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Effects of Industrial Development on the Predator-Prey Relationship Between Wolves and Caribou in Northeastern Alberta

By

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled EFFECTS OF INDUSTRIAL DEVELOPMENT ON THE PREDATOR-PREY RELATIONSHIP BETWEEN WOLVES AND CARIBOU IN NORTHEASTERN ALBERTA submitted by ADAM ROSS COCHRANE JAMES in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

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ABSTRACT

In northeastern Alberta, continued expansion of the oil and gas industry and timber harvesting has raised concerns that the resulting environmental changes may negatively affect the woodland caribou (*Rangifer tarandus caribou*) population in this region. Caribou are an endangered species in Alberta, and populations in northeastern Alberta appear to be stable or slightly decreasing. Between 1993 and 1997, I studied two ways in which industrial development may potentially affect caribou populations by influencing their predator-prey relationship with wolves (*Canis lupus*). (1) The spatial distribution of caribou in relation to alternative prey (commonly moose, *Alces alces*) has been hypothesized to affect the level of wolf predation experienced by caribou populations. I found that selection of fen/bog complexes by caribou and selection of well-drained habitats by moose and wolves resulted in spatial separation. The spatial separation of caribou and moose reduced predation pressure on caribou, but did not provide a total refuge from wolves. Timber harvesting is expected to change the distribution and abundance of moose and may result in increased predation rates on caribou even if increases in moose density do not occur within the fen/bog complexes selected by caribou. (2) The development of linear corridors (seismic lines, etc) has been hypothesized to increase predation pressure on caribou. Of 98 radio-collared caribou, 35 were significantly further from corridors than were random points and 3 were significantly closer to corridors than were random points. Within caribou range, wolf locations were closer to linear corridors than were random points. Caribou mortalities attributed to wolf predation were closer to linear corridors than were live locations from all caribou, indicating that caribou that were close to linear corridors

were at higher risk of being killed by wolves. I found that in winter, the average speed of wolves traveling on corridors (1.4km/hr) was 2.8 times faster than the average speed of travel in the forest (0.5km/hr). I believe increased industrial activity in and near caribou range could have a significant effect on caribou population dynamics by increasing predation. In this thesis I discuss the management implications of these results and provide some recommendations.

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Introduction

Throughout the last century, wildlife managers in Alberta have repeatedly commented on perceived declines in woodland caribou (*Rangifer tarandus caribou*) populations and the need to provide them with protection to maintain their numbers and distribution (Anonymous 1929, Anonymous 1934, Dwyer 1969, Bloomfield 1980, Edmonds 1986). Licensed hunting of caribou was closed in Alberta in 1981 and in 1985 woodland caribou were listed as 'Endangered' under the Alberta *Wildlife Act*. (Recently the validity of the data and arguments used to show a provincial decline in caribou populations (Edmonds 1986) has been questioned (Bradshaw and Hebert 1996). However, despite Bradshaw and Hebert's (1996) review of data, the general perception among provincial biologists remains that caribou have declined and continue to be threatened by increasing human activity in and near caribou range. Indeed, Bradshaw and Hebert (1996) acknowledge that regardless of the true historical changes in caribou populations, there is at present concern for caribou populations in the presence of increasing industrial development.

During the late 1980s and early 1990s, substantial increases in forestry, oil, and natural gas allocations in and near caribou habitat raised concern among provincial wildlife managers. Without complete knowledge of the potential effects of industrial activity in caribou range, wildlife and land use managers took a conservative approach and applied restrictions to industrial activity in areas occupied by caribou. Restrictions focused on the timing of industrial activity and minimizing access development in caribou range. Industry members with operations in caribou areas found these restrictions costly and onerous and by 1990, management conflicts arose over resource development and caribou conservation. In 1991, Alberta Energy issued a Procedural Guide for Oil and Gas Activity on Caribou Range (Information Letter 91-17) which stated that "Petroleum and natural gas exploration and development activities can occur on caribou range, provided the integrity of the habitat is maintained to support its use by caribou." The procedural guide also set out a framework to establish regional Standing Committees consisting of industry and government representatives to foster cooperation and develop area-specific mitigation plans. Regional Standing Committees were established in the northeast (1991), northwest (1994), and west central (1992) areas of the province.

In northeastern Alberta, the Northeast Region Standing Committee (NERSC) realized that better information was required before flexibility in land use restrictions would be possible (Rippin et al. 1996). NERSC established a Research Subcommittee of government biologists, university staff and students, and industry representatives to begin finding the answers needed to assess the effects of industrial development on caribou populations (Rippin et al. 1996, Hamilton and Edey 1998). Initial studies used radio telemetry to determine the distribution and habitat use of caribou and the potential direct disturbance effects of industrial activity on caribou energetics (Bradshaw 1994, Bradshaw et al. 1995, Bradshaw et al. 1997, 1998). After several consecutive years of data collection, researchers found the population to be stable or slightly declining and identified wolf (*Canis lupus*) predation as the most common cause of adult mortality (Stuart-Smith et al. 1997). Members of the research subcommittee became increasingly interested in the potential indirect effects of industrial development on caribou through changes in their prey-predator relationship with wolves. Industrial development could affect caribou-predator interactions by altering the spatial relationship among caribou, wolves, and alternate prey and/or by affecting caribou and wolf movements through the creation of linear corridors.

I joined the NERSC research subcommittee in 1993 and conducted fieldwork in northeastern Alberta between 1994 and 1997 to test these two hypotheses. In *Chapter 2*, I describe the role we believe spatial separation plays in influencing the predation pressure experienced by caribou populations and its relevance to industrial activity. In *Chapter 3*, I describe the distribution of caribou and wolves in relation to linear corridors and in *Chapter 4*, I examine wolf behaviour and speed on linear corridors. In *Chapter 5*, I discuss the conclusions of this research that both spatial separation and linear corridors play an important role in influencing the level of predation experienced by caribou populations in northeastern Alberta, the management implications of our findings, and some suggestions for future work.

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Chapter 2

Spatial Separation of Caribou from Moose and its Relation to Predation by Wolves[1]

INTRODUCTION

The North American range of woodland caribou (*Rangifer tarandus caribou*) has undergone gradual but significant reduction since European settlement (Bergerud and Elliot 1986, Edmonds 1991, but see Bradshaw and Hebert 1995). A major cause of this decline in western Canada may be predation by wolves (Bergerud 1974, 1985, Bergerud and Elliot 1986, Fuller and Keith 1980,1981, Gauthier and Theberge 1986, Seip 1992). In Alberta, woodland caribou are currently identified as 'Threatened' in the regulations of the Alberta Wildlife Act. In northeastern Alberta, continued expansion of the oil and gas industry, and new interest in trembling aspen (*Populus tremuloides*) as a source of fibre for the production of pulp, has raised concerns that the resulting environmental changes may negatively affect the caribou population in this region.

Industrial development may directly impact caribou through disturbance (Bradshaw et al. 1997, Bradshaw et al. 1998) or habitat alteration. However, the indirect effects of industrial development on caribou-predator relationships may be equally important to caribou population dynamics (Bergerud 1974). Industrial development may affect caribou-predator interactions by altering the spatial relationship among caribou, wolves (*Canis lupus*), and alternate prey.

Spatial separation from alternative prey (commonly moose, *Alces alces*) has been hypothesized as an anti-predator strategy of caribou. It has been argued that caribou populations decline in areas where the biomass of moose allows wolf numbers to increase to (or be maintained at) high levels (Bergerud 1974, 1985, Bergerud et al.

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[1] This chapter will be submitted for publication with the following authorship: Adam R. C. James, Stan Boutin, Daryll M. Hebert, and A. Blair Rippin.

1984, Bergerud and Elliot 1986, Bergerud and Page 1987, Fuller and Keith 1981, Seip 1991). The exclusion of caribou from these areas is likely an example of predator-mediated apparent competition (Holt 1977). Apparent competition arises when a predator has a positive numeric response to each prey type in its diet. An increase in the density of one prey results in increased predator density and, hence, causes higher predation on other prey. If one prey is sufficiently productive, the predator may be maintained at levels high enough to exclude the other prey from the system (Holt 1984). Moose have a high capacity to increase relative to caribou, and wolves are capable of strong numeric response (Fuller 1989, Messier 1994), therefore, caribou are expected to be excluded in these systems. The exclusion of prey species by a predator has been demonstrated in field studies of many different communities (e.g., Bergerud 1967, 1983, Macan 1977, review in Jeffries and Lawton 1984).

The spatial distribution and movements of predators and prey may however result in encounter rates for prey species that are not directly proportional to their densities (Skogland 1991, Huggard 1993), and variation in the spatial and temporal overlap of predators and their prey may play a major role in determining which prey are eaten (Hassell and Southwood 1978, Schluter 1981, Williamson and Stoeckel 1990, Williamson 1993). Therefore, the spatial separation of two prey types that share a common predator, under certain conditions of predator mobility, may lead to a refuge for prey species with high sensitivity to predation (Hanski 1981, Holt 1984, Comins and Hassell 1987, Holt and Kotler 1987). Examples of spatial patchiness leading to the coexistence of prey that share a common predator can be found in many communities (e.g., Gilbert 1984, Kotler 1984, Lawton 1986).

Much of the evidence for the importance of spatial separation of caribou from moose comes from mountainous areas of British Columbia where moose populations have recently expanded northward to the detriment of caribou herds (Seip 1992). In this system caribou avoid valley bottoms now inhabited by moose, but suffer higher mortality in areas where elevational migrations bring moose and caribou into close proximity. However, in northern Alberta, caribou, moose, and wolves have coexisted for centuries, and in most areas there is little or no topographic relief. It was not known if caribou mortality rates due to predation were influenced by spatial separation from moose in this region.

Understanding the role of spatial separation in caribou-moose-wolf dynamics is important for determining the potential effects of industrial development on threatened caribou populations. Moose are adapted to early successional stages after forest fires, and the greater quantity and quality of regenerating browse in recently burned areas often allow moose densities to increase (Peek 1974, Gasaway et al. 1989). We predict that moose densities will also increase in areas regenerating after aspen timber harvest; however, we know little about how this might affect caribou in the boreal mixed-woods of northern Alberta. Caribou numbers in northeastern Alberta appear to be stable or slightly decreasing (Fuller and Keith, 1981, Stuart-Smith et al. 1997), therefore, small changes in predation pressure may have significant consequences to the long-term viability of the population.

Telemetry locations of radio-collared caribou in northeastern Alberta over the last 5 years indicate that caribou show strong preference for fen/bog complexes and avoid well-drained areas (Stuart-Smith et al., 1997). In this paper, we do not attempt to determine the ultimate cause of caribou habitat selection, but rather we assess the importance of the proximate effects of spatial separation on predation rates experienced by caribou. Our hypothesis is that caribou in northeastern Alberta experience lower predation rates because they occupy large fen/bog complexes that provide spatial refuges from moose and wolves (Spatial Separation Hypothesis). To assess this hypothesis we tested the following three predictions:

Prediction 1. Differential habitat use by caribou, wolves, and moose: -- If occupying fen/bog complexes spatially separates caribou, we should be able to detect a significant difference in the use of fen/bog and well-drained habitats between moose and caribou and between wolves and caribou. Fen/bog and well-drained habitats are highly separated in northeastern Alberta; therefore, habitat separation implies spatial separation.

Prediction 2. Wolf predation pressure is higher in and near patches selected by moose: -- The Spatial Separation Hypothesis implies that wolves concentrate their hunting activity in areas with high moose densities. Therefore, we predict predation pressure will be higher in and near habitat patches selected by moose. If fen/bog complexes are effective refuges, then by definition predation pressure should be lower in these areas.

Prediction 3. Disproportionate predation by wolves: -- If spatial separation from alternative prey results in a lower predation rate on caribou, then the relative frequency of caribou in the diet should be lower than the relative frequency of caribou in the environment (or predation has not been reduced).

This project was conducted as part of a long-term study of caribou in northeastern Alberta, ongoing since 1991 (see Bradshaw 1994, Bradshaw et al. 1995, Bradshaw et al. 1997, 1998, Stuart-Smith et al. 1997, James and Stuart-Smith, in preparation, James and Boutin, in preparation).

STUDY AREA

This study was conducted in northeastern Alberta, Canada (56° N, 112° W), encompassing approximately 20,000 km^2 of boreal mixed-wood and peatland vegetation (Fig. 2.1). Wetlands were dominated by black spruce (*Picea mariana*) or black spruce-tamarack (*Larix laricina*) fens and bogs. Well-drained sites along river valleys and in upland areas were dominated by aspen (*Populus tremuloides*), white spruce (*Picea glauca*), and jack pine (*Pinus banksiana*). See Bradshaw et al. (1995) for a detailed description of vegetation in the study area. Habitat within the study area was classified as either fen/bog or well-drained habitat based on wetland and upland categories in digital Baseline Thematic Maps of the region. Fen/bog (approx. 78% of study area) and well-drained habitats (approx. 22% of study area) are highly separated in the region (Fig. 2.2). Caribou, moose, white-tailed deer (*Odocoileus virginianus*), and mule deer (*Odocoileus hemionus*) were the main ungulate prey available to wolves. Black bears (*Ursus americanus*) and Lynx (*Lynx canadensis*) were also present in the study area.

METHODS

Habitat use of caribou, wolves, and moose

As part of a long-term study, 117 adult caribou were fitted with VHF radio-collars with mortality switches between 1991 and 1997 (Stuart-Smith et al. 1997). We attempted to capture animals throughout the study area, preferentially selecting females over males to obtain information on reproduction and calf survival. One hundred and nine of these collars were active during this study (1993-1997). Between 1994 and 1997, we placed VHF collars on 20 wolves in 7 packs (Bourgoin, Upper, Joli, Iron, Grand, Crooked, and Horsetail) and on 3 loners. To ensure our sample was not biased, we actively attempted to collar wolves within fen/bog complexes by establishing three bait stations in this habitat type (see Fig. 2.7). We also obtained location information from 37 female moose collared as part of a concurrent study conducted by T. Osko (University of Alberta, Edmonton) to evaluate the effects of timber harvesting on moose abundance and distribution.

We located radio-collared individuals of all three species approximately every 2 weeks by aerial telemetry and recorded the latitude and longitude of each location with a Global Positioning System (GPS) unit. GPS locations were not differentially corrected. In addition to regular telemetry locations, we located wolves twice a day (to locate predation sites) and caribou and moose every 3 days for 15 days during winter in 1995, 1996, and 1997 and during the calving season of 1995. We also collected three additional sets of locations for each of the three species during calving season in 1996 and 1997 and additional wolf locations were obtained to confirm den site locations for newly collared packs. We classified all locations into three seasons: Winter (November – February) Spring (March – June) and Fall (July – October). We entered caribou ($n = 3,382$), wolf ($n = 710$) and moose ($n = 1754$) locations into a Geographical Information System (GIS).

