



PEACE/WILLISTON  
FISH & WILDLIFE  
COMPENSATION  
PROGRAM

**BChydro** 



# **Spatial and Temporal Patterns of Predation Risk on Woodland Caribou in the Wolverine and Chase Herds, North-Central British Columbia**

**1991 – 2006**

---

R. Scott McNay  
March 2009

PWFWCP Report No. 323

The Peace/Williston Fish & Wildlife Compensation Program is a cooperative venture of BC Hydro and the provincial fish and wildlife management agencies, supported by funding from BC Hydro. The Program was established to enhance and protect fish and wildlife resources affected by the construction of the W.A.C. Bennett and Peace Canyon dams on the Peace River, and the subsequent creation of the Williston and Dinosaur Reservoirs.

**Peace/Williston Fish and Wildlife Compensation Program, 1011 Fourth Ave.  
3<sup>rd</sup> Floor, Prince George B.C. V2L 3H9**

Website: [www.bchydro.com/pwcp/](http://www.bchydro.com/pwcp/)

**This report has been approved by the Peace/Williston Fish and Wildlife  
Compensation Program Wildlife Technical Committee.**

Citation: McNay, R.S. 2009. Spatial and temporal patterns of predation risk on woodland caribou in the Wolverine and Chase Herds, north-central British Columbia, 1991-2006. Peace/Williston Fish and Wildlife Compensation Program Report No. 323. 28 pp. plus appendices

Author(s): R. Scott McNay<sup>1</sup>

Address(es): <sup>1</sup>Wildlife Infometrics Inc., #3-220 Mackenzie Blvd., Mackenzie, B.C. V0J 2C0

## EXECUTIVE SUMMARY

Where woodland caribou populations are declining, reversing the population trend in the short-term will depend on mitigating predation rates until other factors (e.g., forest age structure) are managed in ways that discourage overlap among predators and caribou. In other work, I proposed to test the notion that removal of sufficient predators (wolves) can be accomplished by regulated, licensed trap line holders if their trapping is focused (spatially and temporally) on that objective. If proven successful, the need for a broader indiscriminate approach to wolf reduction may be unnecessary. I therefore assessed the utility of predation risk models to discriminate specific locations where radio-tagged caribou were killed by wolves from other sites used by caribou when they were alive, and from random sites on the landscape. I assembled 58,411 relocations of 231 radio-tagged caribou, 43 of which died from predation by wolves, and used logistic regression to distinguish wolf kill sites from other sites based on the possible combinations of seven independent factors: (1) caribou age class at death, (2) caribou sex, (3) season of death, and factors (4)-(7) which were four spatial estimators of predation risk: (i) shortest linear distance to roads, (ii) shortest linear distance to early-seral forest, (iii) weighted distance to areas of predicted predation risk based on a previously published logistic regression model, or (iv) location relative to high or low classes of predicted predation risk based on a previously published Bayesian Belief Network. Age class of caribou at death, season, and the Bayesian model of predation risk provided a robust description of mortality sites where death was due to predation by wolves. Although more adults died than calves, the probability that a kill site was a calf was higher than for adults, kill sites for both age classes were more likely to occur during winter and spring migration than during other seasons, and kill sites were most likely within the zone of modeled predation risk. Also, caribou kill sites were more often and more successfully discriminated when nonrespondent data were caribou relocations rather than random locations. It was apparent from these results that radio-tagged caribou may have been selecting for range that had lower predation risk than otherwise but needed to undergo relatively short periods of high risk coincident with migration in order to do so. Although the Bayesian model performed well in most seasons, the predicted zone of risk failed to account for 12 deaths, most of which were calves that died either just prior to or during calving when the probability of

a kill site being for an adult was lowest. With that qualification, I concluded that predation risk models can be useful tools to advance recovery planning for declining caribou populations because their use can help identify spatial and temporal parameters that characterise risk of predation by wolves. Knowing this can help managers focus management actions where and when they will be most effective; actions such as: reduction of wolves' primary prey, vegetation management that deters population increases in wolves' primary prey, and/or site-specific removal of wolves.

