that the pack would use the first line "encountered". If the line was not used, then the line use subroutine would loop, meaning that there was a 25% chance that the pack would use the second line in the cell. If this line wasn't used, then it was assumed that travel in this cell was restricted to forest habitat. Note that line use was reevaluated for each time step (i.e., line use was not continuous from cell to cell; after the pack moved to another cell, probability of line use was determined via the line use subroutine). Variation in line use was examined in Chapter 3.

Line vs forest speed

If the pack used a line, then it took 1 time step to cross the cell. If no lines in the cell were used or if the pack traveled in a line-free cell, it took 3 time steps to cross the cell. This yielded a 3:1 ratio of line:forest speed as per James (1999). These rates yielded a maximum search area of 3 km^2/day if traveling strictly in forest cells or 9 km^2/day if traveling strictly in forest cells with lines. Note that this area represents a "straight line" search path (i.e., between the beginning and end points of daily movements; Jedrzejewski *et al*. 2001). The actual daily movement distance (DMD) would be much longer. For example, Jedrzejewski *et al*. (2001) found that straight line distances (SLD) approximated 21% of the actual distance wolves traveled per day (e.g., 4.4 SLD km/day vs 22.8 DMD km/day).

Pack dynamics

The pack moved as a cohesive unit (i.e., a single hunting unit roamed the territory). In reality, individuals may move independently of the pack throughout the year, although the movements are often outside of the territory (e.g., extraterritorial forays and/or dispersal; Messier 1985*b*; Peterson *et al*. 1984; Fuller 1989; Ballard *et al*. 1997). Lone wolves may also be part of the population and move through established pack territories and/or are limited to the areas between territories (e.g., in Alberta, 10-13% of the population may be loners; Fuller and Keith 1980; Bjorge and Gunson 1989; also see Peterson *et al*. 1984; Messier 1985*b*; Thurber and Peterson 1993). Models based on multiple wolf movements are discussed in Chapter 5.

Prey distribution and movement

Caribou were always found in peatlands and baseline models restricted moose to uplands (see Chapter 4 for the effect of variation in moose distributions). Distributions were generated from a random number generator. Prey movement was mimicked via random redistribution of individual caribou and moose each time step (cell by cell movement of individual prey was much more complex to program because of the variable time step). As such, prey movement speed was dictated by how fast the pack moved. Straight line distances for moose and caribou are usually estimated at less than 2 km/day, but this varies seasonally (Cederlund *et al*. 1987; Bradshaw *et al*. 1997, Stuart-Smith *et al*. 1997; Smith *et al*. 2000; Rettie and Messier 2001; Ferguson and Elkie 2004). Still, movement in the models is greater than the empirical data suggests (i.e., varied from 3 to 9 km/day), although sensitivity analyses suggest that this did not affect model results (see below).

Prey response to lines

Prey avoidance behaviors were incorporated into the models by assuming that no prey animal would be found in a cell with lines. This assumption is largely based on caribou, which are usually 250 m or more from a linear feature (James and Stuart-Smith 2000; Dyer *et al*. 2001). Moose response to lines is not well studied, so I assumed that prey behavior was similar for all simulations (i.e., if caribou avoided lines, so did moose). Variation in prey response to lines was investigated in Chapter 3.

Prey encounters and kills

A prey encounter occurred when the pack was in the same 1 km^2 cell as a prey animal. Ten percent of encounters led to a successful kill (average based on data in Fuller and Keith 1980 (17%); Mech 1981 (8-10%); Peterson *et al*. 1984 (5%)). I assumed that the 10% kill success would incorporate small scale behaviors and conditions not incorporated into the models (i.e., direct tracking of prey, short-term prey response to wolf presence, prey condition and age, etc.). If successful, the pack would remain at a moose kill for 2 d and a caribou kill for 1 d (based on Ballard *et al*. 1997, in which mean pack size was 7; for an Alberta comparison, a pack of ~10 wolves took an average of 2.5 days to handle an adult moose; Fuller and Keith 1980).

Prey survival

Models assumed that kills directly reflected on annual rates of prey survival. Furthermore, models assumed that overall prey survival reflected directly on female adult survival as there was no evidence to suggest that gender affects survival rates of moose or caribou in Alberta (i.e., a 10% in model survival meant a 10% decline in female survival; Fuller and Keith 1981; Hauge and Keith 1981). It was also assumed that prey mortality was only a function of wolf predation (i.e., the effects of starvation, disease, etc., were not included in the models).

Simple example of cell transitions

Starting from a random upland location, the pack would "make a decision" and move from their existing cell to an adjacent cell. If the new cell contained no prey, the pack would make another move to a different cell. If the cell contained prey and the pack captured and kill it, they would remain in the cell while handling the prey (time in cell depended on if it was a moose or caribou kill). If no kill was made, the pack would move to a new cell. A move to a new cell also depended on the time step interval (i.e., if the pack was on a line or traveling in forest) but always occurred at the beginning of the next time step. This pattern would loop for a "year" (i.e., until $t = 3289$).

Sensitivity Analyses

The model structure describe above was subjected to a series of sensitivity analyses, in which parameters were varied to assess their effects on model output (i.e., moose survival, caribou survival, and wolf kills/year) (e.g., Turner *et al*. 2001). For the most part, changes in model structure had no qualitative or quantitative effect on results. Uncertainty analyses, in which parameters were varied based on their reported range of variation (e.g., Turner *et al*. 2001), were performed on select parameters in later chapters (e.g., wolf use of lines and prey avoidance of lines (Chapter 3), moose distributions (Chapter 4), and moose and wolf densities (Chapter 5)).

Unless otherwise indicated, all sensitivity analyses assumed that:

(1) The territory was free of linear features;

(2) Wolves moved randomly as a cohesive unit;

(3) Prey distributions were random (but restricted to their appropriate habitats);

(4) Moose density was $0.24/\text{km}^2$;

(5) The probability of a kill, if a moose or caribou was encountered, was 10%;

(6) A pack took 2 d to handle a moose and 1 d to handle a caribou.

Cell size within the territory

The number of cells, as determined by cell size, can affect model results (Chen and Mynett 2003). However, cell size did not have a large and/or consistent effect on survival and kill rate in this study. For example, caribou survival only varied 3% even if the number of cells was doubled (0.71 km x 0.71 km or 1225 cells) or halved (1.40 km x 1.40 km or 324 cells; note that the overall grid remained constant at 625 km^2) (Figure 2.2.). Moreover, simulations were about twice as fast in a 625 cell grid than in a 1225 cell grid.

The number of peatland and upland patches within the territory

Models assume a very simplified landscape; in reality, uplands and peatlands are much more integrated. As such, an actual wolf territory would consist of a number of upland and peatland patches. However, a simple 2-habitat territory yielded similar results to territories with multiple upland and peatland patches that were randomly distributed throughout the territory (Figure 2.3.).

Line configuration

For simplicity, line configurations were fixed in the models, and thus could bias model results. However, alternative line configurations did not affect model output (e.g., Figure 2.4.).

Moose density

Moose density does vary in Alberta, particularly with respect to the northeast and northwest portions of the province (Schneider and Wasel 2000). However, qualitative patterns assuming 0.24 or 0.48 moose/km^2 were the same (see Chapter 5; note that this is also true for 0.12 and 1 moose/km^2; *unpublished results*).

Start position

"Start position" did affect caribou survival (i.e., survival was 7% lower if wolves started in peatlands; Figure 2.5.), but wolves in northern Alberta primarily center their territories in upland habitat (James *et al*. 2004). Moreover, qualitative results from later chapters were unaffected by start position (*unpublished results*). As such, start position was not changed in subsequent models.

Wolf movement

In addition to the wolf movement strategies described above (i.e., random movement and movement assuming a 45 km^2 giving up rule), I also ran simulations in which the pack moved non-randomly by "giving-up" after 4.5, 9, 12, 18, 24, 30, 66, 90, 135, and 225 km^2 of unsuccessful search (note that this range was chosen arbitrarily and is not based on any biological data). I also varied the amount of north/south movement that accompanied a "give-up", but this did not affect results unless under extreme parameter conditions (i.e., if all "giving-up" movement was in north or south direction) (Figure 2.6.).

As previously stated, differences in prey survival and wolf kill rates indicated that wolf movement has an effect on model output and was therefore a sensitive parameter.

Caribou survival ranged from 86 to 93%, but peaked at intermediate giving-up areas of 45 to 90 km^2 (Figure 2.7.). Moose survival showed the opposite trend, but was less variable (i.e., ranged from 81 to 85%). Kill rates ranged from 5 to 30/year (Figure 2.8.). Kills peaked at intermediate giving-up areas (45 km^2 to 90 km^2) and then declined as giving-up areas approached completely random movement. Kill rates were the lowest when the pack moved randomly or used a 4.5 km^2 to 12 km^2 giving-up rule. Based on these results, I ran models assuming movement patterns that yielded the lowest (random movement) and the highest (movement using a 45 km^2 giving up rule) rates of prey survival and kills.

Prey movement

In the models, prey movement is greater than the empirical data suggests (i.e., varied from 3 to 9 km/day). However, this was not expected to alter results as models with prey movement yielded the same results as those as models in which prey distributions were fixed (i.e., no prey movement; Figure 2.9.).

Kill success

Baseline models assumed that 10% of encounters led to a successful kill. However, sensitivity analyses indicated that kill success was a sensitive parameter. For example, kills increased from 13 to 53/year as kill success increased from 5 to 20% (Figure 2.10.). Large changes in moose and caribou survival were also evident. However, qualitative patterns based on changes in line density, moose overlap, and wolf density were unaffected by kill success (*unpublished results*). Prey-specific kill rates also had no effect on qualitative model results (*unpublished results*), and thus I did not differentiate between the kill success rates for moose and kill success rates for caribou (see Lessard 2005 for some discussion of this). As such, kill success was not changed in subsequent models.

Handling time

Handling time did affect kill rates (e.g., kill rates decreased from ~29 to 22 kills/year as handling time increased to 5 d; Figure 2.11.). However, prey survival varied little across handling time unless it was very long (e.g., 5 days). Moreover, qualitative patterns based on changes in line density, moose overlap, and wolf density were unaffected by handling time (*unpublished results*). As such, handling time was not changed in subsequent models.

Model convergence

Models have built-in stochasticity (e.g., wolves did not always start in the same spot, prey positions were not fixed, etc.), which meant that results varied from one simulation run to the next. I determined how many simulation runs were necessary for the mean prey survival to stabilize by running simulations 5, 25, 50, 75, 100, and 150 times (e.g., Bugmann *et al*. 1996). Results indicated that the mean after 50 runs approximated the "true mean" (i.e., the mean based on all runs) as equally well as the mean after 100 or more runs (Figure 2.12.).

Model assessment

Model validation is not possible for this study as there is no existing data set that documents the effects of line use and line density, overlap between moose and caribou, and wolf density on wolf kill rates and prey survival. However, the realism of baseline models can be assessed by comparing kill rates and prey survival to the existing literature. Fuller and Keith (1980; 1981) and Hauge and Keith (1981) are the main studies for comparison as they describe wolf, moose, and caribou population dynamics in northeast Alberta in the 1970s and early 1980s. Relative to current developments, linear feature density in these studies was low (e.g., Schneider 2002). Moose and caribou densities in the northeast region of Fuller and Keith (1980) were also comparable to the 0.28 prey/km^2 in the models (0.27 prey/km^2 based on Fuller and Keith 1981 and Hauge and Keith 1981). Models were assessed by comparing the empirical literature to model estimates of moose and caribou survival, days between kills, and changes in wolf densities based on biomass intake.

Depending on the wolf movement strategy, annual moose survival ranged from 81 to 85% and annual caribou survival ranged from 85 to 93%. This is close to the data in Fuller and Keith (1981) and Hauge and Keith (1981), in which combined male and female moose survival was estimated at 75% while combined male and female caribou survival was estimated at 85 to 88%. Some of the discrepancy between models and data may stem from only including wolf-based mortality (i.e., models do not consider mortality from other predators, disease, hunting, etc.). While wolves appear to be the primary predator of both species (i.e., they accounted for ~64% of the moose mortality in Hauge and Keith 1981 and at least 50% of caribou mortality in Fuller and Keith 1981), 36 to 50% of the mortality still remains unaccounted for. One interesting result was the inverse relationship between moose and caribou survival (i.e., when moose survival was low, caribou survival was high). This suggests that time spent handling one prey type reduces the amount of time spent handling another (e.g., Holt and Kotler 1987). This finding will be examined more thoroughly in Chapter 4.

Days between kills was also similar to the empirical data. Simulation results predicted that days between kills would range from 12 to 17 days (this primarily reflects moose kills), which is higher than Fuller and Keith (1980) but was still close to the observed range (average: 7 days/moose kill; range: 5 to 13 days/moose kill). Kill rates should yield enough prey/year to support a pack of six wolves. Average moose density in northeast Alberta is higher than the threshold moose density below which a pack may no longer be sustained and/or reproduce (i.e., 0.24 moose/km^2; Schneider and Wasel 2000 vs 0.20 moose/km^2; Messier 1985*a*). Wolves require 0.06 and 0.13 kg prey/kg wolf/day for over winter survival and a litter of pups, respectively (Kolenosky 1972; Mech 1977). Based on data in Fuller and Keith (1980) and Bjorge and Gunson (1989), each pack member weighs 41 kg and the average winter pack size across Alberta is six. This translates into a minimum of 7 183 kg prey for over winter survival of the whole pack and a minimum of 15 564 kg of prey for over winter survival and a successful litter of pups (note that values assume a 75% consumption rate of prey; Peterson 1978; Fuller and Keith 1980; Peterson *et al*. 1984; Ballard *et al*. 1997). If kill rates are converted into biomass rates (e.g., #moose killed*435 kg/moose*0.75 + #caribou killed*154 kg/caribou*0.75; prey kg are based on Fuller and Keith 1981; Hauge and Keith 1981; Renecker and Hudson 1993; Smith 1993), models predict that wolves will have enough food for over winter survival (i.e., pack size will remain stable), but not enough food for reproductive success (i.e., pack size won't increase; Figure 2.13.). This tentatively agrees with the existing knowledge of wolf densities in northern Alberta. While wolf population trends are poorly studied across the province, there is no obvious indication that they are currently decreasing or increasing (but see Gunson 1992 and Stelfox and Stelfox 1993 for a more historical account of wolf numbers in Alberta). Overall, models appear to perform reasonably well despite their simplicity.

References

Ballard, W.B., Ayres, L., Krausman, P.R., Reed, D.J., and Fancy, S.G. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. Wildlife Monographs 135: 1-47.

Bascompte, J., and Vila, C. 1997. Fractals and search paths in mammals. Landscape Ecology 12: 213-227.

Bayne, E.M., Van Wilgenburg, S.L., Boutin S., and Hobson, K.A. 2005. Modeling and field-testing of Ovenbird (*Seiurus aurocapillus*) responses to boreal forest dissection by energy sector development at multiple spatial scales. Landscape Ecology 20: 203-216.

Berec, L. 2002. Techniques of spatially explicit individual-based models: construction, simulation, and mean-field analysis. Ecological Modeling 150: 55-81.

Bjorge, R.R., and Gunson, J.R. 1989. Wolf, *Canis lupus*, population characteristics and prey relationships near Simonette River, Alberta. Canadian Field Naturalist 103: 327-334.

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

Bugmann, H., Fischlin, A., and Kienast, F. 1996. Model convergence and state variable update in forest gap models. Ecological Modeling 89: 197-208.

Cederlund, G., Sandegren, F., and Larsson, K. 1987. Summer movements of female moose and dispersal of their offspring. Journal of Wildlife Management 51: 342-352.

Chen, Q., and Myntt, A.E. 2003. Effects of cell size and configuration in cellular automata based prey-predator modeling. Simulation Modeling Practice and Theory 11: 609-625.

DeAngelis, D.L., and Mooij, W.M. 2005. Individual-based modeling of ecological and evolutionary processes. Annual Review of Ecology and Systematics 36: 147-168.

Dieckmann, U., Law, R, and Metz, J.A.J, Editors. 2000. The geometry of ecological interactions: simplifying spatial complexity. Cambridge University Press, Cambridge, UK. 564 pp.

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

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

Ferguson, S.H., and Elkie, P.C. 2004. Seasonal movement patterns of woodland caribou (*Rangifer tarandus caribou*). Journal of Zoology London 262: 125-134.

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

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

Fuller, T.K., and Keith, L.B. 1981. Woodland caribou population dynamics in northeastern Alberta. Journal of Wildlife Management 45: 197-213.

Gardner, R.H., and Gustafson, E.J. 2004. Simulating dispersal of reintroduced species within heterogeneous landscapes. Ecological Modeling 171: 339-358.

Green, R.F. 1984. Stopping rules for optimal foragers. American Naturalist 123: 30-43.

Grimm, V. 1999. Ten years of individual-based modeling in ecology: what have we learned and what could we learn in the future? Ecological Modeling 115: 129-148.

Grimm, V., and Railsback, S.F. 2005. Individual-based modeling and ecology. Princeton University Press, Princeton, Princeton, USA, 428 pp.

Gunson, J.R., Jalkotzy, M., Carbyn, L.N., and Roy, L.D. 1993. Predation. In Hoofed Mammals of Alberta. Edited by J.B. Stelfox. Lone Pine Publishing, Edmonton, Alberta. pp. 69-80.

Hauge, T.M., and Keith, L.B. 1981. Dynamics of moose populations in northeastern Alberta. Journal of Wildlife Management 45: 573-597.

Holt, R.D., and Kotler, B.P. 1987. Short-term apparent competition. American Naturalist 130: 412-430.

Huggard, D.J. 1993. Prey selectivity of wolves in Banff National Park. II. Age, sex, and condition of elk. Canadian Journal of Zoology 71: 140-147.

Iwasa, Y., Higashi, M., and Yamamura, N. 1981. Prey distribution as a factor determining the choice of optimal foraging. American Naturalist 117: 710-723.

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

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

James, A.R.C., Boutin, S., Hebert, D.M., and Rippin, A.B. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. Journal of Wildlife Management 68: 799-809.

Jedrzejewski, W., Jedrzejewska, B., Okarma, H., Schmidt, K., Zub, K., and Musiani, M. 2000. Prey selection and predation by wolves in Bialowieza Primeval Forest, Poland. Journal of Mammalogy 81: 197-212.

Jedrzejewski, W., Schmidt, K., Theuerkauf, J., Jedrzejewska, B., and Okarma, H. 2001. Daily movements and territory use by radiocollared wolves (*Canis lupus*) in Bialowieza Primeval Forest in Poland. Canadian Journal of Zoology 79: 1993-2004.

Jedrzejewski, W., Schmidt, K., Theuerkauf, J., Jedrzejewska, B., Selva, N., Zub, K., and Szymura, L. 2002. Kill rates and predation by wolves on ungulate populations in Bialowieza Primeval Forest (Poland). Ecology 83: 1341-1356.

Kolenosky, G.B. 1972. Wolf predation on wintering deer in east-central Ontario. Journal of Wildlife Management 36: 357-369.

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

Kunkel, K., and Pletscher, D.H. 2001. Winter hunting patterns of wolves in and near Glacier National Park, Montana. Journal of Wildlife Management 65: 520-530.

Kunkel, K.E., Pletscher, D.H., Boyd, D.K., Ream, R.R., and Fairchild, M.W. 2004. Factors correlated with foraging behavior of wolves in and near Glacier National Park, Montana. Journal of Wildlife Management 68: 167-178.

Kunkel, K.E., Ruth, T.K., Pletscher, D.H., and Hornocker, M.G. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park, Montana. Journal of Wildlife Management 63: 901-910.

Lee, P. and Boutin, S. 2006. Persistence and developmental transition of wide seismic lines in the western Boreal Plains of Canada. Journal of Environmental Management 78: 240-250.

Lima, S.L. 2002. Putting predators back into behavioral predator-prey interactions. Trends in Ecology and Evolution 17: 70-75.

Lima, S.L., and Zollner, P.A. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution 11: 131-135.

McNair, J.N. 1982. Optimal giving-up times and the marginal value theorem. American Naturalist 119: 511-529.

Mech, L.D. 1977. Population trend and winter deer consumption in a Minnesota wolf pack. In Proceedings of the 1975 Predator Symposium. Edited by R.L. Philips and C. Jonkel. Montana Forest and Conservation Experiment Station, University of Montana, Missoula. pp. 55-83.

Mech, L.D. 1981. The wolf: the ecology and behavior of an endangered species. University of Minnesota Press, Minneapolis, 384 pp.

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

Mech, L.D., and Boitani, L. 2003. Wolf Social Ecology. In Wolves: Behavior, Ecology, and Conservation. Edited by L.D. Mech and L. Boitani. The University of Chicago Press, Chicago. pp. 1-34.

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

Messier, F. 1985b. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. Canadian Journal of Zoology 63: 239-244.

Moustakas, A., Silvert, W., and Dimitromanolakis, A. 2006. A spatially explicit learning model of migratory fish and fishers for evaluating closed areas. Ecological Modeling 192: 245-258.

Peterson, R.O. 1978. Wolf ecology and prey relationships on Isle Royale. National Park Service Scientific Monograph Series 11. 210 pp.

Peterson, R.O., Woolington, J.D., and Bailey, T.N. 1984. Wolves of the Kenai Peninsula, Alaska. Wildlife Monographs 88: 1-52.

Potvin, F., Jolicoeur, H., and Huot, J. 1988. Wolf diet and prey selectivity during two periods for deer in Quebec: decline versus expansion. Canadian Journal of Zoology 66: 1274-1279.

Renecker, L.A., and Hudson, R.J. 1993. Morphology, bioenergetics and resource use: patterns and processes. In Hoofed Mammals of Alberta. Edited by J.B. Stelfox. Lone Pine Publishing, Edmonton, Alberta. pp. 141-163.

Rettie, W.J., and Messier, F. 2001. Range use and movement rates of woodland caribou in Saskatchewan. Canadian Journal of Zoology 79: 1933-1940.

Schneider, R.S. 2002. Alternative futures: Alberta's boreal forest and the crossroads. Federation of Alberta Naturalists, Edmonton, Alberta, 152 pp.

Schneider, R.S., and Wasel, S. 2000. The effect of human settlement on the density of moose in northern Alberta. Journal of Wildlife Management 64: 513-520.

Smith, H.C. 1993. Alberta Mammals: an atlas and guide. Provincial Museum of Alberta, Edmonton, Alberta, 250 pp.

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.

Stelfox, J.B., and Stelfox, J.G. 1993. Population dynamics and reproduction. In Hoofed Mammals of Alberta. Edited by J.B. Stelfox. Lone Pine Publishing, Edmonton, Alberta. pp. 141-163.

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

Theuerkauf, J., Jedrzejewski, W., Schmidt, K., Okarma, H., Ruczynski, I., Sniezko, S., and Gula, R. 2003. Daily patterns and duration of wolf activity in the Bialowieza Forest, Poland. Journal of Mammalogy 84: 243-253.

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

Tischendorf, L. 1997. Modeling individual movements in heterogeneous landscapes: potentials of a new approach. Ecological Modeling 103: 33-42.

Turner, M.G., Gardner, R.H., and O'Neill, R.V. 2001. Introduction to models. Pages 47 to 69 In Landscape ecology in theory and practice: pattern and process. Springer-Verlag New York, Inc., New York, 401 pp.

Vuilleumier, S., and Metzger, R. 2006. Animal dispersal modeling: handling landscape features and related animal choices. Ecological Modeling 190: 159-170.

Wissel, C. 2000. Grid-based models as tools for ecological research. Pages 94 to 115 In The geometry of ecological interactions: simplifying spatial complexity. U. Dieckmann, R. Law, and J.A.J. Metz, Editors. Cambridge University Press, Cambridge, UK.

Zollner, P.A., and Lima, S.L. 1999. Search strategies for landscape-level interpatch movements. Ecology 80: 1019-1030.

Table 2.1. Basic parameter values used in the models. Some parameters (e.g., wolf density, wolf use of lines, moose density, moose distributions, and prey behavior) were varied in subsequent models.

Parameters	Value
territory size[1]	625 km^2
cell size	1 km x 1 km
#of upland and peatland patches	1 each (325 and 300 km2, respectively)
line densities[2]	0 to 5 km/km2
#lines/cell (in lined territories only)	2 to 5
prey avoidance buffers around lines[3]	0.25 km
prey response to lines	none (random) and avoid
moose overlap with caribou	none
wolf pack size[4]	6, but moved as a cohesive unit
caribou density[5]	0.04/km2 (25 caribou)
moose density[6]	0.24/km2 (150 moose)
start position	randomly selected upland cell
wolf movement	random or use of a 45 km2 giving-up rule
h/d spent travelling[7]	9 (i.e., 9 one hour time steps)
probability of using a line, if encountered[8]	25%
line:forest speed[9]	3:1
prey movememt	randomly redistributed each time step
kill success[10]	10%
handling time[11]	2 d for moose; 1 d for caribou
length of simulation	1 year (i.e., 3289 time steps)

[1]Fuller and Keith 1980; Bjorge and Gunson 1989, [2]Bayne *et al*. 2005; Lee and Boutin 2006, [3]Dyer *et al*. 2001, [4]Fuller and Keith 1980; Bjorge and Gunson 1989, [5]Fuller and Keith 1981; Edmonds 1988; Stuart-Smith *et al*. 1997; James *et al*. 2004, [6]Schneider and Wasel 2000; [7]Fuller and Keith 1980; Mech 1981; Peterson *et al*. 1984;Theuerkauf *et al*. 2003; [8]James 1999; [9]James 1999; [10]Fuller and Keith 1980; Mech 1981; Peterson et al. 1984; [11]Ballard *et al*. 1997

Figure 2.1. Example of virtual model setup in a line free territory. Note that this is only a subset of the model, which is actually 625 km^2 (25 km x 25 km or 25 cells x 25 cells).

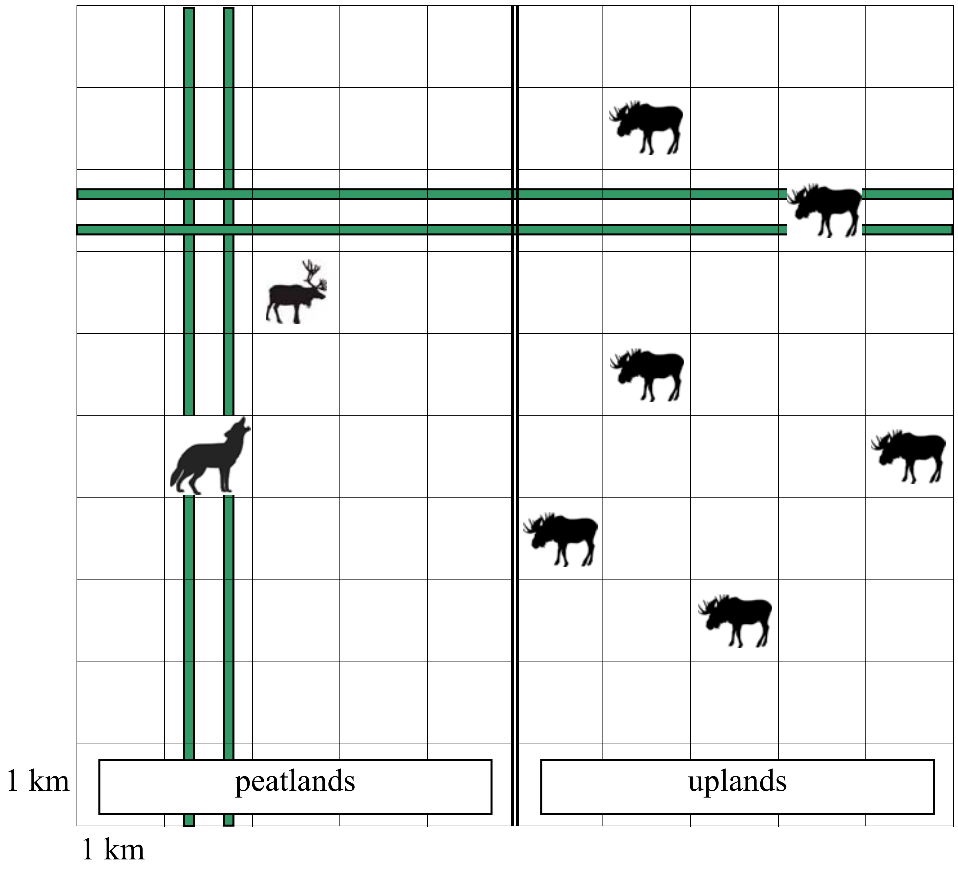


Figure 2.2. The effect of cell size (as reflected by the number of cells) on moose survival (■), caribou survival (●), and wolf kills (✖) in a line free territory. Results are means ± 95% confidence intervals after 50 simulations.

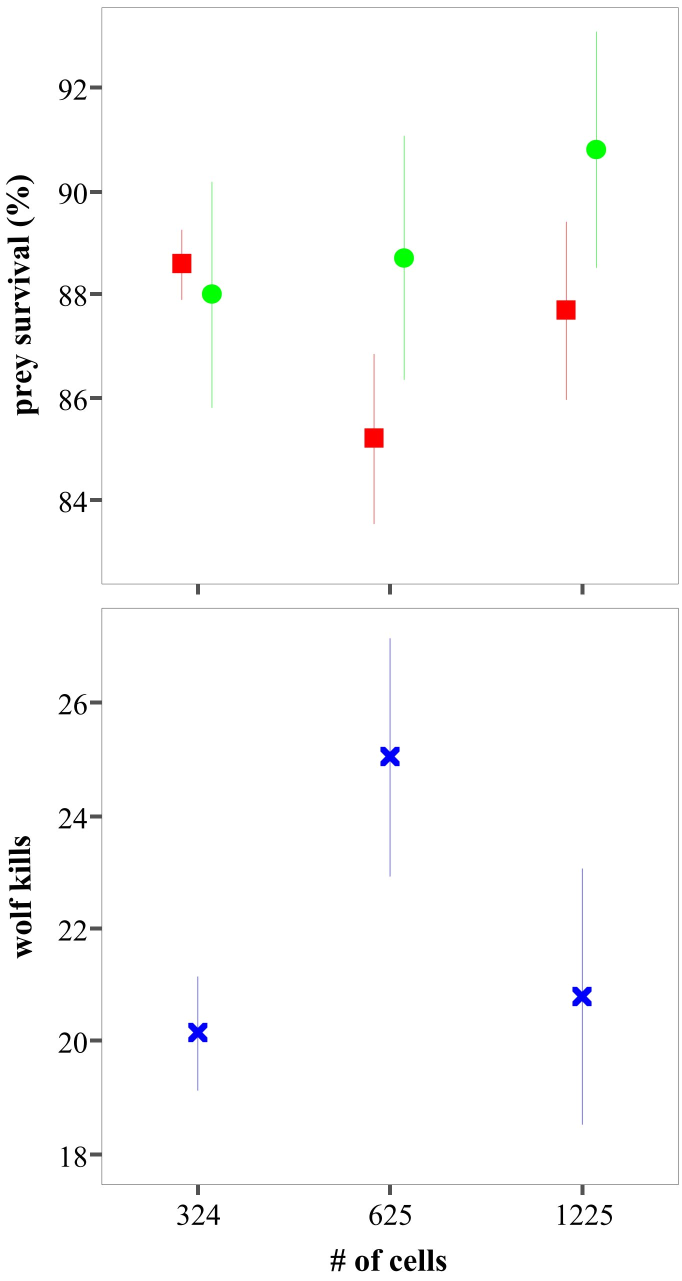


Figure 2.3. The effect of patch number on moose survival (■), caribou survival (●), and wolf kills (✖) in a line free territory. A 2 patch-territory consisted of 1 upland and 1 peatland patch, a 4 patch-territory consisted of 2 upland and 2 peatland patches, and a 8 patch territory consisted of 4 upland and 4 peatland patches. Results are means ± 95% confidence intervals after 50 simulations.

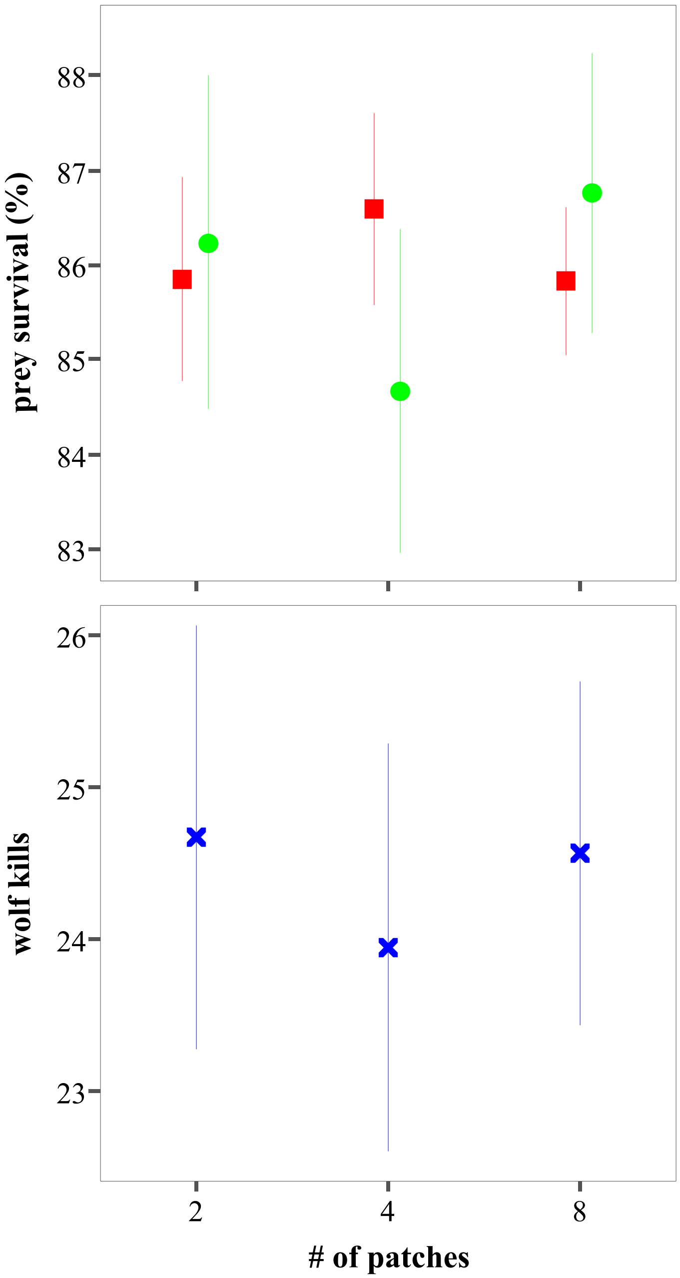


Figure 2.4. The effect of line placement on moose survival, caribou survival, and wolf kills in 4 and 5 km/km^2 territories. Different symbols refer to different line configurations (variation 1: ■; variation 2: ●). Simulations assumed that there was a 25% chance a pack would use a line (see *Wolf use of lines* for details). Results are means ± 95% confidence intervals after 50 simulations.