Caribou: -- We used the GIS to determine the habitat type (fen/bog or well drained) that each caribou location fell within. We determined the proportion of locations in fen/bog and well-drained habitat for each collared individual by season. We used these proportions to calculate the mean proportion of each habitat used by caribou in each season. To compare habitat use to availability, we calculated Ivlev's electivity index (Krebs 1989) using the proportion of fen/bog and well-drained habitat within the minimum convex polygon around all caribou locations and the mean proportion of each habitat used by caribou in each season.

Wolves: -- We used the GIS to determine the minimum convex polygon around all wolf locations and then calculated the proportion of locations in the two habitat types for each collared wolf, the mean of all collared wolves, and electivity for wolves by season as above. We also used individual wolf locations to create a data set of "pack locations." In the pack location data set, when >2 collared individuals in the same pack were located together (i.e., when a difference in location was not distinguishable from aerial telemetry), we considered this to be one location. However, when individuals from the same pack were located apart, we used each location. This made a data set of 592 locations. The proportion of locations in each habitat type was calculated for each pack and the mean proportion and electivity were calculated for the pack data set by season as above. Using wolf location data for packs as a whole removes any bias introduced by having different numbers of collared wolves between packs. Comparing individual locations to pack locations also provides information on the frequency of individual versus group forays in the two habitat types.

Moose: -- In addition to telemetry locations, we completed aerial grid surveys of the moose study area in March 1995 and 1997 to provide additional information on moose distribution. Transects were flown east-west at 1 minute of latitude intervals and the locations of all animals seen on or between flight lines were recorded. The grid surveys indicated that the distribution of collared moose was not representative of the true distribution of moose in the study area. The surveys indicated there were relatively more moose in the well-drained areas than were represented by collared individuals. Moose were captured with a net-gun fired from a helicopter, which requires sufficient openings in the forest canopy to maneuver and shoot the net. Capturing animals is much easier in the open wetlands than in the densely forested river valley. Therefore, although unintentional, we believe moose were not captured at random. Caribou and wolves were also captured with a net gun fired from a helicopter, however, after 6 years of studying caribou in the area, we have no information to suggest caribou collaring was biased. We also believe we had at least one collar in every wolf pack within the polygon around wolf locations.

We determined the proportion of moose telemetry locations in fen/bog and well-drained habitat types for each individual by season. To correct for the collaring bias, we categorized each collared moose as Upland or Wetland based on its winter locations. We randomly sampled a total of 37 moose from the Upland and Wetland categories in proportion to the number of Upland and Wetland moose observed on the winter grid surveys. This procedure was repeated 1000 times, and the resulting data was used to determine the mean proportion of each habitat used by moose and the electivity for each season. This is a conservative approach because the grid survey data is also biased towards fen/bogs due to easier sightability in that habitat; therefore, we were more likely to find no support for the prediction.

Wolf predation higher in and near patches selected by moose

While locating radio-collared wolves by telemetry during winter, we found 76 predation sites where wolves had killed an ungulate (18 moose, 20 deer, and 38 unknown) and recorded their location with a GPS. Kills were distinguished from scavenging by the presence of blood spread around kill sites. No identifiable caribou kill sites were found while locating radio-collared wolves. Wolf predation site locations were entered into the GIS. We compared the proportion of predation sites found in fen/bog and well-drained habitats to the proportion of those habitat types in the minimum convex polygon around wolf locations using Ivlev's electivity index.

We used data from aerial caribou calf surveys conducted by helicopter in March 1994, 1995, 1996 and 1997 to assess whether caribou that use areas near the edges of fen/bogs have a higher probability of losing their calves than do those located further from moose habitat. We used the GIS to determine the distance to well-drained habitat of groups with and without calves and compared these distances using a General Linear Model (GLM) with year as a random factor. We also used the GIS to determine the mean distances to well-drained habitat for all locations for each female caribou by season and by year. We then identified caribou as being in a group with calves or in a group without calves during the calf survey for each year. We compared the mean distance to well-drained habitat between the With Calf and Without Calf categories by season for the 12 months preceding each calf survey using a GLM. We included season as a fixed factor and year as a random factor in the GLM. In this analysis individual caribou cows could not be classified as being with or without a calf. Rather, all cows in a group with at least one calf were included in the With Calf category because the calf could have belonged to any of them. The error introduced by doing this makes the analysis less likely to show support for the prediction because cows without calves are being included in the With Calf category, reducing the ability to detect differences between the With Calf and Without Calf categories. These analyses of calf survival are both based on the assumption that all female caribou are equally likely to get pregnant and produce a calf regardless of location. We have no reason to believe this assumption is false. The adult female pregnancy rate in 1994 was 86% (Stuart Smith et al. 1997).

Disproportionate predation by wolves

To assess the proportion of caribou and moose in the diet of wolves we collected 969 wolf scats from the study area between 1994 and 1996. Scats were collected along seismic lines and roads, at den and rendezvous sites, and when found opportunistically, as described by Kennedy and Carbyn (1981). The scats were analysed by T. Packer (Alberta Natural Resources Service forensic lab, Edmonton) to identify hair and other contents of the scats. Ungulate hairs were identified as caribou, moose or deer (white-tailed and mule deer were not differentiated) where possible. Some hairs, particularly fragments, could not be positively identified and were classified as Unknown Ungulate. Other hairs were identified as Deer/Moose, having features of these species such as colour or banding that rule out caribou, but that were not distinctive enough to confirm which of the three species (moose, white-tailed deer or mule deer) they came from. Non-deer family hair was either classified as Non-Ungulate or identified to species.

To be conservative (by reducing the likelihood of finding support for the prediction), we compared the proportion of caribou and moose in the diet using only the data from hairs identified to species. We used Weaver's (1993) equation for the relationship between the body mass (kg) of prey (X) and the mass (kg) of prey per scat (Y): $Y = 0.439 + 0.008X$, to adjust the proportion seen in scats to a proportion of individuals. We assumed a mean mass of 115kg for caribou and 425kg for moose . These are a low estimate for caribou and a high estimate for moose. The use of these values in our calculations biases the analysis toward finding no support for the prediction because the larger the difference in assumed mass, the larger the proportion of caribou in the diet will appear. We determined the upper and lower 95% confidence limits for the proportion of caribou in the diet based on the binomial distribution and sample size (Sokal and Rohlf, 1987 p.333).

We used two approaches to determine if caribou were being eaten in proportion to their availability in the environment. We first compared the proportion of caribou in the diet to the proportion of caribou in the environment based on density estimates of caribou and moose from stratified random block surveys. Stuart-Smith et al. (1997) reported a winter (1993/1994) density estimate of 7.7 (SD = 5.5) caribou/100km^2 in the study area and winter (1993/1994) density estimates of moose in the four Wildlife Management Units that overlap the study area were 10, 11, 21 and 28 moose/100km^2 (Alberta Natural Resources Service unpublished data from WMUs

519, 518, 512, and 516 respectively). To be conservative we used the highest moose density of 28 moose/100km^2 in our analyses. Because of the large uncertainty associated with the density estimate for caribou, our second approach was to assess the probability of disproportionate predation without using the caribou density estimate. We did this by asking "If caribou were eaten in proportion to their availability in the environment, then what would their density be, based on the proportions of caribou and moose in the scats and the density of moose?" We estimated the density of caribou (C) with the equation $C = p_c/p_m(M)$, where p_c and p_m are the proportions of caribou and moose in the diet respectively and M is the density of moose. We then multiplied C by the area of the study site and compared the resulting estimate of caribou numbers to the minimum number of caribou known to be in the study area during March calf surveys to test the assumption that caribou were eaten in proportion to their availability.

RESULTS

Habitat use of caribou, wolves and moose

The proportion of caribou locations within well-drained habitat was low for all seasons, with the highest proportion among these occurring in Fall (Fig. 2.3). A high proportion of wolf locations was within well-drained habitat in all seasons, with the lowest level occurring in Fall. The proportion of locations in well-drained habitat was higher for pack locations than for individual wolf locations in all seasons. Moose showed the lowest use of well-drained habitat in Spring. Wolves and moose had a higher proportion of locations in well-drained habitat than did caribou during all seasons.

Based on habitat availability within the minimum convex polygons around caribou, wolf, and moose telemetry locations (Fig. 2.4), caribou selected against well-drained habitat while moose and wolves selected for it (Fig. 2.5) during all seasons. Caribou and moose both showed the lowest use of well-drained habitat in Spring. Caribou showed strong selection for different habitat from moose and wolves; habitat types were highly separated in the environment; therefore, caribou must have been spatially separated from moose and wolves. The spatial separation of caribou and wolves was evident from the distribution of telemetry locations (Fig. 2.6).

Habitat use was similar among wolf packs. None of the wolf packs within the study area had territories that were predominantly in fen/bog habitat (Fig. 2.7). Rather, pack territories tended to be centred on the Athabasca River valley or in the Pelican Hills in the southwest portion of the study area. Many of the minimum convex polygons around pack locations include a considerable proportion of fen/bog habitat; however, all packs had a majority of locations in well-drained habitat. Only one wolf was captured at a bait station within fen/bog habitat. This wolf was a member of the Joli pack, which had the highest proportion of locations in fen/bog habitat. The Joli pack appeared to be a small, unstable pack with a poorly established territory between the Bourgoin and Upper packs along the Athabasca River, and as such, may have been squeezed into the fen/bog complexes on either side of the river. Many of the telemetry locations within fen/bog habitat from other packs were associated with major creeks draining into the Athabasca River.

Wolf predation higher in and near patches selected by moose

Of the 76 predation sites found during telemetry locations of wolves, 57 (75%) were found in well-drained habitat. Based on the habitat available within the minimum convex polygon around wolf locations, predation sites had an electivity index for well-drained habitat of 0.57. None of the predation sites found while locating wolves were identified as a caribou.

The locations of caribou groups with calves observed during the March calf surveys were on average 439 m further from well-drained habitat than were groups without calves, although this difference was not quite significant ($F_{1,152} = 5.13$, $P = 0.097$). Telemetry locations of caribou that were found in groups with calves during the March calf surveys were also further ($F_{1,567} = 71.29$, $P = 0.001$) from well-drained habitat than were locations of caribou in groups without calves throughout the previous 12 months (Fig. 2.8). There was no effect of season or year on the distance of caribou locations from well-drained habitat.

Disproportionate predation by wolves

Caribou formed only a small proportion of the wolves' diet based on scat analysis (Table 2.1). Moose was the most common item in the scats.

Table 2.1. Contents of 969 wolf scats collected in northeastern Alberta between 1994 and 1996.

Contents	Number of Items	%
Moose	415	42.8
Caribou	3	0.3
Deer	61	6.3
Moose/Deer	140	14.4
Unknown Ungulate	126	13.0
Beaver	95	9.8
Other Non-Ungulate	74	7.6
Plant Matter	55	5.7

Correcting the occurrence of caribou and moose in scats to reflect individuals consumed provides a ratio of 0.0354 [3(0.439 + 0.008 * 115)/115] caribou to 3.7475 [415(0.439 + 0.008 * 425)/425] moose, or 0.94% caribou. The upper 95% confidence limit is 2.48% caribou, or 0.0254 caribou per moose. The density estimates for caribou (7.7/100km^2) and moose (28/100km^2) provide a caribou to moose ratio of 0.275:1, or 21.6% caribou.

Working in the other direction and assuming caribou are eaten in proportion to their availability in the environment, caribou density was estimated to be 0.7/100km^2 (28 moose/100km^2 * 0.0254 caribou per moose). Multiplying by the area of the study site (20,000km^2) provides a population estimate of 143 caribou. Minimum population estimates from calf surveys in 1994, 1995, 1996, and 1997 were 190, 195, 354, and 273 respectively.

DISCUSSION

Our data support all three predictions of the Spatial Separation Hypothesis. Caribou and moose selected different habitat types while wolves and moose selected the same habitat type. This resulted in a spatial separation between caribou and wolves. Wolf predation pressure was higher in well-drained areas, and the probability of caribou calf survival appeared to be influenced by the distance of cows to well-drained habitat. Lower use of well-drained habitat by moose during spring may reflect dispersion into low predation risk areas by calving females. Caribou also showed the lowest use of well-drained habitat during spring, a time when wolves are more restricted in their movements to the area around their den sites. Deer were also found in the study area and comprised a portion of the wolves' diet. We believe deer in the study area were more closely associated with upland habitat than were moose based on incidental observations of deer during the study. Deer provided additional alternate prey in well-drained habitat and likely increased the attractiveness of well-drained sites as foraging areas for wolves.

The difference between habitat use determined by wolf pack locations and habitat use determined by individual wolf locations indicated that collared wolves in the same pack traveled together slightly more often in fen/bog complexes than in well-drained habitat. This difference may have given wolves a higher probability of killing prey on encounter in fen/bogs, or may reduce the area searched. Comparing the electivity of wolf predation sites and individual wolf locations, there were more kills made per unit time in well-drained habitat than in fen/bog complexes. However, comparing the electivity of predation sites to pack locations suggests that an equal number of kills were made per unit time in each habitat. Given the lower density of prey in fen/bog complexes, packs must have had higher success rate per encounter in this habitat.

We used conservative assumptions in our estimate of the proportion of caribou in the diet to bias the analysis toward finding no selection, and we still found that caribou were not eaten in proportion to their availability. The ratio of caribou to moose in the environment based on density estimates was an order of magnitude greater than the ratio of caribou to moose in the wolves' diet. We knew that considerably more caribou were present in the study area than was estimated with the assumption of proportionate predation. Although there is error involved in both of these calculations, we believe the magnitude of the difference and the consistent results were strong evidence that caribou were not killed in proportion to their availability in the study area.

Our results were consistent with studies of caribou–moose–wolf interactions in British Columbia (Bergerud et al. 1984, Seip 1992) and Ontario (Cumming et al. 1996), and with caribou avoidance of fen/upland boundaries previously reported from northeastern Alberta (Stuart-Smith et al. 1997). Stuart-Smith et al. (1997) did not however detect higher predation pressure near fen/upland boundaries based on the mortality locations of collared caribou. Nor did they detect a difference in calf survival between two areas with different landscape patterns of fen/bog and well-drained habitats. This suggests that fen/bog complexes in both areas were sufficiently large to provide a spatial refuge for caribou. Our data suggest that within these areas, caribou near well-drained habitat are more likely to lose their calves than individuals that remain more distant from well-drained habitat.

These results support the theoretical predictions that multiple prey species may persist under predator-mediated apparent competition when prey species occupy different habitat patches (Holt 1984). In this instance, predator aggregation in patches with high prey density results in a refuge for prey in lower density patches. However, Holt and Kotler (1987) demonstrate that the theoretical outcome of shared predation between two species of prey is dependent not only on the spatial distribution of prey types, but also on the foraging behaviour of the predator. If predators forage optimally among patches, spatially separated prey should experience apparent mutualism (increases in one prey type result in increases of the other prey type). Or, if predators use patches independently of prey availability and are not limited by prey density, alternate prey may also experience apparent mutualism because the consumption of individuals of one prey species reduces the time available to predators to prey on the other species (Holt 1977, Holt and Kotler 1987). Under either of these conditions one may expect increased moose densities to result in increased caribou densities. However, if predators are limited by prey density (i.e. respond numerically to increases in prey density) and there is any predator 'spillover' between patches, then a predator population supported by productive prey in one patch, can exploit prey in another patch to the point of extinction (Holt 1984).