## ACKNOWLEDGEMENTS

I am indebted to M. Wood (Peace Williston Fish and Wildlife Compensation Program), C. Johnson (University of Northern BC), and A. Lance (International Forest Services) who provided data on radio-tagged caribou preceding my involvement in this study in 1999. Capture and collaring of caribou was undertaken by crews under the management of J. Innis, by Bighorn Helicopters (C. Wilson and crew), by Altoft Helicopter Services (G. Altoft and crew), and in earlier years by Northern Mountain Helicopters (Bob Batchelor, Wade Ross). Others involved in animal captures were: K. Connors, F. Corbould, B. Culling, C. Cushway, R. Dawson, L. Giguere, D. Heard, P. Hengeveld, C. Johnson, J. Joy, G. Keddie, B. McLellan, C. Ritchie, S. Walshe, G. Watts, L. Wilson, M. Wood, R. Woods, and K. Zimmerman. Aerial support for monitoring radio-tagged caribou was performed by Northern Thunderbird Air (K. Connors, L. Frey, V. Miller, and L. Scott), Northern Lights (L. Frey and E. Steir), and Vanderhoof Flying Services (L. Frey). Telemetry biologists included: J. Caldwell, H. Davis, L. Giguere, P. Hengeveld, C. Johnson, G. Keddie, E. Muller, M. Rankin, K. Schmidt, S. Walshe, L. Wilson, M. Wood, and C. Wright. Mortality site investigation was led by L. Giguere with support from P. Hengeveld, J. Joy, G. Keddie, S. Walshe, and L. Wilson. In the earlier studies, mortality investigations were performed by C. Johnson and by staff of the Peace-Williston Fish and Wildlife Compensation Program. Application of the published predation risk models and management of other spatial data was conducted by V. Brumovsky and R. McKinley. V. Brumovsky provided graphical support and L. Giguere and J. Caldwell provided support with data management. J. Voller and D. Heard helped edit earlier versions of the manuscript and later versions were greatly improved through helpful comments received from David Guistine, Doug Heard, Elena Jones, Andrew Walker, and Mari Wood. The data collection and initial data management was funded by Peace Williston Fish and Wildlife Compensation Program (1991-1997), University of Northern BC (1996-1999), Forest Renewal BC (1998-2002), BC Forest Investment Account (Land Based Investment Program – 2003-2006), Slocan Forest Products Ltd. (now Canadian Forest Products, Ltd. – 1998-2006), Abitibi Consolidated Company of Canada (now Abitibi-Bowater – 1998-2006), and BC Ministry of Environment. This report was funded by Peace Williston Fish and Wildlife Compensation Program.

## TABLE OF CONTENTS

Executive Summary .....	i
Acknowledgements.....	iii
Table of Contents.....	iv
List of Figures.....	v
List of Tables .....	v
1.0 Introduction.....	1
1.1 Background .....	1
2.0 Study Area .....	3
2.1 Wolverine .....	3
2.2 Chase .....	4
3.0 Methods.....	5
3.1 Relocation of Radio-tagged Caribou.....	5
3.2 Mortality Investigations .....	6
3.3 Modeled Predation Risk .....	7
3.4 Analytical Methods .....	10
4.0 Results.....	11
4.1 Compiled Data.....	11
4.2 Discriminating Kill Sites from Caribou Relocations .....	14
4.3 Discriminating Kill Sites from Random Locations.....	14
5.0 Discussion.....	14
6.0 Management Implications.....	20
7.0 References.....	21
8.0 Appendix A.....	1

## LIST OF FIGURES

Figure 1. Location of recovery plan areas (RPA) for herds (Wolverine, Chase, Takla, and Scott) of threatened woodland caribou in north-central British Columbia.....	4
Figure 2. Frequency of observations (purple bars - caribou relocations, blue bars – random locations, orange triangles – caribou killed by wolves) and the shortest, straight-line distances to (A) early-seral forests, (B) roads, (C) modeled risk of predation (Logistic), and (D) modeled risk of predation (Bayesian). Distances to predation risk for the Logistic model was a weighted index calculated following methods of Johnson et al. (2002). The Bayesian model was calculated following methods of (McNay et al. 2006). .....	13
Figure 3. Sites where radio-tagged caribou were killed by wolves (black pins, 1991-2006, north-central British Columbia), in relation to an area of predicted low predation risk (darker shade) modeled with a Bayesian Belief Network (McNay et al. 2006). .....	15
Figure 4. Probability of a kill site due to mortality by wolf predation for radio-tagged caribou calves and adults during specific seasons, within two zones of predation risk (High and Low) in north-central British Columbia, 1991-2006. Risk zones were previously modeled using a Bayesian Belief Network (McNay et al. 2006). .....	18

## LIST OF TABLES

Table 1. Spatial/temporal models of predation risk and the number of independent parameter estimates used to assess the relative ability of models to discriminate where radio-tagged woodland caribou were killed by wolves in north-central British Columbia, from other sites used while they were alive or from other random sites on the landscape. See text for a description of all models and model factors <sup>a</sup> , including the determination of spatial predation risk factors (Roads, Blocks, Logistic, and Bayesian). ..	8
Table 2. General characteristics of four predation-risk models assessed using sites where radio-tagged woodland caribou were killed by wolves. ....	9
Table 3. Number of animals, deaths from predation by wolves, and relocations collected for radio-tagged caribou in north-central British Columbia, 1991-2006. ....	11