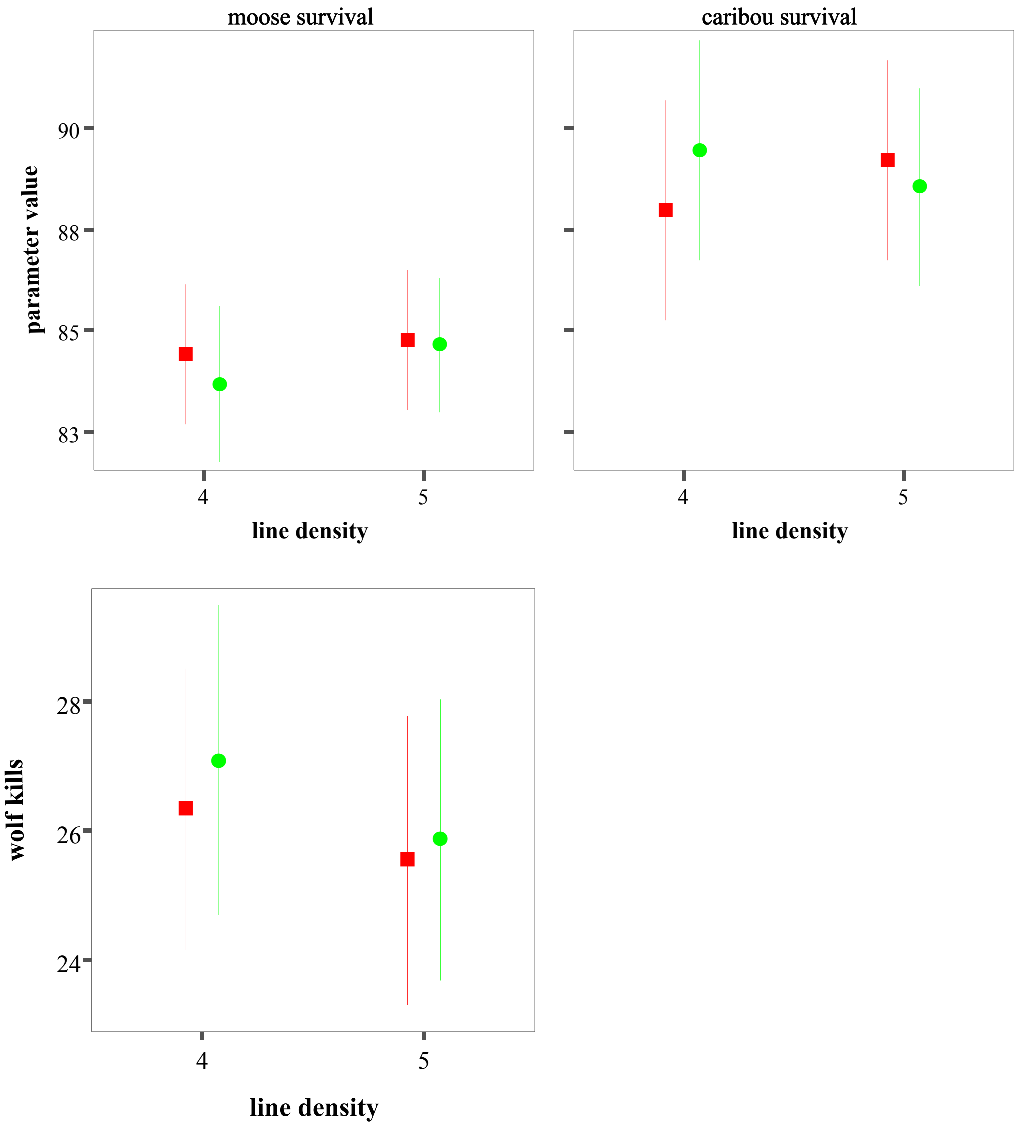


Figure 2.5. The effect of pack “start position” on moose survival (■), caribou survival (●), and wolf kills (✖) in a line free territory. Results are means ± 95% confidence intervals after 50 simulations.

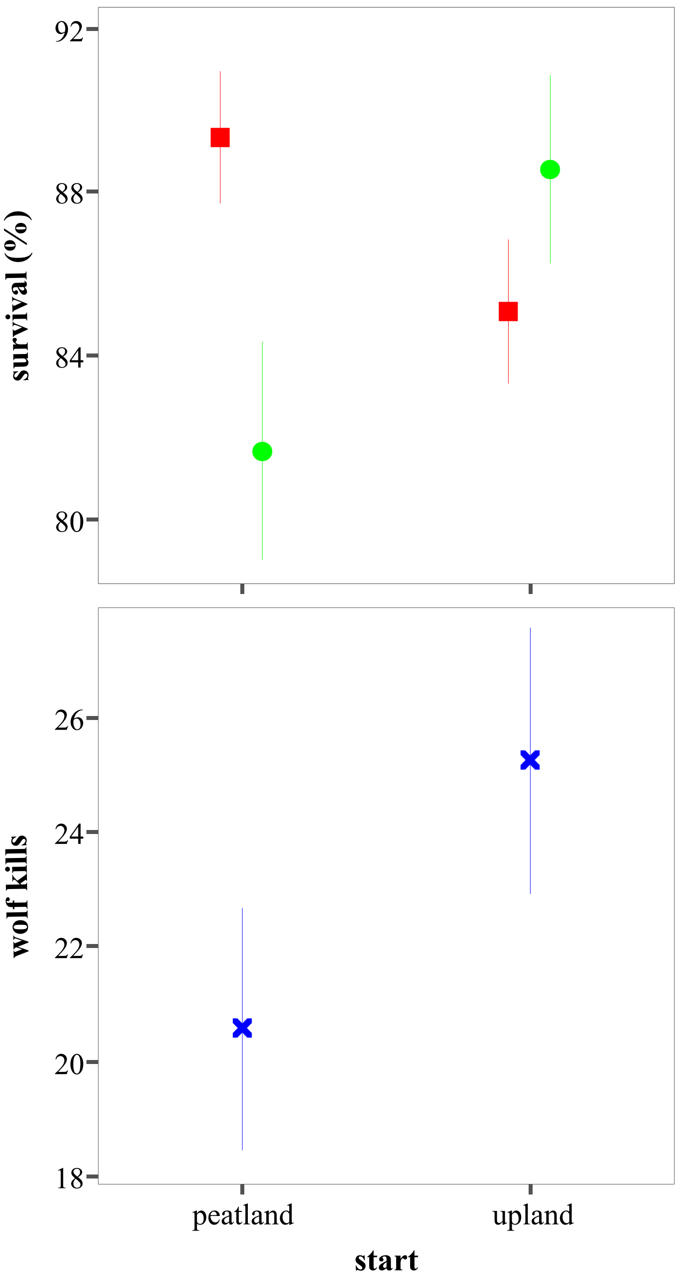


Figure 2.6. The effect of “northness or southness” on moose survival (■), caribou survival (●), and wolf kills (✖) in a line free territory. “Northness or southness” reflects what percent of a “retreat” was spent moving directly north or south. Runs assumed that the pack was using a 45 km^2 giving up rule in a 0 km/km^2 territory. Results are means ± 95% confidence intervals after 50 simulations.

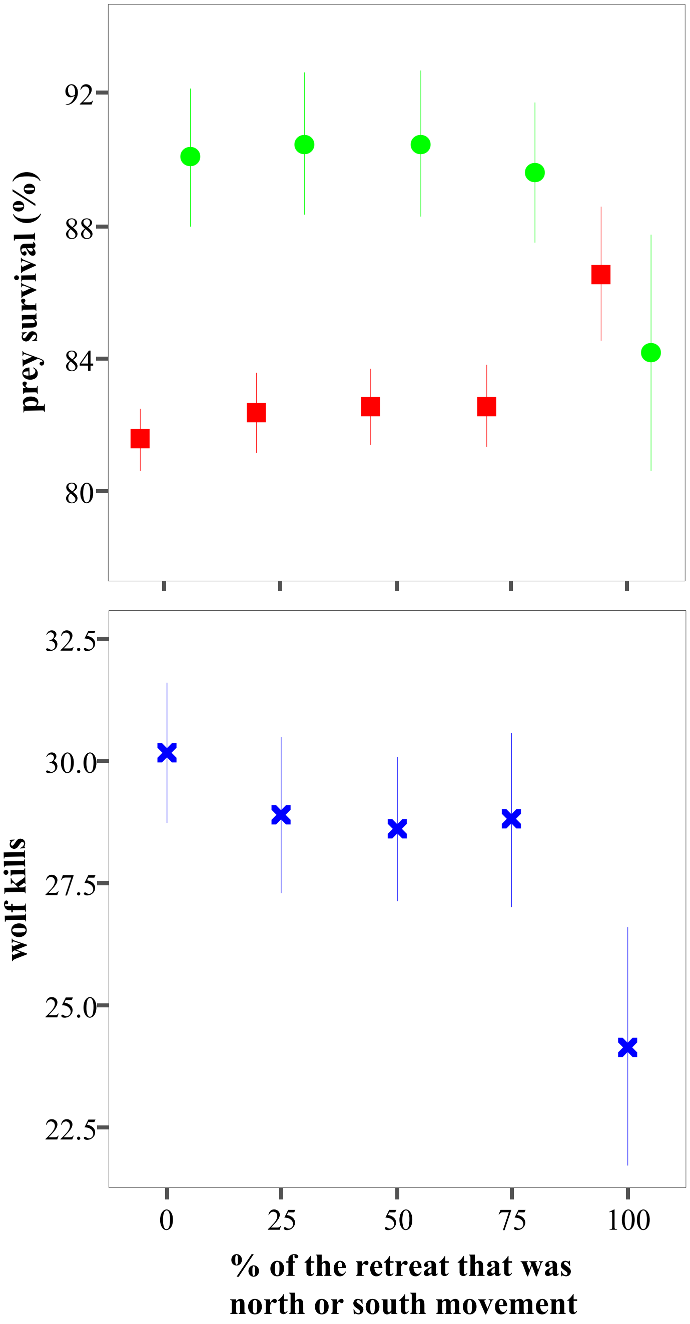


Figure 2.7. Moose and caribou survival across different wolf movement strategies. R refers to random movement (note that the axis is not continuous). Results are means ± 95% confidence intervals after 50 simulations.

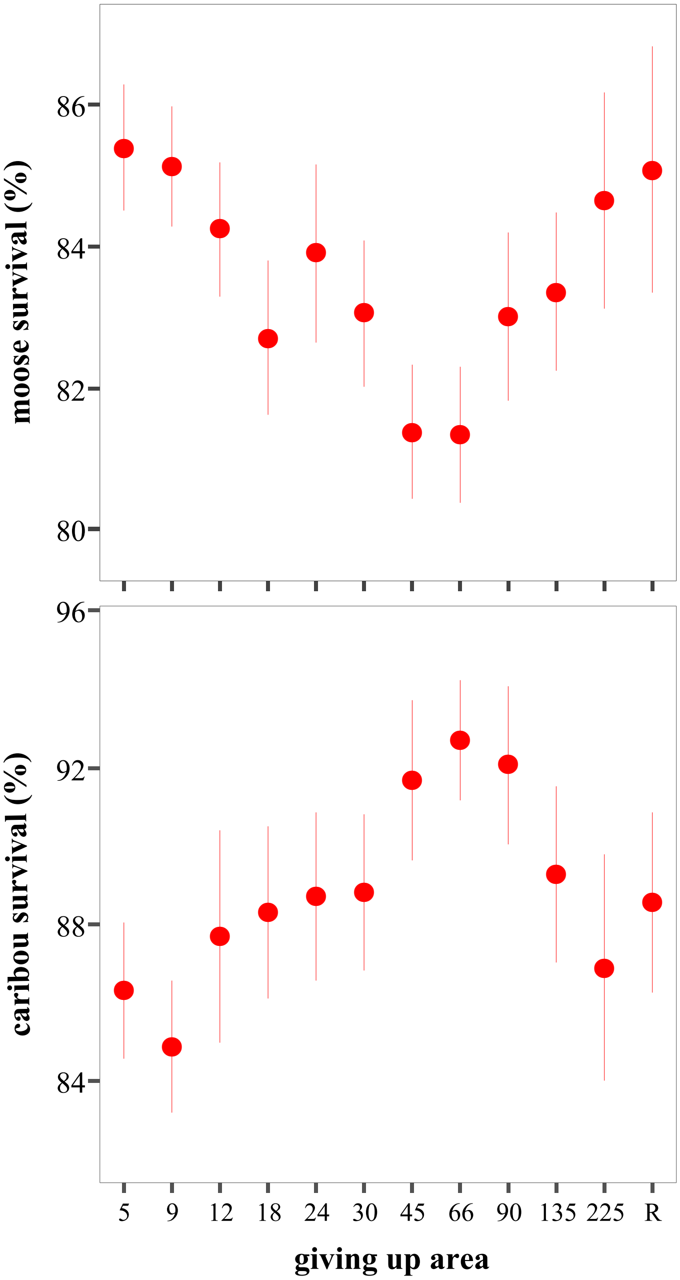


Figure 2.8. Kill rates across different wolf movement strategies. R refers to random movement (note that the axis is not continuous). Results are means ± 95% confidence intervals after 50 simulations.

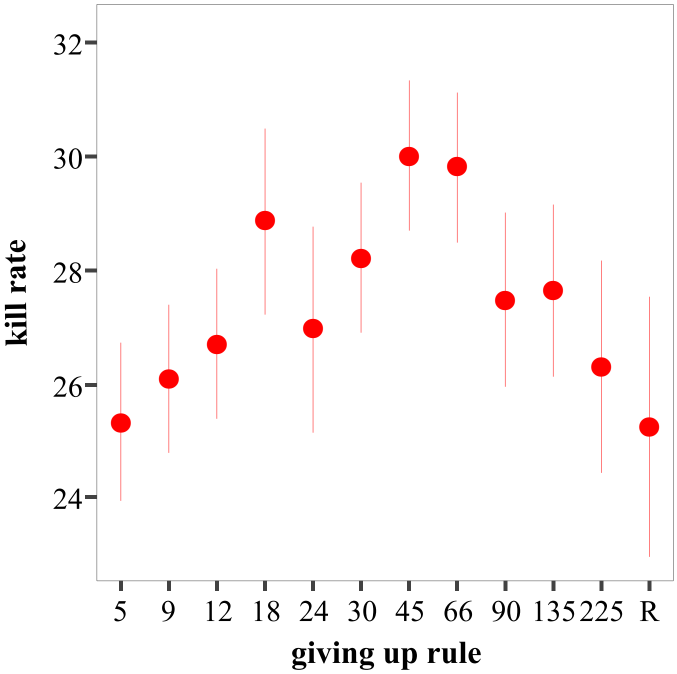


Figure 2.9. Moose and caribou survival as a function of prey behavior and prey movement. Different colors represent different parameter combinations: random prey, redistributed each time step (●), random prey, fixed across time (●), 100% avoid prey, redistributed each time step (●), and 100% avoid prey, fixed across time (●). Results are means ± 95% confidence intervals after 50 simulations.

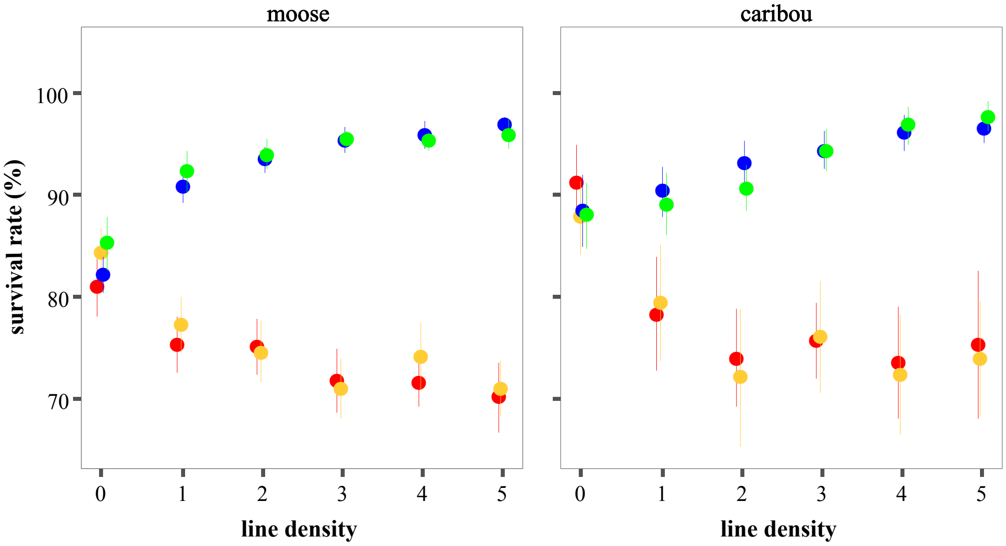


Figure 2.10. The effect of kill success (%) on moose survival (■), caribou survival (●), and wolf kills (✖) in a line free territory. Results are means ± 95% confidence intervals after 50 simulations.

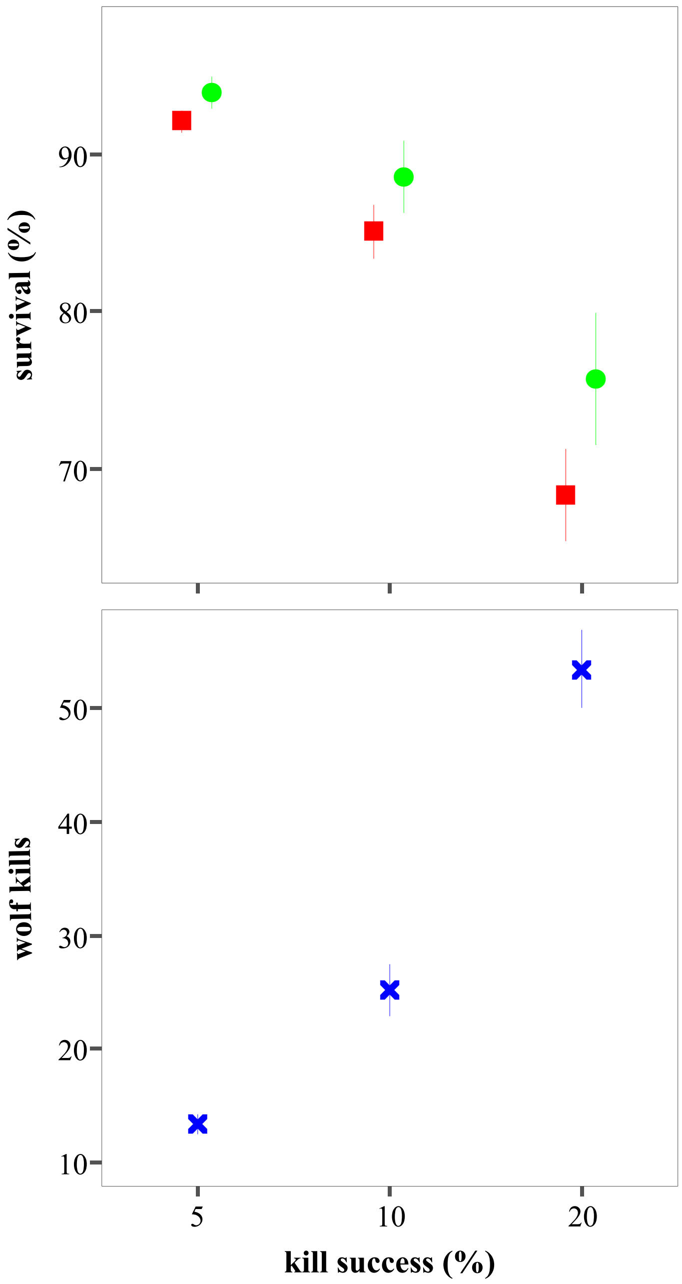


Figure 2.11. The effect of handling time on moose survival (■), caribou survival (●), and wolf kills (✖) in a line free territory. Results are means ± 95% confidence intervals after 50 simulations.

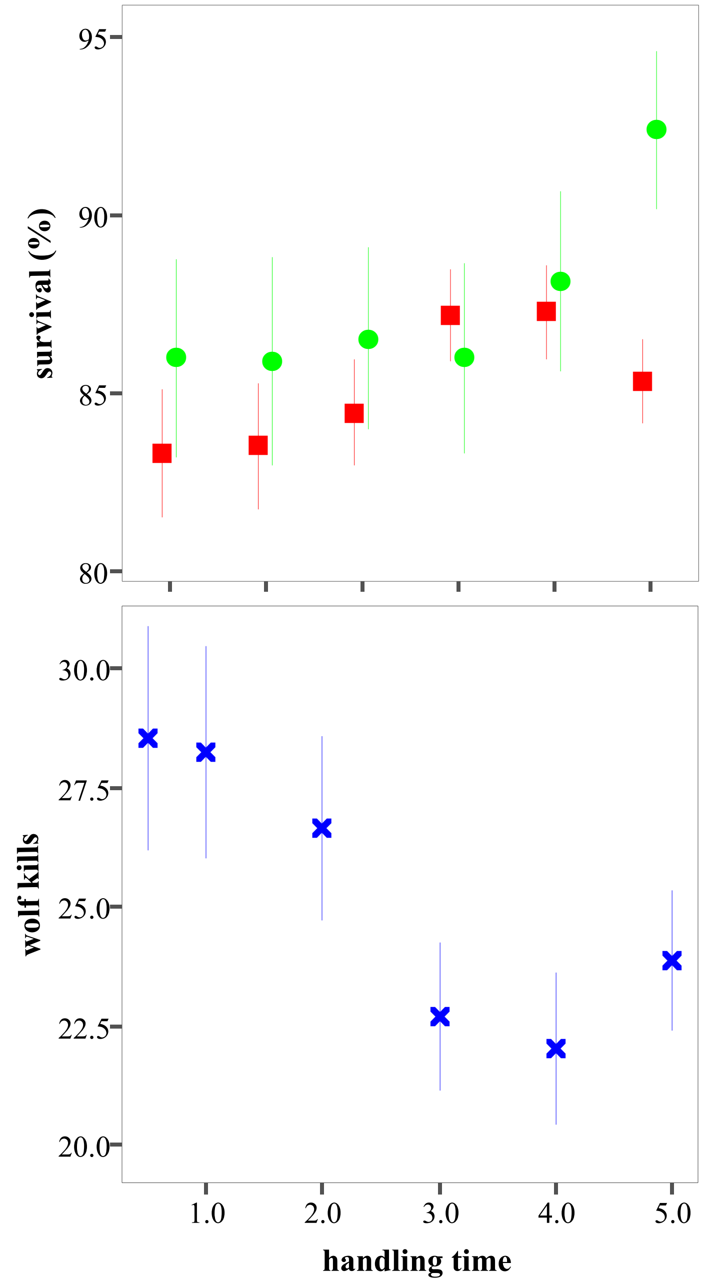


Figure 2.12. Moose survival (■), caribou survival (●), and wolf kills (✖) across a different number of simulation replicates. Reference lines refer to average survival across all runs. Results are means ± 95% confidence intervals.

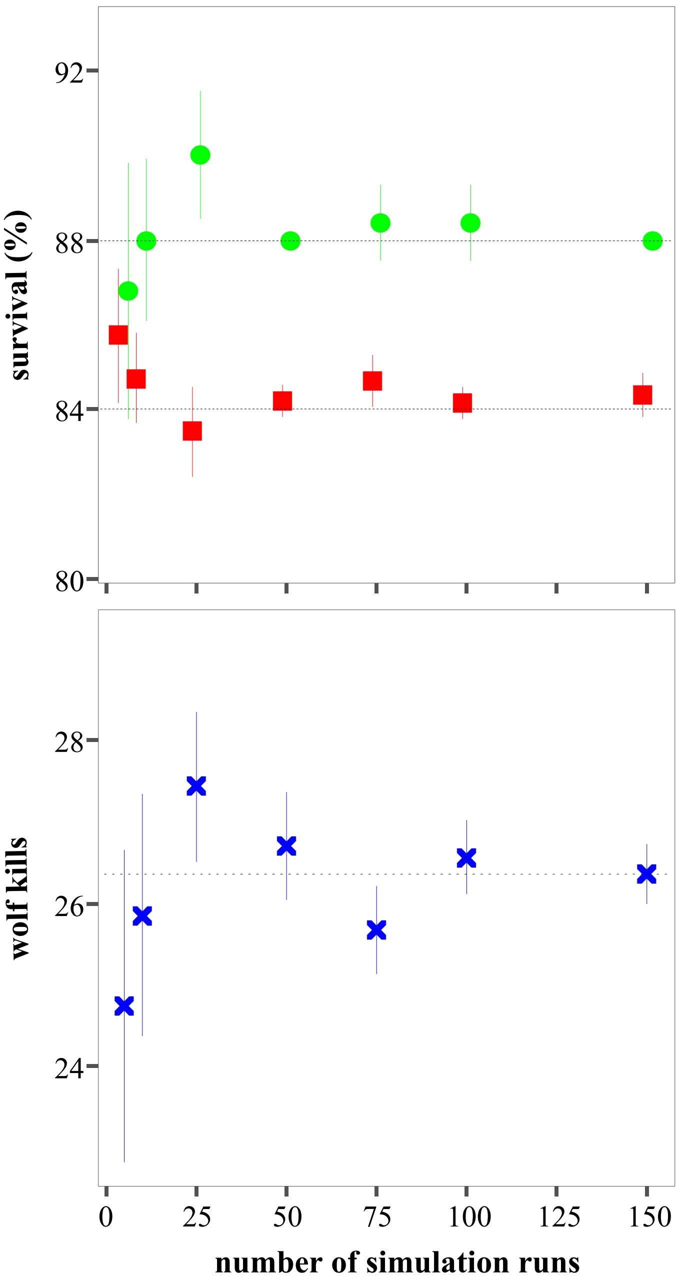
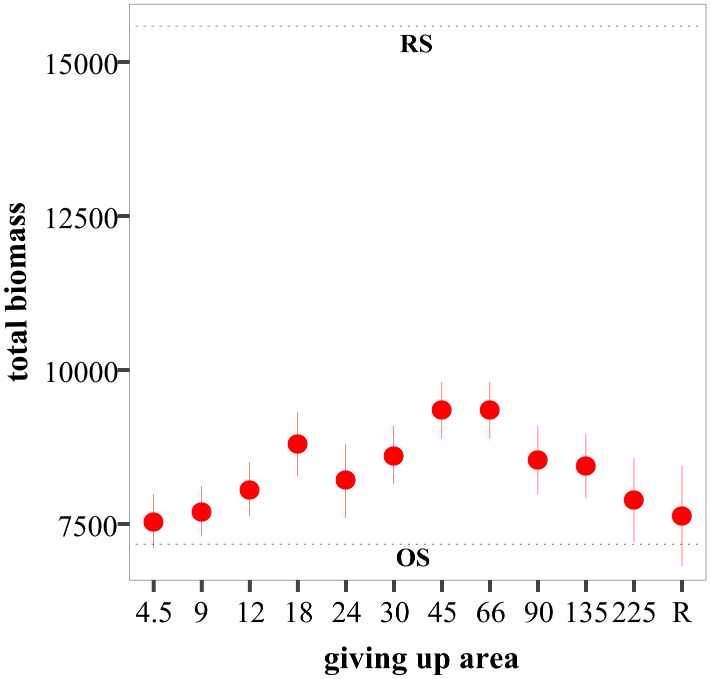


Figure 2.13. Biomass rates across different wolf movement strategies. R refers to random movement (note that the axis is not continuous), while in the biomass figure, RS refers to the reproductive threshold, and OS refers to the over wintering survival threshold. Results are means ± 95% confidence intervals.



Chapter 3: Does wolf use of lines increase wolf-caribou interactions?

Introduction

Wolves (*Canis lupus*) often use natural and anthropogenic features that facilitate faster movement and/or increase their probability of encountering prey (e.g., Mech 1981; Thurber *et al*. 1994; Musiani *et al*. 1998; Kuyzk *et al*. 2004; Bergmann *et al*. 2006). For example, wolves in northeastern Alberta are found on or near linear features more often than expected by chance (James and Stuart-Smith 2000). These features – which are dominated by seismic lines but also include roads, pipelines, and gas lines – are semi-permanent to permanent paths that cut through the forest (MacFarlane 1999; Schneider 2002; Lee and Boutin 2006). They are prevalent in Alberta and are part of the oil and gas exploration and extraction process (Schneider 2002). For example, seismic lines, in association with explosive charges, are used to find and map oil and gas deposits (Schneider 2002). Seismic lines vary from 1 to 8 m or more in width and can be as dense as 10 km/km^2 (Schneider 2002; Lee and Boutin 2006).

Wolf use of linear features has also been noted in other areas (Mech 1981; Thurber *et al*. 1994; Musiani *et al*. 1998; Kunkel and Pletscher 2000; Whittington *et al*. 2005; Neufeld 2006) and is a behavior that can facilitate faster travel (Musiani *et al*. 1998; James 1999). For example, James (1999) found that speed on lines was three times greater than speed in the forest. Line use should mean more wolf-prey encounters because wolves are able to search a given area more quickly. This implies that line use will mimic the effects of prey density on wolf functional responses (e.g., Messier 1994; Marshall and Boutin 1999). Functional responses depict how kill rate (i.e., the number of prey killed per predator) changes with prey density and are typically described as linear

(Type I), asymptotic (Type II), or sigmoidal or “S-shaped” (Type III) (Holling 1959; also see Messier 1994). Kills should increase with line density because lines are more likely to be encountered (e.g., James 1999) and thus yield a travel advantage.

Increased mobility should translate into increased prey mortality via increased predator-prey encounters (e.g., if kills increase asymptotically with line density, then survival should decrease asymptotically with line density). In northeastern Alberta, wolves mainly prey on moose (*Alces alces*) whereas use of woodland caribou (*Rangifer tarandus caribou)*is largely incidental (i.e., moose and caribou comprise >40% and <1% of the wolf diet, respectively; Stuart-Smith *et al*. 1997; James *et al*. 2004). Low use of caribou likely stems from their small size and scarcity relative to moose (154 kg/caribou vs 435 kg/moose; 0.04 caribou/km^2 vs 0.24 to 0.53 moose/km^2; mass and density estimates averaged from data in Fuller and Keith 1981; Hauge and Keith 1981; Edmonds 1988; Renecker and Hudson 1993; Smith 1993; Stuart-Smith *et al*. 1997; Schneider and Wasel 2000; James *et al*. 2004; also see Cumming *et al*. 1996 for an explicit description of moose vs caribou profitability). Furthermore, caribou are found in peatlands whereas moose are predominantly found in adjacent uplands (Bradshaw *et al*. 1995; Stuart-Smith *et al*. 1997; James *et al*. 2004; McLoughlin *et al*. 2005). Habitat segregation should means that peatlands are a spatial refuge from wolves because wolves spend most of their time hunting in upland habitat (James *et al*. 2004; also see Holt 1984). The use of spatial refuges has been well documented for a number of caribou herds across Canada and is generally associated with their local persistence (Bergerud and Page 1987; Bergerud 1988; Ferguson *et al*. 1988; Bergerud *et al*. 1990; Seip 1992; Cumming *et al*. 1996; Rettie and Messier 2000).

However, if predator mobility between refuge and alternative prey habitats is high, then the value of the refuge may decrease (Holt 1984). In northern Alberta, average adult female caribou survival declines ~9% as line density increases from 0.7 to ~3.5 km/km^2 (r^2= 0.68; based on data in Dzus 2001; Dunford 2003; McLoughlin *et al.* 2003; Neufeld 2006; Figure 3.1). This suggests that wolf use of lines may be compromising peatlands as refuge space. Moreover, female adult survival has high elasticity (Fancy *et al.* 1994; also see Gaillard *et al.* 1998), meaning that a small decline in survival can mean a large decline in herd size. As such, wolf use of lines may also explain why many of Alberta's woodland caribou (*Rangifer tarandus caribou*) herds are declining (McLoughlin *et al.* 2003). This trend that has led to the designation of caribou as provincially threatened (COSEWIC 2005). Although the data is limited by small sample sizes, there is some indication that the declines are more likely or greater for herds with lower adult survival (based on data in Dunford 2003; McLoughlin *et al.* 2003; Neufeld 2006; Alberta Caribou Committee, *unpublished results*). Low female adult survival has also been linked to population declines in other caribou herds in Canada (Schaeffer *et al.* 1999; Wittmer *et al.* 2005*a*).

While the link between wolf use of lines and caribou declines seems logical, there are two factors which question the likelihood of this relationship: degree of line use by wolves and prey response to lines. Wolf use of may be too low to affect existing wolf-moose and wolf-caribou interactions. Data from James (1999) indicates that only 26% of wolf locations were on a line, which is similar to two other Alberta studies (i.e., Whittington *et al.* 2005; Neufeld 2006, in which locations on a line were 25% and 30%, respectively). Low line use is unlikely to be a function of few wolf-line encounters, as average line density in all three studies was 1 km/km^2 or higher (James 1999; Whittington *et al*. 2005; Neufeld 2006). Low line use is often linked to human presence (Thurber *et al*. 1994; Kuzyk *et al*. 2004; Whittington *et al*. 2005), although this seems unlikely in northern Alberta. Lines are dense enough that human activity on any one line is probably low unless the line is part of an active exploration project.

To complicate things further, the average caribou is a minimum of 250 m from a linear feature (Dyer *et al*. 2001; also see Nellemann and Cameron 1996; 1998; James and Stuart-Smith 2000; Nellemann *et al*. 2001; Vistnes and Nellemann 2001; Cameron *et al*. 2005). The underlying reason for avoidance is not known but has been attributed to the association of lines with predation risk and human activity (James and Stuart-Smith 2000; Dyer *et al*. 2001). However, the consequence of this behavior is clear: avoidance should negate the effects of line use because predator and prey never “cross paths”. Although the response of moose to linear features has not been as well studied, it is conceivable that they would avoid lines as they do other risky habitats (e.g., Edwards 1983; Bowyer *et al*. 1999; White and Berger 2001; Dussault *et al*. 2005). For example, moose in northwestern Alberta were 36-55% less likely to be found in transects within 200 m of a road than in transects 200-400 m from a road (Intera Environmental Consultants 1973).

Still, prey behavior is not absolute. Some caribou are actually closer to seismic lines than expected while others are randomly distributed with respect to lines (i.e., 3% and 61% respectively; James and Stuart-Smith 2000; also Dyer *et al*. 2001; Oberg 2001). Similarly, some moose may use lines as travel routes or as a source of regenerating vegetation (e.g., Rempel *et al*. 1997; also see Jalkotzy *et al*. 1997). If enough of the prey population is randomly distributed with respect to lines, then line use should still increase wolf encounters and kills. It is also possible that low line use by wolves is a response to prey behavior, in which there is little value in using lines when prey are never near them. This suggests that low line use reflects a “game” between predator and prey (Lima 2002), which can further complicate line-wolf-prey interactions but ultimately means that line use does increase wolf hunting success.

The main objectives of this study were to use simulation models to (1) determine if line use mimicked the functional response such that kills increased, and prey survival decreased, with line density, (2) determine how kill rate:line density and survival rate:line density relationships were affected by the degree of line use and prey avoidance behaviors, (3) determine if low line use minimized the effects of prey avoidance behaviors, and (4) determine if line use could account for the negative correlation between female adult caribou survival and line density. Understanding these relationships is important for Alberta’s caribou management strategies. There are currently a number of mitigation efforts in Alberta that are designed to reduce wolf use of lines, either via line reclamation or line blocking (Boreal Caribou Committee 2001; Golder Associates 2006; Neufeld 2006). However, the usefulness of these techniques for caribou conservation is questionable, namely because a wolf-line-caribou relationship has yet to be empirically or theoretically established. If no relationship exists, then money used in line reclamation and blocking could obviously be put to better use elsewhere. However, if a relationship does exist, then this study should be able to identify the line density where reclamation or blocking is useful. For example, if caribou survival follows a sigmoid or threshold type response (i.e., a large decrease in survival over a small increase in line density) (e.g., With and Crist 1995; Huggett 2005; Luck 2005), then one management objective would be to maintain line density below this line density. Alternatively, if this threshold has already been passed, then line mitigation may be too expensive and labor-intensive to be feasible. This suggests that alternative management strategies may be necessary to conserve caribou (e.g., wolf control).