The spatial separation of caribou and moose reduced predation pressure on caribou, but did not provide a total refuge from wolves. Caribou were not an important component of wolves' diet, however wolf predation was the main proximate limiting factor for caribou in northeastern Alberta (Stuart-Smith et al. 1997). Although prey densities were apparently insufficient to allow wolves to permanently occupy fen/bog complexes, forays from well-drained habitat must have been sufficient to allow some predation on caribou to occur (based on the large proportion of caribou mortalities attributed to predation by Stuart-Smith et al. 1997). Therefore, increases in moose density do not need to occur within fen/bog habitat to result in higher predation pressure on caribou through apparent competition.

Our study was not designed to determine the ultimate reasons why caribou, moose, and wolves show selection for the habitats they do. For example, caribou may have been avoiding moose, or simply avoiding wolves, or they may have occupied fen/bogs because they prefer to forage on the lichens found in these areas. However, regardless of why caribou in northeastern Alberta selected fen/bog habitat, this selection reduced the level of predation they experienced. It is this proximate result of habitat use on the level of predation experienced by caribou populations that is of primary concern for their conservation.

We believe timber harvesting close to fen/bog complexes occupied by caribou may considerably increase the predation pressure on caribou. In such a scenario (Fig. 2.9), we expect the regenerating browse immediately after timber harvesting to cause an initial decrease in predation pressure on caribou as existing moose concentrate in the new high forage areas (Gasaway et al. 1989, Peek 1974). Then, as moose respond numerically to the new browse (Franzmann and Schwartz 1985), they should fill in previously occupied habitat and return to their original density in fen/bog complexes, while maintaining elevated densities in the logged area. Elevated moose densities may persist for several decades (Bangs et al. 1985, Kelsall et al. 1977, Schwartz and Franzmann 1989) and may peak at densities many times the original level (Peek 1974,). These elevated moose densities will cause a numeric response in wolves (Messier 1994). Wolves are expected to increase in at least a linear fashion with respect to moose density (Marshal 1997) and may show a sharp increase at low moose densities (Messier 1994). Elevated wolf densities should increase the incidental predation on caribou. If wolf behavior does not change, the increase in predation pressure would be directly proportional to the numeric increase in wolves. However, wolves are predicted to spend more time in the new high moose density areas resulting in a lower increase in predation pressure for caribou than expected by the numeric response alone. After a time, regenerating trees will outgrow the reach of moose and moose numbers are expected to decline. However, there will likely be a time lag in the wolf population response, and the abundant wolves may turn proportionately more towards alternate prey in the face of declining moose densities. It is at this point, 20 to 40 years after harvesting, that caribou populations may experience the greatest increase in wolf predation rates. Caribou in northeastern Alberta appear to be stable or slightly decreasing (Fuller and Keith, 1981; Stuart-Smith et al. 1997), so even small changes in predation pressure may have significant consequences to the long-term viability of local populations.

It is unknown whether increasing moose populations in areas after logging will "spill over" into fen/bog habitats. If the density of moose within fen/bog complexes increased enough to produce a total prey density sufficient to support resident wolves, caribou would then presumably be consumed in proportion to their availability. In this study, caribou were consumed in approximately one tenth of their availability relative to moose. Therefore in this scenario, one could expect an order of magnitude increase in predation rates on caribou. Even if high moose and wolf densities only lasted for a short time, this level of predation may cause the extirpation of caribou from a fen/bog complex. Low movement rates between fen/bog complexes (Stuart-Smith et al. 1997) suggests that recolonization of previously occupied patches would be rare.

Historically, caribou in northeastern Alberta must have survived localized increases in moose densities after wildfires. However, current conditions may not provide caribou with the options they once had. It is possible that fen/bog complexes previously provided a more complete refuge for caribou, and that recently the many new linear corridors created during oil and gas exploration, production and distribution have eroded the effectiveness of these refuges. Wolves in northeastern Alberta use linear corridors more than expected by chance, while caribou avoid them (Chapter 3) and linear corridors may allow wolves to travel more quickly and further into caribou range (Chapter 4). Oil and gas, heavy oil, and peat extraction facilities may also reduce the options available to caribou for movements within patches. In addition, timber harvesting may result in a more widespread increase in moose than wildfires because of the dispersed nature of current two-pass harvesting designs. The juxtaposition of forage and cover in logged areas, a characteristic often cited as important for creating good moose habitat (reviewed by Thompson and Stewart 1997), may be higher than occurred following large fires. Therefore, caribou may be less able to endure increases in moose and wolf populations in the existing landscape in northeastern Alberta.

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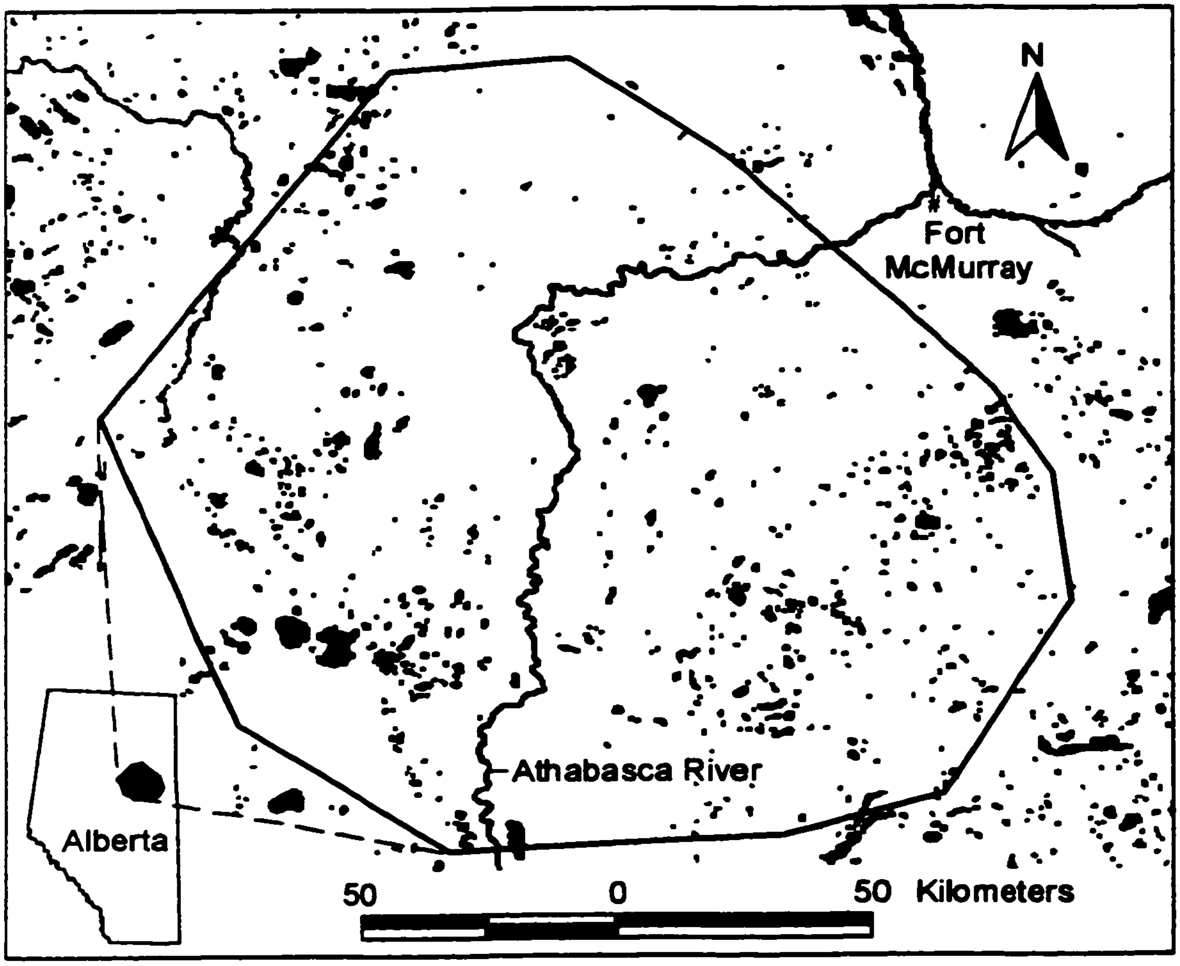

Figure 2.1: Location of study area, lakes, and major rivers in northeastern Alberta, Canada, 1993-97.

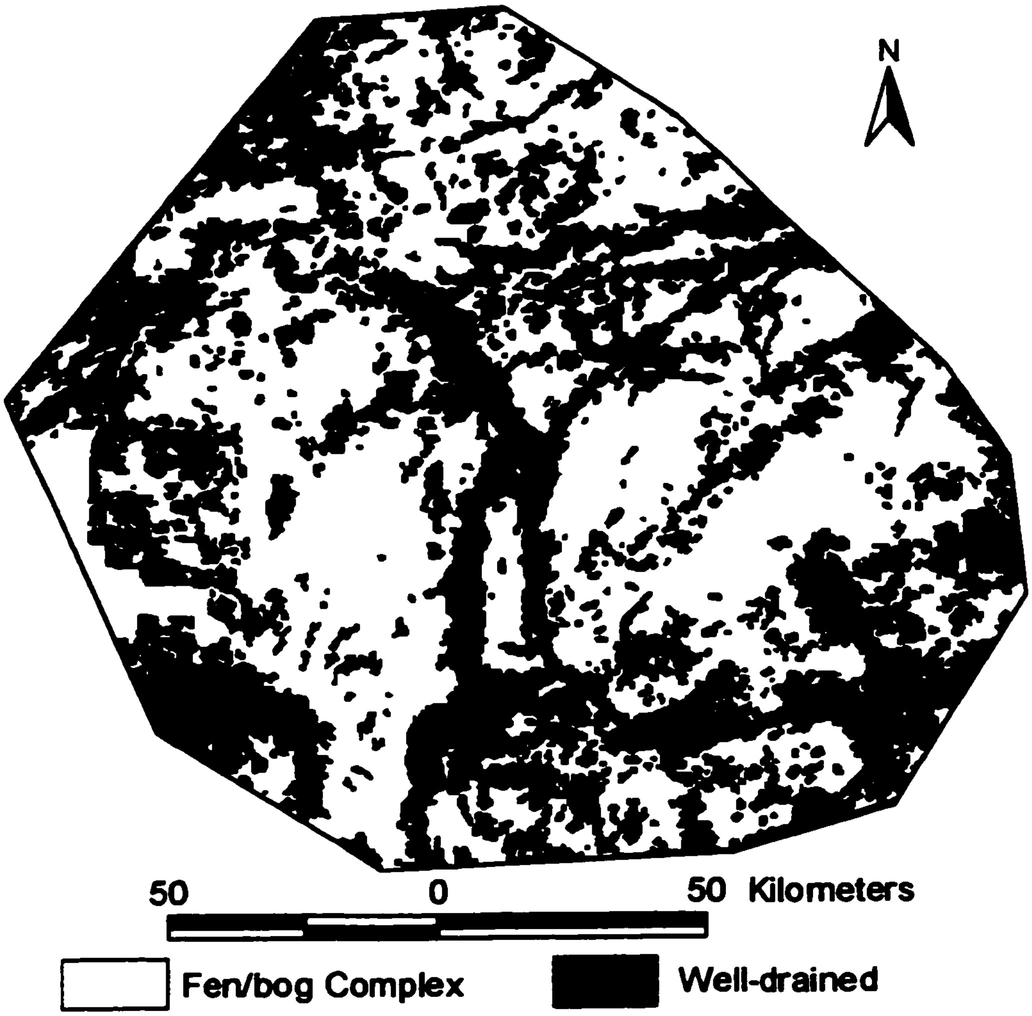

Figure 2.2: Fen/bog and well-drained habitat types in northeastern Alberta, 1993-97.

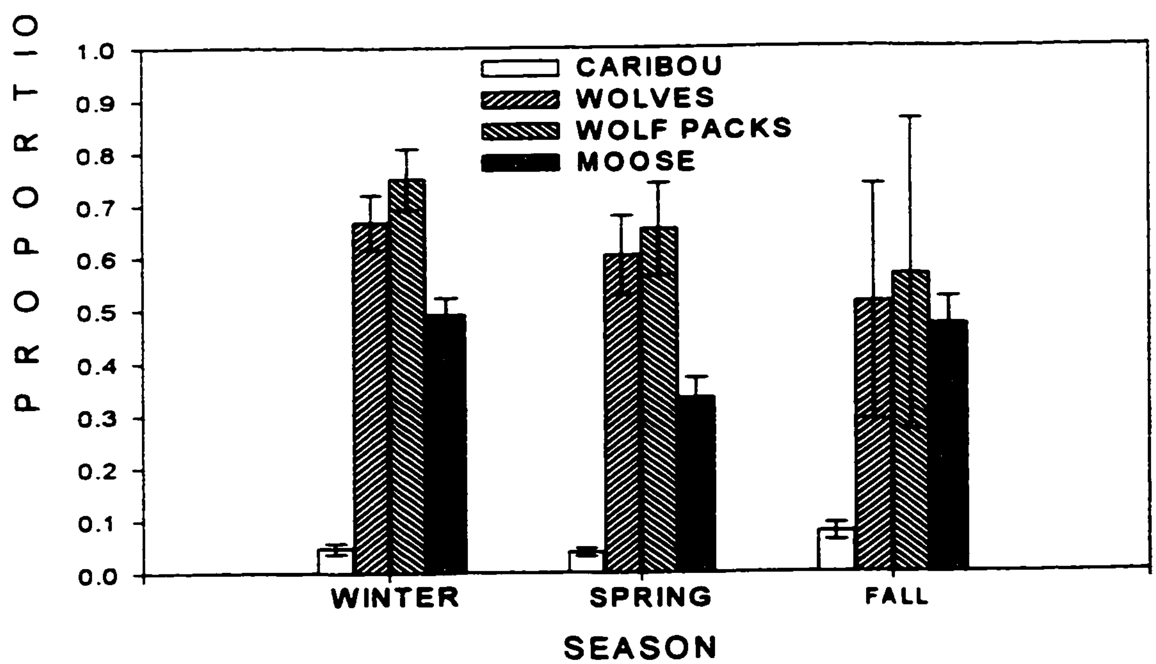

Figure 2.3: Proportion of caribou, wolf, wolf pack, and moose telemetry locations in well-drained habitat in northeastern Alberta, 1993-97. Error bars are S.E.