Table 4. Calculated average distances (and standard deviation in parentheses) away from roads, early-seral forests, and areas of modeled predation risk that were observed for radio-tagged caribou when they were alive, for ransom points ( <i>italicized</i> ), and for caribou when they were found dead. Distances to roads and early-seral forests were the shortest straight-line distances. Distances to predation risk was a weighted index calculated following methods of Johnson et al. (2002). .....	12
Table 5. Comparison of logistic regression models used to discriminate sites where radio-tagged woodland caribou were killed by wolves in north-central British Columbia from other sites used while caribou were alive or from random sites on the landscape. Nonrespondent data (NRD) were referred to as caribou relocations or random locations, respectively. Decreasing model rank was assessed using Akaike's information criterion for small sample sizes (AICc), AICc difference from the model with lowest AICc ( $\Delta_n$ ), AIC weight ( $W_m$ ), area under the receiver operating characteristics curve (AUC), Wald $\chi^2$ , and number of independent parameters estimated (df). All models had significance levels ( $P$ ) <0.001. ....	16
Table 6. Logistic regression models used to discriminate sites where radio-tagged woodland caribou were killed by wolves in north-central British Columbia, from other sites used while they were alive or from other random sites on the landscape. Nonrespondent data (NRD) were referred to as caribou relocations or random locations, respectively. Caribou relocation, nonrespondent data led to the selected model based on age class of caribou at death, season, and a previously constructed Bayesian Belief Network (McNay et al. 2006), the latter used to predict zones of high predation risk ( $n = 57,748$ , Wald $\chi^2 = 92.51$ , $P < 0.001$ , AUC = 0.783). Random location, nonrespondent data led to the selected model based on the Logistic prediction of predation risk ( $n = 39,564$ , Wald $\chi^2 = 37.11$ , $P < 0.001$ , AUC = 0.668). See text for variable and model descriptions.....	17



# 1.0 INTRODUCTION

## 1.1 Background

Woodland caribou (*Rangifer tarandus caribou* (Gmelin 1788)) in the Southern Mountain National Ecological Area were designated “threatened” by the Council On the Status of Endangered Wildlife In Canada in 2002, were added to the Species at Risk Act Schedule 1, and are a species at risk under the Forest and Range Practices Act in British Columbia (BC). Caribou are commonly regarded as an indicator of biodiversity and ecosystem health in the boreal and sub-boreal forests (e.g., see Environmental Non-Government Organizations programs such as Caribou Nation<sup>1</sup>, Grey Ghosts<sup>2</sup>, and Staring at Extinction<sup>3</sup>).

In the late 1970s, the BC government sensed potential mismanagement of caribou after observing an apparent decline in populations while annual harvests were exceeding 1,500 animals (McGregor 1985). After curtailing hunting, some caribou populations continued to decline and now, despite the current legal status, the rate of decline in many herds indicates extirpation in a matter of decades (Wittmer 2004). The common denominator in this decline was considered by Messier et al. (2004) to be increased ungulate (other than caribou) populations that have led to increased numbers of predators and increased predation on caribou: caribou apparently suffer more incidental predation from wolves (*Canis lupus* (Linnaeus 1758)) than would otherwise occur (Bergerud 1983, Seip 1992, Racey et al. 1999). The increased mortality is exacerbated because caribou are possibly more susceptible to wolf predation than other ungulates (Seip 1991, Seip 1992, Thomas 1995). Increases in other ungulate populations have been related to abundance of early-seral forests (Hatter 1950, Wallmo 1969, Spalding 1990, 1992, Rempel et al. 1997, Rettie and Messier 1998). Roads and other linear corridors associated with natural resource development may also benefit predator search rates and allow predator’s access to caribou in places where they would otherwise be less accessible as prey (Jalkotzy et al. 1997, Bradshaw et al. 1997, James and Stuart-Smith 2000, Dyer et al. 2001).

Corrective measures to reverse the decline of caribou populations therefore must involve mitigation of predation either by managing the amount of early-seral forests, roads and linear corridors, other ungulates, predators, or a combination of these factors. A review of predator management and its effect on prey was undertaken in Alaska after the control of wolves was suspended in 1994 (NRC 1997) concluding that, although some of the best data on the topic

---

<sup>1</sup> <http://www.caribounation.org>

<sup>2</sup> <http://23120.vws.magma.ca/work/caribou/index.php>

<sup>3</sup> <http://www.forestethics.org/article.php?id=1122>

come from studies in Alaska, more science was required to meet requirements for reinstating control of wolf populations. Other than the experimental reduction of wolf populations (Elliot 1985, Janz 1989, Seip 1992, Boertje et al. 1996, Youds and Roorda 2001, Hayes et al. 2003), other mitigation techniques have had relatively little attention from managers. Also, published accounts expounding on the relative management efficacy of mitigation techniques are rare (but see Boertje et al. 1996 and Hayes et al. 2003) but demonstrate reduced predation rates and more abundant ungulate populations following experimental reduction of wolves. These same accounts also indicate however, that the result is feasible only with considerable long-term and widely spread effort, the effects of which may be short-lived once the program stops (Boertje et al. 1996, Hayes et al. 2003, NRC 1997). Nevertheless, where recovery of caribou is considered feasible, short-term mitigation of predation is likely to occur while habitat is being restored (MCTAC 2003, Seip 2005, McNay et al. 2008).