Methods

Models were programmed as described in Chapter 2. Based on the results from Chapter 2, simulations were run assuming that (1) wolves moved randomly or (2) that wolves moved non-randomly using a 45 km^2 giving up rule. Models were also programmed to reflect a "northeast Alberta scenario" (i.e., 0.24 moose/km^2; Schneider and Wasel 2000).

I determined if kill rate:line density relationships mimicked the functional response by curve-fitting simulated results to linear ($y = ax + b$), asymptotic ($y = ax/(b + x) + c$), and sigmoid ($y = ax^d/(b + x^d) + c$) functions (e.g., Messier 1994; Vucetich *et al.* 2002). In these equations, y = the kill rate, x = line density, *a* = the asymptotic kill rate, *b* = the line density at half the maximal kill rate, *c* = the y – intercept (which, when added to a, gave the actual asymptotic kill rate), and *d* was the power function that shifts the curve from an asymptotic to a sigmoid response (e.g., Messier 1994; Marshall and Boutin 1999). I determined if prey survival:line density relationships showed the opposite trends by curve fitting simulated results to linear ($y = ax + b$), asymptotic ($y = ab/(b + x) + c$), and sigmoid ($y = ab^d/(b + x^d) + c$) decaying responses. In these equations, y = prey survival rate, x = line density, *a* = the amount survival declined from 0 km/km^2 to the line density at which survival reached an asymptote, *b* = the line density at half the minimal survival rate, and *c* = the rate at which survival reached an asymptote (which, when added to *a*, gave the y-intercept). Parameters *a* and *b* were used to identify the line densities at which a threshold existed and/or at which no more or little change in kill or survival was expected.

I determined how kill and prey survival:line density curves were affected by the degree of line use by running simulations in which the probability of line use, if a cell with lines was encountered, was 0, 25, 50, 75, and 100% (note: additional simulations at 12.5, 33, and 67% line use did not alter results and were not included in the analysis). I also determined how the curves were affected by prey avoidance behaviors by running simulations in which prey were randomly distributed with respect to lines and in which 25%, 50%, 75%, or 100% of the prey population avoided lines (note: results based on 40% avoidance and in which all prey were on lines were not included in the analysis as they did not alter interpretation of results). All of these avoidance behaviors were run across each degree of line use, which allowed me to determine if line use minimized the effects of prey avoidance. If kill rate:line density or prey survival:line density relationships switched during these simulations (e.g., from an increase to a decrease in kills as prey avoidance increased), I used the appropriate but opposite function (e.g., a decaying vs a positive linear function).

All curves were fitted using Table 2D Curve (Version 5.01). Best fit curves were selected using an *F*-test, in which alpha = 0.05 (Zar 1996; note that this method was used over AIC because of the ambiguity of using statistics with modeling data and the fact that the asymptotic and sigmoid models were nested). R-squared was adjusted based on the number of degrees of freedom (Zar 1996). One issue with the asymptotic and sigmoid equations used in this study is that they take a long time to asymptote. As such, I determined the line density at which 90% of the kill rate or survival asymptote had been reached. I also determined how much of the asymptote was reached by 1 to 5 km/km^2, which highlighted where most of the change in kills or survival occurred. The overall effects of line use and avoidance were also assessed by summarizing the change in kills or survival from 0 to 5 km/km^2 and scaling it to the kill or survival rate at 0 km/km^2. This yielded a quick index of positive or negative change in the metric of interest based on specific parameter combinations.

Comparisons to the empirical data

Model results from 0 to 3 km/km^2 were compared to the empirical data set that describes caribou survival as a function of linear feature density. Results were also placed in a population context by determining how changes in caribou survival affected the finite rate of increase in an "average herd" and two previously stable herds (i.e., more recent data than McLoughlin *et al*. 2003 suggests these herds are now also declining; Alberta Caribou Committee, *unpublished results*). Based on the data in McLoughlin *et al*. (2003), an average herd would have a survival rate of 88.7±2.4% and calf:cow recruitment ratio of 0.161±0.04 (i.e., 16.1 calves per 100 cows; note that this only includes the data from Alberta). The Cold Lake Air Weapons range (CLAWR) herd was considered stable with an average female survival of 92.9±2.1% and an average calf:cow recruitment ratio of 0.114±.05. The West Side of the Athabasca (WSAR) herd was also considered stable with an average female survival of 89.1±2.4% and an average calf:cow recruitment ratio of 0.227±0.04. For each prey behavior and line use combination, change in survival from 0 to 3 km/km^2 was determined based on simulation results. This change was then applied to the CLAWR, WSAR, and average herd survival rate (i.e., if survival declined 2% from 0 to 3 km/km^2, the resulting survival rate for the CLAWR herd would be 91%). Finite rate of increase was subsequently calculated assuming that λ = (1-annual adult female mortality)/(1-calf recruitment) (i.e., in which calf recruitment is the cow:calf ratio; Hatter and Bergerud 1991). A λ of 1 or more would mean that the herd would hypothetically remain stable or increase. Calf recruitment was assumed to remain stable for all herds, namely because the intent of the model was to determine how changes in adult survival affected λ. In reality, calf recruitment varies within and among herds (McLoughlin *et al*. 2003).

Results

Effect of line density

Kill rates increased with line density if the pack used lines as travel routes. Kill rate:line density relationships were best described by asymptotic or sigmoid functional responses. Use of lines always lead to increased moose kills and as such, moose survival decreased with line density. Moose survival:line density relationships were best described by asymptotic or sigmoid decaying functions. However, line use only increased caribou kills if wolf use of lines was 50% or more. Corresponding declines in caribou survival were best described as linear or asymptotic.

Effect of degree of line use

The degree of line use affected the shape of the kill rate and prey survival:line density curves. For example, the kill rate:line density curve shifted from an asymptotic to a sigmoid functional response as line use increased from 50 to 75% (i.e., at 25 and 50% line use, a sigmoid response did not improve curve fit) (Figure 3.2.). Similarly, moose survival shifted from an asymptotic to a sigmoid decaying response as line use increased from 25 to 50% or from 50 to 75% (i.e.; patterns reflecting random wolf movement vs movement with giving up rules, respectively) (Figure 3.3.). Line use had to be at least 50% before caribou survival decreased with line density (Figure 3.4.). Moreover, higher degrees of line use did not lead to the threshold responses evident in the kill rate and moose survival:line density relationships. Caribou survival:line density curves either followed an asymptotic decaying function from 50 to 100% line use or shifted from a linear to an asymptotic decaying function as line use increased from 50 to 75% (i.e., patterns reflecting random wolf movement vs movement with giving up rules, respectively).

Line use also affected the line density at half the maximal kill rate and the line density at half the minimal prey survival rate (parameters b_{kills}, b_{moose}, and $b_{caribou}$). Half saturation rates decreased as line use increased, which meant that asymptotes for all asymptotic or sigmoid responses occurred at progressively lower line densities as line use increased (see Table 1 and 2 for details). For example, if wolves moved randomly, b_{kills} was 2.12 km/km^2 at 25% line use and 0.01 km/km^2 at 75% line use. This also meant that thresholds for sigmoid responses occurred at lower line densities as line use increased. Line use did not have a clear effect on the rate at which kills or survival saturated. For the most part, asymptotic rates were similar across different degrees of line use (although they did differ across movement strategies; see below for more details).

Effect of wolf movement

Qualitative patterns assuming random movement were usually similar to those assuming that the pack used giving up rules. However, there were quantitative differences in the results. For example, giving up rules always yielded higher rates of caribou survival, regardless of line density or degree of line use. Yet, while giving up rules always yielded more kills and lower rates of moose survival at 0% line use (or at 0 km/km^2), this difference was not evident when a pack used lines. Wolf movement also affected the amount kills or survival changed across line density. For example, there was 1.7 to 2 fold increase in kills as line density increased from 0 to 5 km/km^2 if the pack moved randomly, but only a 1.3 to 1.7 fold increase if the pack used giving up rules (the variance reflects different degrees of line use). Similarly, there was a 1.2 to 1.5 fold decrease in caribou survival as line density increased if the pack moved randomly at 50% line use or more, but only a 1.1 fold decrease if the pack used giving up rules. Conversely, there was a 1.1 to 1.2 fold decrease in moose survival as line density increased regardless of the way the pack moved.

Movement patterns affected the line density at half saturation rates and the line density where asymptotes occurred. b_{kills} and b_{moose} were always higher if the pack used giving up rules. For example, at 25% line use, b_{kills} was 2.12 km/km^2 if movement was random but 3.21 km/km^2 if movement was based on a giving up rule (Table 3.1.). Similarly, b_{moose} was 1.66 km/km^2 if movement was random but 3.16 km/km^2 if movement was based on a giving up rule (Table 3.2.). These results indicate that asymptotes will occur at lower line densities if wolves move randomly. For example, at 25% line use, 90% of the asymptote for the kill rate:line density curve was reached by 7.25 km/km^2 if movement was random and by 8.95 km/km^2 if movement was based on a giving up rule. Ninety percent of the moose survival:line density curve was reached by

9.05 km/km^2 if movement was random and by 17.35 km/km^2 if movement was based on a giving up rule.

Contrary to b_{kills} and b_{moose}, $b_{caribou}$ was always lower if the pack used giving up rules. For example, at 75% line use, $b_{caribou}$ was 0.80 km/km^2 if movement was random but 0.06 km/km^2 if movement was based on a giving up rule (Table 3.3.). This suggests that at line use of 50% or more, declines in caribou survival will asymptote at lower line densities if wolves use giving up rules. For example, at 75% line use, 90% of the asymptote for the caribou survival:line density curve was reached by 5.25 km/km^2 if wolves moved randomly and by 0.50 km/km^2 if the movement was based on a giving up rule.

Asymptotic kill and survival rates were also affected by wolf movement. For example, the range of kill and moose survival asymptotes was greater if the pack moved randomly (e.g. 48 to 57 kills/year vs 49 to 52 kills/year; 66 to 73% annual moose survival vs 68 to 70% annual moose survival; note that the values are based on the best-fit curves). The range of asymptotes was also higher for caribou survival rates if the pack moved randomly. Moreover, the survival rate at which curves reached an asymptote was 1.2 to 1.5 times lower if the pack moved randomly then if it used giving up rules (e.g., 57 to 68% caribou survival vs 84 to 85% annual caribou survival).

In general, if there was an asymptotic or sigmoid relationship between wolf kills and line density or survival and line density, more than 65% of any asymptote was reached by 1 km/km^2 (Table 3.4.). In other words, most of the change in kills and prey survival occurred at low line densities, regardless of wolf movement patterns or the degree of line use by wolves.

Effect of prey behavior

The main effect of prey avoidance was to reverse the effects of line density on kill rate and prey survival. As prey avoidance increased to 100%, kill rate:line density curves switched from functional to decaying while moose survival:line density curves showed the opposite trend (Tables 3.5. and 3.6.). For example, at 25% line use, there was a 1.1 fold decrease in kills as line density increased and a 1.01 to 1.02 fold increase in moose survival as line density increased (variance reflects random wolf movement and movement based on giving up rules, respectively) (Figures 3.5. and 3.6.). These patterns were also consistent with caribou survival:line density curves if line use was 50% or more (Table 3.7.).

However, the specific effect of avoidance on curve shape was variable and depended on the measure of interest, the amount of avoidance, the degree of line use, and wolf movement patterns. This variability (and in some cases, the poor fit to the simulated data) made it difficult to make general predictions about how avoidance affected thresholds, asymptotes, and the line densities at which asymptotes occurred (if they occurred). Yet, two consistent patterns were evident. Any relationship with negative consequences (i.e., increases in kill rate/reductions in caribou survival) did not occur if prey avoidance was absolute. Moreover, if the relationship fit a asymptotic or sigmoid curve, the asymptotic kill rate decreased with increasing avoidance and the asymptotic survival rate increased with increasing avoidance (up to a maximum of 100%). For example, if wolves moved randomly at 25% line use, the change in kills dropped from a 1.7 to 1.2 fold increase as prey avoidance increased to 75%.

Yet, intermediate amounts of avoidance still meant that the pack benefited from line use. How much avoidance could be "tolerated" depended on line use and the way in which wolves moved. For example, if wolves moved randomly at 25% line use, kills were higher than expected even if 75% of prey avoided lines (Figure 3.7.). At 75% line use, kills were only higher than expected if 25% or less prey avoided lines. Line use did not affect "tolerance" if wolves used giving up rules. Rather, kills were always higher than expected if 50% or less prey avoided lines. This also means that prey avoidance was more likely to have a positive effect on prey survival if wolf use of lines was high. For example, at 25% line use, moose survival was only higher than expected if 75 to 100% of prey avoided lines (variance reflects patterns assuming giving up rules vs random wolf movement, respectively) (Figure 3.8.). At 75% line use, moose survival was higher than expected if 50 to 75% of prey avoided lines (variance reflects patterns assuming random movement vs movement assuming giving up rules).

Prey avoidance had a negligible effect on caribou survival unless line use was high and wolf movement was random. For example, at 25% line use, caribou survival switched from no to a positive change as avoidance increased or did not change despite increasing avoidance (variance reflects random wolf movement vs movement based on giving up rules, respectively) (Figure 3.9.). If wolves moved randomly at 75% line use, there was a 1.22 fold increase in survival as avoidance increased to 50%. However, if wolves used giving up rules at 75% line use, there was only a 1.04 to 1.05 fold increase in survival as avoidance increased to 75%.

Comparison to the empirical data

The empirical data indicates that average caribou survival declines 9% as line density increases from 0.7 to 3.5 km/km^2 (r^2= 0.68; based on data in Dzus 2001; Dunford 2003; McLoughlin *et al*. 2003; Neufeld 2006). Based on James (1999), wolf use of lines is 26%. Model results indicate that at 25% line use, caribou survival will increase or remain unchanged if line density increases from 0 to 3 km/km^2. These findings were consistent across both wolf movement strategies and all prey behaviors (Table 3.8.). Assuming that recruitment is stable, these results would hypothetically lead to increases in the CLAWR herd, WSAR herd, and an average herd (Table 3.9). Other combinations of parameters approached a 9% decline, but only if line use was 50% or more.

Discussion

In a territory with randomly distributed prey, kill rate:line density relationships followed asymptotic or sigmoid functional curves. This suggests that line use does mimic the functional response between wolves and prey density. However, while increased predator efficiency always lead to an asymptotic or sigmoid decline in moose survival, caribou survival only declined with line density if line use was 50% or more. At 25% line use, caribou survival did not change with line density, which differs from the empirical data in which caribou survival declines 9% as line density increases from 0.7 to 3.5 km/km^2 (based on data in Dzus 2001; Dunford 2003; McLoughlin *et al*. 2003; Neufeld 2006). This suggests that 25% line use is not sufficient to increase mobility between peatlands and uplands, and consequently, line use does not compromise peatlands as a refuge space (note: 33% line use yields the same finding; *unpublished results*). These findings may ultimately be related to the scarcity of caribou. Even with increased mobility, caribou are just too few to be frequently encountered by wolves. For example, 25% line use was still too low to increase wolf use of caribou even if 100% of caribou were on lines (*unpublished results*). Moreover, additional simulations indicate that at 25% line use, caribou density had to triple before line use had a negative effect on survival (*unpublished results*).

There is further evidence to suggest that it is the degree of line use that drives the type of line density relationships. While line density thresholds were evident for kill rate and moose survival, they only occurred if the degree of line use was greater than 25%. At 25% line use, curves were best described by asymptotic relationships (i.e., decaying for moose and increasing for kill rate). Furthermore, asymptotes occurred at progressively lower line densities as degree of line use increased. Yet, even at 25% line use, more than 65% of the asymptote for any line density curve was reached by 1 km/km^2. This means that most of the change in kill or survival rate occurred at low line densities and suggests that even a small amount of linear disturbance may impact wolf-prey relationships in Alberta. A low line density effect is also consistent with other modeling work done for this system (Weclaw and Hudson 2004).

While 25% line use was too low to alter wolf-caribou interactions, it was enough to increase wolf use of their main prey. This could explain why wolves are often associated with linear features (e.g., Mech 1980; Thurber *et al.* 1994; Musiani *et al.* 1998; James 1999; James and Stuart-Smith 2000; Kunkel and Pletscher 2000; Whittington *et al.* 2005). Still, just how much wolves benefited from line use depended on prey behavior (and in particular, moose behavior). If all prey avoided lines, kill rate:line density relationships shifted from increasing to decaying responses while prey survival relationships shifted to increasing responses. This suggests that prey avoidance can negate the effect of line use, and moreover, that line use can be maladaptive if it leads to less kills than what would be expected in a territory with no lines. However, prey behavior is not that static (e.g., Jalkotzy *et al.* 1997; James and Stuart-Smith 2000; Dyer *et al.* 2001; Oberg 2001), which suggests that wolves are likely to benefit from line use.

In fact, wolves may be able to counteract line avoidance by altering their own hunting strategies (i.e., their behavior should also not be static, Brown *et al.* 1999; Lima 2002). While prey avoidance did not have consistent effects on curve shape or curve shape parameters, it did dampen wolf kill rates and improved prey survival. However, low wolf use of lines minimized this effect. For example, kills at 25% line use were still higher than expected even if 75% of prey avoided lines. At 75% line use, kills were only higher than expected if 25% or less prey avoided lines. Of course, the trade-off to low line use was fewer kills if prey were distributed more randomly with respect to lines. Still, low line use seems to be the most effective compromise to moving on a feature that improves efficiency and yet may be avoided by most prey. This may explain why low line use has also been documented for wolves in west-central Alberta (30%; Neufeld 2006) and Jasper National Park (21%; Whittington *et al.* 2005). Results also suggest that random movement is more effective at counteracting avoidance than giving up rules. While movement based on giving up rules was less sensitive to the line use:prey behavior trade-off (i.e., did not depend on degree of line use), kills were only higher than expected if 50% or less prey avoided lines. These patterns also suggest that prey response to lines – in particular, that of moose – should be investigated more thoroughly in the field.

Model results suggest that caribou avoidance of lines may be a response to something other than predation risk. While avoidance of lines certainly improved survival, it was largely a trivial effect given that that there was no effect of wolf use of lines on caribou survival even if all caribou were randomly distribution with respect to lines. For example, Dyer *et al*. (2001) suggested that avoidance may be linked to human activity on or near lines (also see Nellemann and Cameron 1996; 1998; Nellemann *et al*. 2001; Vistnes and Nellemann 2001; Cameron *et al*. 2005). As with wolves, this effect has largely been discounted because human use of individual lines is expected to be low. However, this hypothesis should be revisited because it points to a more direct role of human activity in the caribou declines (aside from direct habitat loss, which overall good body condition and high pregnancy rates suggests is not yet an issue; e.g., McLoughlin *et al*. 2003; Weclaw and Hudson 2004). For example, Bradshaw *et al*. (1997) suggested that disturbance stemming from petroleum exploration may increase energetic costs for caribou during the winter. An initial assessment of human effects is relatively straightforward, as it would simply require monitoring of caribou proximity to lines against different gradients of human use on or near lines.

However, line use may still be linked to the caribou declines if it is more variable than the current data suggests. For example, caribou survival declined 4 to 7% from 0 to 3 km/km^2 if wolves used giving up rules at 75% line use (the range reflects different prey behaviors). A 4-7% decline in female adult survival would yield λ values of 1 to 0.97 for the CLAWR herd, 1.1 to 1.06 for the WSAR herd, and 1.01 to 0.97 for an "average herd". This suggests that line use could also underlie some of the herd declines, especially if recruitment is low (i.e., the CLAWR herd) (e.g., Gaillard *et al*. 1998; 2000).

Models based on random wolf movement also resulted in declines in survival if line use was 50% or more, but these declines were much larger than expected based on the empirical data (i.e., a decline of 14 to 24%, yielding λ values of 0.89 to 0.78 for the CLAWR herd, 0.97 to 0.84 for the WSAR herd, and 0.89 to 0.77 for an "average herd"). Clearly, the amount of time wolves spend on lines should be investigated more thoroughly as it is a critical factor in wolf-caribou interactions.

Wolf movement, which was identified as a sensitive parameter in Chapter 2, also affected the line density relationships, but more in terms of quantitative than qualitative results. For example, when caribou survival did decline with line density, it saturated at lower survival rates if the pack moved randomly. Asymptotes for kills and moose survival also occurred at lower line densities if wolves moved randomly (e.g., at 25% line use, kills saturated at ~7 km/km^2 if movement was random and at ~9 km/km^2 if movement was rule-based). One unexpected and interesting finding is that that line use may actually affect the way wolves move. In a line free territory, giving up rules yielded more kills because it increased the amount of time wolves spend in the more profitable uplands (e.g., Chapter 2). However, random movement yielded equivalent (albeit more variable) results in territories with lines. These differences may stem from how the different movement strategies interact with line use. Random movement combined with line use promotes more linear movement, which allows wolves to traverse their entire territory more quickly. Yet, if wolves use giving-up rules, line use may be less beneficial because when a rule "kicks in", wolves are more likely to leave the line as they move to an alternate habitat.

Overall, these results suggest that line use is too low to account for the declines in caribou survival and herd size and that caribou response to lines may be driven by something other than predation risk. This suggests that current attempts to reduce wolf use of lines are likely to be ineffective at conserving caribou and that alternative management techniques should be considered (e.g., wolf and moose control; see Chapter 5). However, model results must first be tested with field data to assess their validity. At the very least, empirical studies should primarily focus on determining how wolves move in their territories and if relatively low line use is a consistent phenomenon across different caribou ranges. This is important as the degree of line use appears to be critical to wolf-line-prey interactions while wolf movement is important for predicting the quantitative effects of line use on wolf-prey interactions. The other key parameter of interest is the role of moose. Line use increased use of moose even if most of the moose population avoided lines. A better understanding of wolf use of lines and moose response to lines is important for making predictions the effects of line use, as the current data have too many gaps to confidently state how much kills are likely to increase with line density.

A more thorough examination of model results would include correlative work, which should show that kill rates increase with line density while moose survival decreases with line density (this should be true even if most moose avoid lines). Moreover, more than 50% of the change in kills or survival should occur by 1 km/km^2. These predictions can also be tested experimentally by reducing wolf access to lines (kills should decrease while moose survival increases; no effect on caribou survival should be observed) and/or increasing line density (kills should increase while moose survival decreases; no effect on caribou survival should be observed). Still, recent efforts suggest than an access control program must be comprehensive to be effective (i.e., all lines in an area must be blocked or reclaimed) (Neufeld 2006; NAM, *personal observation*). Moreover, even if line use is more variable than current data suggests and comprehensive line manipulation is successful, it is still not clear how feasible such a mitigation strategy would be given that line density is greater than 1 km/km^2 in most caribou ranges.

This again questions the validity of current line mitigation techniques. This is true even when the impact of line use is considered in a larger context. The obvious consequence of a functional kill rate:line density relationship is a numeric response between wolves and line density (e.g., Messier 1994). This may lead to an indirect effect of line use on caribou populations if increased wolf use of moose leads to higher overall wolf numbers that "spillover' into caribou range (e.g., Holt 1984). This suggests that lines can still play a role in the caribou declines, albeit not in a way previously expected (see Chapter 5 for a more thorough discussion of this). Still, it is seems more logical to control the proximate rather than the ultimate cause of the caribou declines given the sheer number of lines and the mitigation effort that would be required to manipulate them.

References

Bayne, E.M., Van Wilgenburg, S.L., Boutin S., and Hobson, K.A. 2005. Modeling and field-testing of Ovenbird (*Seiurus aurocapillus*) responses to boreal forest dissection by energy sector development at multiple spatial scales. Landscape Ecology 20: 203-216.

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

Bergerud, A.T., Ferguson, R., and Butler, H.E. 1990. Spring migration and dispersion of woodland caribou at calving. Animal Behavior 39: 360-368.

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

Boreal Caribou Committee. 2001. Strategic plan and industrial guidelines for boreal caribou ranges in northern Alberta. 35pp.

Bowyer, R.T., van Ballenberghe, V., Kie, J.G., and Maier, J.A.K. 1999. Birth-site selection by Alaskan moose: maternal strategies for coping with a risky environment. Journal of Mammalogy 80: 1070-1083.

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

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

Brown, J.S., Laundre, J.W., and Gurung, M. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80: 385-399.

Cameron, R.D., Smith, W.T., White, R.G., and Griffith, B. 2005. Central Arctic caribou and petroleum development: distributional, nutritional, and reproductive implications. Arctic 58: 1-9.

Committee on the Status of Endangered Wildlife in Canada. 2005. Status of Woodland caribou (*Rangifer tarandus caribou*). Retrieved on Nov. 30th, 2005 at http://www.cosewic.gc.ca/eng/sct1/searchdetail_e.cfm.

Cumming, H.G., Beange, D.B., and Lavoie, G. 1996. Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared predation risk. Rangifer Special Issue 9: 81-94.

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

Dussault, C., Ouellet, J-P., Courtois, R., Huot, J., Breton, L., and Jolicoeur, H. 2005. Linking moose habitat selection to limiting factors. Ecography 28: 619-628.

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

Dzus, E. 2001. Status of the Woodland Caribou (*Rangifer tarandus caribou*) in Alberta. Alberta Environment, Fisheries and Wildlife Management Division, and Alberta Conservation Association, Wildlife Status Report No. 30, Edmonton, AB. 47 pp.

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 Smith, K.G. 1991. Mountain caribou calf production survival, and calving and summer habitat use in west-central Alberta. Wildlife Research Series No. 4, Alberta Fish and Wildlife Division, Edmonton, AB. 16 pp.

Edwards, J. 1983. Diet shifts in moose due to predator avoidance. Oecologia 60: 185-189.

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

Fancy, S.G., Whitten, K.R., and Russell, D.E. 1994. Demography of the Porcupine caribou herd, 1983-1992. Canadian Journal of Zoology 72: 840-846.

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

Fuller, T.K., and Keith, L.B. 1981. Woodland caribou population dynamics in northeastern Alberta. Journal of Wildlife Management 45: 197-213.

Gaillard, J.M., Festa-Bianchet, M., and Yoccoz, N.G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13: 58-63.

Gaillard, J.M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., and Toigo, C. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31: 367-393.

Golder Associates. 2006. Woodland Caribou Research and Information Gap Identification. Prepared for the Alberta Caribou Committee, 19 pp.

Hatter, I.W., and Bergerud, W.A. 1991. Moose recruitment, adult mortality, and rate of change. Alces 27: 65-73.

Hauge, T.M., and Keith, L.B. 1981. Dynamics of moose populations in northeastern Alberta. Journal of Wildlife Management 45: 573-597.

Holling, C.S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Canadian Entomologist 91: 293-320.

Holt, R.D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. American Naturalist 124: 377-406.

Huggett, A.J. 2005. The concept and utility of 'ecological thresholds' in biodiversity conservation. Biological Conservation 124: 301-310.

Intera Environmental Consultants. 1973. Whitecourt Environmental Study - 1973. Intera Environmental Consultants Ltd, Calgary, Alberta, .

Jalkotzy, M.G., Ross, P.I., and Nasserden, M.D. 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.

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

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

James, A.R.C., Boutin, S., Hebert, D.M., and Rippin, A.B. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. Journal of Wildlife Management 68: 799-809.

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

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

Lee, P. and Boutin, S. 2006. Persistence and developmental transition of wide seismic lines in the western Boreal Plains of Canada. Journal of Environmental Management 78: 240-250.

Lima, S.L. 2002. Putting predators back into behavioral predator-prey interactions. Trends in Ecology and Evolution 17: 70-75.

Luck, G.W. An introduction to ecological thresholds. Biological Conservation 124: 299-300.

MacFarlane, A. 1999. Revegetation of well sites and seismic lines in the boreal forest. Honors thesis, University of Alberta, Edmonton, Alberta.

Marshall, J.P., and Boutin, S. 1999. Power analysis of wolf-moose functional responses. Journal of Wildlife Management 63: 396-402.

McLoughlin, P.D., Dunford, J.S., Boutin, S. 2005. Relating predation mortality to broad-scale habitat selection. Journal of Animal Ecology 74: 701-707.

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

Mech, L.D. 1981. The Wolf: the Ecology and Behavior of an Endangered Species. University of Minnesota Press, Minneapolis, 384 pp.

Mech, L.D., and Boitani, L. 2003. Wolf Social Ecology. In Wolves: Behavior, Ecology, and Conservation. Edited by L.D. Mech and L. Boitani. The University of Chicago Press, Chicago. pp. 1-34.

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology 75: 478-488.

Musiani, M., Mamo, C., Boitani, L., Callaghan, C., Cormack-Gates, C., Mattei, L., Visalberghi, E., Breck, S., and Volpi, G. 2003. Wolf depredation trends and the use of fladry barriers to protect livestock in western North America. Conservation Biology 17: 1538-1547.

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

Nellemann, C., and Cameron, R.D. 1996. Effects of petroleum development on terrain preferences of calving caribou. Arctic 49: 23-28.

Nellemann, C., and Cameron, R.D. 1998. Cumulative impacts of an evolving oil-field complex on the distribution of calving caribou. Canadian Journal of Zoology 76: 1425-1430.

Nellemann, C., Vistnes, I., Jordhoy, P., and Strand, O. 2001. Winter distribution of wild reindeer in relation to power lines, roads, and resorts. Biological Conservation 101: 351-360.

Neufeld, L. 2006. Spatial dynamics of wolves and woodland caribou in an industrial forest landscape in west-central Alberta. MSc Thesis, University of Alberta, Edmonton, AB.

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

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

Renecker, L.A., and Hudson, R.J. 1993. Morphology, bioenergetics and resource use: patterns and processes. In Hoofed Mammals of Alberta. Edited by J.B. Stelfox. Lone Pine Publishing, Edmonton, Alberta. pp. 141-163.

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

Schaefer, J.A., Veitch, A.M., Harrington, F.H., Brown, W.K., Theberg, J.B., and Luttich, S.N. 1999. Demography of decline of the Red Wine Mountains caribou herd. Journal of Wildlife Management 63: 580-587.

Schneider, R.S. 2002. Alternative futures: Alberta's boreal forest and the crossroads. Federation of Alberta Naturalists, Edmonton, Alberta, 152 pp.

Schneider, R.S., and Wasel, S. 2000. The effect of human settlement on the density of moose in northern Alberta. Journal of Wildlife Management 64: 513-520.

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.

Smith, H.C. 1993. Alberta Mammals: an atlas and guide. Provincial Museum of Alberta, Edmonton, Alberta, 250 pp.

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

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

Vistnes, I., and Nellemann, C. 2001. Avoidance of cabins, roads, and power lines by reindeer during calving. Journal of Wildlife Management 65: 915-925.

Vucetich, J.A., Peterson, R.O., and Schaefer, C.L. 2002. The effect of prey and predator densities on wolf predation. Ecology 83: 3003-3013.

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

White, K.S., and Berger, J. 2001. Antipredator strategies of Alaskan moose: are maternal trade-offs influenced by offspring activity? Canadian Journal of Zoology 79: 2055-2062.

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

With, K.A., and Crist, T.O. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76: 2446-2459.

Wittmer, H.U., McLellan, B.N., Seip, D.R., Young, J.A., Kinley, T.A., Watts, G.S., and Hamilton, D. 2005*a*. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. Canadian Journal of Zoology 83: 407-418.

Zar, J.H. 1996. Biostatistical Analysis. 3rd Edition. Prentice-Hall, Inc., New Jersey, 662 pp.

Table 3.1. The effect of line use and wolf movement on the kill rate:line density relationship, b_{kills}, and the asymptotic kill rate.

Wolf movement	degree of line use			
	25%	50%	75%	100%
Random				
best fit curve	Type II	Type II	Type III	Type III
Type of curve	functional[1]	functional[2]	functional[3]	functional[4]
b_{kills}	2.12	0.91	0.01	0.001
asymptotic kill rate	51	54	48	57
r^2	0.98	0.98	0.88	0.90
Giving up rules				
best fit curve	Type II	Type II	Type III	Type III
Type of curve	functional[5]	functional[6]	functional[7]	functional[8]
b_{kills}	3.21	1.21	0.16	0.13
asymptotic kill rate	49	52	48	50
r^2	0.95	0.96	0.98	0.98

[1] $y = 25.64x/(2.12 + x) + 25.69$; [2] $y = 27.05x/(0.91 + x) + 26.60$; [3] $y = 20.32x^{2.57}/(0.01 + x^{2.57}) + 27.94$; [4] $y = 30.18x^{2.98}/(0.001 + x^{2.98}) + 26.68$; [5] $y = 19.62x/(3.21 + x) + 29.08$; [6] $y = 22.89x/(1.21 + x) + 28.70$; [7] $y = 19.79x^{1.61}/(0.16 + x^{1.61}) + 28.71$; [8] $y = 18.10x^{1.42}/(0.13 + x^{1.42}) + 31.48$

Table 3.2. The effect of line use and wolf movement on the moose survival:line density relationship, b_{moose}, and the asymptotic survival rate.

Wolf movement	degree of line use			
	25%	50%	75%	100%
Random				
best fit curve	asymptotic	sigmoid	sigmoid	sigmoid
type of curve	decaying[1]	decaying[2]	decaying[3]	decaying[4]
b_{moose}	1.66	0.34	0.002	0.0002
asymptotic survival rate	69	72	73	66
r^2	0.98	0.97	0.71	0.77
Giving up rules				
best fit curve	asymptotic	asymptotic	sigmoid	asymptotic
type of curve	decaying[5]	decaying[6]	decaying[7]	decaying[8]
b_{moose}	3.16	1.33	0.14	0.34
asymptotic survival rate	70	68	70	68
r^2	0.91	0.94	0.97	0.97

[1] $y = 15.95*1.66/(1.66 + x) + 69.02$; [2] $y = 11.64*0.34/(0.34 + x^{1.98}) + 71.74$;

[3] $y = 10.19*0.002/(0.002 + x3.40) + 73.48$; [4] $y = 17.18*0.0002/(0.0002 + x^{3.51}) + 66.38$;

[5] $y = 12.60*3.16/(3.16 + x) + 69.56$; [6] $y = 13.82*1.33/(1.33 + x) + 68.25$;

[7] $y = 11.95*0.14/(0.14 + x1.82) + 70.39$; [8] $y = 12.23*0.34/(0.34 + x) + 68.34$

Table 3.3. The effect of line use and wolf movement on the caribou survival:line density relationship, $b_{caribou}$, and the asymptotic survival rate.