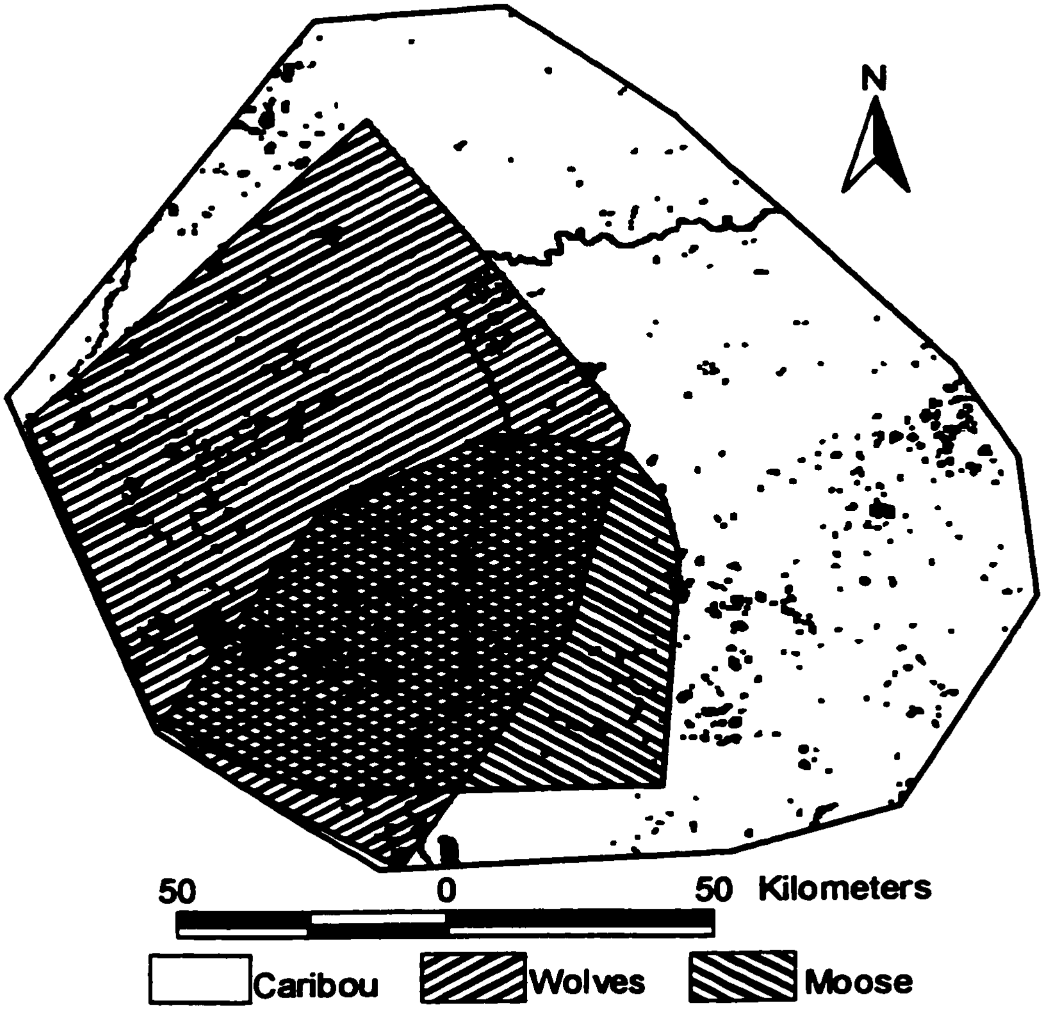

Figure 2.4: Minimum convex polygons around caribou, wolf, and moose telemetry locations in northeastern Alberta, 1993-97.

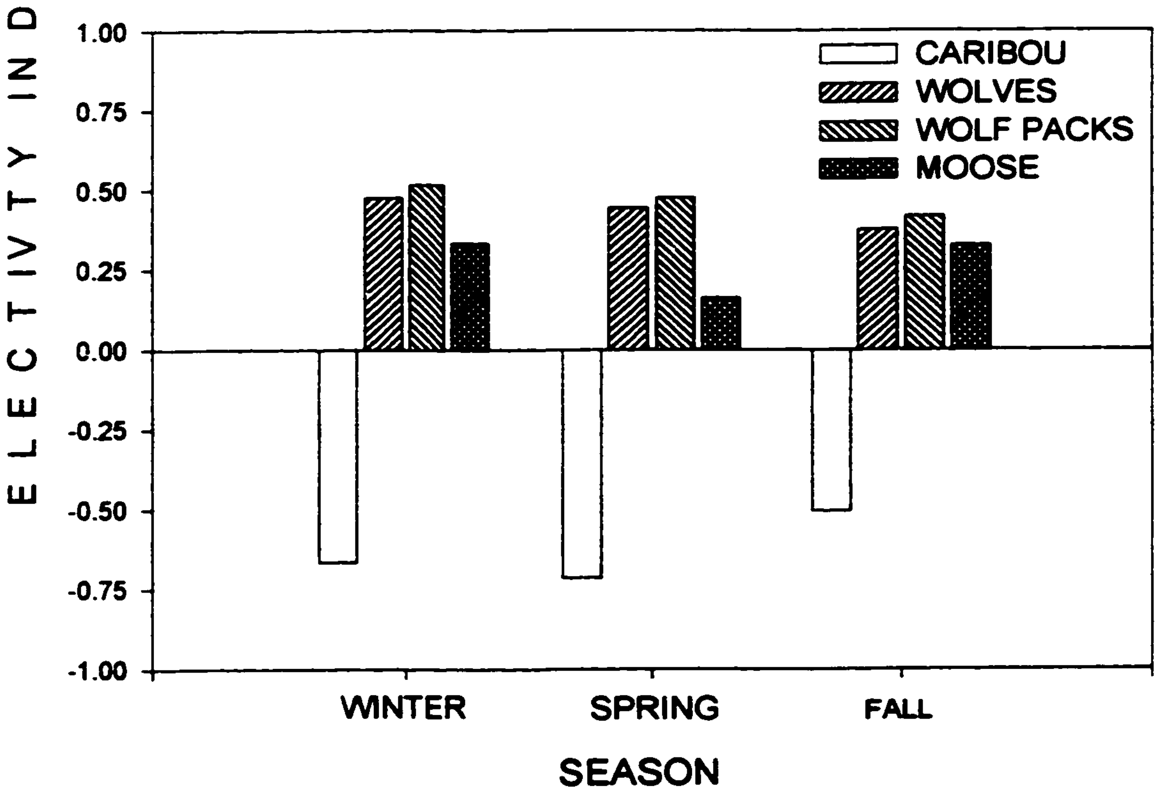

Figure 2.5: Ivlev's electivity index for well-drained habitat from caribou, wolf and moose telemetry locations in northeastern Alberta, 1993-97.

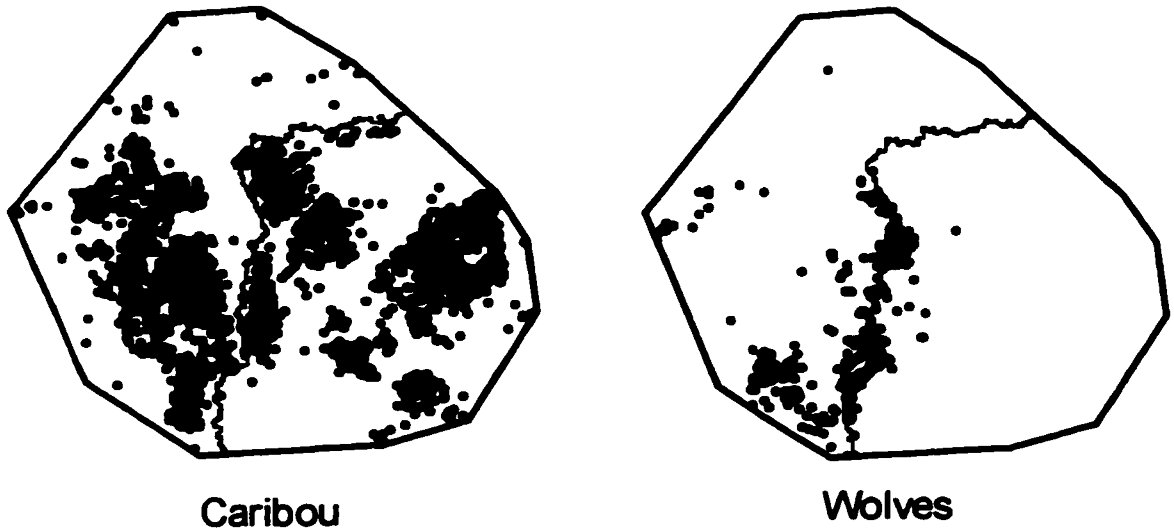

Figure 2.6: Telemetry locations of caribou and wolves in northeastern Alberta, 1993-97

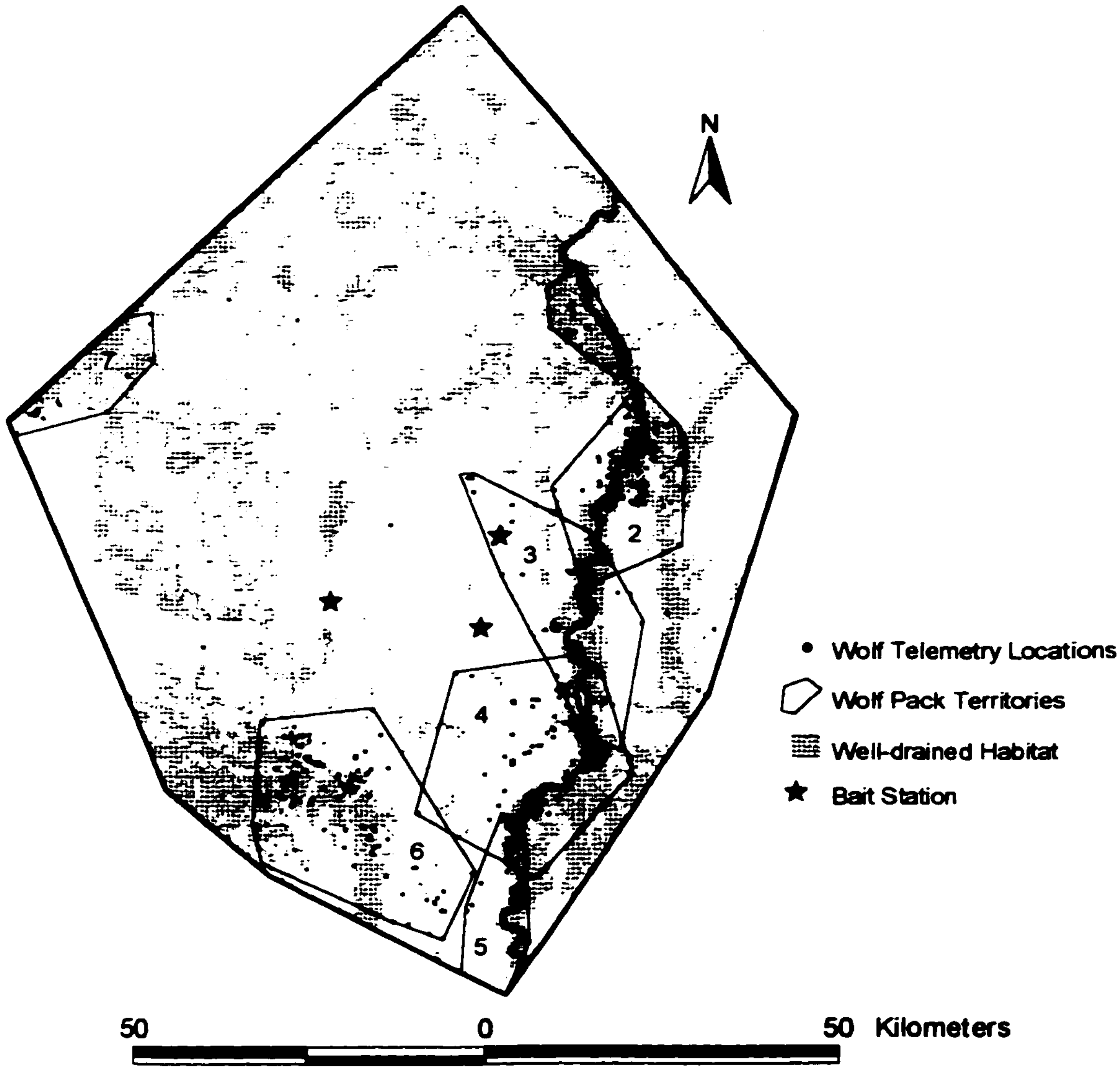

Figure 2.7: Location of wolf pack territories, wolf telemetry locations, and initial collaring bait stations in northeastern Alberta, 1994-1997. Pack names are (1) Grande, (2) Bourgoin, (3) Joli, (4) Upper, (5) Iron, (6) Crooked, and (7) Horsetail.

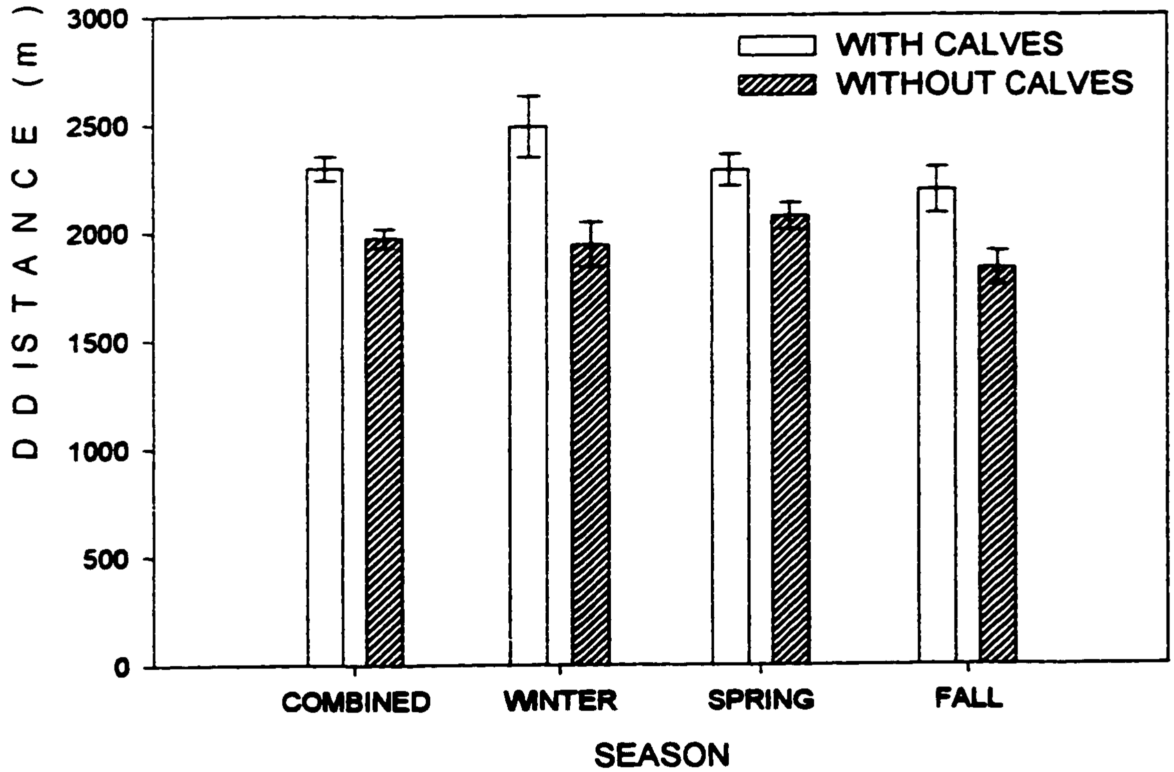

Figure 2.8: Mean distance of caribou locations (from the preceding 12 months) to well-drained habitat for individuals found in groups with and without calves during March calf surveys conducted in northeastern Alberta, 1994-1997. Error bars are S.E.