In other research, I have posed the question: can sufficient reduction in predation risk be achieved through regulated, licensed trapping to avoid a special and broader-spread regulatory policy to reduce wolves for the purpose of caribou recovery? I assumed predation risk to be defined as the probability of caribou encountering, or being killed by, predators (Johnson et al. 2002, Lima and Dill 1990). Based on previous investigations, caribou survival and mortality rates (McNay and Voller 2007), and modeling of caribou habitat supply (McNay et al. 2006); I considered that removal of wolves within or adjacent to caribou migration routes would benefit caribou survival and would likely, temporarily at least, increase calf recruitment and total population size estimated for caribou. To test this notion would first require the determination or prediction of spatial and temporal characteristics of predation risk. Most mortality to radio-tagged caribou in north-central BC has occurred as predation by wolves (McNay and Voller 2007). Furthermore, predation appeared to occur mostly during or immediately subsequent to migration (McNay and Voller 2007). It seemed likely therefore, that most predation-related deaths should be located where migration routes intersect local areas of high use by wolves (i.e., places of high predation risk). My objective in preparation for the larger study was to test this prediction by assessing published models of predation risk with previously collected caribou mortality data. I considered the hypothesis that death sites of radio-tagged caribou killed by wolves could be discriminated from other sites chosen by caribou and from random sites on the landscape through predictions of predation risk. Presumably, radio-tagged caribou would reveal a general habitat use pattern of avoiding areas frequented by predators such as wolves. Avoidance (Johnson 1980) may be active avoidance in which case individuals that did so would have lower likelihood of being encountered and killed by wolves. However, avoidance may also be the result of previous predation leading to bias in our sample of radio-tagged caribou. I

considered that a comparison of models based on live caribou relocations versus random non-respondent data may elucidate the degree to which caribou actively select risk-free habitat.

## **2.0 STUDY AREA**

This study was located in north-central BC west of Williston Reservoir in the Omineca Mountains ecoregion between the Nation and Ingenika River drainages extending into the southern portion of the Northern Mountains and Plateau ecoregion. The study area encompassed two of four Recovery Planning Areas (RPAs; McNay et al. 2008) for herds of woodland caribou in that area (Figure 1): the Chase and Wolverine herds (Heard and Vagt 1998). First Nations reported historic seasonal use of the area by wolves and described an increase in the abundance of wolves and their more persistent presence following the first appearances of moose in the early 1920's (McKay 1997). Predators of caribou, other than wolves, included grizzly bear (*Ursus arctos* (Linnaeus 1758)), black bear (*Ursus americanus* (Pallas 1780)), lynx (*Lynx Canadensis*) and wolverine (*Gulo gulo* (Linnaeus 1758)). Occasional, infrequent reports of cougar (*Puma concolor* (Linnaeus 1771)) have been made apparently consistent with periodic increases in deer (*Odocoileus* spp. (Rafinesque 1832)) and elk (*Cervus elaphus* (Linnaeus 1758)) although I have yet to encounter a caribou killed by cougar in this study area. Other ungulates in the area include Stone's sheep (*Ovis dalli stonei* (Nelson 1884)) and mountain goats (*Oreamnos americanus* (de Blainville 1816)). Regulated hunting of mature male caribou occurred in the Chase area and the northern half of the Wolverine area for 12 weeks beginning every August 15<sup>th</sup> but only 1-3 bulls are killed annually. Regulated hunting was discontinued in the southern portion of the Wolverine area prior to 1981. Hunting by aboriginal people is permitted in all areas but I assumed too few caribou are killed to have a substantial influence on population dynamics.

### **2.1 Wolverine**

The Wolverine RPA is 844,313 ha, ranging in elevation from 676 to 2134 m in rolling high-elevation foothills, and includes four major watersheds of the Omineca, Manson, Klawli, and Germansen Rivers. It is roughly bounded in the north by the headwaters of Goat, Nina, and Big Creeks, in the west by Takla, Tsayta, and Indata Lakes, in the south by Tchentlo, and Chuchi Lakes, and in the east by Sylvester and Gaffney Creeks and the eastern slopes of the Wolverine Mountain Range. At low- to mid-elevations, the area is dominated by a Boreal White and Black