Wolf movement	degree of line use			
	25%	50%	75%	100%
Random				
best fit curve	none	asymptotic	asymptotic	asymptotic
type of curve	none	decaying[1]	decaying[2]	decaying[3]
$b_{caribou}$	--	3.12	0.80	0.56
asymptotic survival rate	--	63	57	68
r^2	--	0.94	0.93	0.78
Giving up rules				
best fit curve	none	linear	asymptotic	asymptotic
type of curve	none	decaying[4]	decaying[5]	decaying[6]
$b_{caribou}$	--	--	0.06	0.05
asymptotic survival rate	--	--	85	84
r^2	--	0.78	0.66	0.64

[1] $y = 25.36*3.13/(3.13 + x) + 63.12$; [2] $y = 30.31*0.80/(0.80 + x) + 57.47$; [3] $y = 17.73*0.56/(0.56 + x) + 68.15$; [4] $y = -1.18x + 89.93$; [5] $y = 7.13*0.06/(0.06 + x) + 84.72$; [6] $y = 7.62*0.05/(0.05 + x) + 84.49$

Table 3.4. Percent of kill rate, moose survival, and caribou survival asymptote reached by 1 to 5 km/km^2.

Wolf movement	degree of line use			
	25%	50%	75%	100%
Kill Rate				
Random				
1 km/km^2	66	76	99	100
3 km/km^2	79	88	100	100
5 km/km^2	85	92	100	100
Giving up rules				
1 km/km^2	69	76	94	96
3 km/km^2	79	87	99	99
5 km/km^2	84	91	100	100
Moose Survival				
Random				
1 km/km^2	86	96	100	100
3 km/km^2	92	99	100	100
5 km/km^2	94	100	100	100
Giving up rules				
1 km/km^2	86	88	98	95
3 km/km^2	91	94	100	98
5 km/km^2	93	96	100	99
Caribou Survival				
Random				
1 km/km^2	--	70	77	91
3 km/km^2	--	79	89	96
5 km/km^2	--	85	93	97
Giving up rules				
1 km/km^2	--	--	100	100
3 km/km^2	--	--	100	100
5 km/km^2	--	--	100	100

Table 3.5. The effect of prey avoidance, line use, and wolf movement on the kill rate:line density relationship, b_{kills}, and the asymptotic kill rate.

Wolf movement	% of the prey population that avoids lines				
	Random	25%	50%	75%	100%
25% line use					
Random					
best fit curve	asymptotic	asymptotic	sigmoid	linear	linear
type of curve	increasing[1]	increasing[2]	increasing[3]	increasing[4]	decaying[5]
b_{kills}	2.12	2.52	0.49	--	--
asymptotic kill rate	51	46	33	--	--
r^2	0.98	0.96	0.95	0.18	0.64
Giving up rules					
best fit curve	asymptotic	linear	linear	none	asymptotic
type of curve	increasing[6]	increasing[7]	increasing[8]	none	decaying[9]
b_{kills}	3.21	--	--	--	0.06
asymptotic kill rate	49	--	--	--	27
r^2	0.95	0.76	0.53	--	0.48
75% line use					
Random					
best fit curve	sigmoid	asymptotic	linear	asymptotic	asymptotic
type of curve	increasing[10]	increasing[11]	decaying[12]	decaying[13]	decaying[14]
b_{kills}	0.01	0.10	--	1.13	0.30
asymptotic kill rate	48	39	--	26	27
r^2	0.88	0.54	0.21	0.85	0.94
Giving up rules					
best fit curve	sigmoid	asymptotic	asymptotic	sigmoid	asymptotic
type of curve	increasing[15]	increasing[16]	increasing[17]	decaying[18]	decaying[19]
b_{kills}	0.16	0.77	1.17	<0.001	0.11
asymptotic kill rate	48	42	35	29	31
r^2	0.98	0.96	0.80	0.84	0.94

[1] $y = 25.64x/(2.12 + x) + 25.69$; [2] $y = 19.23x/(2.52 + x) + 26.81$; [3] $y = 6.54x^{2.37}/(0.49 + x^{2.37}) + 26.22$;

[4] $y = 0.63x + 27.18$; [5] $y = -1.18x + 27.51$; [6] $y = 19.62x/(3.21 + x) + 29.08$; [7] $y = 1.66x + 29.56$; [8] $y = 0.92x + 29.43$;

[9] $y = 3.59*0.06/(0.06 + x) + 27.36$; [10] $y = 20.32x^{2.57}/(0.01 + x^{2.57}) + 27.94$; [11] $y = 12.28x/(0.10 + x) + 26.90$;

[12] $y = -1.14x + 28.53$; [13] $y = 14.48*1.13/(1.13 + x) + 11.55$; [14] $y = 27.35*0.30/(0.30 + x)$;

[15] $y = 19.79x^{1.61}/(0.16 + x^{1.61}) + 28.71$; [16] $y = 12.67x/(0.77 + x) + 29.56$; [17] $y = 6.85x/(1.17 + x) + 27.76$;

[18] $y = 4.08*(1.09e\text{-}08)/(1.09e\text{-}08 + x^{13.01}) + 25.25$; [19] $y = 10.88*0.11/(0.11 + x) + 20.15$

Table 3.6. The effect of prey avoidance, line use, and wolf movement on the moose survival:line density relationship, b_{moose}, and the asymptotic survival rate.

Wolf movement	% of the prey population that avoids lines				
	Random	25%	50%	75%	100%
25% line use					
Random					
best fit curve	asymptotic	asymptotic	sigmoid	linear	linear
type of curve	decaying[1]	decaying[2]	decaying[3]	decaying[4]	increasing[5]
b_{moose}	1.66	1.43	0.21	--	--
survival rate	69	73	80	--	--
r^2	0.98	0.95	0.86	0.45	0.42
Giving up rules					
best fit curve	asymptotic	Type I	Type I	none	Type I
type of curve	decaying[6]	decaying[7]	decaying[8]	none	increasing[9]
b_{moose}	3.16	--	--	--	--
survival rate	70	--	--	--	--
r^2	0.91	0.72	0.47	--	0.18
75% line use					
Random					
best fit curve	sigmoid	none	linear	sigmoid	asymptotic
type of curve	decaying[10]	--	increasing[11]	increasing[12]	increasing[13]
b_{moose}	0.002	--	--	0.29	0.31
survival rate	73	--	--	91.40	100.00
r^2	0.71	--	0.39	0.88	0.95
Giving up rules					
best fit curve	sigmoid	asymptotic	linear	asymptotic	asymptotic
type of curve	decaying[14]	decaying[15]	decaying[16]	increasing[17]	increasing[18]
b_{moose}	0.14	0.81	--	0.11	0.08
survival rate	70	81.98	--	85.66	88.57
r^2	0.97	0.94	0.56	0.76	0.97

[1] $y = 15.95*1.66/(1.66 + x) + 69.02$; [2] $y = 11.33*1.43/(1.43 + x) + 73.03$;

[3] $y = 4.92*0.21/(0.21 + x4.14) + 79.67$; [4] $y = -0.64x + 83.75$; [5] $y = 0.56 + 83.42$; [6] $y = 12.60*3.16/(3.16 + x)$;

[7] $y = -1.06x + 81.75$; [8] $y = -0.68x + 81.97$; [9] $y = 0.37x + 82.30$; [10] $y = 10.19*0.002/(0.002 + x3.40) + 73.48$;

[11] $y = 1.15x + 83.37$; [12] $y = 5.84*x^{6.32}/(0.29 + x^{6.32}) + 85.64$; [13] $y = 16.61x/(0.31 + x) + 84.10$;

[14] $y = 11.95*0.14/(0.14 + x1.82) + 70.39$; [15] $y = 7.79*0.81/(0.81 + x) + 74.20$; [16] $y = -0.70x + 82.74$;

[17] $y = 4.87x/(0.11 + x) + 80.78$; [18] $y = 8.54x/(0.08 + x) + 80.03$

Table 3.7. The effect of prey avoidance, line use, and wolf movement on the caribou survival:line density relationship, $b_{caribou}$, and the asymptotic survival rate.

Wolf movement	% of the prey population that avoids lines				
	Random	25%	50%	75%	100%
25% line use					
Random					
best fit curve	none	asymptotic	asymptotic	asymptotic	linear
type of curve	none	increasing[1]	increasing[2]	increasing[3]	increasing[4]
$b_{caribou}$	--	0.02	0.72	1.38	--
survival rate	--	91	93	98	--
r^2	--	0.49	0.47	0.90	0.68
Giving up rules					
best fit curve	none	none	none	none	none
type of curve	none	none	none	none	none
$b_{caribou}$	--	--	--	--	--
survival rate	--	--	--	--	--
r^2	--	--	--	--	--
75% line use					
Random					
best fit curve	asymptotic	asymptotic	linear	none	asymptotic
type of curve	decaying[5]	decaying[6]	decaying[7]	none	increasing[8]
$b_{caribou}$	0.80	0.88	--	--	0.70
survival rate	57	64	--	--	100
r^2	0.93	0.97	0.78	--	0.73
Giving up rules					
best fit curve	asymptotic	asymptotic	asymptotic	asymptotic	none
type of curve	decaying[9]	decaying[10]	decaying[11]	decaying[12]	none
$b_{caribou}$	0.06	0.14	0.07	0.08	--
survival rate	85	85	87	87	--
r^2	0.66	0.78	0.50	0.62	--

[1]$y=4.64x/(0.02 + x) + 86.03$; [2]$y = 5.68x/(0.72 + x) + 86.85$; [3]$y = 10.02x/(1.38 + x) + 87.55$;
[4]$y = 1.04x + 90.53$; [5]$y = 30.31*0.80/(0.80 + x) + 57.47$; [6]$y = 25.56*0.88(0.88 + x) + 63.69$;
[8]$y = 13.89x/(0.70 + x) + 86.95$; [9]$y = 7.13*0.06/(0.06 + x) + 84.72$; [10]$y = 7.19*0.14/(0.14 + x) + 85.34$;
[11]$y = 5.34*0.07/(0.07 + x) + 86.67$; [12]$y = 5.16*0.08/(0.08 + x) + 86.89$

Table 3.8. Change in caribou survival (%) from 0 to 3 km/km^2. Survival is a function of different wolf movement strategies, degree of line use, and prey avoidance behaviors.

Model Settings	change in survival (%) from 0 to 3 km/km^2		
	25% line use	50% line use	75% line use
Random wolf movement			
Random Prey	4	-14	-24
25% Avoid Prey	4	-16	-19
50% Avoid Prey	5	-5	-4
75% Avoid Prey	8	6	2
100% Avoid Prey	7	8	8
Movement using a giving-up rule			
Random Prey	-1	-6	-7
25% Avoid Prey	-1	-3	-7
50% Avoid Prey	0	-3	-7
75% Avoid Prey	-1	-1	-5
100% Avoid Prey	-3	-2	-4

Table 3.9. Hypothetical effect of declining survival on λ for two stable herds and for an "average herd." Estimates are based on Hatter and Bergerud (1991), in which λ = (1-mortality)/(1-recruitment).

% change in survival	CLAWR	WSAR	Average
0	1.05	1.15	1.06
-1	1.04	1.14	1.05
-2	1.03	1.13	1.03
-3	1.01	1.11	1.02
-4	1.00	1.10	1.01
-5	0.99	1.09	1.00
-6	0.98	1.08	0.99
-7	0.97	1.06	0.97
-8	0.96	1.05	0.96
-9	0.95	1.04	0.95
-10	0.94	1.02	0.94
-11	0.92	1.01	0.93
-12	0.91	1.00	0.91
-13	0.90	0.98	0.90
-14	0.89	0.97	0.89
-15	0.88	0.96	0.88
-16	0.87	0.95	0.87
-17	0.86	0.93	0.85
-18	0.85	0.92	0.84
-19	0.83	0.91	0.83
-20	0.82	0.89	0.82
-21	0.81	0.88	0.81
-22	0.80	0.87	0.80
-23	0.79	0.86	0.78
-24	0.78	0.84	0.77

Figure 3.1. Average adult female caribou survival as a function of linear feature density (km/km^2) ($r^2 = 0.68$, based on data in Dzus 2001; Dunford 2003; McLoughlin *et al*. 2003; Neufeld 2006). Different data points represent survival in different caribou ranges across northern Alberta: CM or Caribou Mountains herd, CLAB or Cold Lake Air Weapons Range herd, WSAR or West Side of the Athabasca herd, ESAR or the East Side of the Athabasca herd, REDE or the Red Earth herd, and LS or the Little Smoky herd.

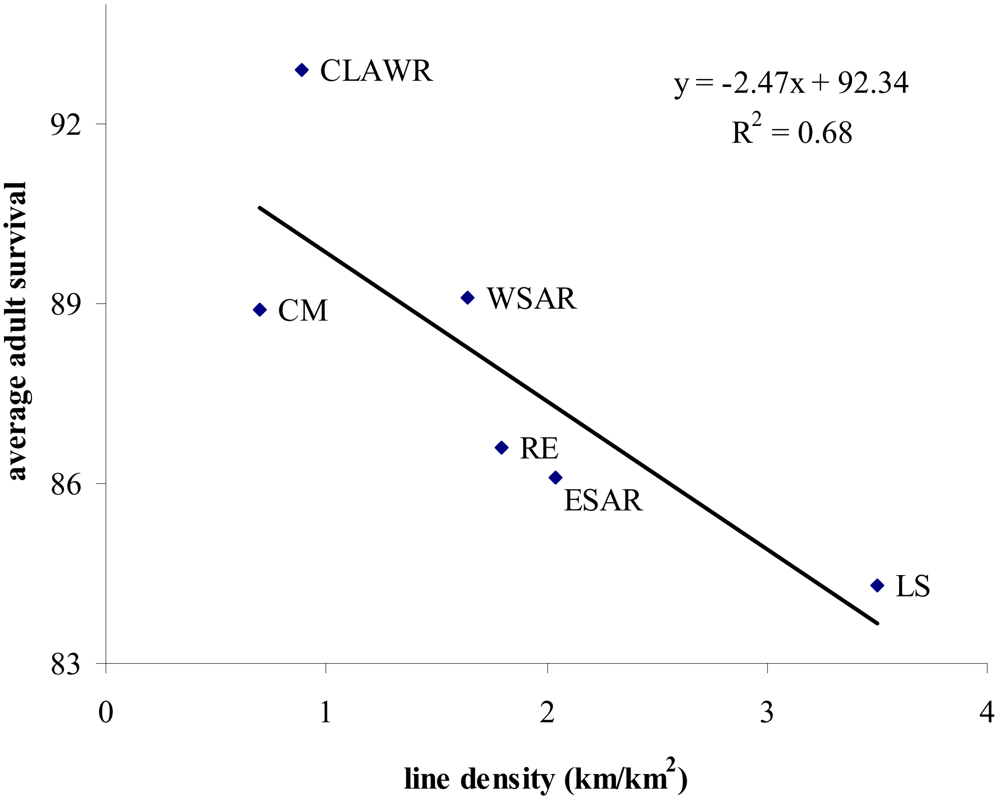
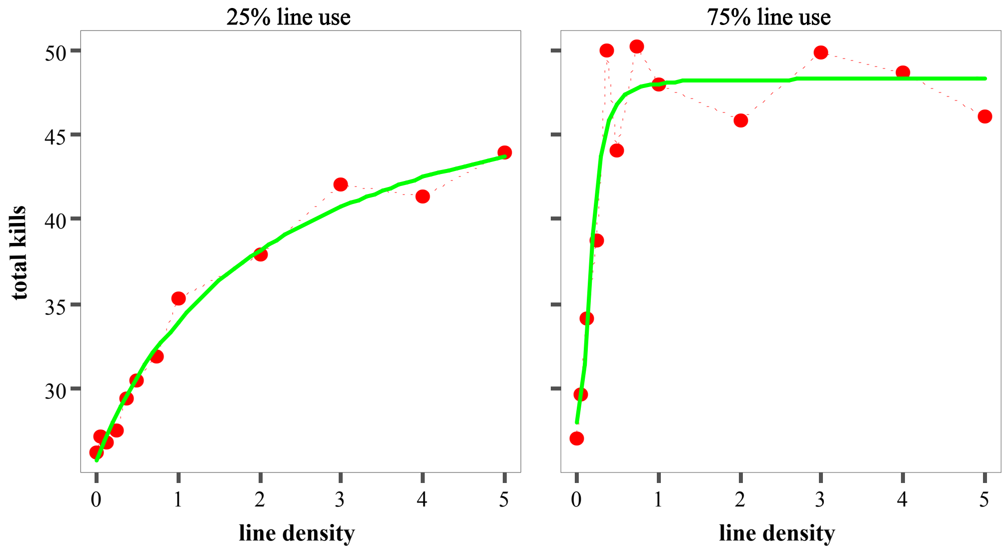
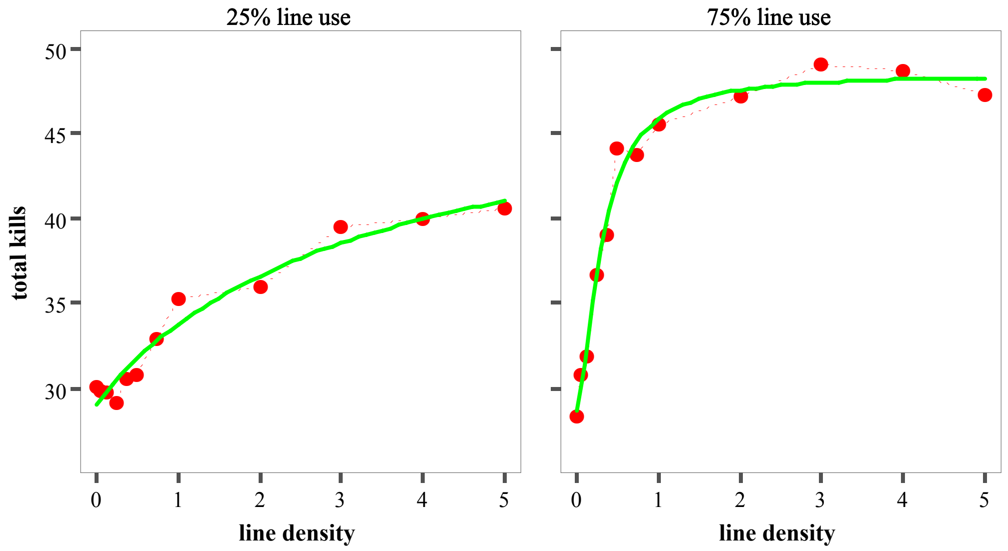


Figure 3.2. The effect of line density, line use, and wolf movement on total kills per year. Simulated data (--●--) was best described by an asymptotic curve (——) at 25% line use and a sigmoid curve (——) at 75% line use.

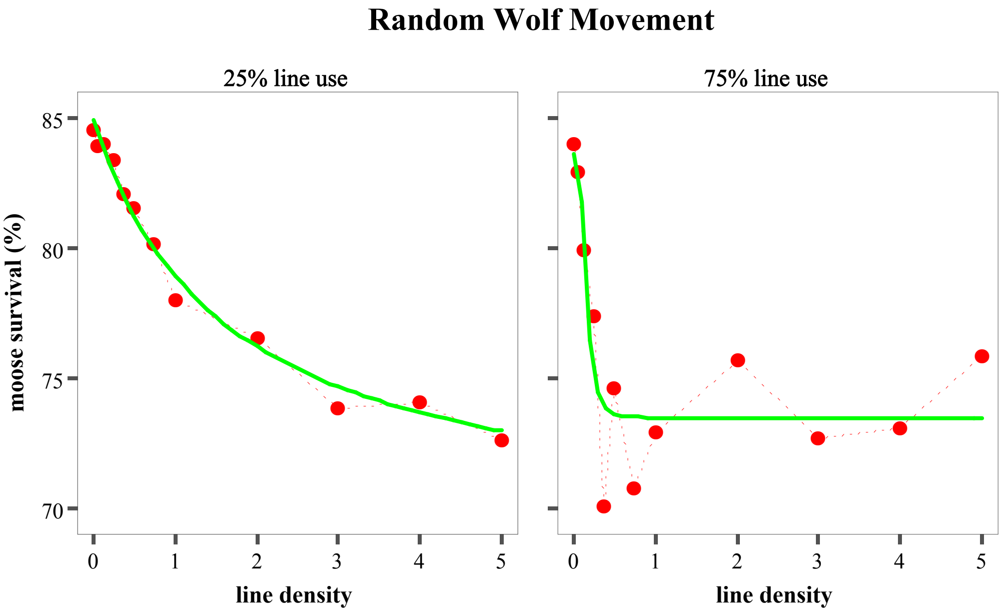


Random Wolf Movement

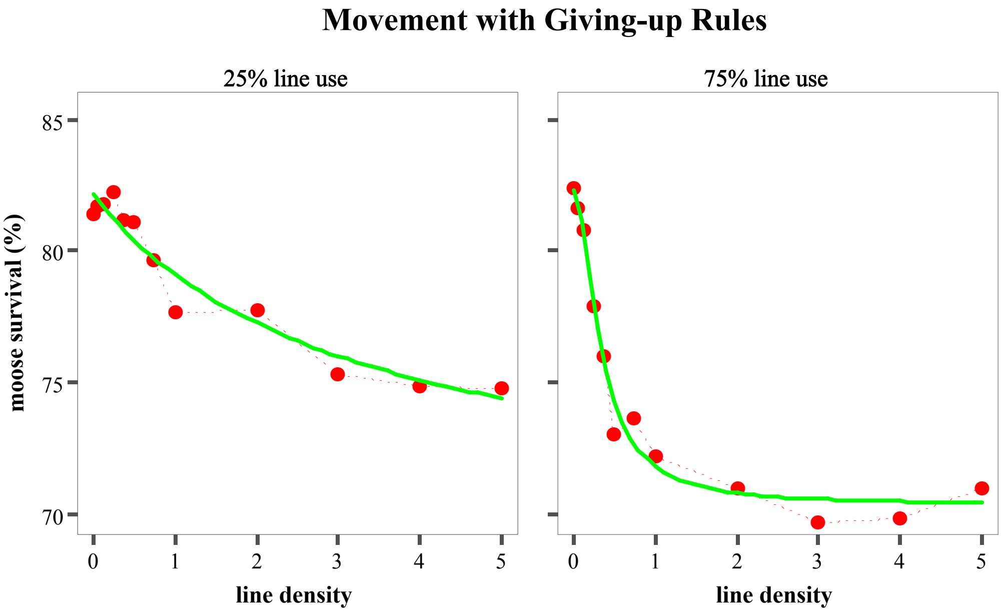


Movement with Giving-up Rules

Figure 3.3. The effect of line density, line use, and wolf movement on moose survival. Simulated data (--●--) was best described by a decaying asymptotic curve (——) at 25% line use and a decaying sigmoid curve (——) at 75% line use.



Random Wolf Movement



Movement with Giving-up Rules

Figure 3.4. The effect of line density, line use, and wolf movement on caribou survival. Simulated data (--●--) did not change across line density at 25% line use but was best described by a decaying asymptotic curve (——) at 75% line use.

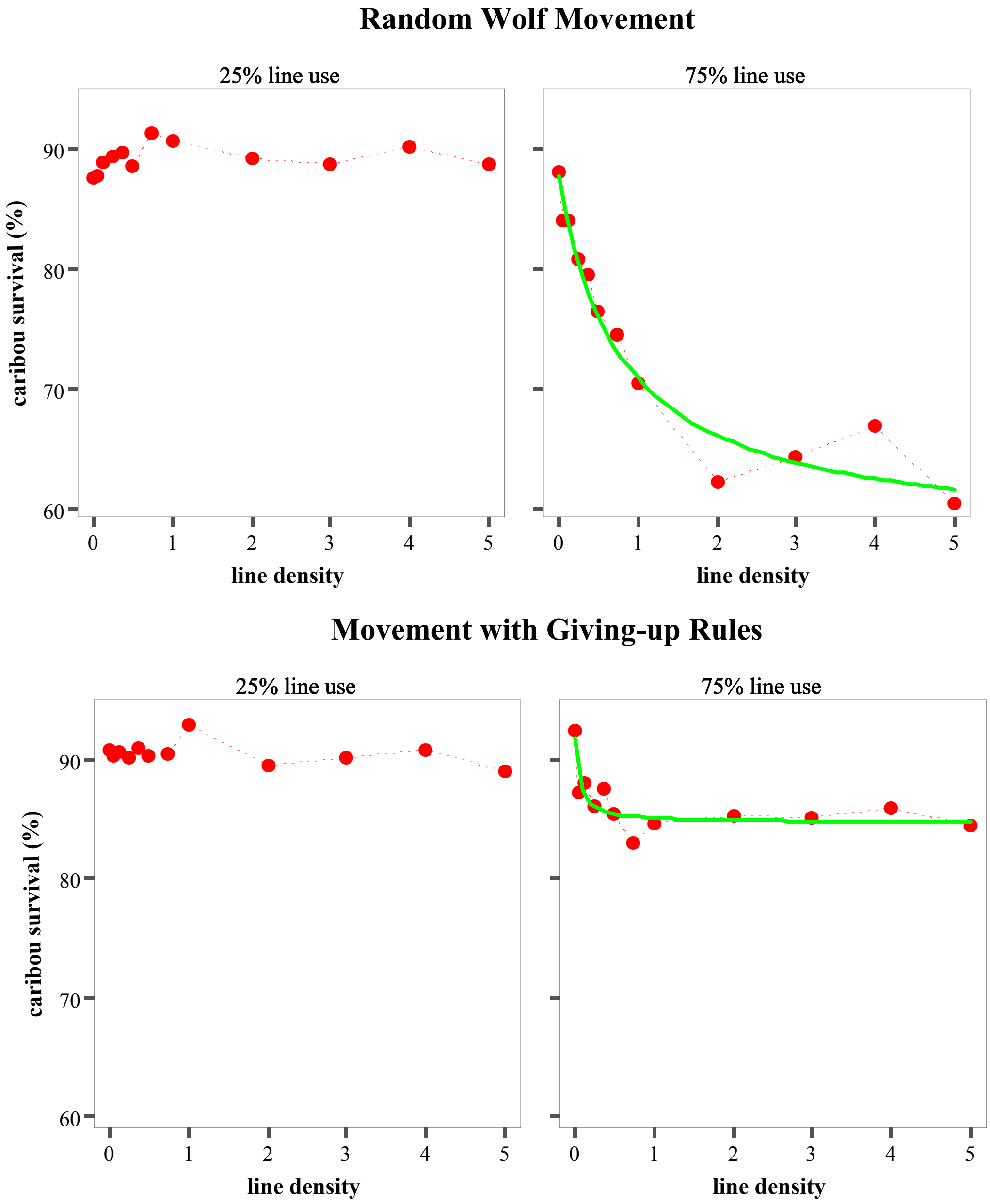


Figure 3.5. The effect of prey behavior on kill rate:line density relationships assuming that wolves move randomly at 25% line use. Simulations based on randomly distributed prey (--●--) were best described by an asymptotic curve (——) whereas simulations in which all prey avoided lines (--●--) followed a decaying linear curve (——).

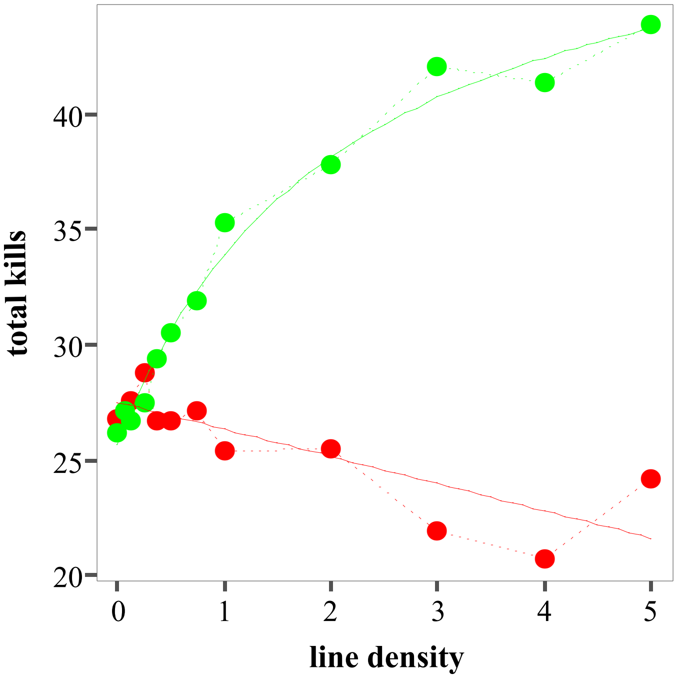


Figure 3.6. The effect of prey behavior on prey survival:line density relationships assuming that wolves move randomly at 25% line use. For moose, simulations based on randomly distributed prey (--●--) were best described by a decaying asymptotic curve (——) whereas simulations in which all prey avoided lines (--●--) followed a linear curve (——). Line density had no effect on caribou survival if all prey were randomly distributed (--●--), but the survival:line density curve was best described by a linear curve (——) if all prey avoided lines (--●--).

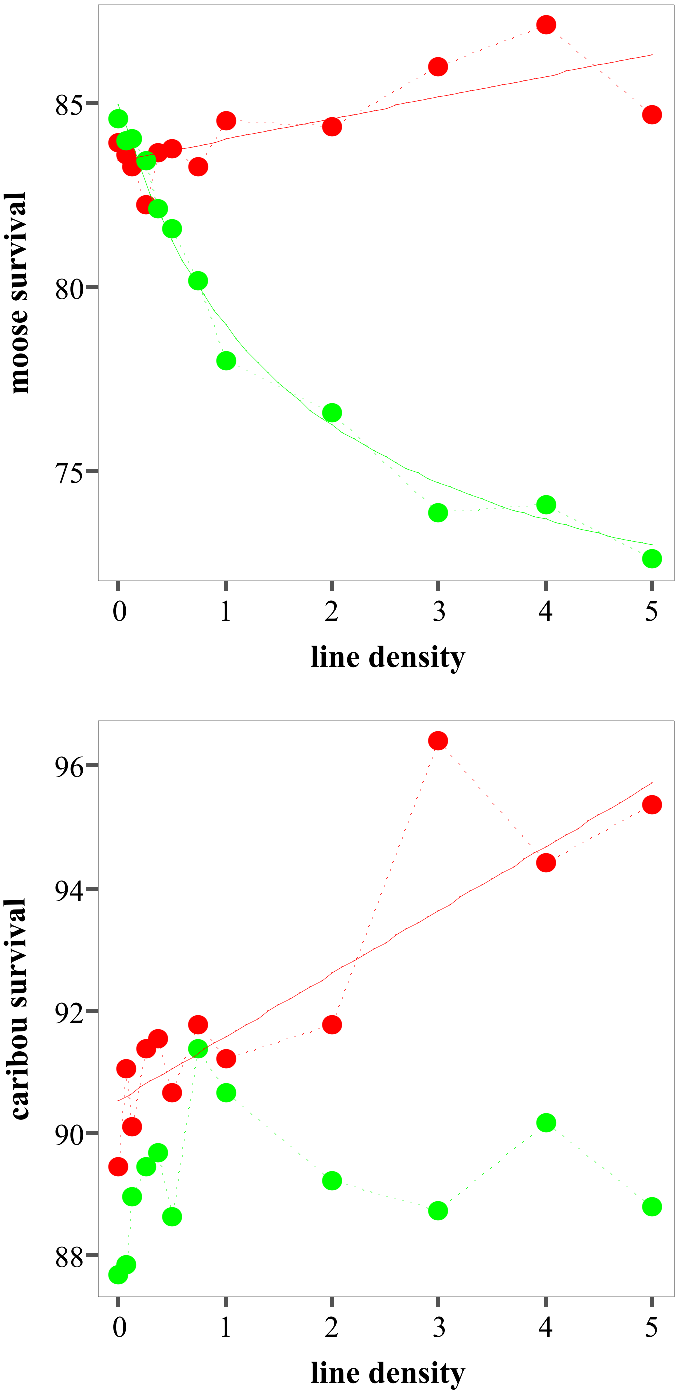


Figure 3.7. The effect of prey avoidance on the change in kill rates from 0 to 5 km/km^2 assuming that wolves move randomly or use a giving up rule. Bars represent line use of 25% (🟥) and 75% (🟩). Values above 1 indicate an increase in kill rate, values equal to 1 indicate no change in kill rate, and values below 1 indicate a decrease in kill rate.

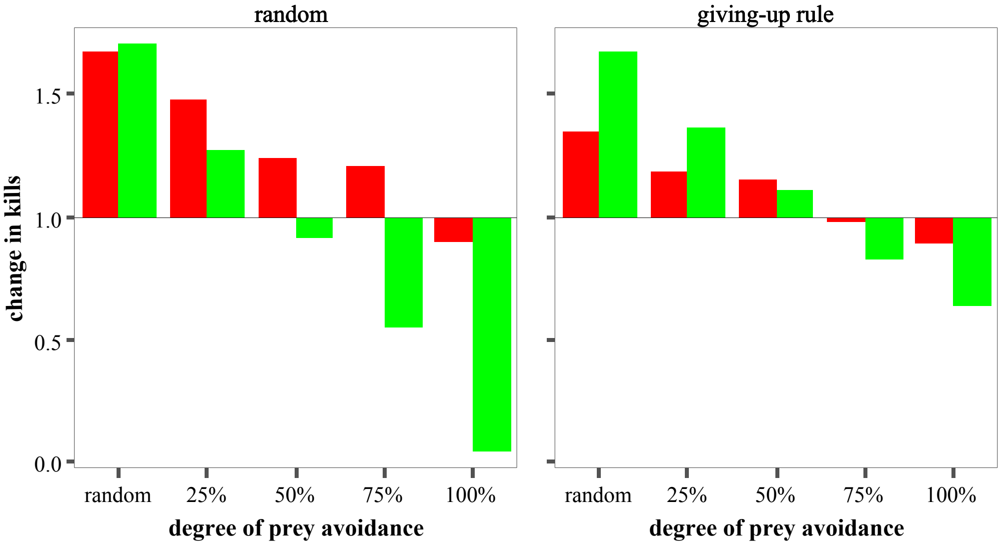


Figure 3.8. The effect of prey avoidance on the change in moose survival from 0 to 5 km/km^2 assuming that wolves move randomly or use a giving up rule. Bars represent line use of 25% (🟥) and 75% (🟩). Values above 1 indicate an increase in survival rate, values equal to 1 indicate no change in survival rate, and values below 1 indicate a decrease in survival rate.