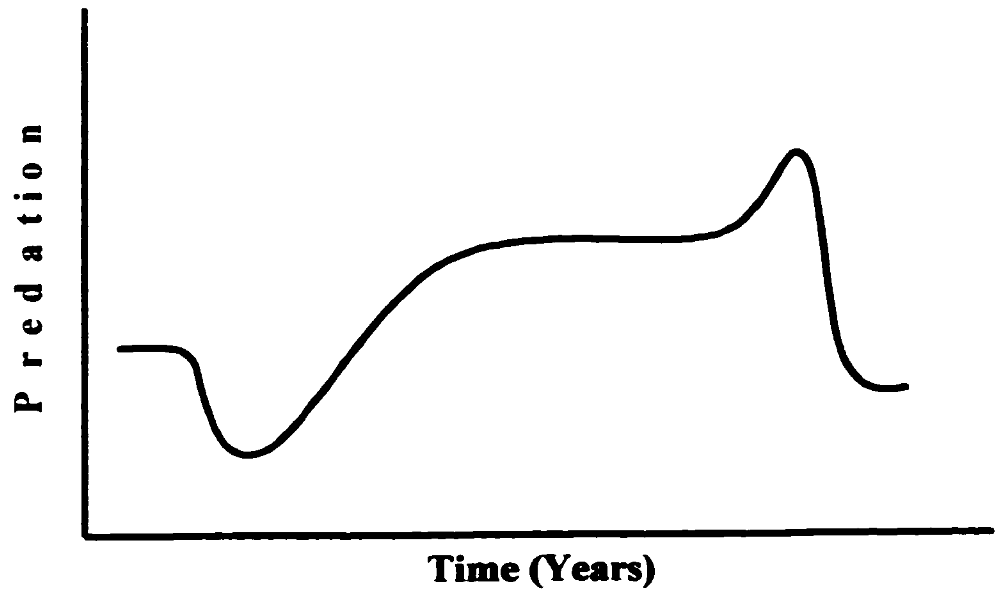

Figure 2.9: Predicted changes in predation pressure experienced by caribou populations in northeastern Alberta following timber harvesting.

Chapter 3

The Distribution of Caribou and Wolves in Relation to Linear Corridors[2]

INTRODUCTION

Linear corridors such as roads, seismic lines, power lines, and pipeline right-of-ways are a common component of industrial operations in forested areas. There is considerable evidence that these corridors can affect the distribution, movements, and population dynamics of many wildlife species (see Jalkotzy et al. 1997 for an extensive literature review).

Woodland caribou (*Rangifer tarandus caribou*) populations in Alberta have declined over the last century (Edmonds 1988, but see Bradshaw and Hebert 1996) and are currently identified as 'Threatened' in the regulations of the Alberta Wildlife Act. Increasing industrial development by the petroleum and forest industries in northeastern Alberta has raised concern about the potential effects of linear corridor development on woodland caribou populations. Human harvest or predation by wolves (*Canis lupus*) is often cited as the main cause of caribou mortality (Bergerud 1974, 1978, 1983, 1988, Fuller and Keith 1980, Bergerud et al. 1984, Edmonds and Bloomfield 1984, Johnson 1985, Edmonds 1988, Seip 1992). Linear corridors may provide increased access for hunters into caribou range, thereby increasing legal and illegal hunting pressure. It has been hypothesized that linear corridors may also affect wolf-prey dynamics (Bergerud et al. 1984, Edmonds and Bloomfield 1984). Wolves are often reported to be less abundant in areas with many roads (Thiel 1985, Jensen et al. 1986, Mech et al. 1988, Fuller 1989, Fuller et al. 1992); however, roads and other corridors that receive little human use may be attractive to wolves as easy travel routes (Horejsi 1979, Edmonds and Bloomfield 1984, Eccles and Duncan 1986, Thurber et al. 1994).

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[2] This chapter has been submitted for publication to the Journal of Wildlife Management with Adam R. C. James and A. Kari Stuart-Smith as authors.

In northeastern Alberta, human harvest and wolf predation accounted for 19% and 56% of caribou mortalities respectively between 1991 and 1995 (Stuart-Smith et al. 1997). Caribou in this area predominantly inhabit large fen/bog complexes (Bradshaw et al. 1995, Stuart-Smith et al. 1997) and wolves are most commonly found in surrounding well-drained habitats (Chapter 2). It has been suggested that linear corridors may provide wolves with increased access into caribou range (Bergerud et al. 1984) and allow them to travel more quickly through their environment. Caribou populations are stable or declining slowly in northeastern Alberta (Stuart-Smith et al. 1997); therefore, small changes in hunting or predation pressure may have a significant effect on caribou population dynamics.

To test the hypotheses that linear corridors affect the distribution of caribou and their risk of predation or being shot, we compared the distance from caribou telemetry locations and wolf telemetry locations to the nearest linear corridor with the distance from random points to the nearest linear corridor. We also compared the distances to linear corridors between caribou mortalities and live caribou locations, and between wolf predation sites and wolf locations. Our predictions were:

i) Caribou locations are further than random to linear corridors.
ii) Caribou mortality sites are closer than live caribou locations to linear corridors.
iii) Wolf locations are closer than random to linear corridors.
iv) Wolf predation sites are closer than wolf locations to linear corridors.

This project was conducted as part of a long-term study of woodland caribou in northeastern Alberta, ongoing since 1991 (see Bradshaw 1994, Bradshaw et al. 1995, Bradshaw et al. 1997, 1998, Stuart-Smith et al. 1997).

STUDY AREA

This study was conducted in northeastern Alberta, Canada (56° N, 112° W), encompassing approximately 20,000 km^2 of boreal mixed-wood and peatland vegetation. The Athabasca River flows through the middle of the study area. Elevation varied from 500 to 700 m above sea level with little topographic relief. Wetlands were dominated by black spruce (*Picea mariana*) or black spruce-tamarack (*Larix laricina*) fens and bogs; well-drained sites were dominated by aspen (*Populus tremuloides*), white spruce (*Picea glauca*), and jack pine (*Pinus banksiana*). See Bradshaw et al. (1995) for a more detailed description of vegetation in the study area. Caribou range polygons were defined for the study area by Bradshaw (1994) based on caribou habitat selection and peatland habitat mapping (Fig. 3.1). Maximum snow depths in the area did not exceed 60 cm during the study (E. Dzus pers. com.).

METHODS

As part of a long-term study, 117 adult caribou were fitted with VHF radio-collars with mortality switches between 1991 and 1997 (Stuart-Smith et al. 1997). We attempted to capture animals throughout the study area, preferentially selecting females over males to obtain information on reproduction and calf survival. Ninety-eight of these collars were active during this study (1994-1997). We located radio-collared individuals approximately every 2 weeks by aerial telemetry and recorded the latitude and longitude of each location with a Global Positioning System (GPS) unit. GPS locations should be accurate to within 100m (Wells 1986) and error associated with telemetry may add to the total location error. However, neither source of error is directionally biased. We entered caribou locations (n = 2,616) into a Geographical Information System (GIS) for analysis and used the GIS to determine the minimum convex polygon home range for each individual. Twenty-seven collared caribou died during the study. We classified the cause of each mortality as human (shot), predator, disease/injury, or unknown, based on remains and signs found near the radio-collar. We recorded a GPS location at each mortality site and entered these into the GIS.

Between 1994 and 1997, we placed VHF collars on 20 wolves from 7 packs (Bourgoin, Upper, Joli, Iron, Grand, Crooked, and Horsetail) and on 3 loners. We located radio-collared wolves by aerial telemetry every 2-3 weeks and collected additional locations twice a day for 15 consecutive days during the winters of 1996 and 1997 to locate wolf predation sites. When > 2 collared individuals in the same pack were located together, we considered this to be one location. However, when individuals from the same pack were located apart, we used each location. We recorded 592 wolf locations and used the GIS to determine the minimum convex polygon home range for each pack. We had insufficient data from lone wolves to describe individual home ranges so we considered all loner locations together. We also used the GIS to determine whether individual wolf locations fell within caribou range. We found 76 predation sites (18 moose, 20 deer, and 38 unknown) and recorded their location with a GPS. No identifiable caribou kill sites were found while locating wolves by aerial telemetry.

All of the linear corridors within the study area in 1997 were digitized from aerial photos and entered into the GIS. The location error for the digital linear corridor data was approximately 50m (R. Farries, Lormel Consultants, personal communication). We did not classify linear corridors into categories (e.g. road, pipeline, seismic line, etc.), however the majority (approximately 25,500 km) of linear corridors in the study area were seismic lines, trails, or pipeline right-of-ways. There were few gravel roads and one paved road (approximately 1,350 km combined).

We used the GIS to generate 10,000 random points within the study area, from which we determined a random set for each caribou and each wolf pack based on their minimum convex polygon home ranges. Each random set was identified with a caribou collar number or pack number. The number of points in each random set was dependent on the home range size and ranged from 62 to 1074 for caribou and from 24 to 1039 for wolf packs. We determined the perpendicular distance of all locations and random points to the nearest linear corridor using the GIS. Using the 1997 distribution of linear corridors in our analyses reduces the power to detect differences from random because we began collecting caribou and wolf locations in 1994 when some of the linear corridors may not have been present. This reduces the chances of detecting differences in the analyses described below, but does not introduce any directional bias.

We used a General Linear Model (GLM) to compare the distance to the nearest corridor between caribou locations and random points. We included collar number as a fixed factor in the GLM and explored a significant interaction between collar number and point type by running separate analyses for each collared caribou. For each collar we calculated the difference between mean caribou distance to corridor and mean random distance to corridor. We used a t-test to test the null hypothesis that the average of these differences was equal to zero. We also repeated these analyses using only caribou locations and random points that fell within peatland types selected by caribou (Bradshaw et al. 1995) to avoid any potential confounding effects of habitat selection. However, the distribution of linear corridors was not related to the distribution of fen/bog or well-drained habitat types (Dyer in prep.). Additionally, the density of linear corridors within fen/bog habitat would not allow the comparison of distance to nearest corridor to be influenced by the distribution of corridors in well-drained habitat. An example of the distribution of linear corridors, habitat types, and caribou locations is shown in Fig. 3.2.

We used a GLM to compare the distance to nearest corridor among caribou mortalities and both random points and live locations from all caribou. Post hoc tests were completed using Least Significant Difference (LSD) if the assumption of equal variance was met, or Tamhane's T2 if the assumption was not met. We reanalyzed the caribou mortalities to consider the cause of death. For wolf- and human-caused mortalities, we used the Wilcoxon paired-sample test to compare the distance to nearest corridor of each mortality location with the mean distance to nearest corridor of the live locations from the individual that died.

We conducted a similar comparison of the distance to nearest corridor between wolf locations and random points. We suspected that the use of linear corridors might differ between wolf packs and between an individual's movements in caribou range (as described by Bradshaw 1994) versus the well-drained matrix habitat. We included pack number and habitat (caribou range or well drained) as fixed factors in the GLM and explored a significant interaction between habitat and point type by running separate analyses for locations from each habitat type. Within well-drained habitat we further explored a significant interaction between pack number and point type by running separate analyses for each pack.

We used a General Linear Model to compare the distance to nearest corridor among predation sites and both random points and wolf locations within caribou range. We included pack number as a fixed factor. Post hoc tests were completed using LSD if the assumption of equal variance was met, or Tamhane's T2 if the assumption was not met.

RESULTS

Caribou Locations

When comparing the distance of caribou locations and random points from linear corridors, we found a significant point type * collar interaction ($F_{97,3780} = 4.7$, $P < 0.001$) indicating that individual caribou responded differently to linear corridors. Of the 98 caribou, 35 were significantly further from linear corridors than were random points and 3 caribou were significantly closer (Fig. 3.3). The mean difference between the distance to the nearest corridor from caribou locations and the distance to the nearest corridor from random points (106m) was significantly different than zero ($T = 5.1$, $df = 97$, $P < 0.001$). We found the same pattern when we used only caribou locations and random points that fell within the peatland types selected by caribou.

Caribou Mortalities

The distance to linear corridors of caribou mortalities ($n = 27$) was not significantly different than the distance to linear corridors of random points or live caribou locations. However, when we considered the cause of mortality we found that mortalities attributed to wolf predation (n = 5) were closer to linear corridors than were live caribou locations (mean difference = 316m, SE = 213.2, T2 P = 0.035), but not significantly closer than random (mean difference = 219m, SE = 213.8, T2 P = 0.113). Human-caused mortalities (n = 5) were closer, but not significantly different than live caribou locations (mean difference = 174m, SE = 213.2, T2 P = 0.604) or random points (mean difference = 77m, SE = 213.1, T2 P = 0.936). Two of the five human-caused mortalities were within 30m of a linear corridor. When we compared the distance of the mortality location and the live locations for each individual, we found that all 5 of the mortalities attributed to wolves were closer to linear corridors (Fig. 3.4), with a mean difference of 204m (Wilcoxon T- = 0, $T_{0.05(2),5}$ = 0, P = 0.05). Human-caused mortality sites were not significantly different from individual live locations.

Wolf Locations and Predation Sites

When comparing wolf locations and random points we found a significant point type * habitat interaction ($F_{1,2173}$ = 9.2, P = 0.002) indicating that the relationship between wolf locations and random points differed between habitat types.

Within Caribou Range:-- Wolf locations were on average 134m closer to corridors than were random points ($F_{1,1197}$ = 9.3, P = 0.002). There was also a significant pack effect ($F_{7,1197}$ = 5.7, P < 0.001) reflecting the different densities of linear corridors within each pack's territory. Wolf locations were consistently closer than random to corridors in all pack territories. Predation sites were on average 55m closer to corridors than random points and 79m further from linear corridors than wolf locations; however, neither of these differences were significant.

Outside Caribou Range:-- We found a significant point type * pack interaction ($F_{6,976}$ = 5.8, P < 0.001) indicating that different packs responded differently to linear corridors in outside caribou range. Three packs were significantly closer to corridors (Bourgoin [305m, $F_{1,225}$ = 33.7, P < 0.001], Upper [73m, $F_{1,241}$ = 4.8, P = 0.03], Crooked

[71, $F_{1,218} = 6.3$, $P = 0.01$]), three packs (Iron, Grand, Joli) and loners were no different than random, and the Horsetail pack did not have any outside caribou range.

Table 3.1 summarizes the distance relationships among telemetry locations and random points relative to linear corridors.