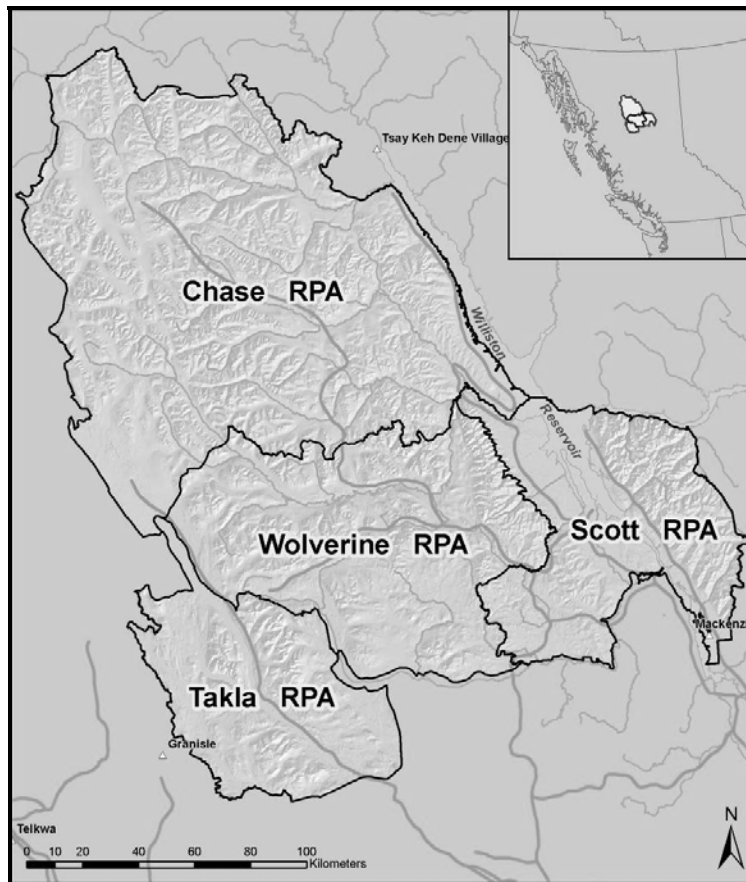


Figure 1. Location of recovery plan areas (RPA) for herds (Wolverine, Chase, Takla, and Scott) of threatened woodland caribou in north-central British Columbia.

Spruce subzone (BWBSdk1), two of the Sub-Boreal Spruce subzones (SBSmk1 and SBSmk2 variants), and an Engelmann Spruce-Subalpine Fir subzone (ESSFmv3) dominates the mid- to high-elevations. The Alpine Tundra (AT) prevails above tree line. Extensive areas within the study area have been managed for production of timber.

## 2.2 Chase

The Chase RPA is 1,733,039 ha situated in steep mountainous terrain ranging in elevation from 671 to 2466 m, and has three major watersheds including the Ingenika, Osilinka, and Mesilinka Rivers. It is roughly bounded in the north by the most northerly portion of the Finlay River, in the west by Thutade, Sustut and Driftwood Rivers, in the south by Ominicetla Creek, back end of Osilinka River, headwater of Wasi and Flegezand Creeks, and in the east by the Williston Reservoir. At low- to mid-elevations, the area is dominated by the BWBSdk1 and SBSmk2

biogeoclimatic variants, and at mid- to high-elevations the ESSF Omineca variant (ESSFmv3) predominates. The AT prevails above the tree line.

### 3.0 METHODS

#### *3.1 Relocation of Radio-tagged Caribou*

Research teams<sup>4</sup> fit caribou from the Wolverine and Chase herds with Very High Frequency (VHF) radio transmitters containing mortality sensors from 1991 to 2004. Some transmitter deployments also contained Global Positioning System (GPS) technology. Animals were captured in the Wolverine herd from 1991 to 2004, and in the Chase herd in 1991 to 1992 and then again from 1997 to 2003. Animals were caught using a net propelled by a .308 calibre rifle fired while hovering above the animal in a rotary-wing aircraft. Animals were blindfolded, hobbled, and manually restrained without the use of drugs while fitting radio transmitters. We determined caribou life stage by examination of tooth wear and replacement at the time of capture. This technique was sufficient to classify caribou as calves or yearling (<2 yr old, henceforth calves unless specified otherwise), or adult (>2 yr old). We assigned all caribou common birthdates of June 30 (i.e., the date when neonatal calf mortality subsided (McNay and Giguere 2007)).

Radio transmitters were attached to ear tags for animals caught as calves, expandable collars for animals caught as yearlings, and fixed-size collars for adults. Ear tags were replaced by expandable collars if calves lived to be yearlings and expandable collars were replaced with fixed-size collars once animals were adults. Collars and ear tags were fit to minimize disturbance to the animal. We generally monitored radio-tagged caribou  $\geq 2$  times per month until the radio transmitter faded or the animal died. More frequent (e.g., daily) observation was conducted during capture sessions to check the status of recently handled animals and to assess whether calves were properly reunited with mothers. Visual VHF locations were assumed to have a precision of <100m (or to be within 100m of their true location) or <250 m if the animal was not seen. All VHF locations were obtained during daylight hours using a Cessna 185, fixed-wing aircraft. GPS data were collected using Televilt (GPS-Simplex g01-01010, Televilt International, Lindesberg, Sweden) or Lotek (GPD 1000, Lotek Engineering, Newmarket, Ontario) GPS receivers. Random locations were gathered from within the Chase and Wolverine RPAs and were systematically assigned to age, sex, and season strata.