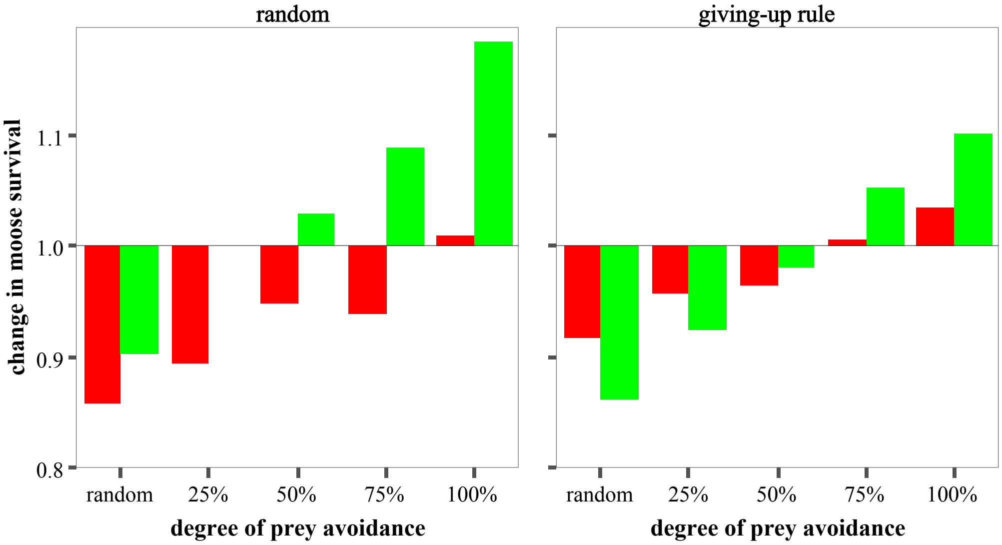
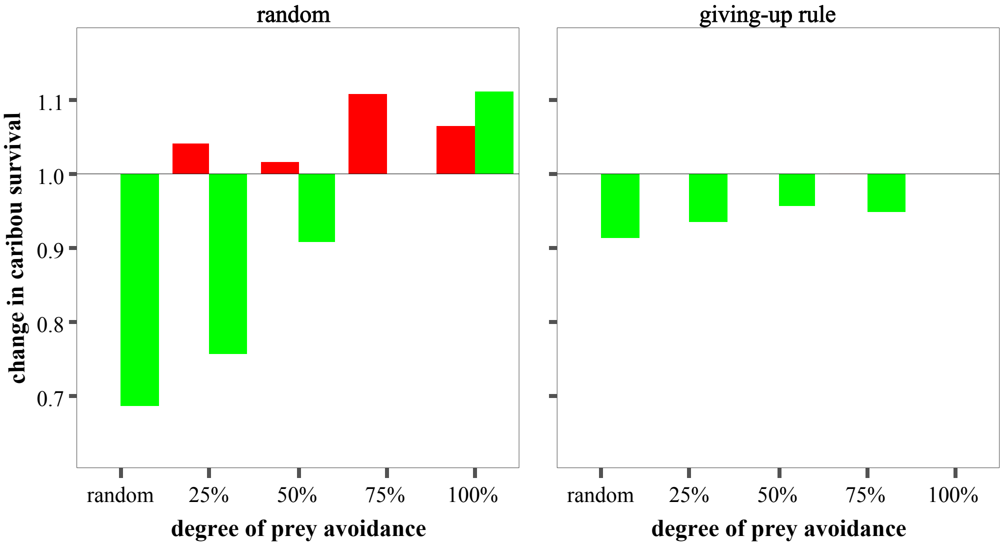


Figure 3.9. The effect of prey avoidance on the change in caribou survival from 0 to 5 km/km^2 assuming that wolves move randomly or use a giving up rule. Bars represent line use of 25% (🟥) and 75% (🟩). Values above 1 indicate an increase in survival rate, values equal to 1 indicate no change in survival rate, and values below 1 indicate a decrease in survival rate.



Chapter 4: The effect of overlap between moose and caribou on caribou survival

Introduction

Many studies have documented the spatial segregation of woodland caribou (*Rangifer tarandus caribou*) from other ungulates (Bergerud 1985; 1988; Bergerud and Page 1987; Seip 1992; Cumming *et al*. 1996). One of the benefits of this "spacing away" strategy is reduced encounters with predators like wolves (*Canis lupus*) (Bergerud 1985; 1988; Bergerud and Page 1987; Bergerud *et al*. 1990; Cumming *et al*. 1996; Ferguson *et al*. 1988; Seip 1992; Rettie and Messier 2000). Wolves concentrate on alternative prey because they are usually more abundant and/or provide more biomass than caribou (e.g., Cumming *et al*. 1996). In northeastern and west-central Alberta, for example, boreal caribou are found in peatlands whereas wolves and moose (*Alces alces*) are predominantly found in the adjacent uplands (Bradshaw *et al*. 1995; Stuart-Smith *et al*. 1997; Dzus 2001; James *et al*. 2004). Moose occur at higher densities and are larger than caribou (0.24 to 0.53 moose/km^2 vs 0.04 caribou/km^2 and ~435 kg vs ~154 kg; averages based on density and mass estimates from Fuller and Keith 1981; Hauge and Keith 1981; Edmonds 1988; Renecker and Hudson 1993; Smith 1993; Stuart-Smith *et al*. 1997; Schneider and Wasel 2000; James *et al*. 2004), which potentially renders uplands the more profitable patch (e.g., Holt 1984). As such, wolves spend little time in peatlands and rarely incorporate caribou into their diet (James *et al*. 2004). However, boreal caribou are currently in decline and the species is now listed as provincially threatened (Dzus 2001; McLoughlin *et al*. 2003; COSEWIC 2005). These declines have been documented since 1993 and in some herds, have been quite extensive (i.e., a ~15 to 50%+

cumulative decline since study inception; McLoughlin *et al*. 2003). This strongly suggests that peatlands may no longer be a spatial refuge from wolf predation.

Spatial refuges may be compromised if there are changes in the abundance of alternative prey species and/or if mobility between the refuge and alternative prey habitat increases (Holt 1984). Changes in alternative prey distributions can also affect refuge prey if alternative prey move into the refuge habitat (e.g., Holt and Kotler 1987). The presence of alternative prey will mean that the refuge is more profitable, and as a direct consequence, predator activity in the refuge should increase (e.g., Holt and Kotler 1987). For example, recent work in the WSAR caribou range suggests that moose and caribou are no longer segregated (i.e., D. Latham, *unpublished results*). This is contrary to James *et al*. (2004), who suggest that moose strongly select for upland habitat and caribou strongly select for peatland habitat. The extent of overlap between moose and caribou in other caribou ranges is not known, nor is it clear why moose distributions are changing. The concern is that moose are drawing wolves into peatlands (which recent work suggests is occurring; D. Latham, *unpublished results*), thereby increasing the likelihood of wolf-caribou interactions (e.g., Holt and Kotler 1987). If so, then changes in moose distribution may account for at least some caribou declines in Alberta.

Declines in caribou survival may also result from an interaction between overlap and wolf use of linear features as travel routes (James and Stuart-Smith 2000). These features are prevalent in Alberta and include seismic lines, pipelines, and roads (Schneider 2002). Seismic lines, which are the dominant line type in Alberta, vary from 1 to 8 m or more in width and can be as dense as 10 km/km^2 (Schneider 2002; Lee and Boutin 2006). Line use results in a three fold increase in wolf travel speed (James 1999;

also see Musiani *et al*. 1998), which simulation models predict will increase wolf search efficiency and mobility between uplands and peatlands (Chapter 3). In fact, simulations suggest that line use mimics the wolf functional response (e.g., Messier 1994; Marshall and Boutin 1999). Functional responses depict how kill rate (i.e., the number of prey killed per predator) changes with prey density and are typically described as linear (Type I), asymptotic (Type II), or sigmoidal or "S-shaped" (Type III) (Holling 1959; also see Messier 1994). This should mean increased wolf use of caribou (and moose; see Chapter 3), such that caribou survival:line density curves decline linearly, asymptotically, or sigmoidally (i.e., are opposite of the kill rate:line density curves). In fact, this may explain why average female adult survival declines 9% as line density increases from 0.7 to 3.5 km/km^2 (based on data in Dzus 2001; Dunford 2003; McLoughlin *et al*. 2003; Neufeld 2006).

However, the role of linear features in the wolf-caribou system is complicated by a number of factors. Caribou typically avoid linear features (James and Stuart-Smith 2000; Dyer *et al*. 2001), which models suggest negates or at the very least, minimizes the effect of line use on caribou survival (Chapter 3). Furthermore, data from James (1999) suggest that line use is only 26% (also see Whittington *et al*. 2005; Neufeld 2006), which models predict is too low to increase wolf use of caribou (Chapter 3). These results suggest that linear features per se are not responsible for declines in survival. Yet, increasing overlap between moose and caribou may change this outcome because wolves may search more efficiently and are more likely to be in the peatlands. This should be true even if 100% of caribou avoid lines, because low line use still means that most hunting occurs off-line. If so, then overlap may change the nature of the caribou survival:line density relationships, ultimately contributing to the observed declines in survival and herd size.

The main objectives of this study were to (1) determine how overlap between moose and caribou affected caribou survival, (2) determine if overlap changed the nature of survival:line density relationships under different degrees of prey avoidance, and (3) determine if a combination of overlap and line use could account for the negative correlation between female adult survival and line density. Addressing these objectives will help determine if the declines in caribou survival could be a function of overlap alone or possibly stem from an interaction between overlap and line use. This is important to know because current mitigation efforts in Alberta are predominantly designed to reduce wolf use of lines, either via line reclamation or line blocking (Boreal Caribou Committee 2001; Golder Associates 2006; Neufeld 2006). However, the usefulness of these techniques for caribou conservation is questionable, namely because a wolf-line-caribou relationship has yet to be empirically or theoretically established (see Chapter 3). No effort has been made to investigate the effects of moose distributions. As such, this study is important for determining if empirical work should focus on moose use of peatlands and its consequences for caribou survival in northern Alberta. It will also have implications for caribou, moose, and line management, as results may indicate the need to control moose activity in caribou range and/or to minimize line densities in ranges where moose and caribou overlap.

Methods

Models were programmed as described in Chapter 2. Based on the results from Chapter 2 and 3, simulations were run assuming that (1) wolves moved randomly and (2) that wolves moved non-randomly used a 45 km^2 giving up rule. For each movement strategy, I ran simulations in which (a) prey were randomly distributed with respect to lines, (b) 50% of prey avoided lines, and (c) 100% of prey avoided lines. In simulations with linear features, the probability of line use was set at 25% (note: patterns based on higher levels of line use did not differ from those in Chapter 3; *unpublished results*). Models were also programmed to reflect a "northeast Alberta scenario" (i.e., 0.24 moose/km^2; Schneider and Wasel 2000).

I determined how overlap between moose and caribou affected caribou survival by reprogramming the 0 km/km^2 models such that there was 0%, 25%, 50%, 75%, and 100% overlap between moose and caribou. Twenty five percent overlap implies that the moose population extended 25% into caribou range. Note that overall moose density in the territory did not change.

I then determined if overlap changed the nature of the survival:line density relationships observed in Chapter 3 by reprogramming the lined territories to reflect 0%, 25%, 50%, 75%, and 100% overlap between moose and caribou. Simulated results were then fitted to linear ($y = ax + b$), asymptotic ($y = ab/(b + x) + c$), and sigmoid ($y = ab^d/(b + x^d) + c$) decaying responses. In these equations, y = prey survival rate, x = line density, a = the amount survival declines from 0 km/km^2 to the line density at which survival asymptotes, b = the line density at half the minimal survival rate, c = the rate at which survival asymptotes (which, when added to a, gives the y-intercept), and d = the power function that shifts the curve from an asymptotic to a sigmoid response. In some instances, prey survival increased with line density (e.g., if all prey avoided lines) and were best fit linear ($y = ax + b$), asymptotic ($y = ax/(b + x) + c$), and sigmoid ($y = ax^d/(b

+ x^d) + c) increasing curves. In these equations, a = the asymptotic survival rate, b = the line density at half the maximal survival rate, and c = the y – intercept (which, when added to a, gives the actual asymptotic survival rate). Parameters a and b were used to identify key line densities at which a threshold existed and/or at which no more or little change in survival was expected.

I also determined how the curves were affected by prey avoidance behaviors by running simulations in which prey were randomly distributed with respect to lines and in 50% and 100% of the prey population avoided lines. All of these avoidance behaviors were run across 0, 50, and 100% overlap.

All curves were fitted using Table 2D Curve (Version 5.01). Best fit curves were selected using an *F*-test, in which alpha = 0.05 (Zar 1996). R-squared was adjusted based on the number of degrees of freedom (Zar 1996). One issue with the asymptotic and sigmoid functions used in this study is that they take a long time to asymptote. As such, I determined the line density at which 90% of any survival asymptote had been reached. The overall effects of overlap were also assessed by plotting average survival from 0 to 5 km/km^2 across the different prey behaviors.

Comparisons to the empirical data

Model results describing the relationship between caribou survival and linear feature density at different degrees of overlap and prey behaviors were compared to the empirical data set that describes caribou survival as a function of line density (i.e., a 9% decline from 0.7 to 3.5 km/km^2, $r^2 = 0.68$; based on data in Dzus 2001; Dunford 2003; McLoughlin *et al*. 2003; Neufeld 2006). More generally, results were placed in a population context by determining how changes in caribou survival affected the finite rate of increase in an “average herd” and two previously stable herds (i.e., more recent data than McLoughlin *et al*. 2003 suggests these herds are now also declining; Alberta Caribou Committee, *unpublished results*) (see Methods and Table 3.9. in Chapter 3 for how λ was calculated).

Results

The effect of overlap

The effect of overlap on caribou survival depended on wolf movement patterns. If wolves moved randomly, caribou survival changed little despite increasing overlap between moose and caribou (i.e., less than a 1% change in caribou survival; Figure 4.1.). However, if wolves used giving up rules, survival declined 5% as overlap increased from 0 to 100%.

The effect of overlap on line density relationships

The effect of overlap on caribou survival:line density relationships depended on how wolves moved. If wolves moved randomly, the survival:line density curve shifted from no relationship to an asymptotic curve as overlap increased to 100% (Table 4.1.; Figure 4.2.). This suggests that overlap will lead to an asymptotic increase in survival. For example, at 100% overlap, survival increased 7% from 0 to 5 km/km^2. Ninety percent of this asymptote was reached by 0.9 km/km^2.

However, if the pack used giving up rules, overlap had the opposite effect on survival. Survival:line density curves shifted from no relationship to a decaying linear curve if overlap was 50% or more (Table 4.2.). For example, at 50 and 100% overlap, survival decreased 6% as line density increased to 5 km/km^2.

If survival was averaged across line density, then changes in lined territories were similar to those in a 0 km/km^2 territory. For example, if wolves moved randomly, average survival changed little despite an increase in overlap (i.e., there was less than a 1% change in survival) (Figure 4.3.). If wolves used giving up rules, average survival decreased 7% as overlap increased to 100%.

The effect of avoidance

Avoidance always improved survival rates if wolves moved randomly. For example, survival:line density curves shifted from no relationship to a linear or asymptotic curve at 0% and 50% overlap. At 100% overlap, the survival:line density curve was best described by an asymptotic curve across all prey behaviors but avoidance meant that survival saturated at a higher rates (e.g., 90 vs 97%, reflecting random prey distributions vs 100% prey avoidance) (Figure 4.4.). However, $b_{caribou}$ increased from 0.03 to 1.73 km/km^2 as avoidance increased, indicating that asymptotes occurred at higher line densities if avoidance was high. Still, 94% of the asymptote was reached by 1 km/km^2 even if all prey avoided lines. More generally, there was a 2 to 5% increase in survival across line density if 50% of prey avoided lines and a 5 to 8% increase in survival across line density if all prey avoided lines (variance reflects different degrees of overlap).

However, avoidance had a more variable effect on survival rates if wolves used giving up rules. Avoidance had no effect on the survival:line density relationship if there was no overlap between caribou and moose. However, at 50 and 100% overlap, the survival:line density curves shifted from decaying linear curves to no relationships if all prey avoided lines (Figure 4.5.). This suggests that avoidance will negate the effect of overlap on wolf use of lines. The survival:line density curve still followed a linear decaying response if only 50% of prey avoided lines (i.e., survival declined ~5% with line density), but the relationship was weak at both levels of overlap (i.e., r^2 of 0.32 or less).

Avoidance also minimized the overall effects of overlap from 0 to 5 km/km^2. For example, average survival only decreased 2% from 0 to 100% overlap if wolves used giving up rules and 50% or more prey avoided lines (Figure 4.6.). If wolves moved randomly, average survival did not change despite increasing overlap or changes in prey behavior.

Comparison to empirical data

Empirical data indicates that average caribou survival declines 9% as line density increases from 0.7 to 3.5 km/km^2 (r^2= 0.68; based on data in Dzus 2001; Dunford 2003; McLoughlin *et al*. 2003; Neufeld 2006). Actual caribou avoidance of lines (other than more or less than expected; James and Stuart-Smith 2000) and overlap between caribou and moose (other than preliminary data for the WSAR region; D. Latham, *unpublished results*) is not known. Despite changes in moose overlap and prey behavior, model results predict that caribou survival will increase or remain unchanged if line density increases from 0 to 3 km/km^2 and wolves move randomly at 25% line use (Table 4.3.). This would lead to stability or increases in the CLAWR, WSAR, and "average herd" (see Table 3.9., Chapter 3). If wolves used giving up rules at 25% line use, survival decreased by 1 to 5% if 50% or less prey avoided lines and overlap was 50% or higher. A 1 to 5% decline would yield λ values of 1.04 to 0.99 for the CLWAR herd, 1.14 to 1.09 for the

WSAR herd, and 1.05 to 1.00 for an average herd, suggesting primarily stable or increasing herds.

Discussion

Model results suggest that the effect of overlap on caribou survival depends on how wolves move within their territories. Overlap did not affect caribou survival if wolves moved randomly. However, if wolves used giving-up rules, survival decreased 5% as overlap between caribou and moose increased to 100%. This difference stems from how wolf movement patterns were affected by prey density. Random movement means that wolves will move between habitats independently of prey density (e.g., Holt and Kotler 1987). Even if they are hunting in peatlands, wolves are more likely to encounter moose because moose are more abundant than caribou. This suggests that while caribou may no longer have a spatial refuge, they can still find refuge in alternative prey numbers. This agrees with Holt and Kotler's (1987) theoretical findings in which refuge prey survival depends on the functional response of predators to alternative prey (see Farnell *et al*. 1996 and Retie and Messier 1998 for anecdotal evidence of this). In other words, time spent handling moose means less time for hunting caribou. This is interesting as it implies that a spatial refuge per se is not necessary for caribou persistence, which is contrary to other theoretical and empirical work (e.g., Holt 1977; 1984; Bergerud 1985; Cumming *et al*. 1996; Ferguson *et al*. 1988; Seip 1992; Schaefer *et al*. 2001).

However, if wolves use giving-up rules, they will only leave a given habitat after so much time/distance traveled has passed since their last kill (Chapter 2; also see Iwasa *et al*. 1981; McNair 1982; Green 1984; Jedrzejewski *et al*. 2001; Mech and Boitani

2003). The presence of moose will mean that kills occur more frequently in peatlands, which will delay the "decision" to leave the habitat. This increases the amount of time wolves have to encounter caribou, ultimately leading to higher rates of caribou mortality (i.e., short-term apparent competition; Holt and Kotler 1987). In fact, overlap between moose and caribou could mean that peatlands become the more productive patch because overall prey density and prey biomass is higher than in the uplands. This means that wolves should spend more time in peatlands than uplands if they use giving up rules. These findings are consistent with empirical work that stresses the importance of spatial refuges for caribou persistence (Bergerud 1985; Cumming *et al*. 1996; Ferguson *et al*. 1988; Seip 1992; Schaefer *et al*. 2001). Clearly, wolf movement patterns should be investigated further as the type of pattern can lead to vastly different predictions about the effects of overlap. While there is some evidence to suggest that wolves do use "rules" while hunting (e.g., Jedrzejewski *et al*. 2001; Mech and Boitani 2003), the only Alberta work to comment on wolf movement suggests there was no pattern to pack movement (Fuller and Keith 1980). However, the topic as a whole remains poorly studied.

Overlap should also augment the effects of wolf use of lines simply because wolves are hunting more efficiently and are more likely to be in peatlands. This implies that overlap will change the nature of the line-wolf-caribou interaction, which previous simulations suggest does not occur because wolf use of lines is too low (Chapter 3). However, the type of effect that overlap had on wolf use of lines again depended on wolf movement patterns. If movement was random, caribou survival:line density curves shifted from no relationship to asymptotic curves if moose completely overlapped with caribou. This means that overlap actually improved survival for caribou in territories with lines (i.e., survival increased 7% with line density). Again, this likely reflects higher encounter rates with moose, which, when combined with more efficient hunting, should mean that wolves spend most of their time handling moose.

Yet, overlap did augment the effects of line use if wolves used giving up rules. Survival:line density curves shifted from no relationship to decaying linear curves even if moose only extended 50% into caribou range (i.e., survival declined 6% with line density at 50% overlap or more). This suggests that even with higher moose densities offsetting wolf predation, increased wolf presence in peatlands combined with increased hunting efficiency will lead to declines in caribou survival. The more general effects of overlap also persisted in lined territories. When averaged across all line densities, average survival in a territory with no prey segregation was 7% less than in a territory with prey segregation. This implies that overlap alone could underlie both the survival and herd declines (note that a 7% decline was also evident if survival was only averaged from 0 to 3 km/km^2). For example, a 7% decline would yield λ values of 0.97 for the CLWAR herd, 1.06 for the WSAR herd, and 0.97 for an "average" caribou herd. If so, then these results could mean that moose overlap varies across caribou ranges. Moreover, this variation may be correlated to linear feature density. Moose response to lines is not well studied, but there is some anecdotal evidence to suggest that they may use lines as travel routes and/or as a place to feed on regrowth (e.g., as they do with older clearcuts; Rempel *et al*. 1997; also see Jalkotzy *et al*. 1997). If so, then more lines may mean more moose movement into peatlands, which could account for the negative correlation between caribou survival and line density (Alberta Caribou Committee, *unpublished results*). There is also evidence that deer (*Odocoileus* sp.) are encroaching on peatlands (D.

Latham, *unpublished results*), possibly for the same reasons as moose. This is disconcerting as any species that increases prey biomass in peatlands is likely to have a negative effect on caribou survival, if wolves use giving up rules.

However, these results do not account for the fact that caribou typically avoid linear features (James and Stuart-Smith 2000; Dyer *et al*. 2001; also see Nellemann and Cameron 1996; 1998;; Nellemann *et al*. 2001; Vistnes and Nellemann 2001; Cameron *et al*. 2005). Previous simulations suggest that avoidance minimizes (and if extensive enough, negates) the effect of line use on wolf kills (Chapter 3). As such, avoidance behaviors can lead to an increase in caribou survival as line density increases (Chapter 3). Model results suggest that avoidance also minimized the effects of overlap and/or simply improved survival rates. If wolves moved randomly, avoidance lead to a 2 to 8% increase in survival as line density increased (variance reflects different degrees of overlap and avoidance). If wolves used giving up rules, the decaying survival:line density relationship shifted to no relationship if all prey avoided lines and only a weakly declining relationship if 50% of prey avoided lines. Avoidance also minimized the overall effects of overlap. For example, average survival from 0 to 5 km/km^2 only decreased 2% if moose and prey completely overlapped and 50% or more prey avoided lines. Still, caribou response to lines is variable (e.g., James and Stuart-Smith 2000; Oberg 2001), which means that overlap may still augment the effects of line use. The exact amount of avoidance has not been explicitly quantified nor has it been studied in every caribou range. Yet, caribou avoidance should be more thoroughly investigated given its potential importance to the moose-caribou-overlap relationships.

Still, even without accounting for avoidance, survival declines may not be extensive enough to drive the existing herd declines. Survival declined 1 to 5% as line density increased from 0 to 3 km/km^2, depending on prey behavior and the degree of overlap. This is 4 to 8% less than the empirical data set. A 1 to 5% decline would yield λ values of 1.04 to 0.99 for the CLWAR herd, 1.14 to 1.09 for the WSAR herd, and 1.05 to 1.00 for an average herd, suggesting largely stable or increasing herd sizes. Even the 7% decline in average survival across increasing overlap was reduced to 2% once prey avoidance behaviors were considered. However, these conclusions may reflect the simplifying assumptions of the models and the sole focus on adult survival. If calves were also included in the models, then it is possible that increasing overlap would also lead to higher rates of calf mortality. Lower recruitment, combined with lower female survival, could lead to population declines (e.g., Fancy *et al*. 1994; Gaillard *et al*. 1998; 2000). Furthermore, models do not account for finer scale behaviors like prey preference (i.e., encounters are solely a function of relative prey density). This differs from a number of studies which suggest that wolves do select certain types of prey (i.e., a certain species and/or age class is taken more than expected based on availability) (e.g., Fuller and Keith 1980; Peterson *et al*. 1984; Bjorge and Gunson 1989; Huggard 1993; Mattioli *et al*. 1995; Kunkel *et al*. 1999; Kunkel and Pletscher 2001). If wolves prefer caribou over moose where the two species overlap, then it is conceivable that declines in caribou survival would be extensive enough to trigger population declines. As such, studies investigating overlap should also determine if the proportion of caribou taken simply reflects their availability or something more complicated. They should also determine the effect of overlap on calf survival and recruitment.

Overall, these results suggest that overlap between caribou and moose can increase predation pressure on caribou, although the effect may not be extensive enough to have herd-level impacts. This implies that overlap is not the sole factor underlying the caribou population declines. Results also suggest that overlap between moose and caribou is necessary for wolf use of lines to have an effect on caribou survival. This suggests that overlap is a more critical factor for caribou survival than linear features, although this assumes that the primary effect of linear features is how they change wolf hunting efficiency (see Chapter 5 for the other potential effects of line use). Future empirical work should investigate the degree of overlap between moose and caribou in all of the caribou ranges. If models do mimic the wolf-prey system in Alberta, caribou survival should be lower in ranges in which moose are present. Moreover, survival should be lower in ranges with moose and lines than lines alone. The effect of overlap on caribou survival can also be tested experimentally by removing or adding moose to caribou range, which should lead to an increase or a decrease in caribou survival, respectively. Moose removals/additions should reflect changes in distribution and not abundance (i.e., relocating moose to uplands or peatlands) to avoid potential spillover effects (e.g., Holt 1984; furthermore, the movement of moose into peatlands is thought to reflect a change in distribution and not abundance; D. Latham, *personal communication*). If these data are too difficult or costly to collect, then a conservative management strategy would be to remove all alternative prey from caribou range. Given model results from this Chapter and Chapter 3, managing moose distributions would be much more effective in improving caribou survival than managing linear features. It might also be more feasible, given the vast number of linear features that are present in any given caribou range.

However, model results depend on two key behaviors: wolf movement and prey response to lines. If wolves actually do move randomly in their territories (as Fuller and Keith 1981 suggest), then overlap is not expected to affect caribou survival. This conclusion is also true if line avoidance within the caribou population is high. This suggests that researchers should more thoroughly investigate the role of moose distributions, wolf movement, and prey behavior to wolf-caribou interactions before employing extensive moose management strategies. There simply is not enough information to make more definitive recommendations. Nevertheless, these results suggest an alternative reason for the caribou declines, which may mean that current mitigation strategies – which are primarily line based (Boreal Caribou Committee 2001; Golder Associates 2006; Neufeld 2006) – need to be modified to consider the effects of alternative prey.

References

Bergerud, A.T. 1985. Antipredator strategies of caribou: dispersion along shorelines. Canadian Journal of Zoology 63: 1324-1329.

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

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

Bergerud, A.T., Ferguson, R., and Butler, H.E. 1990. Spring migration and dispersion of woodland caribou at calving. Animal Behavior 39: 360-368.

Boreal Caribou Committee. 2001. Strategic plan and industrial guidelines for boreal caribou ranges in northern Alberta. 35pp.

Bjorge, R.R., and Gunson, J.R. 1989. Wolf, *Canis lupus*, population characteristics and prey relationships near Simonette River, Alberta. Canadian Field Naturalist 103: 327-334.

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

Cameron, R.D., Smith, W.T., White, R.G., and Griffith, B. 2005. Central Arctic caribou and petroleum development: distributional, nutritional, and reproductive implications. Arctic 58: 1-9.

Committee on the Status of Endangered Wildlife in Canada. 2005. Status of Woodland caribou (*Rangifer tarandus caribou*). Retrieved on Nov. 30th, 2005 at http://www.cosewic.gc.ca/eng/sct1/searchdetail_e.cfm.

Cumming, H.G., Beange, D.B., and Lavoie, G. 1996. Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared predation risk. Rangifer Special Issue 9: 81-94.

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

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

Dzus, E. 2001. Status of the Woodland Caribou (*Rangifer tarandus caribou*) in Alberta. Alberta Environment, Fisheries and Wildlife Management Division, and Alberta Conservation Association, Wildlife Status Report No. 30, Edmonton, AB. 47 pp.

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

Fancy, S.G., Whitten, K.R., and Russell, D.E. 1994. Demography of the Porcupine caribou herd, 1983-1992. Canadian Journal of Zoology 72: 840-846.

Farnell, R., Barichello, N., Egli, K., and Kuzyk, G. 1996. Population ecology of two woodland caribou herds in southern Yukon. Rangifer Special Issue 9:63-72.

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

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

Fuller, T.K., and Keith, L.B. 1981. Woodland caribou population dynamics in northeastern Alberta. Journal of Wildlife Management 45: 197-213.

Gaillard, J.M., Festa-Bianchet, M., and Yoccoz, N.G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13: 58-63.

Gaillard, J.M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., and Toigo, C. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31: 367-393.

Golder Associates. 2006. Woodland Caribou Research and Information Gap Identification. Prepared for the Alberta Caribou Committee, 19 pp.

Green, R.F. 1984. Stopping rules for optimal foragers. American Naturalist 123: 30-43.

Hauge, T.M., and Keith, L.B. 1981. Dynamics of moose populations in northeastern Alberta. Journal of Wildlife Management 45: 573-597.

Holling, C.S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Canadian Entomologist 91: 293-320.

Holt, R.D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. American Naturalist 124: 377-406.

Holt, R.D., and Kotler, B.P. 1987. Short-term apparent competition. American Naturalist 130: 412-430.

Huggard, D.J. 1993. Prey selectivity of wolves in Banff National Park. II. Age, sex, and condition of elk. Canadian Journal of Zoology 71: 140-147.

Iwasa, Y., Higashi, M., and Yamamura, N. 1981. Prey distribution as a factor determining the choice of optimal foraging. American Naturalist 117: 710-723.

Jalkotzy, M.G., Ross, P.I., and Nasserden, M.D. 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.

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

James, A.R.C., Boutin, S., Hebert, D.M., and Rippin, A.B. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. Journal of Wildlife Management 68: 799-809.

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

Jedrzejewski, W., Schmidt, K., Theuerkauf, J., Jedrzejewska, B., and Okarma, H. 2001. Daily movements and territory use by radiocollared wolves (*Canis lupus*) in Bialowieza Primeval Forest in Poland. Canadian Journal of Zoology 79: 1993-2004.

Kunkel, K.E., and Pletscher, D.H. 2001. Winter hunting patterns of wolves in and near Glacier National Park, Montana. Journal of Wildlife Management 65: 520-530.

Kunkel, K.E., Ruth, T.K., Pletscher, D.H., and Hornocker, M.G. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park, Montana. Journal of Wildlife Management 63: 901-910.

Lee, P. and Boutin, S. 2006. Persistence and developmental transition of wide seismic lines in the western Boreal Plains of Canada. Journal of Environmental Management 78: 240-250.

Marshall, J.P., and Boutin, S. 1999. Power analysis of wolf-moose functional responses. Journal of Wildlife Management 63: 396-402.

Mattioli, L., Apollonio, M., Mazzarone, V., and Centofanti, E. 1995. Wolf habits and wild ungulate availability in the Foreste Casentinesi National Park, Italy. Acta Theriologica 40: 387-402.

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

Mech, L.D., and Boitani, L. 2003. Wolf Social Ecology. In Wolves: Behavior, Ecology, and Conservation. Edited by L.D. Mech and L. Boitani. The University of Chicago Press, Chicago. pp. 1-34.

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology 75: 478-488.

McNair, J.N. 1982. Optimal giving-up times and the marginal value theorem. American Naturalist 119: 511-529.

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

Nellemann, C., and Cameron, R.D. 1996. Effects of petroleum development on terrain preferences of calving caribou. Arctic 49: 23-28.

Nellemann, C., and Cameron, R.D. 1998. Cumulative impacts of an evolving oil-field complex on the distribution of calving caribou. Canadian Journal of Zoology 76: 1425-1430.

Nellemann, C., Vistnes, I., Jordhoy, P., and Strand, O. 2001. Winter distribution of wild reindeer in relation to power lines, roads, and resorts. Biological Conservation 101: 351-360.

Neufeld, L. 2006. Spatial dynamics of wolves and woodland caribou in an industrial forest landscape in west-central Alberta. MSc Thesis, University of Alberta, Edmonton, AB.

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

Peterson, R.O., Woolington, J.D., and Bailey, T.N. 1984. Wolves of the Kenai Peninsula, Alaska. Wildlife Monographs 88: 1-52.

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

Renecker, L.A., and Hudson, R.J. 1993. Morphology, bioenergetics and resource use: patterns and processes. In Hoofed Mammals of Alberta. Edited by J.B. Stelfox. Lone Pine Publishing, Edmonton, Alberta. pp. 141-163.

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

Schaefer, J.A., Veitch, A.M., Harrington, F.H., Brown, W.K., Theberg, J.B., and Luttich, S.N. 1999. Demography of decline of the Red Wine Mountains caribou herd. Journal of Wildlife Management 63: 580-587.

Schaefer, J.A., Veitch, A.M., Harrington, F.H., Brown, W.K., Theberge, J.B., and Luttich, S.N. 2001. Fuzzy structure and spatial dynamics of a declining woodland caribou population. Oecologia 126: 507-514.

Schneider, R.S. 2002. Alternative futures: Alberta's boreal forest and the crossroads. Federation of Alberta Naturalists, Edmonton, Alberta, 152 pp.

Schneider, R.S., and Wasel, S. 2000. The effect of human settlement on the density of moose in northern Alberta. Journal of Wildlife Management 64: 513-520.

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.

Smith, H.C. 1993. Alberta Mammals: an atlas and guide. Provincial Museum of Alberta, Edmonton, Alberta, 250 pp.

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

Vistnes, I., and Nellemann, C. 2001. Avoidance of cabins, roads, and power lines by reindeer during calving. Journal of Wildlife Management 65: 915-925.

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

Wittmer, H.U., McLellan, B.N., Seip, D.R., Young, J.A., Kinley, T.A., Watts, G.S., and Hamilton, D. 2005*a*. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. Canadian Journal of Zoology 83: 407-418.

Zar, J.H. 1996. Biostatistical Analysis. 3rd Edition. Prentice-Hall, Inc., New Jersey, 662 pp.

Table 4.1. The effect of overlap, and prey behavior on the caribou survival:line density relationship, $b_{caribou}$, and the asymptotic survival rate. Results are based on random wolf movement.

Wolf movement	random	50% avoid	100% avoid
0% overlap			
best fit curve	none	none	linear
type of curve	none	none	increasing[1]
$b_{caribou}$	--	--	--
asymptotic survival rate	--	--	--
r^2	--	--	0.66
50% overlap			
best fit curve	none	asymptotic	linear
type of curve	none	increasing[2]	increasing[3]
$b_{caribou}$	--	2.80	--
asymptotic survival rate	--	97	--
r^2	--	0.86	0.57
100% overlap			
best fit curve	asymptotic	asymptotic	asymptotic
type of curve	increasing[4]	increasing[5]	increasing[6]
$b_{caribou}$	0.03	0.56	1.73
asymptotic survival rate	90	92	97
r^2	0.46	0.55	0.89

[1] $y = 1.41x + 88.60$; [2] $y = 9.37x/(2.80 + x) + 87.53$; [3] $y = 1.31x + 89.31$;

[4] $y = 5.35x/(0.03 + x) + 84.35$; [5] $y = 5.63x/(0.56 + x) + 87.80$; [6] $y = 9.30x/(1.73 + x) + 87.97$

Table 4.2. The effect of overlap, and prey behavior on the caribou survival:line density relationship, $b_{caribou}$, and the asymptotic survival rate. Results assume that wolves use giving up rules.