Table 3.1. Distance relationships among telemetry locations and random points relative to linear corridors in northeastern Alberta, 1994-1997.

i) Mean distance of collared caribou to corridors	528 m
Mean distance from random points within caribou home ranges to corridors	422 m
Caribou locations were significantly further from corridors (P < 0.001)	
ii) Mean distance from caribou mortalities caused by wolves to corridors	193 m
Mean distance from all live caribou locations to corridors	509 m
Mean distance from live locations for caribou that were killed by wolves	411 m
Wolf caused mortalities were significantly closer to corridors than were all live caribou locations (P = 0.035) or live locations from caribou killed by wolves (P = 0.05).	
iii) Mean distance of collared wolves in caribou range to corridors	328 m
Mean distance from random points within pack territories to corridors in caribou range	462 m
In caribou range, wolf locations were significantly closer to corridors than were random points (P < 0.001).	
iv) Mean distance of collared wolves in caribou range to corridors	328 m
Mean distance from wolf predation sites in caribou range to corridors	407 m
In caribou range, wolf predation sites were not significantly closer to corridors than were wolf locations.	

DISCUSSION

The general trend within the caribou population was towards avoidance of linear corridors. However, there was considerable individual variation in caribou distribution relative to linear corridors. Caribou may avoid corridors as a response to wolf and/or human activity in these areas. Caribou that have had previous encounters along corridors may avoid them as a learned anti-predator strategy. However, caribou may also be attracted to corridors with high quality forage and may also use corridors for ease of travel in areas where encounter rates with wolves and people are otherwise low. There is no evidence that habitat was a limiting factor for caribou in this area. However, given the large number of linear features within the region, even a small level of avoidance may reduce the amount of effective habitat available to caribou. The mean difference of 106m between caribou locations and random points multiplied by approximately 21,000 km of linear corridors within habitat types selected by caribou would represent 2,226 km^2 of potential habitat loss caused by avoidance. This calculation is overly simplistic, but it illustrates that avoidance of otherwise good habitat must be considered when assessing cumulative effects of continued industrial expansion.

Overall, caribou mortalities appeared to be randomly distributed with respect to linear corridors. However, predation-caused mortalities were closer to corridors than live locations of all caribou. This suggests that caribou that occupied habitat near linear corridors were at higher risk of predation than were caribou that lived further from corridors. It also appeared that an individual's risk of predation increased with proximity to linear corridors. We expected that human-caused mortalities would also be closer to linear corridors. The trend was in this direction (human caused mortalities were on average 113m closer to corridors than expected by chance), however, a sample size of 5 was insufficient to show a significant difference. The lack of significance may also be a result of the effective range of modern firearms. Although a shooter may be on a linear corridor, the target could be a considerable distance from the corridor and may run an additional distance after being shot.

Our wolf telemetry data is consistent with past anecdotal evidence that wolves use linear corridors as easy travel routes in areas with limited human activity (Horejsi 1979, Bergerud et al. 1984, Edmonds and Bloomfield 1984, Eccles and Duncan 1986, Thurber et al. 1994). Wolf locations within caribou range were closer to corridors than were random points. This suggests a greater use of linear corridors by wolves than expected by chance, and is consistent with the hypothesis that linear corridors provide wolves with increased access into caribou range (Bergerud et al. 1984, Stuart-Smith et al. 1997). However, these data do not show that wolves are going where they otherwise would not go. Locations from three of the packs were also closer to linear corridors within well-drained habitats. The Iron, Grand, and Joli packs showed no difference from random within well-drained sites. This may be because there were few linear corridors in well-drained sites within these pack's territories.

We expected wolf predation sites within caribou range to be closer to linear corridors than expected by chance. Although the differences between wolf predation sites and random points or wolf locations were not statistically significant, the trend in these data (distance of wolf locations < predation sites < random) may reflect a difference between wolf-prey encounter locations and the final predation sites. Wolves may encounter prey close to linear corridors, but the predation site could be further away after the chase. Although we did not find any caribou kill sites, these data and the caribou mortalities indicate that wolves are not just travelling through caribou range, but are hunting as well.

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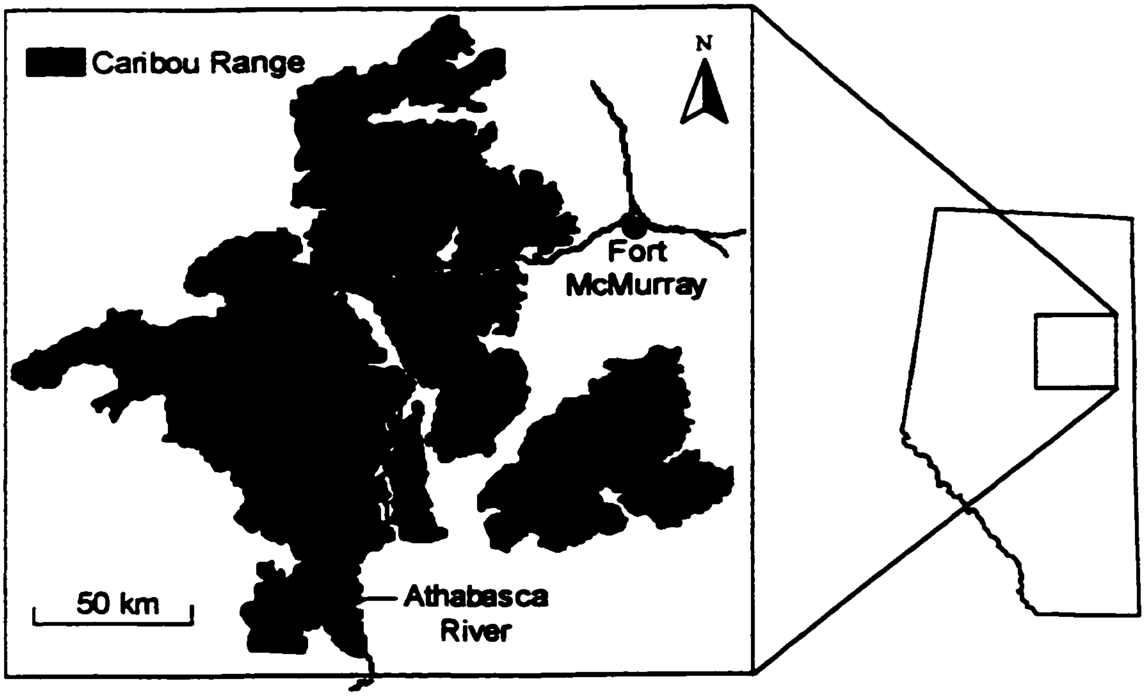

Figure 3.1: Location of study area and caribou range within northeastern Alberta, 1994-97.

Figure 3.2: The distribution of linear corridors, habitat types (white = fen/bog, grey = well-drained), and caribou locations within 4200 km^2 in northeastern Alberta, 1994-97.

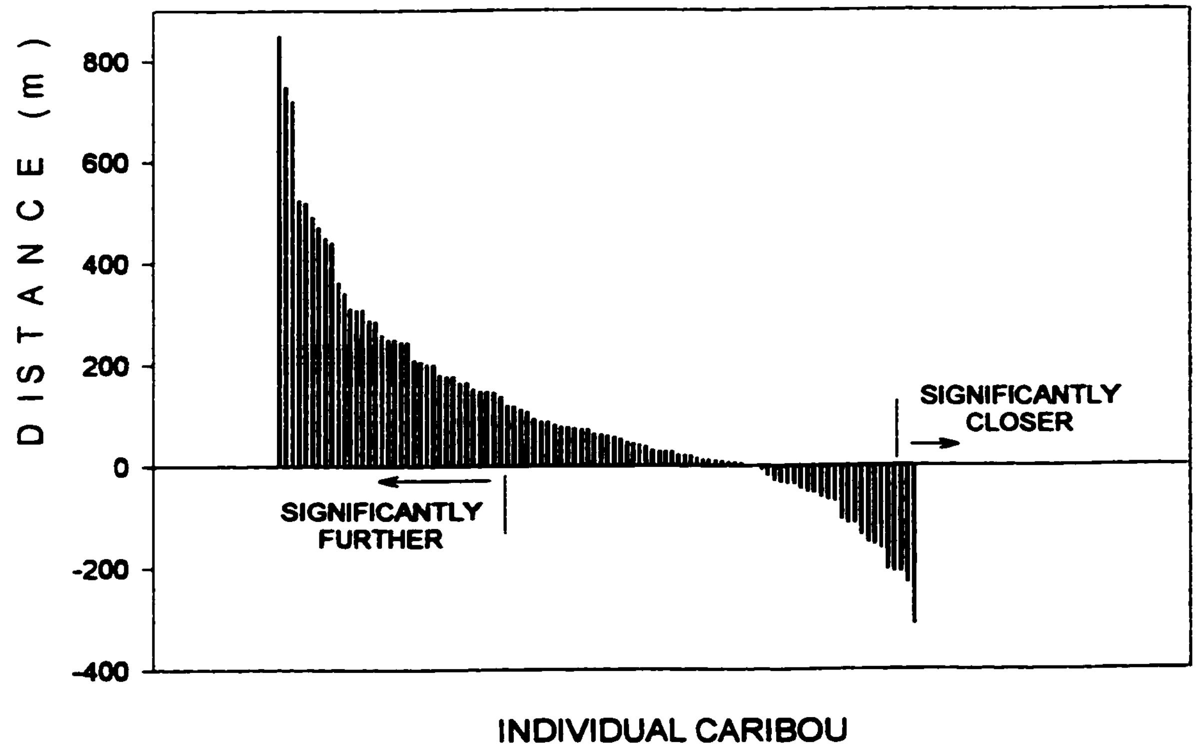

Figure 3.3: Difference in mean distance to nearest corridor between random points and radio telemetry locations for individual caribou in northeastern Alberta, 1994-97 ($n = 98$). Positive values are further than random, negative values are closer than random.

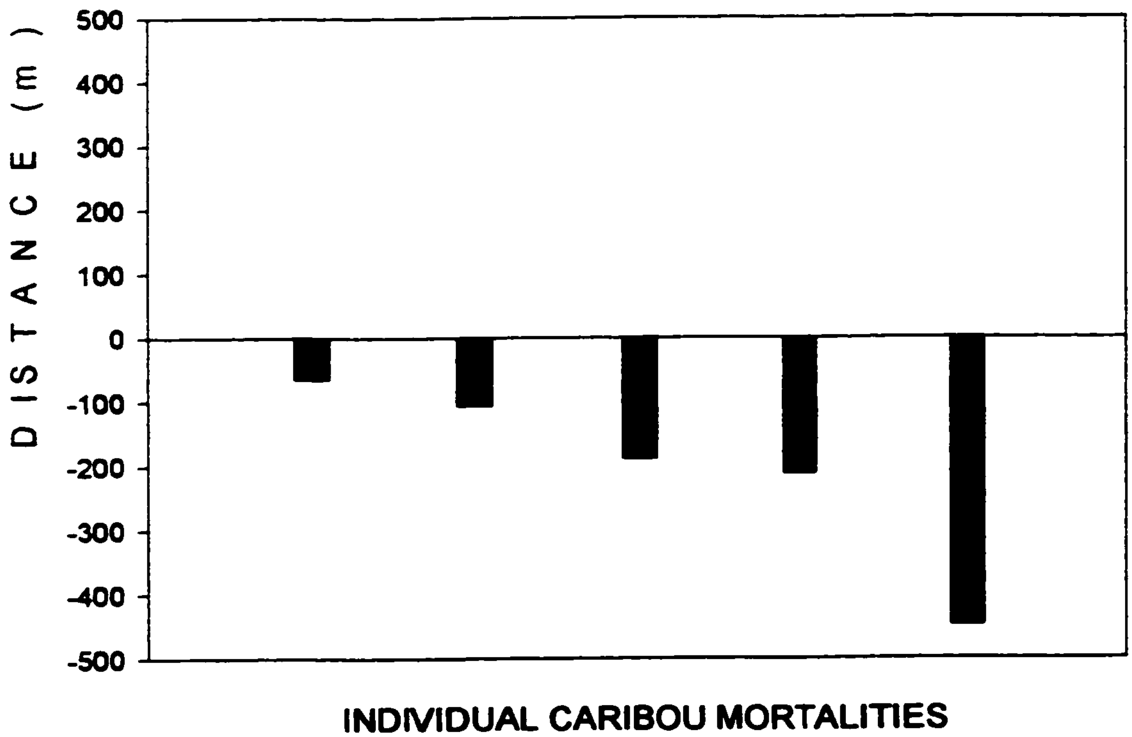

Figure 3.4: Difference between the distance of caribou mortality sites and the mean distance of live locations to nearest corridor for individual caribou that were killed by wolves in northeastern Alberta, 1994-97. Positive values are further than live locations, negative values are closer.

Chapter 4

Wolf Use of Linear Corridors in Caribou Habitat as Revealed by Track Surveys and Global Positioning System Collars[3]

INTRODUCTION

The creation of linear corridors (roads, seismic cutlines, pipeline right-of-ways) associated with the continual expansion of industrial activities in remote areas has the potential to affect the distribution, movements, and population dynamics of many wildlife species (see Jalkotzy et al. 1997 for an extensive literature review). It has been hypothesized that linear corridors may affect wolf-prey dynamics by increasing the mobility of wolves (Bergerud et al. 1984, Edmonds and Bloomfield 1984). Although wolves (*Canis lupus*) are often less abundant in areas with high densities of roads (Thiel 1985, Jensen et al. 1986, Mech et al. 1988, Fuller 1989, Fuller et al. 1992), corridors that receive little human use may be attractive to wolves as easy travel corridors (Horejsi 1979, Fritts and Mech 1981, Edmonds and Bloomfield 1984, Eccles and Duncan 1986, Thurber et al. 1994). Spatially explicit predator-prey models predict that increased predator mobility will increase encounter rates and decrease the stability of predator-prey systems (McCauley et al. 1993).

In northeastern Alberta, there is particular concern about the potential effect of linear corridors on the interaction between wolves and woodland caribou (*Rangifer tarandus caribou*). Wolf predation is often cited as a main cause of caribou mortality (Bergerud 1974, 1978, 1983, 1988, Fuller and Keith 1980, Bergerud et al. 1984, Edmonds and Bloomfield 1984, Edmonds 1988, Seip 1992). Wolf predation accounted for 56% of caribou mortalities in northeastern Alberta between 1991 and 1995, and caribou populations are stable or declining slowly in this area (Stuart-Smith et al. 1997). Therefore, even small changes in predation pressure may have a significant effect on caribou population dynamics.

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[3] This chapter will be submitted for publication with Adam R. C. James and Stan Boutin as authors.