---

<sup>4</sup> Data collected from 1998 to 2007 was augmented from previous studies conducted on the same herds (Terry and Wood 1999, Wood and Terry 1999, Johnson 2000, Lance 2002)

I ensured relocations of each animal contributed equally to the analyses despite sample size differences among animals and seasons following methods described by Apps and McLellan (2006). I assumed  $\geq 5$  temporally independent relocations within each distinct seasonal range were required in order to adequately describe spatial use of seasonal range (Johnson 1980). Six seasons were arbitrarily defined based on the general movement patterns of radio-tagged caribou as follows: winter (January 01 to April 14), spring migration (April 15 to May 31), calving (June 01 to July 31), summer-rut (August 01 to September 30), post-rut (October 01 to November 14), and fall migration (November 15 to December 31). I assumed relocations were temporally independent if separated by an 8-day interval because movements were observed to asymptote at or before that interval (Rankin and McNay 2007). I therefore set a relocation weight  $X$  to 1 if  $\geq 8$  days had elapsed since the previous relocation; otherwise  $X$  was the proportion of 8 days that had elapsed. I also ensured that the temporal representation of data for each animal was balanced seasonally by establishing a relocation weight  $Y$  as the proportion of the total relocations represented by the seasonal locations (i.e., (total relocations / number of seasons) / number of season-specific relocations) observed for each animal in each season and a relocation weight  $Z$  as the proportion of the year represented by the season (i.e., (period length / number of seasons) / season length). Sample schedules for each animal were then standardized by applying a total weight ( $[X * Y * Z] / \sum [X * Y * Z]$ ) to each relocation.

### ***3.2 Mortality Investigations***

Site investigations were conducted as soon as possible after first monitoring mortality signals of radio-tagged caribou, or upon incidental encounter of dead, unmarked caribou. During site investigations we attempted to determine the time and cause of death. Time of death, within a week for calves for the first 10 weeks of calving and within a month for all other investigations, was subjectively determined by the investigator according to evidence at the site (e.g., a qualitative assessment of relative moisture content of the remains) or by investigating patterns in the radio-telemetry data leading up to the first observation of a mortality signal (e.g., screening of GPS data occasionally led to a better estimate of death date than aerial relocations). When sufficient remains were present at the site, we conducted partial necropsies (i.e., to the extent possible), took photos for subsequent inspection, and collected any evidence of the source of mortality and bone for marrow analysis. Death was classified as one of four causes: (1) accident/nutrition (including incidents involving vehicles, avalanches, starvation- and disease-related mechanisms), (2) human (including hunting and capture myopathy), (3) predation (including wolf, wolverine, lynx, or grizzly bear), or (4) unknown. Kills made by wolverine and lynx were generally distinguished by substantial head and/or neck injury and by feeding signs

consisting of burrowing into the carcass. Kills made by wolves were generally scattered in a wide area around the site while remains of caribou killed by bears were often buried. Other evidence at the site, or lack of evidence, was used to help substantiate cause of death such as track patterns, condition of surrounding vegetation, and hair and scat samples. Malnutrition in adult animals was identified by examination of the bone marrow; red, gelatinous bone marrow indicating malnutrition (Cheatum 1949); and confirmed later through an analysis of marrow fat content when samples were available, (Unpubl. data; Wildlife Infometrics Inc.; Mackenzie, British Columbia).

### ***3.3 Modeled Predation Risk***

Potential models of predation risk were based on four independent factors: (1) caribou age class, coded A in two classes (calves, other), (2) caribou sex, coded G in three classes (male, female, unknown), (3) season, coded S in six classes (winter, spring migration, calving, summer-rut, post-rut, fall migration), and (4) one of four estimators used to spatially distinguish sites of high predation risk (Table 1). General comparative characteristics of the four spatial predation risk models (hereafter referenced as blocks, roads, logistic, and Bayesian) are provided in (Table 2). The two simplest spatial estimators of predation risk were: (1) shortest, straight-line distance to roads, coded R as a continuous variable and (2) shortest, straight-line distance to early-seral (<20 year old) forests, coded B as a continuous variable. These data were obtained from planning information used by the forest licensees operating within the RPAs and updated annually to track new industrial development. Roads were all trails, logging roads, and main haul roads.

A third spatial estimator of predation risk was originally modeled by Johnson et al. (2002) and their methods formed the basis for calculating a weighted distance to areas of predicted high predation risk coded K as a continuous variable. Johnson et al. (2002) differentiated wolf relocations and moose kill sites from random locations on the basis of forest cover type using logistic regression. They concluded that predation risk for caribou could be described using the forest cover factors having significant positive regression coefficients in their logistic model (i.e., where caribou were most likely to encounter wolves). Although Johnson et al. (2002) derived forest cover types from interpretation of satellite imagery; I used their detailed cover type descriptions to derive similar cover types based on analysis of the BC Forest Inventory Planning attribute database<sup>5</sup> and the BC Terrain Resource Information Management program data<sup>6</sup>. This

---

<sup>5</sup> <http://srmwww.gov.bc.ca/gis/Databases/>. Accessed March 2007

<sup>6</sup> <http://ilmbwww.gov.bc.ca/bmgs/trim/index.html#> Accessed March 2007

Table 1. Spatial/temporal models of predation risk and the number of independent parameter estimates used to assess the relative ability of models to discriminate where radio-tagged woodland caribou were killed by wolves in north-central British Columbia, from other sites used while they were alive or from other random sites on the landscape. See text for a description of all models and model factors<sup>a</sup>, including the determination of spatial predation risk factors (Roads, Blocks, Logistic, and Bayesian).