Wolf movement	random	50% avoid	100% avoid
0% overlap			
best fit curve	none	none	none
type of curve	none	none	none
$b_{caribou}$	--	--	--
asymptotic survival rate	--	--	--
r^2	--	--	--
50% overlap			
best fit curve	linear	linear	none
type of curve	decaying[1]	decaying[2]	none
$b_{caribou}$	--	--	--
asymptotic survival rate	--	--	--
r^2	0.40	0.22	--
100% overlap			
best fit curve	linear	linear	none
type of curve	decaying[3]	decaying[4]	none
$b_{caribou}$	--	--	--
asymptotic survival rate	--	--	--
r^2	0.67	0.32	--

[1] $y = -0.57x + 87.00$; [2] $y = -0.95x + 90.32$; [3] $y = -0.81x + 84.70$; [4] $y = -1.28x + 89.42$

Table 4.3. Changes in caribou survival from 0-3 km/km^2 across different wolf movement strategies, degrees of overlap, and prey behaviors.

Model Settings	Wolf movement patterns	
	Random	Giving-up Rules
0% Overlap		
100% Avoid Prey	6	-3
50% Avoid Prey	3	-1
Random Prey	2	3
50% Overlap		
100% Avoid Prey	8	-4
50% Avoid Prey	5	-1
Random Prey	5	-2
100% Overlap		
100% Avoid Prey	6	1
50% Avoid Prey	5	-1
Random Prey	4	-5

Figure 4.1. Caribou survival as a function of different wolf movement strategies and degrees of overlap with moose. Results are based on simulations in a 0 km/km^2 territory.

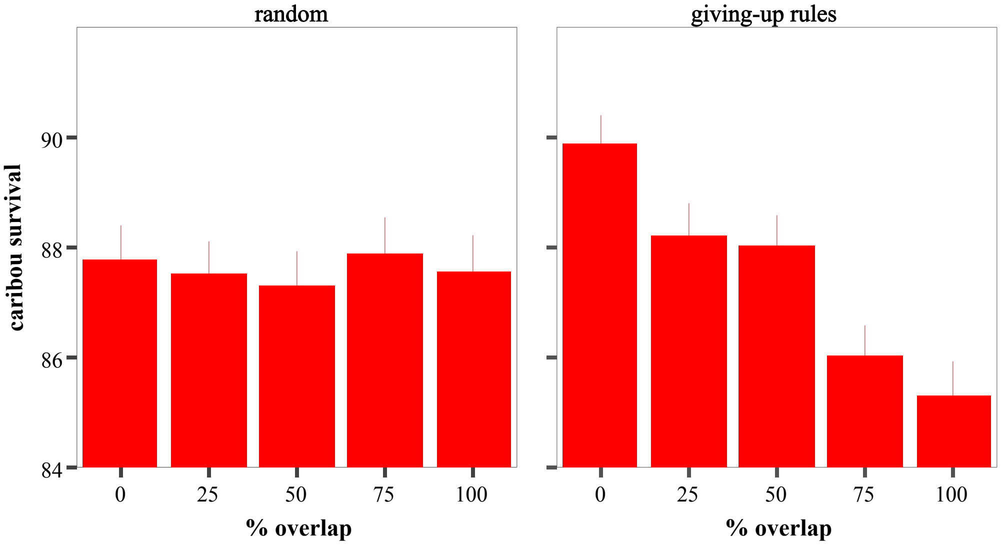


Figure 4.2. The effect of overlap, line density, and wolf movement on caribou survival. Regardless of wolf movement patterns, simulated data did not change across line density at 0% overlap (random: --●--; giving up rules: --●--). At 100% overlap, the survival:line density curve was best described by asymptotic curve (——) if wolves moved randomly (--●--) and a decaying linear curve (——) if wolves used giving up rules (--●--).

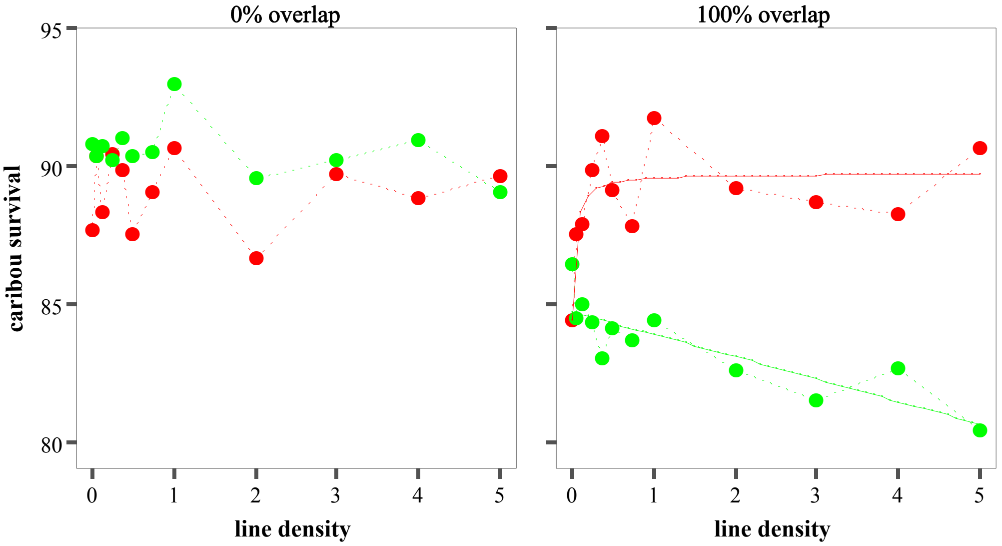


Figure 4.3. Average caribou survival from 0 to 5 km/km^2 as function of overlap and wolf movement strategies.

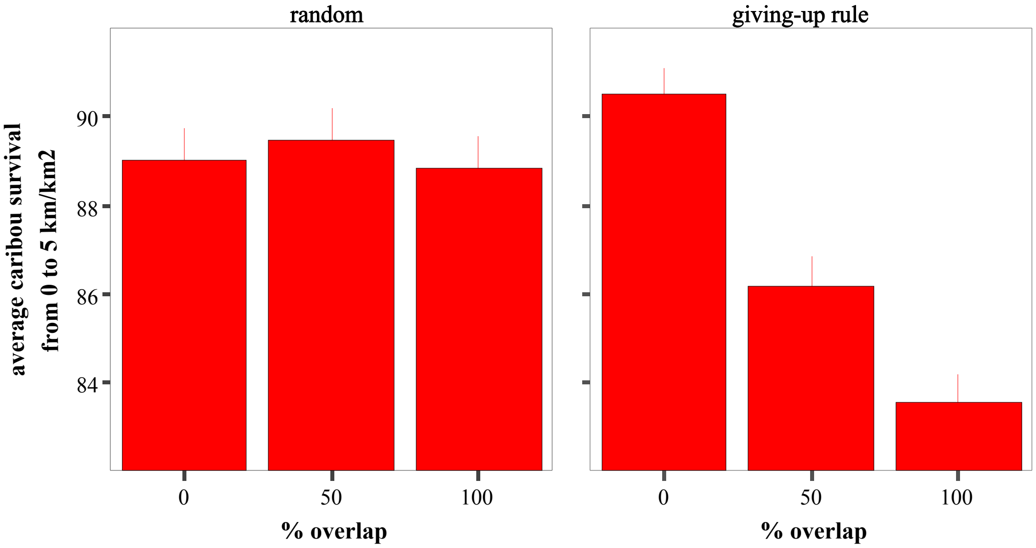


Figure 4.4. The effect of overlap, line density, and prey behavior on caribou survival, assuming that wolves move randomly. Survival:line density relationships are based on simulations in which prey are randomly distributed with respect to lines (--●--) and in which all prey avoid lines (--●--). Simulated data fit a linear curve (——) if all prey avoided lines and overlap was 0%, an asymptotic curve if all prey avoided lines and overlap was 100% (——), and an asymptotic curve if prey were randomly distributed and overlap was 100% (——).

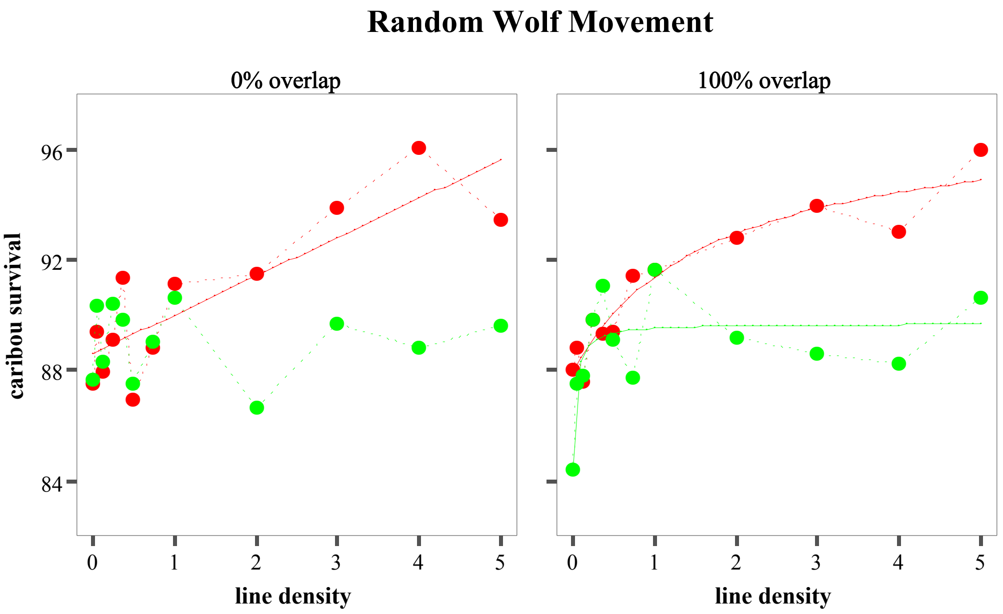


Figure 4.5. The effect of overlap, line density, and prey behavior on caribou survival, assuming that wolves use giving up rules. Survival:line density relationships are based on simulations in which prey are randomly distributed with respect to lines (--●--) and in which all prey avoid lines (--●--). At 100% overlap, the survival:line density curve was best described by a decaying linear curve (——) if all prey were randomly distributed with respect to lines.

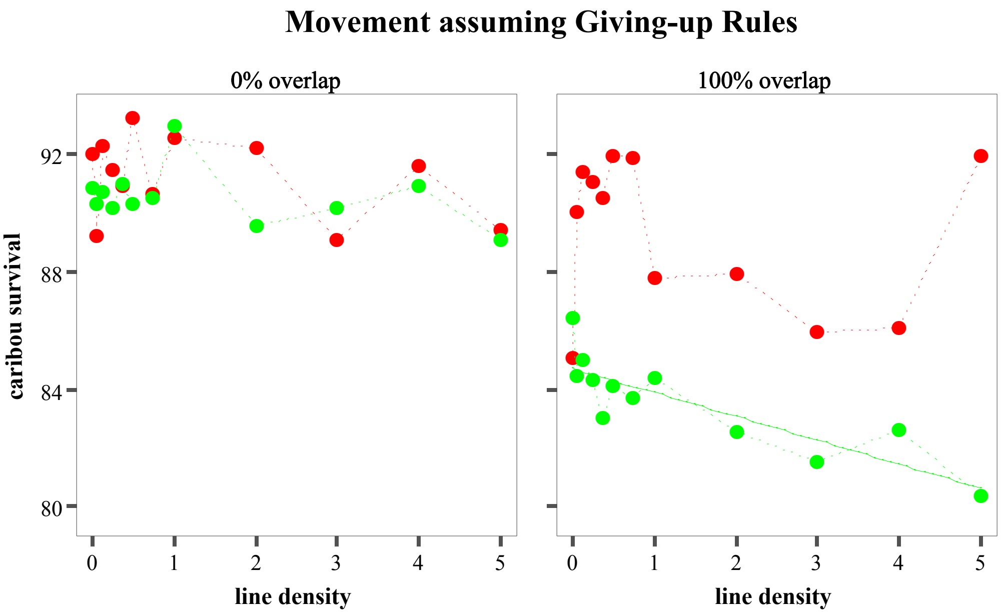
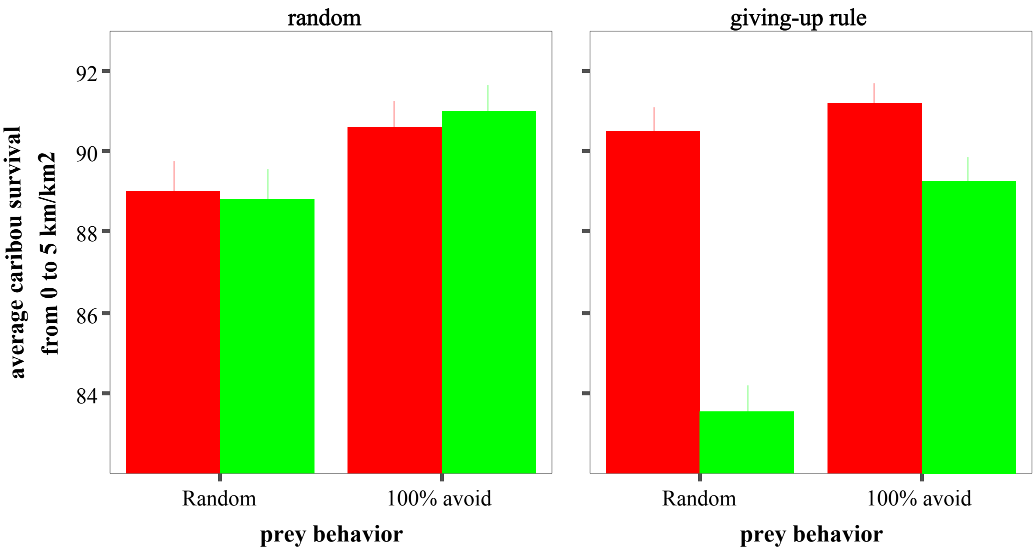


Figure 4.6. Average caribou survival from 0 to 5 km/km^2 as function of overlap (🟥 – 0% overlap, 🟩 – 100% overlap), prey behavior, and wolf movement strategies.



Chapter 5: The effect of predator numbers on woodland caribou survival

Introduction

The persistence of local woodland caribou (*Rangifer tarandus caribou*) herds often depends on the presence of alternative prey. Caribou share predators with other ungulates, leading to interactions that resemble resource competition (i.e., “apparent competition”, Holt 1977; 1984; Holt and Kotler 1987). In some instances, sharing predators may be beneficial if it diverts predation pressure away from caribou. This is more likely if other ungulates are more profitable in terms of size, abundance, and/or probability of encounter (e.g. Krebs and Davies 1993; also see Cumming *et al*. 1996 for an explicit example of this). In northeastern Alberta, for example, wolves (*Canis lupus*) primarily hunt moose (*Alces alces*), which are approximately three times larger and 6 to 13 times more abundant than caribou (~435 kg vs ~154 kg and 0.24-0.53 moose/km^2 vs 0.04 caribou/km^2; Fuller and Keith 1981; Hauge and Keith 1981; Edmonds 1988; Renecker and Hudson 1993; Smith 1993; Stuart-Smith *et al*. 1997; Schneider and Wasel 2000; James *et al*. 2004). Caribou are also spatially separated from moose, as they are predominantly found in peatlands whereas moose are upland-based (Bradshaw *et al*. 1995; Stuart-Smith *et al*. 1997; James *et al*. 2004). This is likely why wolves spend little time in caribou range and rarely incorporate caribou into their diet (James *et al*. 2004). Survival and recruitment rates are often higher for caribou herds that “space away” from other ungulates (Bergerud and Page 1987; Bergerud *et al*. 1990; Seip 1992; Cumming *et al*. 1996; Rettie and Messier 2000; Schaefer *et al*. 2001; McLoughlin *et al*. 2005), a finding that highlights the potential importance of spatial refuges for caribou (Cumming *et al*. 1996; Ferguson *et al*. 1988; Seip 1992; Schaefer *et al*. 2001).

However, the presence of alternative prey may also be detrimental to caribou. Since the mid-1880s, declines in caribou herd size and distribution have been observed throughout North America (Bergerud 1974; 1988; Bergerud and Elliott 1986; Edmonds 1991; Seip 1992; Mallory and Hillis 1998; Schaefer *et al*. 1999; Schaefer 2003; Lessard 2005; Wittmer *et al*. 2005*ab*). While the declines may be explained by a number of factors (i.e., habitat loss, disease, hunting, and climate change), they are often attributed to changes in wolf-moose interactions (e.g., Bergerud and Elliott 1986; Seip 1992; Rettie and Messier 1998; Schaefer *et al*. 1999; Lessard 2005; Wittmer *et al*. 2005*ab*). These changes are typically a function of human activity and/or management of carnivore and ungulate populations (Bergerud and Elliott 1986; Gunson 1992; Rettie and Messier 1998; Schaefer 2003; Wittmer 2005*b*). Timber harvest, for example, may lead to higher moose densities by increasing moose browse (e.g., Rempel *et al*. 1997). More moose should mean more wolves (Fuller 1989; Messier 1994; Joly and Messier 2000), and possibly increased predation pressure on caribou if wolves "spillover" into caribou range (e.g., Holt 1977; 1984).

Increasing predation pressure may also be responsible for the declines in Alberta's boreal caribou, which are now provincially threatened (McLoughlin *et al*. 2003; COSEWIC 2005). These declines have been well documented since the 1990s (McLoughlin *et al*. 2003), but were apparent as early as the 1970s (Stelfox and Stelfox 1993). Coinciding with these declines were changes in moose and wolf densities. Moose densities peaked in the mid 1960s/early 1970s following a period of wolf control from 1957 to 1966 (Gunson 1992; Stelfox and Stelfox 1993). However, in the late 1960s, wolf control switched to protection, leading to an increase in wolf densities (Gunson 1992).

This may have triggered the onset of the caribou declines if incidental wolf activity in peatlands increased. Although use of caribou is incidental (James 1999), wolves account for at least half of adult caribou mortality and are considered to be a main limiting factor (Stuart-Smith *et al*. 1997; also see Bergerud and Elliott 1986; 1998; Bergerud 1988; Rettie and Messier 1998; Schaeffer *et al*. 1999; Wittmer *et al*. 2005*a*). This means that even a small change in predation pressure may be detrimental to local herds (Bergerud 1988).

In northeastern Alberta, moose density is now 7 times lower than in the 1970s (Charest 2005). Low moose densities should eventually lead to lower wolf densities (which some anecdotal studies indicate is occurring; Gunson 1992; also see Fuller 1989; Messier 1994 for more general descriptions of wolf density:prey density relationships), and over time, reduced predation pressure on caribou. Yet, moose densities have been low and relatively stable since the 1980s (Charest 2005; Northern Moose Management program 1998), while caribou populations continue to decline. However, low moose densities may actually increase wolf predation on caribou if wolves are forced to search alternative patches for food (e.g., Holt and Kotler 1987; also see Rettie and Messier 1998 and Farnell *et al*. 1996; Hayes *et al*. 2000 for anecdotal evidence of this). Low moose densities can also affect pack cohesion above and beyond what would be expected given normal pack activities (i.e., extraterritorial forays and dispersal; Messier 1985*ab*; Peterson *et al*. 1984; Fuller 1989; Ballard *et al*. 1997). For example, Messier (1985*a*) found that forays by single or small groups of wolves were more likely to occur when moose were low in abundance (i.e., 0.23 moose/km^2, which is only 0.01 moose/km^2 less than average density in northeast Alberta). Individuals and pairs are capable of killing large prey like moose and caribou (Mech 1981; Thurber and Peterson 1993) and may "favor" peatlands because low overall wolf presence should reduce the likelihood of intraspecific strife (e.g., Mech 1994). Moreover, kill rates may still be high for small packs and individuals because of the amount of prey lost to scavengers (Thurber and Peterson 1993). As such, it is possible that the current declines in Alberta's northeastern caribou may be a consequence of low moose densities, which drive changes in pack dynamics and ultimately lead to more individual wolf forays into peatlands.

Moose-wolf-boreal caribou relationships are somewhat different in west-central Alberta and in fact, may reflect the more "traditional" effects of moose on wolf-caribou interactions. In general, moose are more abundant in the west and there is some speculation that they are increasing as a result of timber harvest (~0.53 moose/km^2 vs the provincial average of 0.24 moose/km^2; Schneider and Wasel 2000; Lessard 2005). This increase, presumably followed by increases in wolf numbers, may also explain why both mountain and boreal caribou are declining in this part of the province (Dzus 2001; Lessard 2005).

Changes in wolf numbers – however they may arise – may be furthered by anthropogenic disturbance. Linear features are a prevalent part of Alberta's forests and include seismic lines, roads, and pipelines (Schneider 2002). Wolves use these features as travel routes and in fact, travel three times faster on lines than they do in undisturbed forest (James 1999; James and Stuart-Smith 2000; also see Musiani *et al*. 1998). Seismic lines, which are the dominant line type in Alberta, vary from 1 to 8 m or more in width and can be as dense as 10 km/km^2 (Schneider 2002; Lee and Boutin 2006). Line use should increase wolf efficiency because a pack can search more area within a given amount of time, resulting in higher encounter and kill rates (Chapter 3). More lines should mean more efficiency, which implies that line use mimics the functional response between wolves and prey density (Chapter 3). Functional responses depict how kill rate (i.e., the number of prey killed per predator) changes with prey density and are typically described as linear (Type I), asymptotic (Type II), or sigmoidal or "s-shaped" (Type III) (Holling 1959; also see Messier 1994). This should mean increased wolf use of caribou such that caribou survival:line density curves decline linearly, asymptotically, or sigmoidally (i.e., are opposite of the kill rate:line density curves; also note that similar relationships are expected for moose; see Chapter 3).

As such, line use could explain why average adult female caribou survival declines 9% as line density increases from 0.7 to ~3.5 km/km^2 (r^2= 0.68; based on data in Dzus 2001; Dunford 2003; McLoughlin *et al*. 2003; Neufeld 2006). Female adult survival has high elasticity (Fancy *et al*. 1994; also see Gaillard *et al*. 1998; 2000), meaning that this relationship could also mean that wolf use of lines is also contributing to the overall herd declines. However, simulations suggest that wolf time on lines is too low to increase wolf use of caribou (i.e., 26%; Chapter 3; low line use is also evident in Whittington *et al*. 2005; Neufeld 2006). Prey also tend to avoid linear features (Intera Environmental Consultants 1973; Jalkotzy *et al*. 1997; James and Stuart-Smith 2000; Dyer *et al*. 2001), which models suggest minimizes (and if absolute, negates) the effects of line use (Chapters 3 and 4). Yet, if more individual wolves are using lines, then a combination of increased predator efficiency and more overall forays into caribou range could account for the declines in caribou survival. This should be true even if all prey avoid lines, as 25% line use still means that wolves spend most of their time hunting off line.

Moreover, models suggest that line use does increase wolf use of moose, even if most moose avoid lines (i.e., if 75% of the prey population avoids lines; Chapter 3). As such, it is reasonable to assume that line use also mimics the numeric response of wolves (e.g., Messier 1994). Numeric responses depict how predator density changes with prey density and are typically described as linear (Type I), asymptotic (Type II), and sigmoid or “s-shaped” (Type III) (Holling 1959; also see Messier 1994). More lines should mean more kills, more wolves, and a higher probability of wolf spillover into caribou range. If so, then line use could still drive the caribou declines, albeit indirectly. This implies that linear features, like forestry, can affect wolf-caribou interactions via wolf-moose interactions. It also suggests that herd-specific wolf densities could explain the negative correlation between caribou survival and line density. For example, the Little Smoky herd in west-central Alberta is at immediate risk of extinction (Dzus 2001; Alberta Caribou Committee, *unpublished results*). This status may reflect the combined effects of high moose densities and line use on wolf populations.

The main objectives of this study were to (1) determine how increasing the number of predators within a territory affected caribou survival, (2) determine if adding predators changed the nature of survival:line density relationships across different degrees of prey avoidance, (3) determine if line use mimicked the numeric response of wolves to prey density across different degrees of prey avoidance, and (4) determine if a combination of more predators and line use could account for the negative correlation between female adult survival and line density. Understanding the interactive effects of predator number and wolf use of lines is important for managing wolves, moose, and caribou in Alberta. Current mitigation strategies are largely line based and designed to reduce wolf use of lines (i.e., reclaiming lines and/or line blocking; Boreal Caribou Committee 2001; Golder Associates 2006; Neufeld 2006). Yet, a wolf-line-caribou relationship has yet to be empirically or theoretically established, which may ultimately mean that line mitigation has limited value. If the number of predators is key (as opposed to the number of lines or wolf use of lines), then managing predator and alternative prey numbers may be a more effective way of conserving caribou. As such, this study is important for guiding future empirical and management-based work.

Methods

Models were programmed as described in Chapter 2. Based on the results from Chapter 2 and 3, simulations were run assuming that (1) wolves moved randomly and (2) wolves moved nonrandomly used a 45 km^2 giving up rule. For each movement strategy, I ran simulations in which (a) prey were randomly distributed with respect to lines, (b) 50% of prey avoided lines, and (c) 100% of prey avoided lines. In simulations with linear features, the probability of line use was set at 25% (note: patterns based on higher levels of line use did not differ from those in Chapter 3; *unpublished results*). I assumed that there was no overlap between moose and caribou, namely because predictions at different degrees of overlap did not differ qualitatively from those in Chapter 4 once more predators were added to the territory (*unpublished results*). Simulation were run in a “northwest scenario” (i.e., 0.48 moose/km^2) and a “northeast scenario” (i.e., 0.24 moose/km^2) (based on Schneider and Wasel 2000).

Caribou survival

I determined how predator number affected caribou survival by reprogramming the 0 km/km^2 models such that there were 1, 2, 3, 4, 5, and 6 individual hunting units in the territory (i.e., the range of predators if a single pack was moving cohesively and if all pack members were hunting individually). Pack size was not changed to reflect differences in moose density because the empirical data indicates that average pack size is the same in both regions (i.e., six wolves; Fuller and Keith 1980; Bjorge and Gunson 1989). This suggests that while there are probably more wolves in high density areas, it is not reflected in pack size per se. Each additional hunting unit was added consecutively as preliminary simulations indicated that concurrent and consecutive runs in a 0 km/km^2 landscape yielded the same results (*unpublished results*).

I then determined if the number of predators changed the nature of the survival:line density relationships observed in Chapter 3 by reprogramming the lined territories to incorporate 1, 2, and 3 hunting units. Simulated results were then fitted to linear ($y = ax + b$), asymptotic ($y = ab/(b + x) + c$), and sigmoid ($y = ab^d/(b + x^d) + c$) decaying responses. In these equations, y = prey survival rate, x = line density, a = the amount survival declines from 0 km/km^2 to the line density at which survival asymptotes, b = the line density at half the minimal survival rate, c = the rate at which survival asymptotes (which, when added to a, gives the y-intercept), and d = the power function that shifts the curve from an asymptotic to a sigmoid response.

I also determined how the curves were affected by prey avoidance behaviors by running simulations in which prey were randomly distributed with respect to lines and in 50% and 100% of the prey population avoided lines. All of these avoidance behaviors were run across 1, 2, and 3 hunting units. In some of these simulations, prey survival increased with line density (e.g., if all prey avoided lines) and were best fit with linear ($y = ax + b$), asymptotic ($y = ax/(b + x) + c$), and sigmoid ($y = ax^d/(b + x^d) + c$) curves. In these equations, a = the asymptotic survival rate, b = the line density at half the maximal survival rate, and c = the y – intercept (which, when added to a, gives the actual asymptotic survival rate). Parameters a and b were used to identify key line densities at which a threshold existed and/or at which no more or little change in survival was expected.

Wolf functional and numeric responses to line density

The functional response between kills and line density in a 0.24 moose/km^2 territory were examined in Chapter 3. I also determined if the kill rate:line density curve in a 0.48 moose/km^2 territory mimicked the functional response between wolves and prey density by curve-fitting simulated results based on both wolf movement patterns and all three prey behaviors to linear, asymptotic, and sigmoid curves (e.g., Messier 1994). In these equations, y = the kill rate, x = line density, a = the asymptotic kill rate, b = the line density at half the maximal kill rate, c = the y – intercept (which, when added to a, gives the actual asymptotic kill rate). If kill rate:line density relationships switched during these simulations (e.g., from an increase to a decrease in kills as prey avoidance increased), I used the appropriate but opposite function (e.g., a decaying vs a positive linear function).

To determine if wolf use of lines mimicked the numeric response between wolves and moose density, simulations were first run across moose densities ranging from 0.02/km^2 to 3/km^2. This was done for both movement strategies and across all three prey behaviors. This moose density range reflects the variability observed across northern Alberta (i.e., 0.02 to 2.67 moose/km^2; Schneider and Wasel 2000). Increases in kills relative to line density were then compared to the equivalent rate of increase based on moose density. This comparison was done by estimating moose densities from kills and fitting the subsequent curve to an exponential equation (i.e., “reversing” the kill rate:moose density curve such that moose density = $a + b^{(\text{-kills}/c)}$). This equation was then used to “back-calculate” moose density based on the kill rate:line density relationships in the 0.24 and 0.48 moose/km^2 territories.

Estimated moose densities were then applied to Fuller’s (1989) equation, which describes wolf density as a function of ungulate biomass (i.e., wolves/1000 km^2 = 3.4 + 3.7*(ungulate biomass index/km^2), $r^2 = 0.72$; note that un updated equation in Mech and Boitani 2003 did not alter the key results). For example, given the ungulate densities in northeastern Alberta, wolf density in Fuller and Keith (1980) should be 0.008 wolves/km^2 (Fuller and Keith 1981; Hauge and Keith 1981; Fuller 1989). This is close to the actual 0.006 to 0.007 wolf/km^2 reported in the study (Fuller and Keith 1980). To determine the type of wolf density:line density relationship, I also curve-fit results to linear, asymptotic, and sigmoid “numeric” curves (e.g., Messier 1994). In these equations, y = wolf density, x = line density, *a* = the asymptotic wolf density, *b* = the line density at half the maximal wolf density rate, *c* = the y – intercept (which, when added to *a*, gives the actual asymptotic wolf density rate). If wolf density:line density relationships switched during these simulations (e.g., from an increase to a decrease in wolves as prey avoidance increased), I used the appropriate but opposite function (e.g., a decaying vs a positive linear function).

All curves were fitted using Table 2D Curve (Version 5.01). Best fit curves were selected using an *F*-test, in which alpha = 0.05 (Zar 1996). R-squared was adjusted based on the number of degrees of freedom (Zar 1996). One issue with the asymptotic and sigmoid functions used in this study is that they take a long time to asymptote. As such, I determined the line density at which 90% of any kill, wolf density, or caribou survival asymptote had been reached. The overall effect of the number of hunting units was summarized by averaging the change in kills, wolf density, and caribou survival from 0 to 5 km/km^2 across different moose densities, wolf movement patterns, and prey avoidance behaviors.

Comparisons to the empirical data

Model results describing the relationship between caribou survival and linear feature density assuming 1, 2, or 3 hunting units were compared to an empirical data set that describes caribou survival as a function of line density (based on data in Dzus 2001; Dunford 2003; McLoughlin *et al*. 2003; Neufeld 2006). More generally, results were placed in a population context by determining how changes in caribou survival affected the finite rate of increase in an "average herd" and two previously stable herds (i.e., the CLAWR and WSAR herds, though more recent data than McLoughlin *et al*. 2003 suggests these herds are now also declining; Alberta Caribou Committee, *unpublished results*) (see Methods and Table 3.9. in Chapter 3 for how λ was calculated).

Results

The effect of predator number

Caribou survival declined an average of 8 to 10% for each additional hunting unit in the territory. Overall, survival declined a total of 42 to 49% as the number of predators in the territory increased from 1 to 6 (Figure 5.1.; note that the variance reflects the effects of moose density and wolf movement patterns). For any given number of predators, survival was an average of 3 to 4% lower in the 0.24 moose/km^2 territory when compared to the 0.48 moose/km^2 territory. Moreover, overall declines were 5% larger if wolves moved randomly in a 0.24 moose/km^2 territory than if they used giving up rules. This difference was not evident in a 0.48 moose/km^2 territory.

Based on Hatter and Bergerud's (1991) equation and assuming that calf recruitment is stable, an extra predator would yield λ values of 0.94 to 0.96 for the CLAWR and an average herd and λ values of 1.02 to 1.05 for the WSAR herd. Two extra predators would yield λ values of 0.82 to 0.87 for the CLAWR and an average herd and λ values of 0.89 to 0.95 for the WSAR herd.

The effect of predator number on line density relationships

The effect of predator number on caribou survival:line density relationships depended on how wolves moved. If movement was random, then there was usually no relationship between survival and line density despite a doubling and tripling of the number of predators in the territory (Table 5.1.). This was true for both moose densities (Figure 5.2.). The only exception to this was a shift to a positive linear response when the number of predators hunting in a 0.48 km/km^2 territory tripled. Under these parameter settings, survival increased 10% as line density increased to 5 km/km^2.

However, if wolves used giving-up rules, there was a shift from no relationship to a decline in survival as the number of predators in the territory doubled (Table 5.2.). This was true for both moose densities and indicates that caribou survival will decline with line density if there are two or more predators in the territory (albeit to a minimum of 0%) (Figure 5.3.). Declines were greater in territories with fewer moose (i.e., a 9 to 10% decline as line density increased to 5 km/km^2 in a 0.24 moose/km^2 territory vs a 5 to 6% decline as line density increased to 5 km/km^2 in a 0.48 moose/km^2 territory).

The effect of predator number in a 0 km/km^2 territory was also evident when caribou survival was averaged across all territories. Average survival was 9-13% less if the number of predators in a territory doubled and 17-23% less if the number predators in a territory tripled (Figure 5.4.). For any given line density, survival was always lower if moose density was 0.24 moose/km^2 (i.e., an average of 3% lower if wolves moved randomly and an average of 5% lower if wolves used giving up rules). Differences in survival related to wolf movement were in the range of 1 to 2% for both moose densities.

The effect of prey avoidance

If wolves moved randomly, prey avoidance of lines always improved survival rates. For example, if one or more predators hunted in a 0.24 moose/km^2 territory or 1 to 2 predators hunted in a 0.48 moose/km^2 territory, survival:line density curves shifted from no relationships to linear or asymptotic curves (Figure 5.5.). If three predators hunted in a 0.48 km/km^2 territory, the survival:line density curve was still best described by a linear curve, but survival increased more with line density (e.g., a 10% vs a 17% increase reflecting random and 100% avoid prey results, respectively). Overall, survival increased 6 to 17% as line density increased in a 0.24 moose/km^2 territory and 8 to 15%

as line density increased in a 0.48 moose/km^2 territory (variance reflects the different number of predators; changes in survival were greater in territories with more predators).

However, avoidance had a more variable effect on line density relationships if wolves used giving up rules. There were no survival:line density relationships in territories with a single predator regardless of prey behavior. However, if two or more predators hunted in a territory, survival:line density curves shifted from decaying linear curves to no relationships as the degree of prey avoidance in the population increased (Figure 5.6.). This implies that avoidance negated the interactive effect of predator number and line use on caribou survival.