Spatial separation from alternative prey (commonly moose, *Alces alces*) may be an important anti-predator strategy of caribou (Bergerud 1974, 1985, Bergerud et al. 1984, Bergerud and Elliot 1986, Bergerud and Page 1987, Ferguson et al. 1988, Fuller and Keith 1981, Seip 1991, 1992). Caribou in northeastern Alberta predominantly inhabit large fen/bog complexes (Bradshaw et al. 1995, Stuart-Smith et al. 1997) and wolves are most commonly found in surrounding upland habitats and well-drained river valleys (Chapter 2). Although caribou and wolves appear somewhat spatially separated, it has been suggested that linear corridors may provide wolves with increased access into caribou range (Bergerud et al. 1984). Therefore, an increase in wolf mobility may have significant ramifications for caribou. Not only will encounter rate increase in areas where caribou originally encountered wolves, but linear corridors may also reduce the effectiveness of spatial refuges for caribou. If wolves are able to travel long distances quickly through linear corridors, caribou that were once inaccessible may become much more susceptible to predation. Although there has been considerable speculation about how corridors might affect the movement of wolves, there is little scientific information available.

Radio telemetry data from northeastern Alberta revealed that wolf locations within caribou range were closer to linear corridors than expected by chance (Chapter 3). However, telemetry locations were insufficient to determine whether the use of linear corridors allowed an increase in wolf mobility. In this paper we present location data, from GPS collars deployed on wolves, which confirm the pattern seen in wolf telemetry data and indicate that wolves travel faster on linear corridors than in the forest.

This project was conducted as part of a long-term study of caribou in northeastern Alberta, ongoing since 1991 (see Bradshaw 1994, Bradshaw et al. 1995, Bradshaw et al. 1997, 1998, Stuart-Smith et al. 1997, James and Stuart-Smith, in preparation).

STUDY AREA

This study was conducted in northeastern Alberta, Canada (56° N, 112° W), encompassing approximately 6,000 km^2 of boreal mixed-wood and peatland vegetation. The Athabasca River flows through the middle of the study area. Elevation varies between 500 and 700 m above sea level with little topographic variation. See Bradshaw et al. (1995) for a detailed description of vegetation in the study area. Caribou range polygons were defined for the study area by Bradshaw (1994) based on caribou habitat selection and peatland habitat mapping (Fig. 4.1).

METHODS

Track Data

To obtain information about wolf behaviour around linear corridors within caribou range, we conducted aerial wolf track surveys along transects in forested habitat (Forest), along linear corridors with packed trails from skidoos or plowed roads (Packed LC) and along linear corridors with no snow compaction (Unpacked LC). During the winters of 1996 and 1997, we flew 92 transects (31 Forest, 29 Packed LC, 32 Unpacked LC) in a Cessna 185 traveling at approximately 110km/hr and 60m above ground level. The start and end points of the Forest transects were chosen randomly from easily visible landmarks. Packed and unpacked linear corridors were chosen randomly and transects were flown between easily visible landmarks. Transects varied in length from 1.2km to 8.4km (mean = 3.9km). Wolf tracks were distinguished from other tracks by their size and pattern. We flew surveys 3 to 4 days after fresh snow and recorded the number of wolf tracks crossing the transect from the forest (CFF), crossing the transect on a another linear corridor (CLC), intercepting the transect from the forest and following it (IFF), and the distance tracks followed the transect (D). We converted raw track counts to number of tracks / km / day. To determine whether linear corridors influenced wolf movements, we tested the null hypotheses that:

1. mean # CFF_{forest} = mean # CFF_{packed} = mean # $CFF_{unpacked}$
2. mean # IFF_{forest} = mean # IFF_{packed} = mean # $IFF_{unpacked}$

3. mean D_{forest} = mean D_{packed} = mean $D_{unpacked}$

using the Kruskal-Wallis test and nonparametric Tukey-type multiple comparisons. We also compared the mean # Crossing From Forest and mean # Crossing on a Linear Corridor on all transects with the normal approximation to the Wilcoxon paired sample test.

Global Positioning System (GPS) Data

Seven wolf packs are known to occupy the study area, based on radio telemetry data collected between 1994 and 1997 (Chapter 2). To collect detailed information on wolf movements, wolves were captured from three of these packs (the Grande, Bourgoin and Upper packs) and fitted with Global Positioning System (GPS) collars. We used two Lotek Engineering Inc. GPS collars capable of storing approximately 1000 differentially correctable locations. The collars were programmed to take locations at time intervals ranging from every hour to every 5 minutes and were expected to collect locations for approximately 1 month before running out of storage capacity. These collars did not contain hardware for remote data transfer, and therefore had to be retrieved from the field to obtain the location information. Remple and Rodgers (1997) determined the location error of similar Lotek Eng. Inc. GPS collars under different canopy conditions. They found that in Black spruce forest the median location error was 4.0m for 3D differentially corrected (3Ddiff) locations and 107.4m for 3D uncorrected locations (3D). We assumed that 3Ddiff and 3D wolf GPS locations within caribou range would have location errors similar to those reported by Remple and Rodgers (1997). We calculated the location errors for 2D differentially corrected locations (2Ddiff) based on each location's horizontal dilution of precision using Remple and Rodgers' (1997) predictive log-linear model.

In February, 1996 we deployed one GPS collar on a wolf from the Grande pack and the other on a wolf from the Bourgoin pack. We retrieved both collars in March and returned them to Lotek Eng. Inc. to have the data extracted and the collars refurbished. We deployed the same collars again in January 1997 on a different wolf from the Bourgoin pack and a wolf from the Upper pack. We retrieved both collars in February and again returned them to Lotek Eng. Inc. for data extraction.

We used Lotek Eng. Inc. post processing software to differentially correct all locations possible. We could not correct some locations because of differences in collar and basestation satellite information. We entered the location data into a Geographic Information System (GIS) and determined the minimum convex polygon home range for each individual. The GPS collars collected a total of 2,707 locations. In this paper we examine only 3Ddiff, 2Ddiff and 3D locations within caribou range (as described by Bradshaw 1994) in the analyses ($n = 335$).

All of the linear corridors within the study area were digitized from aerial photos by Lormel Consultants and entered into the GIS. The location error for the digital linear corridor data is approximately 50m (R. Farries, Lormel Consultants, personal communication). Linear corridors were not classified into categories (e.g. road, pipeline, seismic line, etc.); however, approximately 95% of linear corridors in the area of the GPS locations were seismic lines or pipeline right-of-ways with an average width of 8 m and 15 m respectively. We mapped sequential wolf GPS locations and linear corridors in the GIS and "followed" individuals to look for evidence that wolf movements within caribou range were associated with linear corridors.

We used the GIS to generate 3,275 random points within the study area, from which we determined a random set for each GPS-collared wolf based on their minimum convex polygon home range. Each random set was identified with the corresponding wolf collar number. We determined the perpendicular distance of random and wolf GPS locations to the nearest linear corridor. We compared the distance to nearest linear corridor of the wolf GPS locations to random points using a General Linear Model (GLM) with collar number (individual) as a fixed factor.

To compare the speed of wolves on linear corridors and in the forest, we classified each location as on or off linear corridors based on their distance to the nearest corridor and the location error associated with each location and the digital map of linear corridors. We considered GPS locations to be on a linear corridor if the calculated distance to the nearest linear corridor was less than or equal to the corridor location error (50m) + GPS location error (3Ddiff = 4m, 3D = 107m, 2Ddiff calculated). We determined the average speed between locations using the straight-line distance and the time elapsed between locations. We assumed that a portion of the travel between a location on corridor and a location off was traveled on the corridor (i.e. wolves did not leave the corridor immediately after a location). Therefore, to reduce the likelihood of detecting a difference we classified speeds calculated from points originating or ending on linear corridors as speed on corridor. We did not include the speed from locations that were more than 2 hours apart. We also removed one 2Ddiff outlier from the analysis because it had a horizontal dilution of precision of 281 and an estimated location error of 387m. This datum would have been classified as on corridor with a speed of 106 km/hr, therefore its removal is conservative. Of the 335 locations within caribou range, 87 were classified as on and 248 were classified as off corridors.

Because locations were taken as frequently as every 5 minutes, the GPS data categorized as on or off corridors are clearly autocorrelated. Therefore, a GLM of these data is more likely to detect a difference when there is not a true difference (type I error), which makes it a conservative tool to eliminate factors in the analysis that are not significant. We compared wolf speed on and off corridors using a GLM with fix type (3Ddiff, 3D, or 2Ddiff) and collar (individual) as fixed factors to determine if these factors were important. To test the hypothesis that wolf speed was greater on than off corridors, we used a resampling technique to deal with the autocorrelated data. We used Resampling Stats 4.1 software (Resampling Stats Inc., Arlington, Virginia, USA) to sample with replacement 87 data points from the speed on corridor data set and 248 data points from the speed off corridor set. The software calculated the mean for each sample and the difference between the two means (on minus off).

This procedure was repeated 10,000 times and the grand means of the mean speed on and mean speed off and the mean difference (on minus off) were calculated.

If there was no difference in speed on and off corridors, then the mean difference (on minus off) should be equal to 0. We combined the speed on corridor and the speed off corridor data and resampled from the pooled set. We randomly selected (with replacement) groups of 87 and 248 data points, calculated the mean for each group, and determined the difference between means. This procedure was repeated 10,000 times to generate a frequency distribution of the difference between means. We used this distribution to estimate the probability of obtaining a mean difference as great or greater than that observed.

RESULTS

Track Data

The number of tracks Crossing From Forest/km/day were not different between forest, packed LC and unpacked LC transects ($H_c = 3.11$, $P = 0.211$).

The number of tracks Intercepting From Forest/km/day were different among forest, packed LC and unpacked LC transects ($H_c = 7.04$, $P = 0.03$). There were no Intercepting From Forest tracks observed on forest transects. The number of tracks Intercepting From Forest /km/day was higher on packed LC ($Q = 4.2$, $P < 0.001$) and unpacked LC transects ($Q = 3.05$, $P < 0.01$) than on forest transects. There was no difference in tracks Intercepting From Forest /km/day between packed LC and unpacked LC transects ($Q = 0.49$, $p > 0.5$).

The distance wolves traveled was different among forest, packed LC and unpacked LC transects ($H_c = 8.1$, $P = 0.017$). Wolves traveled further on packed LC ($Q = 4.5$, $P < 0.001$) and unpacked LC transects ($Q = 3.5$, $P < 0.002$) than on forest transects. There was no difference in the distance traveled on packed LC and unpacked LC transects ($Q = 0.94$, $p > 0.5$).

There was no detectable difference in the number of tracks Crossing From Forest/km/day and the number of tracks Crossing on a Linear Ccorridor/km/day ($Z = -0.89$, $P = 0.374$).

Global Positioning System (GPS) Data

Mapping sequential wolf locations and linear corridors provided detailed information on wolf movements. There were few instances in which multiple consecutive locations were observed in caribou range. The majority of locations within caribou range appeared to be brief forays from the well-drained river valley. However, the GPS locations did reveal evidence of wolf use of linear corridors (Fig. 4.2).

Distance to linear corridors: -- Wolf GPS locations were on average 81m closer to linear corridors than were random points ($F_{1,702} = 4.83$, $P = 0.028$). There was a significant collar effect ($F_{3,702} = 6.21$, $P < 0.001$) reflecting the different density of linear corridors within each wolf's home range. The collar effect is unlikely to represent a difference in response between individuals because the point type * collar interaction was not significant.

Wolf speed on and off linear corridors: -- Eighty-seven out of 335 locations (26%) were classified as being on a linear corridor. Fix type (3Ddiff, 3D, 2Ddiff) and collar (individual) were not significant factors in the GLM of the speed data. Resampling produced a grand mean for speed on linear corridors of 1.4 km/hr and a grand mean for speed off corridors of 0.5 km/hr. GPS collared wolves traveled 2.8 times faster on linear corridors than in the forest. The mean difference between speed on and off corridors was 0.9 km/hr. Under the null hypothesis of no difference between speed on and off corridors, resampling produced a mean difference 0.9 km/hr twice out of 10,000 iterations. Therefore, the estimated probability that the difference found came from a population of data with a mean difference of 0 is 0.0002.

DISCUSSION

Our wolf track data were consistent with previous anecdotal evidence that wolves use roads and other corridors as easy travel routes in areas with limited human activity (Horejsi 1979, Bergerud et al. 1984, Edmonds and Bloomfield 1984, Eccles and Duncan 1986, Thurber et al. 1994). Wolf tracks only intercepted and followed linear corridors. Interestingly, there was no difference in the number of tracks intercepting and following from the forest or distance traveled between packed LC and unpacked LC, suggesting that it was not solely the ease of travel that influences wolf movements on linear corridors. We suspect that upon encountering a linear corridor, the visual stimulus of being able to see a long distance may have influenced a wolf's decision to change direction and follow the corridor. However, more behavioural research is needed to assess this hypothesis. Because the area of intersection between transects and crossing linear corridors was a small fraction of the transects, the lack of difference between wolf tracks crossing from the forest and crossing on a linear corridor indicated a greater use of linear corridors than expected by chance.

Wolf GPS locations were closer to linear corridors than were random points, also suggesting greater wolf use of corridors than expected by chance. Radio-telemetry locations from seven packs within the same study area showed a similar difference (134m closer to corridors) from random points (Chapter 3). Chapter 3 also showed that although there was considerable individual variation, there was a general avoidance of linear corridors by caribou, and caribou mortalities attributed to wolf predation were closer to corridors than were live locations.

The creation of linear corridors may cause increased caribou mortality by facilitating wolf movements. Our GPS collared wolves traveled more than twice as fast on linear corridors than in the forest (ave. speed on corridor = 1.4km/hr, ave. speed in forest = 0.5km/hr). Wolves in Poland have also been found to travel significantly faster on trails, roads, and frozen rivers than in the forest (Musiani et al. 1998). Wolf predation site data from our study area showed that wolves were hunting while on the move in caribou range and kills were closer to corridors than expected by chance (James and Stuart-Smith, in preparation). An increase in search rate should cause a corresponding increase in encounter rate. If we assume that all locations classified as on a corridor (26%) were indeed on a corridor, then because wolves traveled 2.8 times faster on corridors, the potential increase in encounter rate could be as much as 72.8% of the encounter rate in the absence of corridors (0.26 X 2.8 = 0.728; assuming a linear relationship between search rate and encounter rate). However, our methodology was biased towards classifying locations as on corridor, therefore the actual increase in encounter rate is probably less than the 72.8% calculated above. These data only demonstrated an increased speed during winter. It is unknown if wolves travel faster on corridors during the summer; therefore, it is difficult to predict what the potential increase in annual caribou mortalities would be.

It is possible that the wolves' speed was the same in the forest as it was on corridors, but the 'directness' of travel was different. However, recent findings from Europe suggest that straight-line distances between telemetry locations collected at 15-minute intervals approximate the actual distance traveled by wolves (Musiani et al. 1998). Based on straight-line distances between consecutive locations at longer intervals, linear movements on a corridor could appear faster than convoluted movements in the forest. If this is the case, increased penetration by wolves into caribou range may be an important consequence of linear corridors. Caribou in northeastern Alberta appear to avoid fen-upland boundaries (Stuart-Smith et al. 1997), possibly as a strategy to spatially separate themselves from moose and wolves. Linear corridors may provide more direct access and allow wolves to penetrate further into caribou range (Bergerud et al. 1984, Stuart-Smith et al. 1997).