Aspatial Models	Models Including Spatial Factors				Number of Parameters
	Roads	Blocks	Logistic	Bayesian	
	AGSRd	AGSBI	AGSLg	AGSBa	10
AGS					9
	AGRd	AGBI	AGLg	AGBa	5
	ASRd	ASBI	ASLg	ASBa	8
	GSRd	GSBI	GSLg	GSBa	9
AG					4
AS					7
	ARd	ABI	ALg	ABa	3
GS					8
	GRd	GBI	GLg	GBa	4
	SRd	SBI	SLg	SBa	7
A					2
G					3
S					6
	Rd	BI	Lg	Ba	2

a – model factors were: A – Caribou age at death (calf, adult), G – Caribou sex (male, female, unknown), S – Season (winter, spring migration, calving, summer-rut, post-rut, fall migration), Rd – shortest. Straight-line distance to nearest road, BI – shortest, straight-line distance to early-seral (<20 years old) forest, Lg – weighted distance to predation risk predicted using logistic regression methods described by Johnson et al. (2002), and Ba – position relative to polygons of predation risk (inside or outside) predicted using a Bayesian Belief Network described by McNay et al. (2006).

involved generalizing the description of spruce, pine, and wetland categories in the manner of Johnson et al. (2002) to the following: Spruce sites were dominated (80%) by *Picea engelmannii* (Engelmann 1884) and/or *P. glauca* ([Moench] Voss) and <1100 m in elevation; Pine sites were dominated (80%) by *Pinus contorta* (Douglas); and Wetland sites were any wetland (including



Table 2. General characteristics of four predation-risk models assessed using sites where radio-tagged woodland caribou were killed by wolves.

Characteristic	Predation Risk Model		
	Logistic	Bayesian	Blocks and Roads
Source	Johnson et al. 2002	McNay et al. 2006	NA
Derivation	Logistic Regression	Bayesian Belief Network	Database Query
Variable	Weighted Distance	Categorical High or Low	Linear Distance
Sensitive to annual changes?	No	No	Yes
Sensitive to seasonal changes?	No	Yes	No
Based on vegetation relationships?	Yes	Yes	No

lakes) or double-lined rivers. The weighted distance to areas of high risk following methods of Johnson et al. (2002):

$$\left( \sum_{i=1}^3 D * \frac{1}{RC_i} \right) / 3 \text{ where;}$$

D was the shortest straight-line distance to covertype *i* (Spruce, Pine, or Wetland) and RC was the regression coefficient for covertype *i* from Johnson et al. (2002).

The fourth and last spatial estimator of predation risk was derived using a Bayesian Belief Network described by McNay et al. (2006). This model was used to find areas of predation risk, coded as C in two classes (inside or outside the area of predation risk). Although this model was based primarily on location of early-seral forest types, it differed from the simple model of early-seral forests in four ways: (1) forest stands that contributed to risk were <40 years old rather than <20 years old (Heard et al. 2008), (2) only shrub-dominated sites were considered to have risk rather than all early-seral sites (Heard et al. 2008), (3) risky sites were <1200 m elevation during winter and there was no elevation restriction in other seasons (Thompson and Stewart 1997), and (4) risk was considered to be as probable in a 500-m area surrounding the selected sites as it was within the sites. Risk was labelled “inside” if inside the Bayesian-predicted risk polygons and “outside” if outside the polygons.

### 3.4 Analytical Methods

I used Arcview 9.2 (Environmental Systems Research Institute, Redlands, California) to collect model-specific risk values from sites where caribou were killed by wolves and, to provide a comparison, from sites where we did not observe caribou deaths but presumably could have. I used the following definition for sites where caribou deaths could have occurred: 1) sites known to be used by caribou based on relocations of all radio-tagged caribou excluding any death sites and 2) random sites on the landscape.

Logistic regression was used to model the probability of a kill site  $P(KS)$  with sample weights for responses (i.e., deaths) adjusted to account for nonrespondents (Iannacchione et al. 1991). The philosophy for choosing the model that most closely resembled the observed data was based on information theoretic concepts (White and Garrott 1990, Burnham and Anderson 2002). I restricted the list of potential model factors to those considered the most likely to contribute to the probability of caribou mortality due to predation from wolves (caribou age, caribou gender, season, and spatial proximity to various models of the risk of predation by wolves). Furthermore, I removed potential models involving obviously covariate factors (e.g., tested models were based on one, rather than a combination of, spatial risk predictions). Candidate models used all remaining possible combinations of the independent variables but deemphasized those with less than five response events per parameter estimate (Vittinghoff and McCulloch 2007). Akaike's Information Criterion with small-sample bias adjustment (AICc), was used to help identify model parsimony (Burnham and Anderson 2002). Further, we estimated the relative probability of each model being most parsimonious based on the difference in AIC (Anderson et al. 2000) calculated as:

$$W_m = \frac{\exp(-0.5\Delta_n)}{\sum_{n=1}^N \exp(-0.5\Delta_n)}; \text{ where}$$

$N$  is the total number of models compared and  $\Delta_n$  is the difference in AICc between model  $m$  and the model with the lowest AICc. Finally, we assessed the proportion of kill sites correctly classified (sensitivity) against the proportion incorrectly classified ( $1 - \text{specificity}$ ) for all possible thresholds of  $P(KS)$  using Receiver Operating Characteristic Curve analyses (AUC, Hanley and McNeil 1982). AUCs  $<0.7$  and  $>0.9$  indicate low and high levels of accuracy, respectively while scores between those values indicate moderate accuracy<sup>7</sup>. Wald  $\chi^2$  was used to infer significance of model coefficients (Allison 1999).