Yet, despite avoidance, average survival from 0 to 5 km/km^2 was still 7 to 11% lower if the number of predators in the territory doubled and 14 to 19% lower if the number of predators in the territory tripled. These trends were consistent across both wolf movement patterns (Figures 5.7. and 5.8.). To put it in a different context, if the number of predators in the territory was 2 or more, avoidance only improved survival by 2 to 4% relative to random prey distributions. Moreover, at any given line density, survival was always lower in the low moose density territories (i.e., an average of 2% lower if wolves moved randomly and an average of 4% lower if wolves used giving up rules). However, differences in survival related to wolf movement were less than 1% for both moose densities.

The effect of moose density on wolf kills and caribou survival

The kill rate:moose density curves were best described as asymptotic if wolves moved randomly ($y = 182.33*x/(1.67 + x) + 3.06$, $r^2 = 0.99$, $p<0.001$) and if they used giving up rules ($y = 200.37*x/(1.45 + x) + 0.95$, $r^2 = 0.99$, $p<0.001$) (Figure 5.9.). There was a 22 fold increase in kills as moose density increased from 0.02 to 3/km^2 if wolves moved randomly and a 24 fold increase in kills if wolves used giving up rules. The caribou survival:moose density curves were also best described as asymptotic. Survival increased asymptotically with moose density if wolves moved randomly ($y = 13.24*x/(0.79 + x) + 84.29$, $r^2 = 0.79$, $p<0.001$) and if they used giving up rules ($y = 15.78*x/(0.33 + x) + 83.70$, $r^2 = 0.93$, $p<0.001$). Regardless of wolf movement, there was a 1.1 fold increase in survival as moose density increased from 0.02 to 3/km^2.

The functional response of wolves to line density (assuming a cohesive pack)

Similar to kill rate:line density relationships at 0.24 moose/km^2 (see Chapter 3), kill rate was best described by an asymptotic curve if all prey were randomly distributed in a 0.48 moose/km^2 territory (i.e., Table 5.3.; Figure 5.10.). Seventy percent or more of the increase in kills occurred by 1 km/km^2, again suggesting low line density effects (see Chapters 3 and 4). Overall, there was a 1.6 fold increase in kills as line density increased from 0 to 5 km/km^2 if the pack moved randomly and a 1.3 fold increase if the pack used giving up rules. This was similar to the 1.3 to 1.7 fold increase in kills in a 0.24 moose/km^2 territory (variance reflects rule-based vs random movement respectively).

However, prey avoidance behaviors shifted the asymptotic curves to decaying linear curves. For example, if all prey avoided lines, there was a 1.01 to 1.2 fold decrease in kills as line density increased (variance reflects random wolf movement vs movement using giving up rules, respectively). This is also similar to the 1.1 fold decrease in kills in the 0.24 moose/km^2 territory (note that this decrease reflects both movement strategies and 100% prey avoidance). However, while the change relative to 0 km/km^2 was also similar across moose densities, kills in general were 1.7 fold higher in the 0.48 moose/km^2 territory (i.e., across all prey behaviors and both wolf movement patterns; Figure 5.11.).

The numeric response of wolves to line density

The moose density:kill rate relationship fit a exponential curve if wolves moved randomly ($y = -0.31 + 0.34^{(-x/-52.91)}$, $r^2 = 0.99$, $p<0.001$) and if they used giving up rules ($y = -0.23 + 0.28^{(-x/-55.33),}$ $r^2 = 0.99$, $p<0.001$). Based on these relationships (see Table 5.4. for the back calculations), the wolf density:line density curves were best described as linear or asymptotic if all prey were randomly distributed with respect to lines (Table 5.5.). If the relationships were asymptotic, more than 62% of the change in wolf density occurred by 1 km/km^2. However, increases were greater in the 0.48 moose/km^2 territory and if wolf movement was random. As line density increased in a 0.24 moose/km^2 territory, wolf numbers increased by 1 if wolves used giving up rules and by 3 if the pack moved randomly. As line density increased in a 0.48 moose/km^2 territory, wolf numbers increased by 3 if wolves used giving up rules and by 7 if the pack moved randomly (Figure 5.12.).

Prey avoidance minimized the amount of increase in wolf numbers and in some instances, led to a decline in wolf numbers as line density increased. If all prey avoided lines, the wolf density:line density relationships were best described by decaying linear curves. Declines were 1 wolf or less for all moose density and wolf movement pattern combinations. Yet, wolf numbers still showed an increase – albeit small – with line density even if 50% of prey avoided lines. Under this prey behavior, wolf number:line density curves were best described as linear or asymptotic. Again, increases were greater if wolves hunted in a 0.48 moose/km^2 territory. As line density increased, wolf numbers only increased by 1 or less wolf in a 0.24 moose/km^2 territory, but by 2 to 4 wolves in a 0.48 moose/km^2 territory.

Comparisons to the empirical data

The empirical data suggest that average caribou survival declines 9% as line density increases from 0.7 to ~3.5 km/km^2 (based on data in Dzus 2001; Dunford 2003; McLoughlin *et al*. 2003; Neufeld 2006). Model results suggest this is unlikely if wolf movement is random (this was true across all moose densities, predator numbers, and prey behaviors) (Table 5.6.). However, declines in survival were evident if wolves used giving up rules and most prey were randomly distributed with respect to lines. In particular, survival declined 1 to 5% in if the number of predators was 2 or more and 50% or more prey were randomly distributed with respect to lines. This would lead to stability or increases in the WSAR and "average herd" and a slow decline in the CLAWR herd (i.e., $\lambda = 0.99$) (see Table 2, Chapter 3). A 7% decline was also evident if 100% of prey avoided lines in a 0.24 moose/km^2 territory, but the curve fitting results suggested that there was no relationship between survival and line density under these parameter conditions.

Discussion

In a wolf territory with no lines, caribou survival declined as the number of predators within the territory increased. In fact, the addition of each additional predator caused, on average, an 8 to 10% decline in survival rate (variance reflects different moose densities and wolf movement patterns). An 8 to 10% decline in survival was enough to cause declines in the CLAWR and "average herd", suggesting that even a small change in predation pressure can have substantial implications for caribou in Alberta. More predators mean a greater probability of incidental forays into caribou range and thus more wolf-caribou interactions. While declines in adult survival may be balanced out by calf recruitment (which is also an important population parameter; Gaillard *et al*. 1998; 2000), calculations of λ suggest that even herds with the highest cow:calf ratios declined if the number of predators in the territory tripled (e.g., the WSAR herd). These findings agree with a number of studies suggesting that caribou declines are often precipitated by increases in predation pressure (e.g., Bergerud and Elliott 1986; Seip 1992; Rettie and Messier 1998; Schaefer *et al*. 1999; Weclaw and Hudson 2004; Lessard 2005; Wittmer *et al*. 2005*ab*).

Increasing the number of predators also affected caribou survival:line density relationships, but only if wolves used giving up rules. While no relationship between survival and line density existed if a single predator hunted in a territory, survival declined 5 or 10% as line density increased to 5 km/km^2 in a territory with 2 or 3 predators (variance reflects moose densities and the number of predators). This suggests that number of predators can change the nature of wolf-line-prey relationships in Alberta. This finding is similar to that of Chapter 4, in which overlap between moose and caribou also affected basic line density relationships. Moreover, like the effects of overlap, this result depended on how wolves hunted. If movement was random, there was no negative effect of line density on caribou survival despite changes in the number of predators. However, the more general effects of predator number persisted in lined territories regardless of the way wolves moved. In particular, average survival from 0 to 5 km/km^2 declined 9 to 13% if number of predators in the territory doubled and 17 to 23% if the number of predators in the territory tripled (variance reflects different moose densities and wolf movement patterns).

However, these results do not account for the fact that caribou are usually 250 m or more from lines (James and Stuart-Smith 2000; Dyer *et al*. 2001; also see Nellemann and Cameron 1996; 1998; Nellemann *et al*. 2001; Vistnes and Nellemann 2001; Cameron *et al*. 2005). Line avoidance negated the decaying relationships driven by higher predator numbers, which is similar to its effects on the degree of line use and overlap (see Chapters 3 and 4). Moreover, comparisons to the empirical data suggest that even if prey were randomly distributed, declines from 0 to 3 km/km^2 were not large enough to cause herd declines (i.e., 5% or less, leading to stable or increasing herds). This suggests that the 9% decline in survival from 0.4 to 2.8 km/km^2 is not driven by more predators using linear features as travel routes.

Yet, avoidance did not negate the overall effects of predator numbers in lined territories. Even if all prey avoided lines, average survival was still 7 to 11% lower if the number of predators in the territory doubled and 14 to 19% lower if the number of predators in the territory tripled. These results imply that the declines could be a function of the number of predators within individual caribou ranges. What is driving this increase is less clear (if it does exist), although it may in part be a function of how moose density affects wolf distributions and pack dynamics. Model results suggest that pre-1980s declines in moose density may have precipitated the original caribou declines in northeastern Alberta. In general, caribou survival decreased as moose density decreased, although presumably this is only a short-term effect until wolf densities adjust to lower prey densities (e.g., Fuller 1989). Yet, caribou are still declining in northeastern Alberta despite stable but low moose densities since the 1980s (Charest 2005). However, current moose density may be low enough to alter pack dynamics such that there are more pairs or individual wolves hunting on their own and/or wolves are hunting more often in peatlands because of low upland resources (e.g., Holt 1977; Messier 1985*b*; Holt and Kotler 1987; Farnell *et al*. 1996; Rettie and Messier 1998). Either scenario will mean more predation pressure on caribou even though wolf density per se may have not changed.

Simulations suggest that an actual increase in the number of predators may stem from wolf use of linear features. Kill rate:line density relationships mimicked the functional response between wolves and prey density even if more than half of the prey population avoided lines (Chapter 3). Line use also mimicked the numeric response between wolves and prey density. As line density increased to 5 km/km^2, predator density increased by 1 to 3 wolves in a 0.24 moose/km^2 territory and by 3 to 7 wolves in a 0.48 moose/km^2 territory. This increase reflects use of moose (Chapter 3). The numeric effects of line use were negated if all prey avoided lines, but it is unlikely that prey behavior is this static (e.g., James and Stuart-Smith 2000; Dyer *et al*. 2001; Oberg 2001). In fact, moose may use lines as travel routes and as a source of regenerating vegetation (e.g., Rempel *et al*. 1997; also see Jalkotzy *et al*. 1997; James and Stuart-Smith 2000; Dyer *et al*. 2001; Oberg 2001). As such, it is possible that line use is "artificially" increasing the number of wolves in Alberta. Moreover, this increase is likely to be higher in west-central Alberta, where timber harvest may be promoting higher moose, and consequently, higher wolf densities. This may explain why the most serious declines are occurring in this part of the province (e.g., McLoughlin *et al*. 2003;

Lessard 2005; Alberta Caribou Committee, *unpublished results*) and suggests an interactive effect of forestry and line use on wolf-moose-caribou dynamics.

The number of predators is clearly important to wolf-caribou interactions in Alberta. It is the only factor examined in this thesis that persisted despite changes in line density, prey behavior, and wolf movement patterns. Additional simulations also suggest that the effect of wolf number is enhanced by increasing overlap between moose and caribou (i.e., similar to the effects observed in Chapter 4; *unpublished results*) and if wolf use of lines increases (i.e., similar to the effects observed in Chapter 3; *unpublished results*). Of course, changes in predation pressure may also reflect the presence of other predator species. For example, while the calving period is usually associated with more predators (Bergerud and Elliot 1986; Bergerud 1988; Mahoney *et al*. 1990; Stephenson *et al*. 1991; Ballard 1994; D. Latham, *unpublished results*), recent surveys in Alberta suggest that coyotes (*Canis latrans*) are also active in peatlands throughout winter (D. Latham, *unpublished results*). This may be a recent trend as coyotes were not considered important in earlier caribou work (James and Stuart-Smith 2000; James *et al*. 2004). There are empirical records of coyotes killing adult caribou (e.g., Stuart-Smith *et al*. 1997), although it is not clear what proportion of caribou they remove from the population. Future empirical work should continue assessing general predator use of peatlands as well as include more detailed investigations of which predators have the largest impact on caribou demography.

Still, it is possible that increased kill rates won't impact wolf numbers. More time spent handling moose will mean less time hunting other prey (e.g., Holt and Kotler 1987), which could mean that line use has a compensatory rather than an additive effect on kill rates. Moreover, satiation effects may mean that the actual effect of line use on wolf kills is much lower than its potential effects. Wolf kills do increase with moose density, but after ~0.5 moose/km^2 this effect reaches a plateau (Messier 1994; also see Hayes and Harestad 2000, which suggests a much lower satiation rate at ~0.20 moose/km^2). This may mean that line use will have a greater effect on wolf kills in low density moose areas, meaning that increased predation pressure in west-central Alberta may be unrelated to linear features (i.e., it could solely be a function of forestry practices). Furthermore, social and territorial behavior may limit wolf numbers if new packs and/or individuals are prohibited from establishing (e.g., Mech 1981). All of these factors stress the need for a better understanding of wolf ecology in northern Alberta and how it is affected by linear features.

Yet, even if line use is not increasing wolf numbers, simulations still suggest that the number of predators has a stronger and more consistent effect on caribou survival than line use and line density. This strongly suggests that predator numbers in and around caribou range should be the immediate focus of empirical work in Alberta. It is also important to investigate pack dynamics, as this will help determine if any change in predator number is real or reflects pack “break-up”. Wolf populations are so poorly studied that this information is largely unknown despite its obvious importance to caribou persistence. If models do resemble the real wolf-prey system in Alberta, then wolf density should increase with line density. These predictions can be tested by experimentally reducing or increasing linear features and determining if these lead to fewer or more wolves. Reduction in line density can be done via line reclamation or through line blocking (e.g., Boreal Caribou Committee 2001; Golder Associates 2006;

Neufeld 2006; ACC, *unpublished results*), although initial study suggests this needs to be comprehensive to be effective (*unpublished results*). Even if the caribou declines are independent of a wolf-line-alternative prey interaction, declines in caribou survival should be correlated with increasing predator density in peatlands. This can be tested by removing predators from caribou range and determining if caribou survival improves as a result. If it doesn't, it strongly suggests that factors other than wolf predation are causing the caribou declines.

Ultimately, these results suggest that wolf management may be necessary to ensure caribou persistence in Alberta. In fact, wolf control is now a mitigation strategy used in at least one caribou range (Golder Associates 2006). While this may be done via management of moose numbers (e.g., Fuller 1989; Lessard 2005), some of the caribou declines are large enough to warrant the direct control of wolves (e.g., the Little Smoky Herd in west-central Alberta). Wolf management is also more feasible and likely to be more successful than current line mitigation techniques (Boreal Caribou Committee 2001; Golder Associates 2006; Neufeld 2006). For example, more than 60% of the asymptotes for the asymptotic numeric curves were reached by 1 km/km^2. This "low line density" effect is consistent with previous simulation results and other theoretical work (Chapters 3 and 4; Weclaw and Hudson 2004) and suggests that any change related to lines will occur early. This suggests that even if managers set a line density target below which wolf numbers do not increase, it will be too low to either reclaim or maintain given current and expected levels of development (e.g., Schneider 2000). This implies that the current line mitigation strategies will have no or little effect on caribou and thus will have little conservation value.

However, while ungulate populations usually increase during periods of wolf control, it isn't always clear that the increases are a result of reduced predator populations or something else entirely (Bergerud and Elliott 1986; 1998; Gasaway *et al*. 1992; Boertje *et al*. 1996; Hayes *et al*. 2003). Moreover, wolf control is a contentious issue, in part because it can upset the existing balance between wolves and their prey (as may have occurred previously in Alberta and may ultimately been the initial cause of both ungulate declines) (also see Bergerud and Elliott 1986; Gasaway *et al*. 1983; 1992; Gunson 1992; Gunson *et al*. 1993). Wolves also recover quickly from control measures (Boertje *et al*. 1996; Bergerud and Elliott 1998), which means that control must be continuous to be effective (at least until alternative strategies are put in place). Still, wolf control is likely to have at least short-term benefits for caribou survival, which may allow enough time for managers and researchers to more clearly establish the ultimate reasons behind the caribou declines in Alberta.

References

Ballard, W. B. 1994. Effects of black bear predation on caribou: a review. Alces 30:25-35.

Ballard, W.B., Ayres, L., Krausman, P.R., Reed, D.J., and Fancy, S.G. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. Wildlife Monographs 135: 1-47.

Bayne, E., Boutin, S., and Moses, R. 2004. Are boreal forest mammals good indicators of cumulative effects? Sustainable Forest Management Network, Edmonton, Alberta, Canada. 43 pp.

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

Bergerud, A.T. 1985. Antipredator strategies of caribou: dispersion along shorelines. Canadian Journal of Zoology 63: 1324-1329.

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

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

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

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

Bergerud, A.T., Ferguson, R., and Butler, H.E. 1990. Spring migration and dispersion of woodland caribou at calving. Animal Behavior 39: 360-368.

Bergman, E.J., Garrott, R.A., Creel, S., Borkowski, J.J., Jaffe, R., and Watson, E.G.R. 2006. Assessment of prey vulnerability through analysis of wolf movements and kill sites. Ecological Applications 16: 273-284.

Bjorge, R.R., and Gunson, J.R. 1989. Wolf, *Canis lupus*, population characteristics and prey relationships near Simonette River, Alberta. Canadian Field Naturalist 103: 327-334.

Boertje, R.D., Valkenburg, P., and McNay, M.E. 1996. Increases in moose, caribou, and wolves following wolf control in Alaska. Journal of Wildlife Management 60: 474-489.

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

Cameron, R.D., Smith, W.T., White, R.G., and Griffith, B. 2005. Central Arctic caribou and petroleum development: distributional, nutritional, and reproductive implications. Arctic 58: 1-9.

Charest, K. 2005. Changes in moose and white-tailed deer abundance in northeastern Alberta and the relationship to cumulative impacts. MSc Thesis, University of Alberta, Edmonton, AB.

Committee on the Status of Endangered Wildlife in Canada. 2005. Status of Woodland caribou (*Rangifer tarandus caribou*). Retrieved on Nov. 30th, 2005 at http://www.cosewic.gc.ca/eng/sct1/searchdetail_e.cfm.

Cumming, H.G., Beange, D.B., and Lavoie, G. 1996. Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared predation risk. Rangifer Special Issue 9: 81-94.

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

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

Dzus, E. 2001. Status of the Woodland Caribou (*Rangifer tarandus caribou*) in Alberta. Alberta Environment, Fisheries and Wildlife Management Division, and Alberta Conservation Association, Wildlife Status Report No. 30, Edmonton, AB. 47 pp.

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. 1991. Status of woodland caribou in western Canada. Rangifer SI 7: 91-107.

Fancy, S.G., Whitten, K.R., and Russell, D.E. 1994. Demography of the Porcupine caribou herd, 1983-1992. Canadian Journal of Zoology 72: 840-846.

Farnell, R., Barichello, N., Egli, K., and Kuzyk, G. 1996. Population ecology of two woodland caribou herds in southern Yukon. Rangifer Special Issue 9:63-72.

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

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

Fuller, T.K., and Keith, L.B. 1981. Woodland caribou population dynamics in northeastern Alberta. Journal of Wildlife Management 45: 197-213.

Gaillard, J.M., Festa-Bianchet, M., and Yoccoz, N.G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13: 58-63.

Gaillard, J.M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., and Toigo, C. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31: 367-393.

Gasaway, W.C., Boertje, R.D., Grangaard, D.V., Kelleyhouse, D.G., Stephenson, R.O., and Larsen, D.G. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs 120: 1-59.

Gasaway, W.C., Stephenson, R.O., Davis, J.L., Sheperd, P.E.K., and Burris, O.E. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs 84: 1-50.

Golder Associates. 2006. Woodland Caribou Research and Information Gap Identification. Prepared for the Alberta Caribou Committee, 19 pp.

Gunson, J.R. 1992. Historical and present management of wolves in Alberta. Wildlife Society Bulletin 20: 3003-339.

Gunson, J.R., Jalkotzy, M., Carbyn, L.N., and Roy, L.D. 1993. Predation. In Hoofed Mammals of Alberta. Edited by J.B. Stelfox. Lone Pine Publishing, Edmonton, Alberta. pp. 69-80.

Hatter, I.W., and Bergerud, W.A. 1991. Moose recruitment, adult mortality, and rate of change. Alces 27: 65-73.

Hauge, T.M., and Keith, L.B. 1981. Dynamics of moose populations in northeastern Alberta. Journal of Wildlife Management 45: 573-597.

Hayes, R.D., and Harestad, A.S. 2000. Wolf functional response and regulation of moose in the Yukon. Canadian Journal of Zoology 78: 60-66.

Hayes, R.D., Farnell, R., Ward, R.M.P, Carey, J., Dehn, M., Kuzyk, G.W., Baer, A.M., Gardner, C.L., and O'Donoghue, M. 2003. Experimental reduction of wolves in the Yukon: ungulate responses and management implications. Wildlife Monographs 152: 1-35.

Holling, C.S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Canadian Entomologist 91: 293-320.

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

Holt, R.D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. American Naturalist 124: 377-406.

Holt, R.D., and Kotler, B.P. 1987. Short-term apparent competition. American Naturalist 130: 412-430.

Intera Environmental Consultants. 1973. Whitecourt Environmental Study - 1973. Intera Environmental Consultants Ltd, Calgary, Alberta, .

Jalkotzy, M.G., Ross, P.I., and Nasserden, M.D. 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.

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

James, A.R.C., Boutin, S., Hebert, D.M., and Rippin, A.B. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. Journal of Wildlife Management 68: 799-809.

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

Joly, D.O., and Messier, F. 2000. A numerical response of wolves to bison abundance in Wood Buffalo National Park, Canada. Canadian Journal of Zoology 78: 1101-1104.

Krebs, J.R., and Davies, N.B. 1993. An introduction to behavioural ecology, 3rd Edition. Blackwell Science, Massachusetts, USA, 420 pp.

Lee, P. and Boutin, S. 2006. Persistence and developmental transition of wide seismic lines in the western Boreal Plains of Canada. Journal of Environmental Management 78: 240-250.

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

Mahoney, S. P., H. Abbott, L. H. Russell, and R. Porter. 1990. Woodland Caribou calf mortality in insular Newfoundland. International Union of Game Biology 19:592-599.

Mallory, F.F., and Hillis, T.L. 1998. Demographic characteristics of circumpolar caribou populations, ecotypes, ecological constraints, releases, and population dynamics. Rangifer 10: 49-60.

McLoughlin, P.D., Dunford, J.S., Boutin, S. 2005. Relating predation mortality to broad-scale habitat selection. Journal of Animal Ecology 74: 701-707.

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

Mech, L.D. 1981. The wolf: the ecology and behavior of an endangered species. University of Minnesota Press, Minneapolis, 384 pp.

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

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

Messier, F. 1985*b*. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. Canadian Journal of Zoology 63: 239-244.

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology 75: 478-488.

Nellemann, C., and Cameron, R.D. 1996. Effects of petroleum development on terrain preferences of calving caribou. Arctic 49: 23-28.

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

Nellemann, C., and Cameron, R.D. 1998. Cumulative impacts of an evolving oil-field complex on the distribution of calving caribou. Canadian Journal of Zoology 76: 1425-1430.

Nellemann, C., Vistnes, I., Jordhoy, P., and Strand, O. 2001. Winter distribution of wild reindeer in relation to power lines, roads, and resorts. Biological Conservation 101: 351-360.

Neufeld, L. 2006. Spatial dynamics of wolves and woodland caribou in an industrial forest landscape in west-central Alberta. MSc Thesis, University of Alberta, Edmonton, AB.

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

Peterson, R.O., Woolington, J.D., and Bailey, T.N. 1984. Wolves of the Kenai Peninsula, Alaska. Wildlife Monographs 88: 1-52.

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

Renecker, L.A., and Hudson, R.J. 1993. Morphology, bioenergetics and resource use: patterns and processes. In Hoofed Mammals of Alberta. Edited by J.B. Stelfox. Lone Pine Publishing, Edmonton, Alberta. pp. 141-163.

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

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

Schaefer, J.A. 2003. Long-term range recession and the persistence of caribou in the taiga. Conservation Biology 17: 1435-1439.

Schaefer, J.A., Veitch, A.M., Harrington, F.H., Kent Brown, W., Theberg, J.B., and Luttich, S.N. 1999. Demography of decline of the Red Wine Mountains caribou herd. Journal of Wildlife Management 63: 580-587.

Schaefer, J.A., Veitch, A.M., Harrington, F.H., Kent Brown, W., Theberg, J.B., and Luttich, S.N. 2001. Fuzzy structure and spatial dynamics of a declining woodland caribou population. Oecologia 126: 507-514.

Schneider, R.S. 2002. Alternative futures: Alberta's boreal forest and the crossroads. Federation of Alberta Naturalists, Edmonton, Alberta, 152 pp.

Schneider, R.S., and Wasel, S. 2000. The effect of human settlement on the density of moose in northern Alberta. Journal of Wildlife Management 64: 513-520.

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.

Smith, H.C. 1993. Alberta Mammals: an atlas and guide. Provincial Museum of Alberta, Edmonton, Alberta, 250 pp.

Stelfox, J.B., and Stelfox, J.G. 1993. Population dynamics and reproduction. In Hoofed Mammals of Alberta. Edited by J.B. Stelfox. Lone Pine Publishing, Edmonton, Alberta. pp. 141-163.

Stephenson, R. O., D. V. Grangaard, and J.Burch. 1991. Lynx, *Felis lynx*, predation on Red Foxes, *Vulpes vulpes*, caribou, *Rangifer tarandus*, and Dall sheep, *Ovis dalli*, in Alaska. Canadian Field Naturalist 105: 255-262.

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

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

Vistnes, I., and Nellemann, C. 2001. Avoidance of cabins, roads, and power lines by reindeer during calving. Journal of Wildlife Management 65: 915-925.

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

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

Wittmer, H.U., McLellan, B.N., Seip, D.R., Young, J.A., Kinley, T.A., Watts, G.S., and Hamilton, D. 2005*a*. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. Canadian Journal of Zoology 83: 407-418.

Wittmer, H.U., Sinclair, A.R.E., and McLellan, B.N. 2005*b*. The role of predation in the decline and extirpation of woodland caribou. Oecologia 144: 257-267.

Zar, J.H. 1996. Biostatistical Analysis. 3rd Edition. Prentice-Hall, Inc., New Jersey, 662 pp.

Table 5.1. The effect of "predator" number, moose density, and prey behavior on the caribou survival:line density relationship. Results are based on random wolf movement.

Wolf Movement	1		2		3	
	random	avoid	random	avoid	random	avoid
0.24 moose/km^2						
best fit curve	none	linear	none	asymptotic	none	asymptotic
type of curve	none	increasing[1]	none	increasing[2]	none	increasing[3]
$b_{caribou}$	--	--	--	1.51	--	2.32
asymptotic survival rate	--	--	--	94.14	--	94.06
r^2	--	0.66	--	0.76	--	0.80
0.48 moose/km^2						
best fit curve	none	linear	none	linear	linear	linear
type of curve	none	increasing[4]	none	increasing[5]	increasing[6]	increasing[7]
$b_{caribou}$	--	--	--	--	--	--
asymptotic survival rate	--	--	--	--	--	--
r^2	--	0.71	--	0.75	0.29	0.79

[1] $y = 1.41x + 88.60$; [2] $y = 17.62x/(1.51 + x) + 76.52$; [3] $y = 26.88x/(2.32 + x) + 67.18$; [4] $y = 1.42x + 89.75$; [5] $y = 2.28x + 81.34$; [6] $y = 1.10x + 71.42$: [7] $y = 3.09x + 73.4$;

Table 5.2. The effect of “predator” number, moose density, and prey behavior on the caribou survival:line density relationship. Results are based on movement using giving-up rules.

Wolf Movement	1		2		3	
	random	avoid	random	avoid	random	avoid
0.24 moose/km^2						
best fit curve	none	none	linear	none	linear	none
type of curve	none	none	decaying[1]	none	decaying[2]	none
$b_{caribou}$	--	--	--	--	--	--
asymptotic survival rate	--	--	--	--	--	--
r^2	--	--	0.77	--	0.79	--
0.48 moose/km^2						
best fit curve	none	none	linear	none	linear	none
type of curve	none	none	decaying[3]	none	decaying[4]	none
$b_{caribou}$	--	--	--	--	--	--
asymptotic survival rate	--	--	--	--	--	--
r^2	--	--	0.60	--	0.66	--

[1] $y = -1.93x + 80.30$; [2] $y = -2.27x + 71.16$; [3] $y = -1.55x + 85.64$; [4] $y = -2.20x + 78.09$

Table 5.3. The effect of prey avoidance, line use, and wolf movement on the kill rate:line density relationship, b_{kills}, and the asymptotic kill rate. Results are based on simulations in a 0.48 moose/km^2 territory.

Wolf Movement	% of the prey population that avoids lines		
	Random	50%	100%
Random			
best fit curve	asymptotic	asymptotic	linear
type of curve	increasing[1]	increasing[2]	decaying[3]
b_{kills}	1.87	3.69	--
asymptotic kill rate	82	72	--
r^2	0.96	0.93	0.30
Giving up rules			
best fit curve	asymptotic	asymptotic	linear
type of curve	increasing[4]	increasing[5]	decaying[6]
b_{kills}	3.73	0.82	--
asymptotic kill rate	80	59	--
r^2	0.93	0.91	0.86

[1] $y = 38.13x/(1.87 + x) + 44.04$; [2] $y = 27.37x/(3.69 + x) + 45.01$; [3] $y = -1.27x + 45.28$;
[4] $y = 29.19x(3.73 + x) + 51.07$; [5] $y = 9.48x/(.82 + x) + 49.29$; [6] $y = -1.97x + 49.40$

Table 5.4. Example of how wolf numbers in 0 to 5 km/km^2 territories were calculated using Fuller's (1989) equation (assuming randomly distributed prey).

Moose density	line density	kills	estimated moose density	ungulate biomass index	wolves per km^2	#wolves in a 625 km^2 territory
0.24 moose/km^2	0	25	0.23	1.47	0.009	5.5
	0.0625	28	0.27	1.68	0.010	6.0
	0.125	28	0.27	1.69	0.010	6.0
	0.25	27	0.25	1.60	0.009	5.8
	0.375	30	0.28	1.79	0.010	6.3
	0.5	30	0.28	1.78	0.010	6.2
	0.75	33	0.32	1.98	0.011	6.7
	1	33	0.33	2.03	0.011	6.8
	2	34	0.33	2.05	0.011	6.9
	3	42	0.43	2.69	0.013	8.3
	4	41	0.43	2.65	0.013	8.2
	5	43	0.46	2.81	0.014	8.6
0.48 moose/km^2	0	42	0.43	13.33	0.013	8.3
	0.0625	45	0.49	14.55	0.015	9.1
	0.125	46	0.50	14.79	0.015	9.2
	0.25	47	0.51	15.09	0.015	9.4
	0.375	49	0.55	15.81	0.016	9.9
	0.5	52	0.60	17.11	0.017	10.7
	0.75	56	0.67	18.48	0.018	11.6
	1	58	0.71	19.40	0.019	12.1
	2	58	0.70	19.16	0.019	12.0
	3	70	0.96	24.90	0.025	15.6
	4	67	0.90	23.62	0.024	14.8
	5	69	0.93	24.42	0.024	15.3

Table 5.5. The effect of prey avoidance, moose density, and wolf movement on the wolf number:line density relationship, b_{wolf}, and the asymptotic density rate.

Wolf Movement	0.24 moose/km^2			0.48 moose/km^2		
	random	50% avoid	avoid	random	50% avoid	avoid
Random						
best fit curve	linear	linear	linear	asymptotic	asymptotic	linear
type of curve	increasing[1]	increasing[2]	decaying[3]	increasing[4]	increasing[5]	decaying[6]
b_{wolf}	--	--	--	1.91	4.78	--
density	--	--	--	18	17	--
r^2	0.86	0.36	0.67	0.92	0.94	0.34
Giving up						
best fit curve	asymptotic	linear	linear	linear	asymptotic	linear
type of curve	increasing[7]	increasing[8]	decaying[9]	increasing[10]	increasing[11]	decaying[12]
b_{wolf}	3.17	--	--	--	0.91	--
density	8	--	--	--	10	--
r^2	0.95	0.20	0.54	0.83	0.66	0.84

[1] $y=0.59x+5.94$; [2] $y = 0.12x + 5.94$; [3] $y = -0.17x + 5.76$; [4] $y = 9.44x/(1.91 + x) + 8.56$;
[5] $y = 7.50x/(4.78 + x) + 9.01$; [6] $y = -0.28x + 9.05$; [7] $y = 2.28x/(3.17 + x) + 5.51$; [8] $y = 0.03x + 5.60$;
[9] $y = -0.07x + 5.46$; [10] $y = 0.55x + 8.90$; [11] $y = 1.76x/(0.91 + x) + 8.47$; [12] $y = -0.31x + 8.50$

Table 5.6. Change in caribou survival from 0-3 km/km^2 across different moose densities, wolf movement strategies, prey behaviors, and numbers of hunting units within the territory.

Moose Density	% change in survival from 0 to 3 km/km^2		
	1 hunting unit	2 hunting units	3 hunting units
0.24 moose/km^2			
Random movement			
100% Avoid Prey	7	15	20
50% Random Prey	5	11	13
100% Random Prey	4	4	5
Giving-up Rules			
100% Avoid Prey	-2	-5	-7
50% Random Prey	0	-3	-1
100% Random Prey	-1	-5	-4
0.48 moose/km^2			
Random movement			
100% Avoid Prey	6	11	14
50% Random Prey	6	11	12
100% Random Prey	1	3	4
Giving-up Rules			
100% Avoid Prey	-2	-3	-3
50% Random Prey	1	1	0
100% Random Prey	0	-2	-5

Figure 5.1. Caribou survival as a function of wolf movement patterns and the number of individual hunting units or predators in a territory. Simulations were run in territories with 0.24 moose/km^2 (🟥) and 0.48 moose/km^2 (🟩).

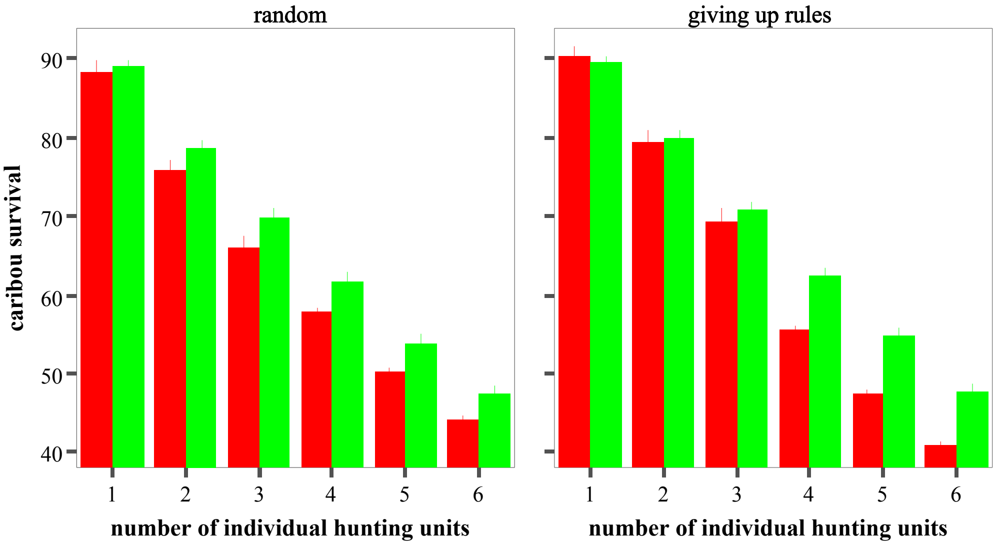


Figure 5.2. Caribou survival as a function of the moose density and line density. Simulations were run in territories with a single hunting unit (--●--) and with two hunting units (--●--). All results are based on random wolf movement.