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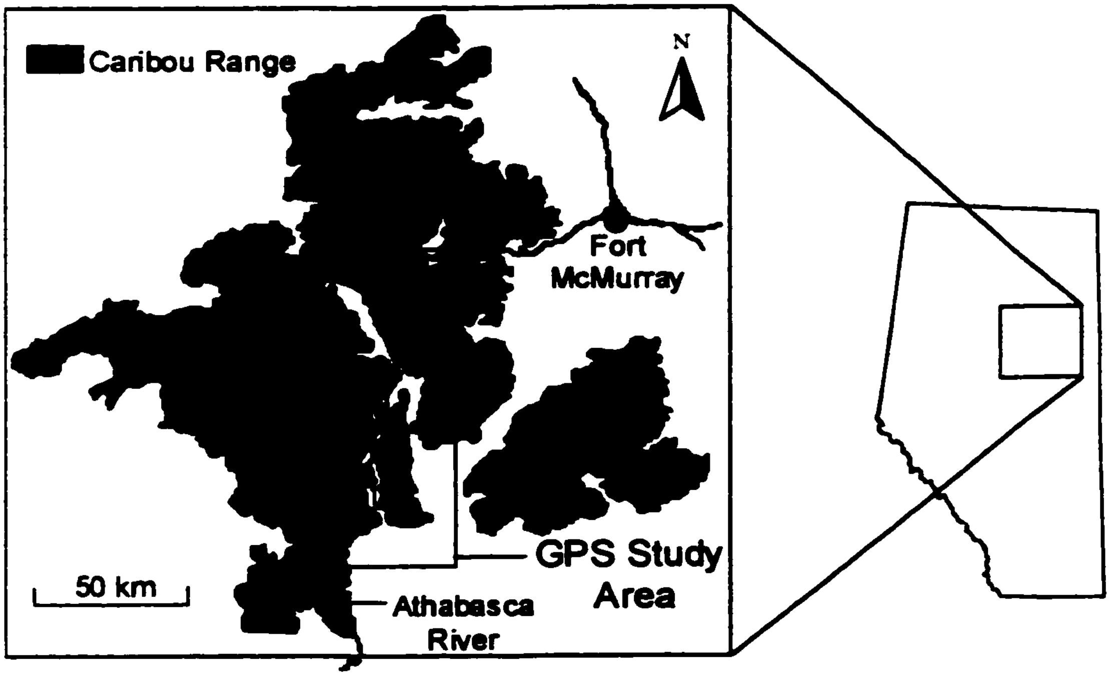

Figure 4.1: Location of study area and caribou range within northeastern Alberta, Canada, 1996-97.

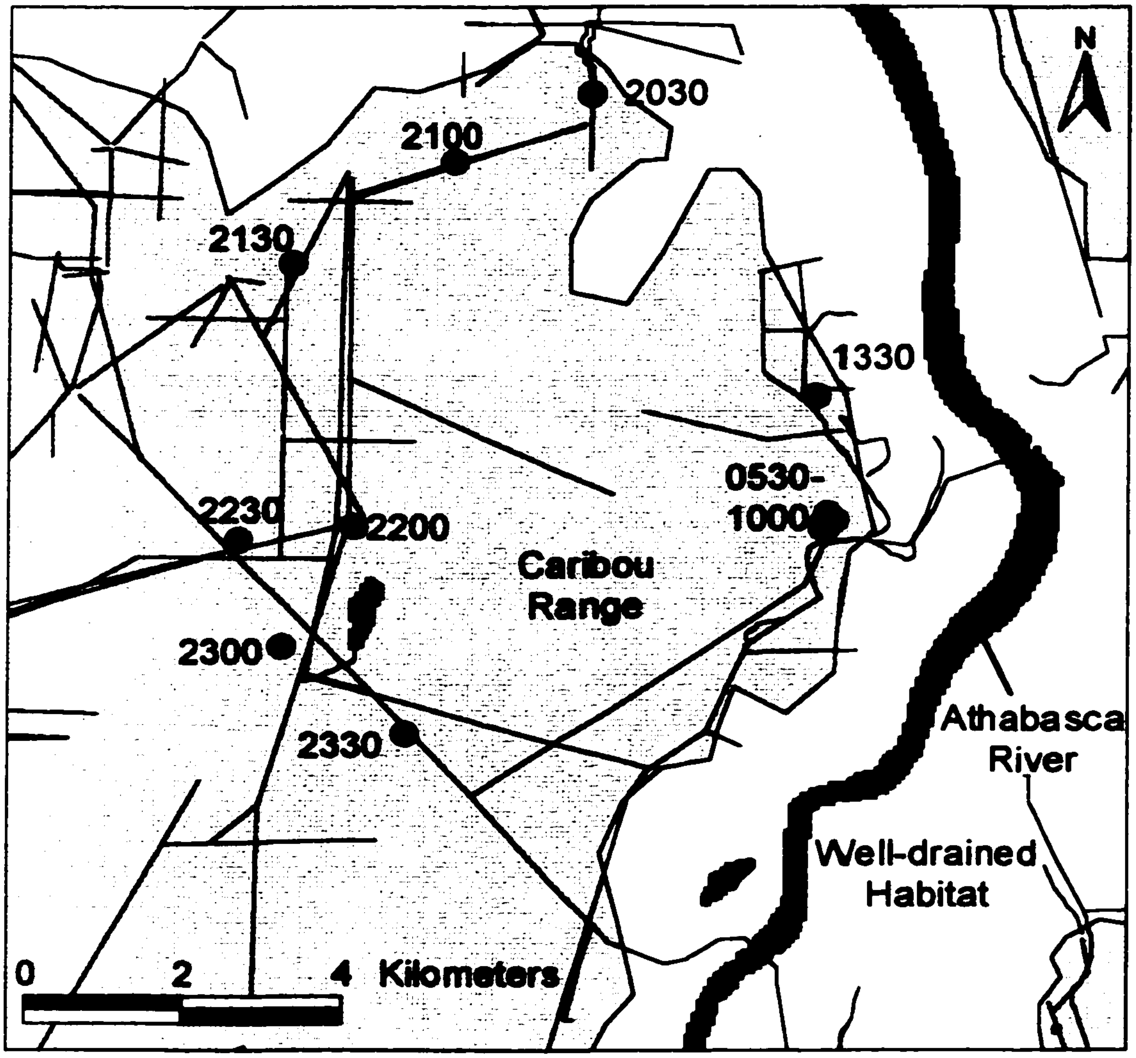

Figure 4.2: Example of sequential locations from a GPS-collared wolf in northeastern Alberta, Canada, 26 Feb. 1996 illustrating wolf use of linear corridors. Dots represent wolf locations and lines represent linear corridors. Locations begin at 0530hrs (centre right) and end 2330hrs (bottom left).

Chapter 5

General Discussion

EXPERIMENTAL DESIGN

I believe the research results presented in chapters 2, 3 and 4 provide strong evidence that industrial development has the potential to affect caribou populations by altering their prey-predator relationship with wolves. The design of this research evolved considerably over the course of the study. My original intentions were to assess the Spatial Separation Hypothesis by using spatial statistics to measure the spatial separation between species, and determine the effect on predation pressure by comparing caribou survival rates between a very large fen/bog complex and a much smaller one surrounded by good moose habitat. It became clear fairly early in the study that the use of spatial statistics on the telemetry point patterns would be confounded by differences in (1) the extent of collar distribution for each species, (2) the proportion of collared individuals of each species and (3) the number of telemetry locations for collared individuals. These differences among the telemetry point patterns of each species would have made the results of nearest neighbor or tessellation analyses virtually meaningless unless large amounts of data were discarded or ignored. Although it would have been nice to have a hard numerical measurement of the spatial separation between species, I believe the argument that spatial separation occurred because of selection for different habitat types that were themselves spatially separated is equally convincing.

The area in which wolves were collared was originally chosen as a natural experiment to compare predation rates between the large Wabasca caribou range and the long, thin Agnes range. The prediction was that predation on caribou would be higher in the Agnes range because caribou are on average closer to good moose habitat than those in the Wabasca range are. However, after studying the system I realized that this was a weak prediction. The Agnes range and other small wetlands appear to be large enough to provide at least a partial refuge for caribou given the tight association between wolves and well-drained habitat. This prediction was possible under the Spatial Separation Hypothesis, but it was not a necessary outcome. I think the comparison of survival and distance to well-drained habitat was a more appropriate test.

One criticism of the experimental design I used to evaluate the Spatial Separation Hypothesis is that is does not provide any information on the ultimate reason why caribou show selection for fen/bog complexes. Do caribou occupy peatlands as a strategy to avoid predation or because they prefer to forage on the lichens found in these areas? Would caribou occupy well-drained habitats in the absence of wolves, or would they be excluded by competition with other ungulates? These are interesting questions and they could potentially be answered through large-scale manipulations of wolf and moose populations. However, regardless of why caribou in northeastern Alberta select fen/bog habitat, this selection reduces the level of predation they experience. I believe it is this proximate result of habitat use on the level of predation experienced by caribou populations that is of primary concern for their conservation.

The experimental design used to evaluate the potential effect of linear corridors on wolf-caribou interactions remained relatively unchanged from its original form. However, in hindsight I would have put more effort into evaluating wolf use of corridors during summer. Wolf use of linear corridors has typically been considered a winter problem on corridors with packed trails. In Chapter 4, I was unable to detect a difference in the use of packed versus unpacked corridors. This raises the question whether wolves use linear corridors in a similar fashion in summer. I expect they do, although their movements may be restricted to areas around den sites during spring.

FUTURE RESEARCH

The Northeast Region Standing Committee on Woodland Caribou research subcommittee, now the Boreal Caribou Research Program has been very successful in generating funds for caribou research. The leveraging of funds from many companies and government has achieved a research program that would be unattainable by individual companies or government alone. The research partnership between industry, government and the University of Alberta has provided exceptional training opportunities for graduate students and has gone a long way towards developing innovative solutions to the problems identified.

Although the research effort has been very successful to date, there is still much to be learned. The 1995 fire at Mariana Lakes, Alberta has provided an excellent opportunity to monitor the long-term changes in caribou, moose and wolf populations after disturbance. Several caribou were collared in the area before the fire, providing pre-disturbance information on habitat use and spatial distribution. Monitoring the changes that occur after the fire would provide valuable information to help predict the effects of logging operations in and near caribou ranges. It would also be interesting to study wolf movements in summer with GPS collars to look at pack dynamics during denning. Are all pack members found near the den site or do non-breeders still travel into peatlands on linear corridors? It would be valuable to compare caribou survival rates among caribou ranges with different densities of linear corridors. This correlative approach may be somewhat weak on its own because of the limited number of distinct ranges and other potential differences between the areas. However, the correlation would be useful to corroborate the results of Chapters 3 and 4. I believe that another important next step is to compare wolf use of different types of linear corridors, particularly between traditional seismic lines and new low impact and heli-portable seismic operations.

Future research should also focus on evaluating the cumulative effects of industrial development. The avoidance of linear corridors by caribou (Chapter 3) illustrates the potential for effective habitat loss that is greater than the physical disturbance of an industrial development. It will be important to determine what types of industrial developments caribou avoid and whether caribou will habituate to these developments over time. I think particular attention should be paid to the development and extraction of heavy oil deposits. Heavy oil will make up an increasing proportion of oil production in Alberta. It requires intensive development, large infrastructure, and currently can not be produced remotely. The many roads needed to truck oil from these wells may affect caribou directly by reducing the availability of effective habitat and indirectly by compromising their ability to avoid wolf predation. Large road networks may also change water movements within peatland complexes, which could greatly alter the vegetation.

MANAGEMENT IMPLICATIONS

Because caribou in northeastern Alberta may already be declining slowly (Stuart-Smith et al. 1997), I recommend a conservative approach to timber planning around fen/bog complexes occupied by caribou. I recommend that areas on the periphery of caribou range be harvested at a conservative rate. It would be unwise to harvest a large proportion of the area surrounding a given caribou range in a short time frame. Harvesting larger, more concentrated blocks may reduce the potential for moose to increase by reducing the interspersion of forage and cover. Such a harvesting pattern would be consistent with the use of natural disturbance patterns in design of harvest plans (Hunter 1993). Because of the low probability of caribou recolonizing areas after extirpation, harvesting planning should consider all caribou ranges at all times.

Wildlife managers may be able to maintain existing moose densities through careful monitoring of moose and liberalized hunting regulations. In Ontario, moose densities increased after disturbance from logging and fire in areas with limited access to hunters, but not in areas easily accessible to hunters (Remple et al 1997). However, current management practices in Alberta attempt to minimize the development of road access into and near caribou range to limit the potential increase in human harvest of caribou. It will be difficult for managers to assess the tradeoffs between increased access allowing the harvest of moose versus caribou until better information is available on human-caused mortality to caribou. There is also societal pressure on wildlife managers to increase the population of moose for subsistence and recreational hunting. It will be difficult to balance the desire to conserve caribou with the desire for increased moose populations, and moose population management through hunting regulations may be insufficient to prevent an increase in predation pressure on caribou.

Caribou and wolf locations were not random with respect to linear corridors. On average caribou locations were further from corridors than expected by chance. This avoidance may contribute to effective habitat loss from industrial development that is considerably greater than the area disturbed. Attempts to assess the cumulative effects of continued industrial expansion should include estimates of habitat lost due to avoidance. Evaluation of future developments should also consider the potential increase in predation pressure resulting from wolf use of linear corridors. Wolf-caused mortalities were closer to linear corridors than live caribou locations, indicating that caribou that are closer to linear corridors are at higher risk of predation. Linear corridors may increase wolf predation efficiency by increasing their search rate and may provide greater access into caribou range. Therefore, increased industrial activity in caribou range could have a significant effect on caribou population dynamics by increasing predation unless the development of new corridors is minimized. Remote production of wells, heli-portable seismic operations, complete roll-back of trees and debris onto new pipeline right-of-ways, and reclamation/replanting or obstruction of unused or unnecessary corridors may help to reduce the total impact of industrial operations on caribou populations.

Wolf control has also been suggested as management tool to mitigate the increases in wolf predation caused by industrial development. However, there is strong public opposition to using wolf control without first doing everything possible to reduce the effects of human activities. For this reason, wolf control is not a viable option at this time.

Implementing these recommendations will only be effective if there is a commitment to caribou conservation from the government and people of Alberta. It appears that there is currently a lack of political will in Alberta to support the conservation of caribou if it means slowing the rate of natural resource extraction in the province. Many of the industrial members of NERSC have made a genuine effort to reduce the effects of their activities on caribou. However, the economic realities of a highly competitive industry and fluctuations in the price of petroleum products often force companies to challenge land use guidelines designed to protect caribou. In the past guidelines have been whittled away based on a lack of scientific data or inadequate support from senior government staff. Many members of oil and gas companies have admitted that economics and competition force them to be a strongly compliance-driven industry. I believe the success of caribou conservation will be determined only partly by how much we learn about them, but mostly by the willingness of Albertans to limit the rate of, and/or change the methods used for resource development in and near caribou range.

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