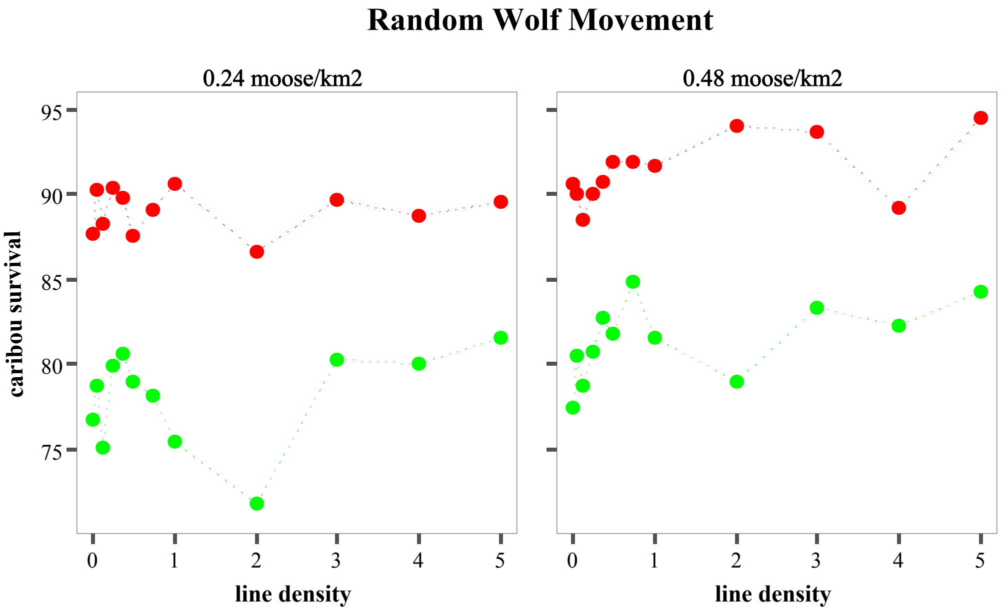


Figure 5.3. Caribou survival as a function of moose density and line density. Simulations were run in territories with a single hunting unit (--●--) and with two hunting units (--●--). Survival:line density curves were best described by decaying linear curves (——) if there was more than one "predator" hunting in the territory. All results are based on wolf movement using giving up rules.

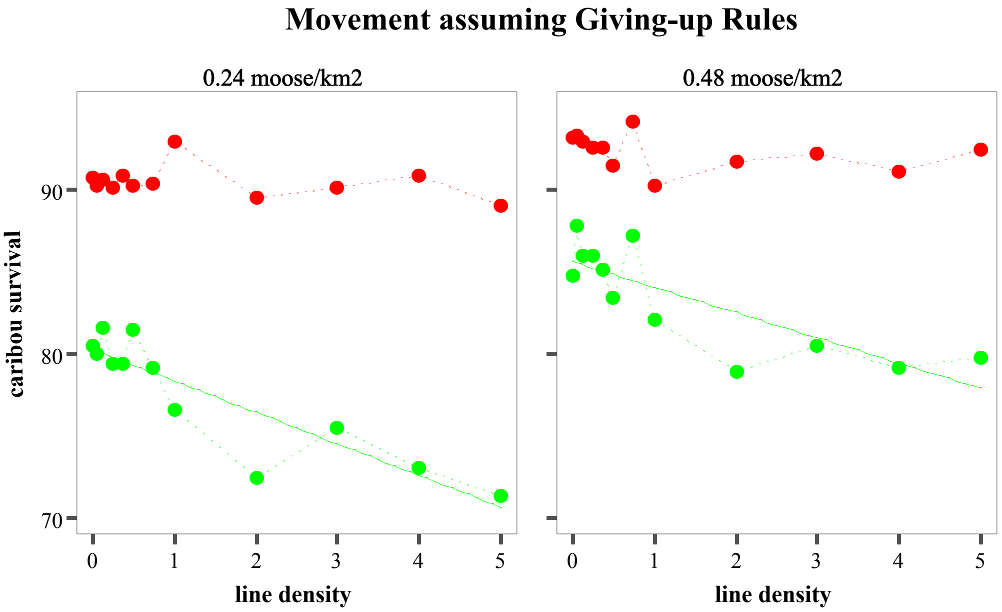


Figure 5.4. Average caribou survival from 0 to 5 km/km^2 as a function of wolf movement patterns and the number of individual hunting units or predators in a territory. Simulations were run in territories with 0.24 moose/km^2 (🟥) and 0.48 moose/km^2 (🟩).

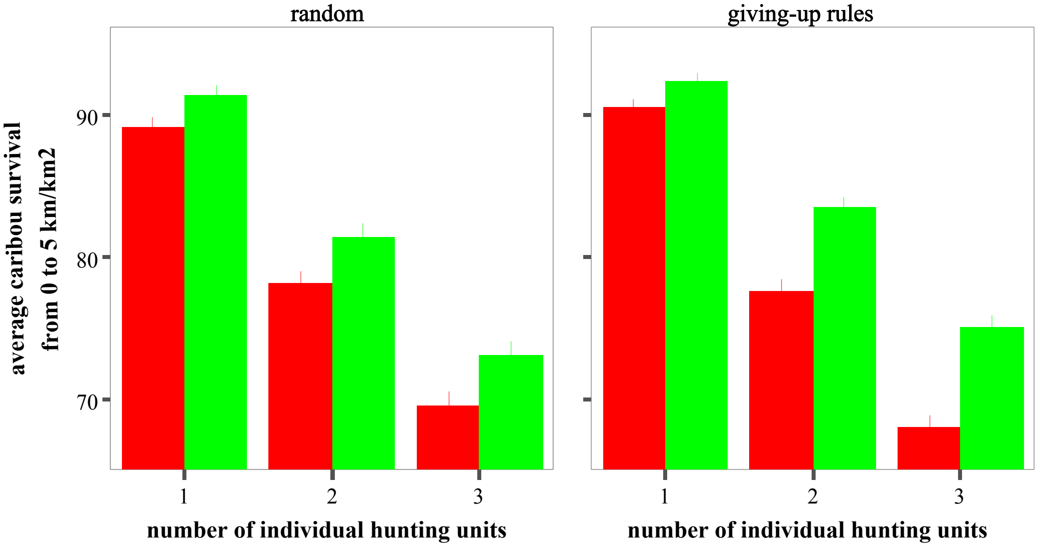


Figure 5.5. Caribou survival as a function of moose density and line density in territories with 3 hunting units. Simulations were run assuming that wolves used giving up rules in territories in which all prey were randomly distributed with respect to lines (--●--) or all prey avoided lines (--●--). Survival:line density curves were best described by an asymptotic curve in a 0.24 moose/km^2 territory if all prey avoided lines (——) and linear curves in a 0.48 moose/km^2 territory if all prey avoided lines (——) or if prey were randomly distributed with respect to lines (——).

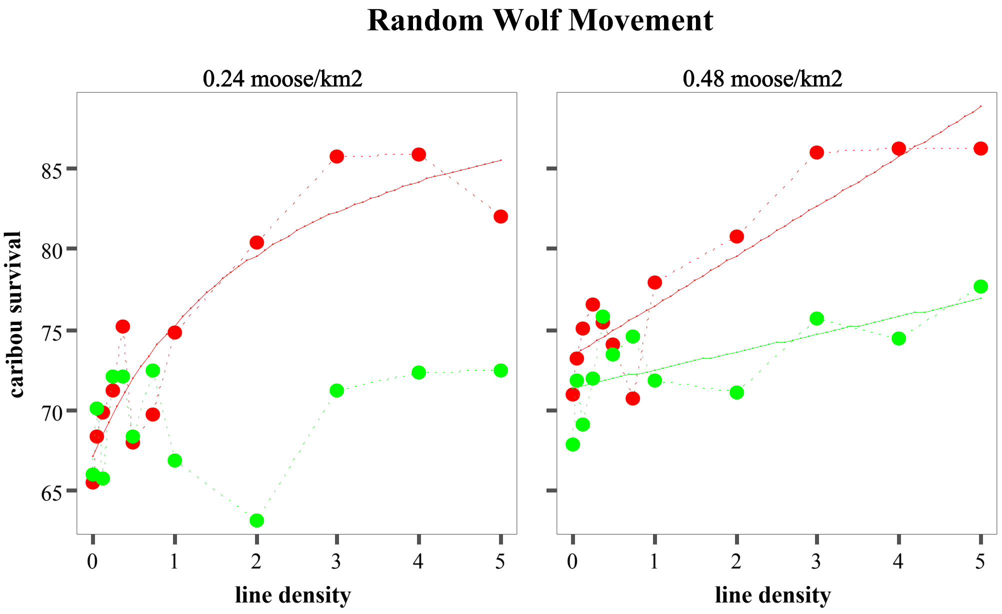
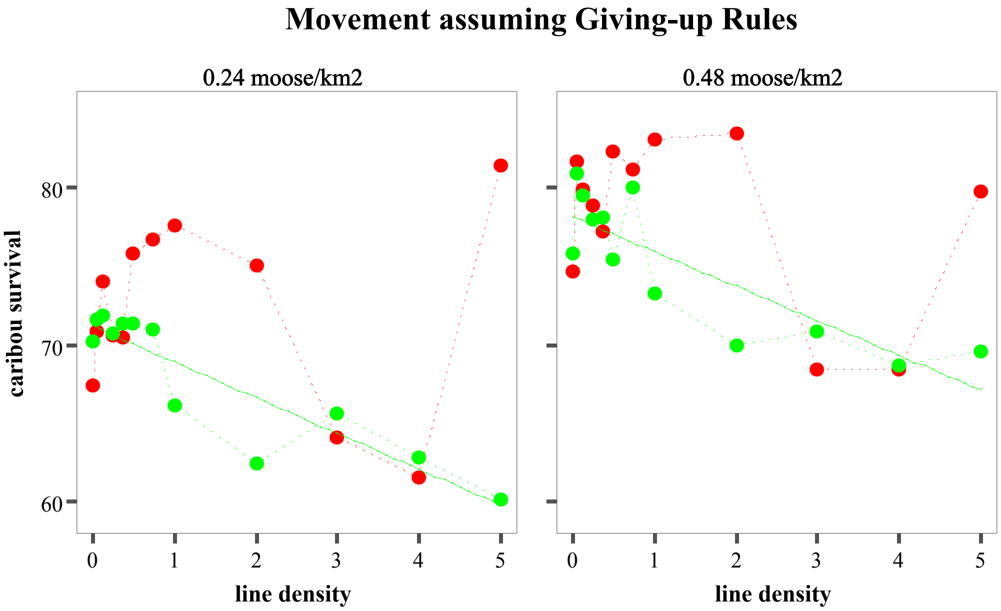


Figure 5.6. Caribou survival as a function of moose density and line density in territories with 3 hunting units. Simulations were run assuming that wolves moved randomly in territories in which all prey were randomly distributed with respect to lines (--●--) or all prey avoided lines (--●--). Survival:line density curves were best described by decaying linear curves if prey were randomly distributed with respect to lines in 0.24 (——) or 0.48 (——) moose/km^2 territories.



Movement assuming Giving-up Rules

Figure 5.7. Average caribou survival from 0 to 5 km/km^2 as a function of moose density and the number of individual hunting units or predators in a territory. Simulations were based on random wolf movement and were run in territories in which all prey avoided lines (🟥) and in which all prey were randomly distributed with respect to lines (🟩).

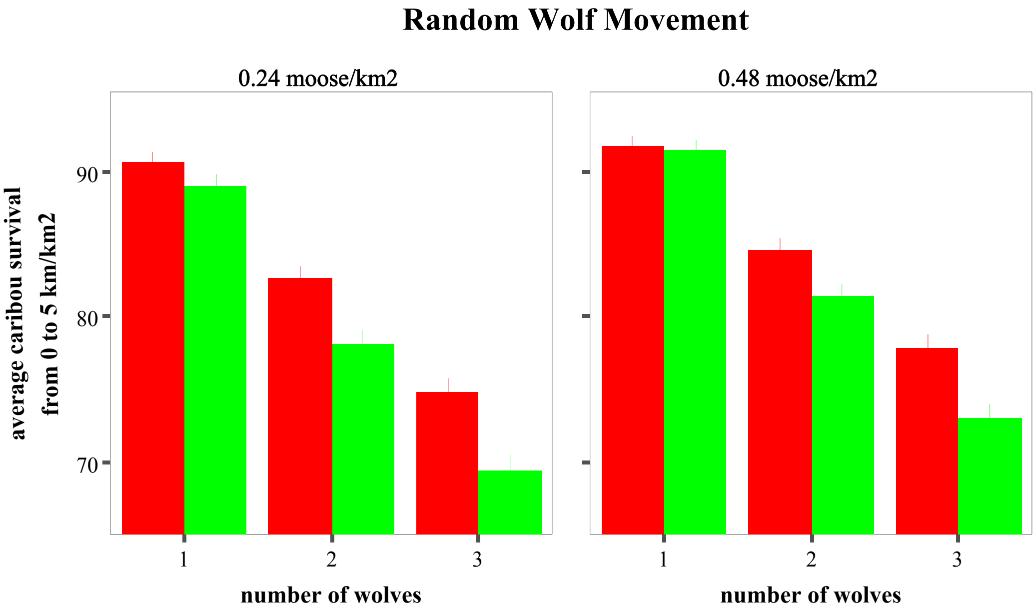


Figure 5.8. Average caribou survival from 0 to 5 km/km^2 as a function of moose density and the number of individual hunting units or predators in a territory. Simulations were based on wolf movement using giving up rules and were run in territories in which all prey avoided lines (🟥) and in which all prey were randomly distributed with respect to lines (🟩).

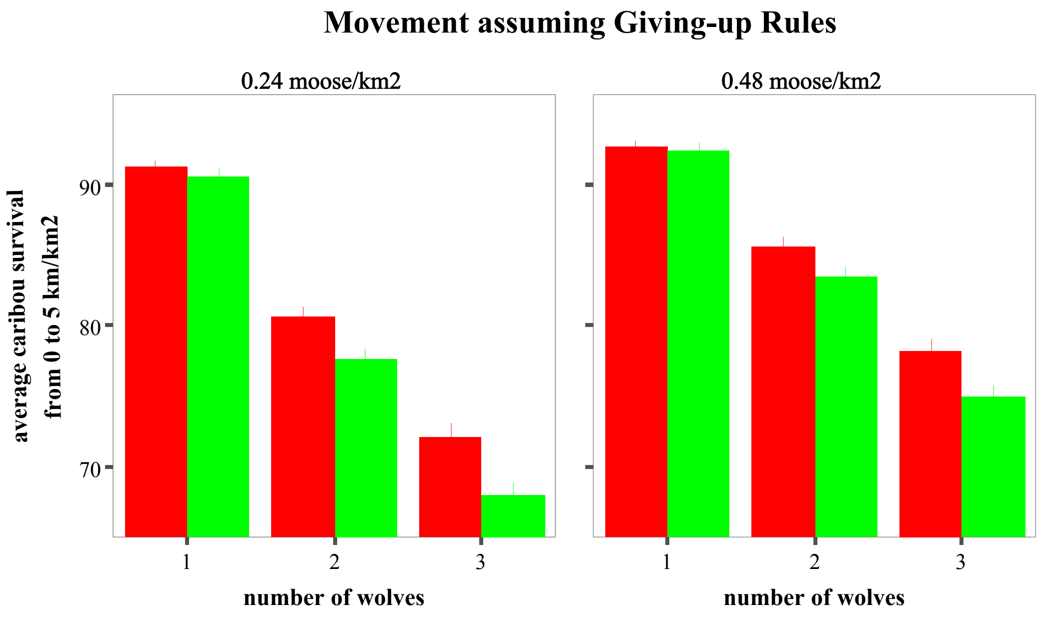


Figure 5.9. Kill rate and caribou survival as a function of moose density. Simulations were based on random wolf movement (--●--) and movement assuming giving up rules (--●--). All curves are best described by asymptotic curves (random: ——; giving up rules: ——).

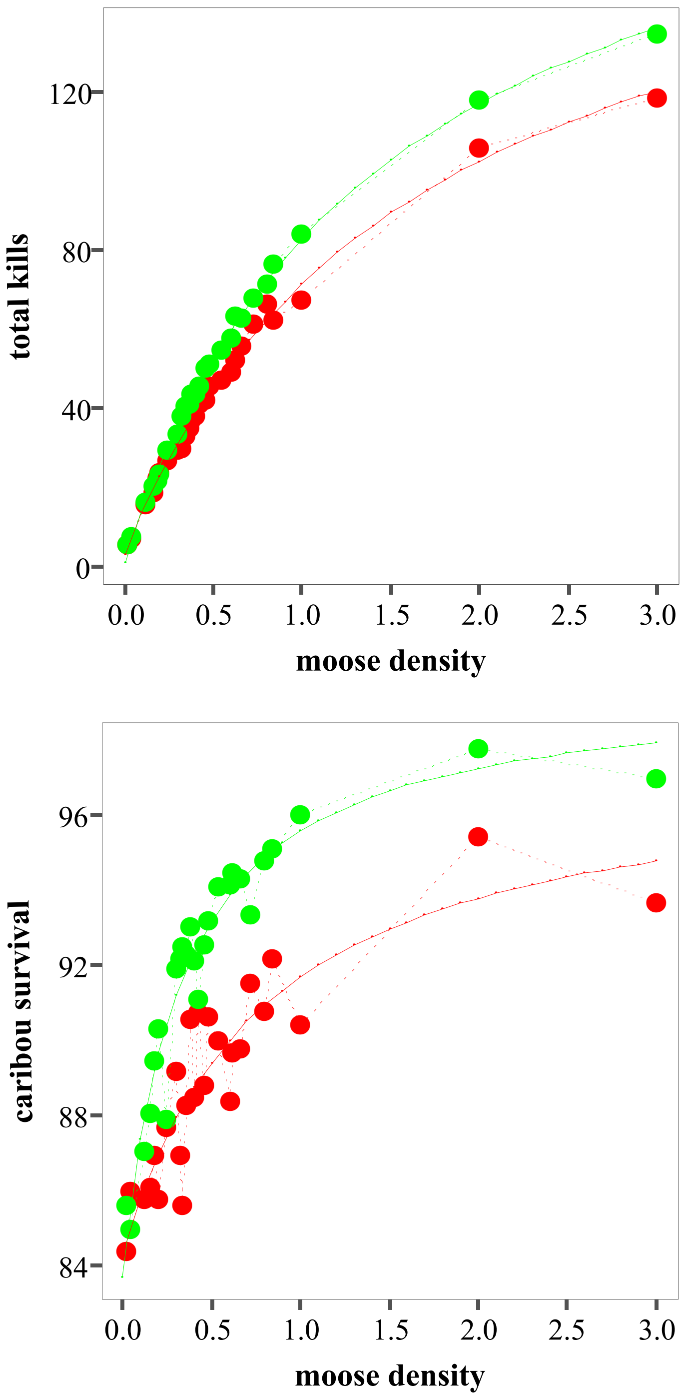


Figure 5.10. The effect of line density and wolf movement patterns on total kills in a 0.48 moose/km^2 territory. Survival:line density relationships are based on simulations in which prey are randomly distributed with respect to lines (--●--) and in which all prey avoid lines (--●--). Regardless of wolf movement, simulated data fit an asymptotic curve (——) if prey were randomly distributed and a decaying linear curve (——) if all prey avoided lines.

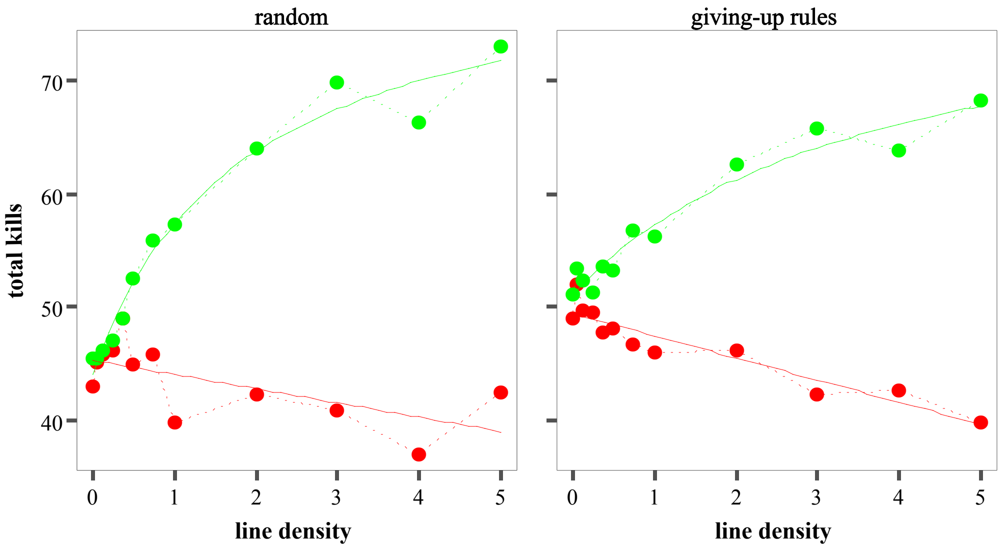
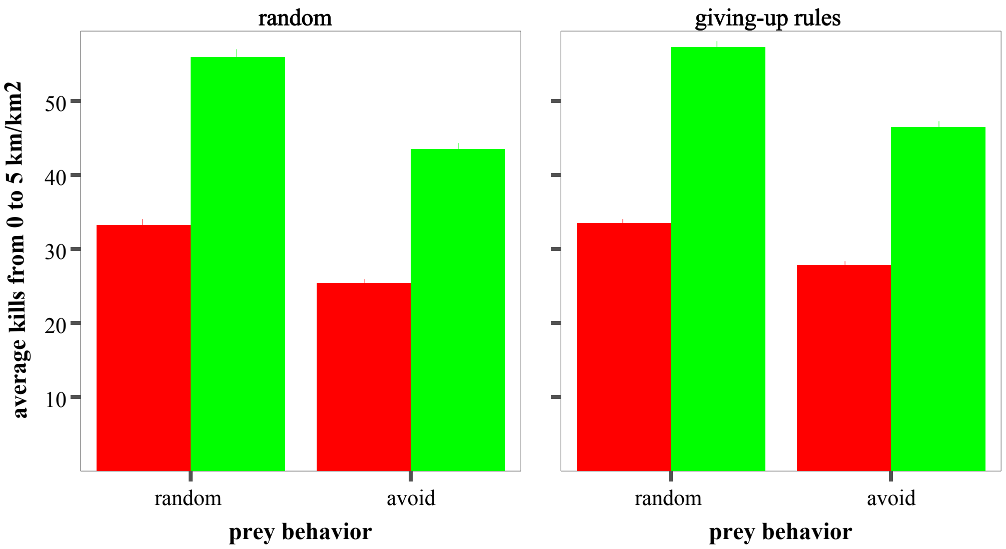
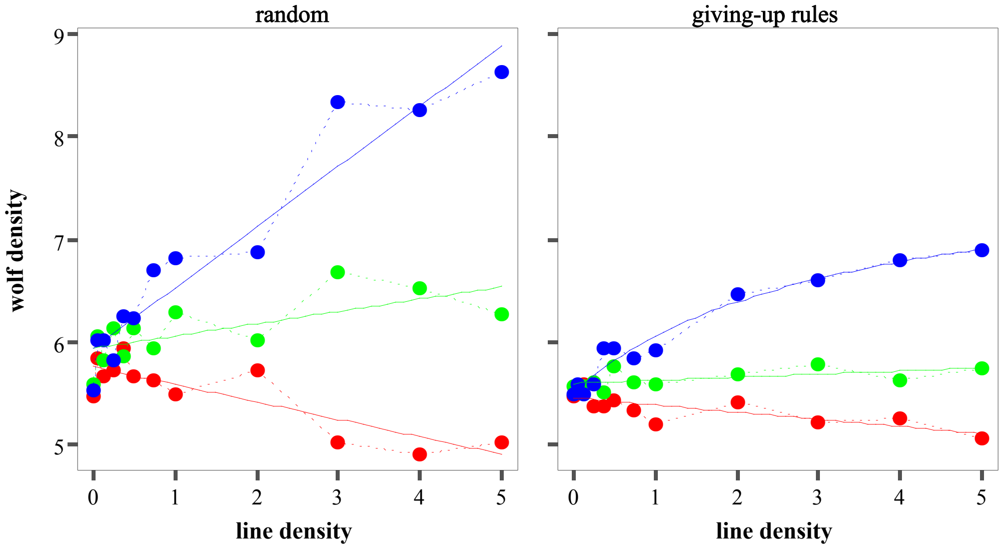


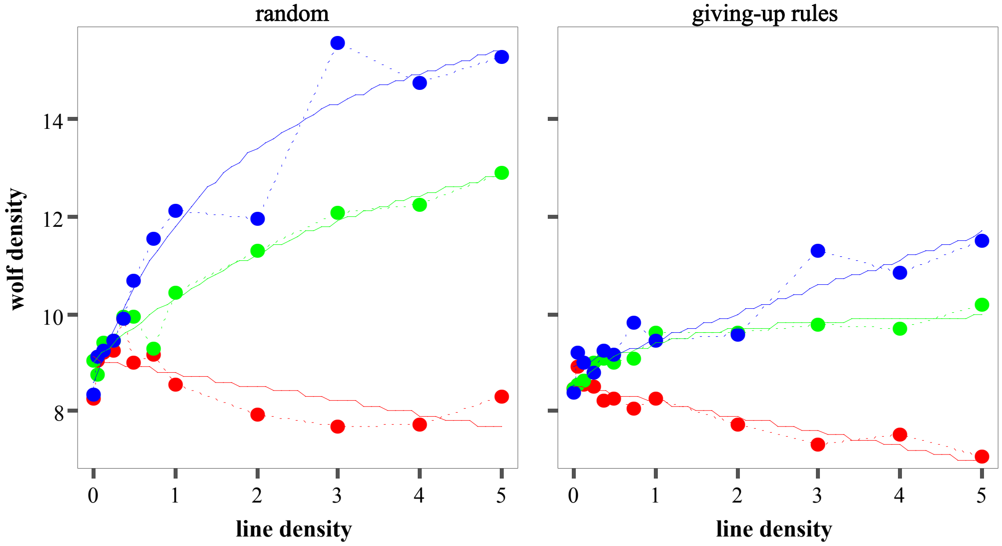
Figure 5.11. Average kills from 0 to 5 km/km^2 as a function of wolf movement patterns and prey behavior. Simulations were run in territories with 0.24 moose/km^2 (🟥) and 0.48 moose/km^2 (🟩).



.

Figure 5.12. The effect of line density, moose density, and wolf movement patterns on wolf density in a 625 km^2 territory. Survival:line density relationships are based on simulations in which prey are randomly distributed with respect to lines (--●--), 50% of prey avoid lines (--●--), and in which all prey avoid lines (--●--). Simulated data fit a linear or asymptotic curve (random: —; 50% avoid: —) if 50% or more prey were randomly distributed with respect to lines and decaying linear curve if all prey avoided lines (—).


0.24 moose/km2


0.48 moose/km2

Chapter 6: General Discussion

The goal of this thesis was to determine the mechanisms underlying the woodland caribou declines in Alberta's boreal forest. These declines have been documented since the early 1990s and are sufficiently extensive that caribou are now provincially threatened (McLoughlin *et al*. 2003; COSEWIC 2005). The declines are presumed to be predator-driven, which essentially implies that peatlands no longer offer refuge from wolf predation. The empirical and theoretical literature suggest three factors that may compromise peatlands as refuge space: (1) increased wolf mobility between uplands and peatlands via wolf use of linear features, (2) the expansion of moose, and consequently wolves, into caribou range, and (3) an increase in the number of wolves hunting in caribou range (Holt 1977; 1984; Holt and Kotler 1987; Fuller 1989; James and Stuart-Smith 2000; James *et al*. 2004; D. Latham, *unpublished results*). I used grid-based simulation models to address my hypotheses, namely because empirical work was virtually impossible for logistical, financial, and ethical reasons (also see Peck 2004).

I first investigated how linear features affect wolf-prey interactions, and in particular, if line use mimicked the functional response between wolves and prey density. Simulation models indicated that while line use did increase wolf use of moose, it was too low to increase wolf use of caribou. This suggests that there is no direct effect of wolf use of lines on caribou survival. This is interesting as it implies that the negative correlation between caribou survival and linear feature density is driven by something else (Alberta Caribou Committee, *unpublished results*). Models also indicate that the while line use mimics the functional effects of prey density on wolf use of moose, the amount of "benefit" wolves receive depends on prey avoidance of lines. More line avoidance meant fewer kills; however, even at 75% prey avoidance, wolves still killed more prey than expected in a territory with no lines. Furthermore, it is possible that wolf use of lines is low because it minimizes the effects of prey avoidance behaviors. This suggests that predators respond to prey distribution in a "game-like fashion" (e.g., Lima 2002). However, while avoidance affected line-wolf-moose interactions, it had no real effect on line-wolf-caribou interactions. This was namely because caribou survival did not change with line density even if all prey were randomly distributed with respect to lines. This suggests that that caribou avoidance of lines is not a response to predation risk and may reflect other factors like human activity (Dyer *et al*. 2001).

I then determined how overlap between moose and caribou affected caribou survival and if overlap could change the nature of the caribou survival:line density relationships evident in Chapter 3. Models did indicate that overlap can increase wolf use of caribou and lead to declining survival:line density relationships, but only under certain parameter conditions. In particular, wolves must move non-randomly and prey distribution must be primarily random before overlap has an effect on caribou survival in unlined and lined territories. Furthermore, model results suggest that even under these conditions, the effect of overlap may not extend beyond female adult survival. This suggests that overlap may contribute to the declines but is not the sole mechanism behind the declines.

Finally, I determined if the declines were a function of the number of wolves and if the number of wolves could change the nature of the caribou survival:line density relationships evident in Chapter 3. Moreover, I determined if an increase in wolf number could stem from the numeric effects of wolf use of lines. Similar to the overlap results, models did indicate that more predators using lines can lead to declining survival:line density relationships, but only if wolves use giving up rules and prey distributions are random. However, models also suggest that overall, caribou survival decreased with the number of individually hunting wolves in both lined and unlined territories, regardless of prey and predator behaviors. Furthermore, the functional effects of line use were extensive enough to facilitate a wolf numeric response. This suggests that line use is artificially increasing wolf numbers in Alberta, ultimately leading to higher rates of caribou mortality and possibly driving the herd declines.

Of the three hypotheses, the number of predators had the most consistent effects on caribou survival. This suggests that most effort – be it research or management wise – should focus on the direct role of predators in the caribou declines. Interestingly enough, more recent work is doing just this (D. Latham, *unpublished results*). This thesis also identified a number of key research gaps in the wolf-prey system in Alberta. Primary areas of interest are: (1) wolf use of lines. The quantitative effect of line use on wolf-prey interactions depended on how much wolves use lines and how much moose avoided lines. If line use is more variable that current data suggests (James 1999; Whittington *et al*. 2005; Neufeld 2006), then the thesis conclusions may be vastly different. I recommend that GPS collars be deployed in caribou ranges across Alberta to determine just how variable line use is. (2) Moose response to lines. Moose avoidance of linear features is largely unstudied, but is critical for determining how much kill rates – and thus wolf density – is expected to improve with line density. Again, studying this would require GPS collars. (3) Wolf movement patterns. Wolf movement primarily had a quantitative effect on model results, although there were a few key exceptions. The outcome of the overlap models, for example, strongly depended on how the pack moved in its territory. This can be investigated in conjunction with (1), in which movement is tracked in ranges across Alberta. (4) Moose densities and distributions in and near caribou range. This will help determine if moose are extending into caribou range and if density is stable or is increasing for anthropogenic-related reasons. In general, a better understanding of moose is likely to yield a better understanding of the caribou declines as wolf-moose interactions appear critical to wolf-caribou interactions. Moose density and distributions can be determined relatively via snow or aerial tracking or more rigorously with VHF and GPS collars. (5) Wolf densities and distributions in and near caribou range. Understanding how many wolves are in and near caribou range as well as their relative activity in caribou range will help determine if the number of wolves can account for the caribou declines (i.e., if declines are greater in areas with more wolves). Similar to moose, wolf density and distributions can be determined via snow or aerial tracking or with collars. (6) The effect of moose density on wolf pack dynamics. Pack "break-up", as driven by moose density, suggests that the number of predators in caribou range can increase without an increase in predator density per se. This can be determined by collaring a number of individuals within a pack and assessing their movements in areas with low and high moose (e.g., northeastern and west-central Alberta, respectively).

Understanding these mechanisms will help elucidate why predation pressure is changing in Alberta. Experimental work in particular can help validate model results (see individual chapters for descriptions of these). However, more immediate action will likely be necessary to preserve Alberta's caribou. Wolf and/or alternative prey control is advocated over line mitigation for two key reasons. First, while line use may be the ultimate cause of the declines via changes in wolf kills and numbers, wolves are still the proximate cause of the declines. Wolf control is a direct conservation action; line control is not. As such, wolf control is likely to have more immediate – and successful – results. Second, line mitigation is a labour intensive endeavour that is unlikely to have any effect on wolf movement given the sheer number of lines in Alberta (i.e., in some areas, lines are 10 km/km^2 or more; Lee and Boutin 2006). This conclusion stems mainly from the model results that indicate most line-related changes will occur by 1 km/km^2. Reclaiming lines back to this density (or maintaining lines under this density) is simply not feasible given the ongoing and projected development in Alberta. Even if lines have non-predator effects on caribou (e.g., loss of habitat), it is still impractical to reclaim them. While it is not desirable to control predator and alternative prey populations for an extended time, such human intervention may be necessary to ensure the persistence of caribou in a province driven primarily by resource extraction.

References

Committee on the Status of Endangered Wildlife in Canada. 2005. Status of Woodland caribou (*Rangifer tarandus caribou*). Retrieved on Nov. 30th, 2005 at http://www.cosewic.gc.ca/eng/sct1/searchdetail_e.cfm.

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

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

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

Holt, R.D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. American Naturalist 124: 377-406.

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

James, A.R.C., Boutin, S., Hebert, D.M., and Rippin, A.B. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. Journal of Wildlife Management 68: 799-809.

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

Lee, P. and Boutin, S. 2006. Persistence and developmental transition of wide seismic lines in the western Boreal Plains of Canada. Journal of Environmental Management 78: 240-250.

Lima, S.L. 2002. Putting predators back into behavioral predator-prey interactions. Trends in Ecology and Evolution 17: 70-75.

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

Neufeld, L. 2006. Spatial dynamics of wolves and woodland caribou in an industrial forest landscape in west-central Alberta. MSc Thesis, University of Alberta, Edmonton, AB.

Peck, S.L. 2004. Simulation as experiment: a philosophical reassessment for biological modeling. Trends in Ecology and Evolution 19: 530-534.

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