---

<sup>7</sup> Tape, T.G. Interpreting diagnostics tests <http://gim.unmc.edu/dxtests/Default.htm> (accessed February 16, 2009)

## 4.0 RESULTS

### 4.1 Compiled Data

Relocation data were retrieved for 231 caribou; 148 adults and 83 calves at first encounter. One hundred and twenty of those animals died, 43<sup>8</sup> (i.e., 36%) from predation by wolves: 33 as adults and 10 as calves (Table 3). Other predation-related deaths were from wolverine (n = 5), grizzly bear (n = 5), black bear (n = 2), and other unconfirmed predators (n = 15) (Appendix A). There were also 39 deaths of unknown causes and 11 deaths from accidents, hunter kills, or malnutrition (McNay and Voller 2007). Too few data were available to analyse predation risk for any predator other than wolves so the sites at which the 43 wolf-related deaths occurred and 58,368 relocations of all caribou composed the sample data set (Table 3). The mode of delay between estimated date of death and investigation (for those samples in which I knew the investigation date) was 7 days (n = 25). Summary statistics for the continuous, spatial variables are provided in Table 4. In general, caribou kill sites were located closer to roads than most caribou relocations when they were alive but caribou were also closer to roads than would be expected based on random locations. The same general pattern held for distance to early-seral forests although immediate adjacency was less than would be expected (Figure 2). The reverse was apparent of weighted distance to zones of predation risk defined by the Logistic model

Table 3. Number of animals, deaths from predation by wolves, and relocations collected for radio-tagged caribou in north-central British Columbia, 1991-2006.

Age Class	Sex	Caribou Herd Area					
		Chase			Wolverine		
		Animals	Deaths	Relocations	Animals	Deaths	Relocations
Adults	Female	41	10	9215	76	16	38747
	Male	22	3	5007	24	1	3091
	Unknown	2	1		4	2	
Calves	Female	15	1	776	15	0	706
	Male	15	5	406	15	2	420
	Unknown	0	0		2	2	
Subtotal		95	20	15404	136	23	42964
Total					231	43	58368

<sup>8</sup> Seven of these were incidental observations of recently killed caribou that were only observed the one time and were not actually radio-tagged.

Table 4. Calculated average distances (and standard deviation in parentheses) away from roads, early-seral forests, and areas of modeled predation risk that were observed for radio-tagged caribou when they were alive, for ransom points (*italicized*), and for caribou when they were found dead. Distances to roads and early-seral forests were the shortest straight-line distances. Distances to predation risk was a weighted index calculated following methods of Johnson et al. (2002).

Spatial variable	Age Class	Sex and status					
		Male		Female		Unknown	
		Alive	Dead	Alive	Dead	Alive	Dead
Sample size (caribou/random)		8,521 / 9,873	4	48,566 / 9,883	26	0	3
Distance to nearest road (m)		3,869 (3,427) <i>5,614 (7,338)</i>	1,366 (2,157)	4,775 (3,980) <i>5,504 (7,279)</i>	4,324 (4,158)		1,044 (387)
Distance to nearest early-seral forest (m)	Adult	7,170 (5,963) <i>10,792 (12,403)</i>	2,422 (2,587)	7,424 (5,969) <i>10,667 (12,323)</i>	6,076 (5,467)		7,924 (5,572)
Weighted distance to nearest predation risk		34,538 (28,287) <i>32,152 (27,819)</i>	16,900 <i>(25,575)</i>	38,865 <i>(22,484)</i> <i>32,114 (27,964)</i>	19,635 <i>(28,231)</i>		4,068 (1,748)
Sample size		403 / 9,797	7	291 / 9,970	1	0	2
Distance to nearest road (m)		5,667 (5,523) <i>5,691 (7,508)</i>	5,625 (6,206)	6,913 (6,333) <i>5,475 (7,245)</i>	6,453		1,354 (1,055)
Distance to nearest early-seral forest (m)	Calf	8,288 (8,109) <i>10,762 (12,464)</i>	14,239 <i>(15,499)</i>	10,673 (9,175) <i>10,530 (12,336)</i>	7,000		13,250 <i>(4,978)</i>
Weighted distance to nearest predation risk		41,857 (22,910) <i>31,860 (27,490)</i>	45,554 <i>(47,823)</i>	44,595 <i>(22,801)</i> <i>32,004 (27,697)</i>	51,098		18,398 <i>(9,349)</i>

## Frequency of observations

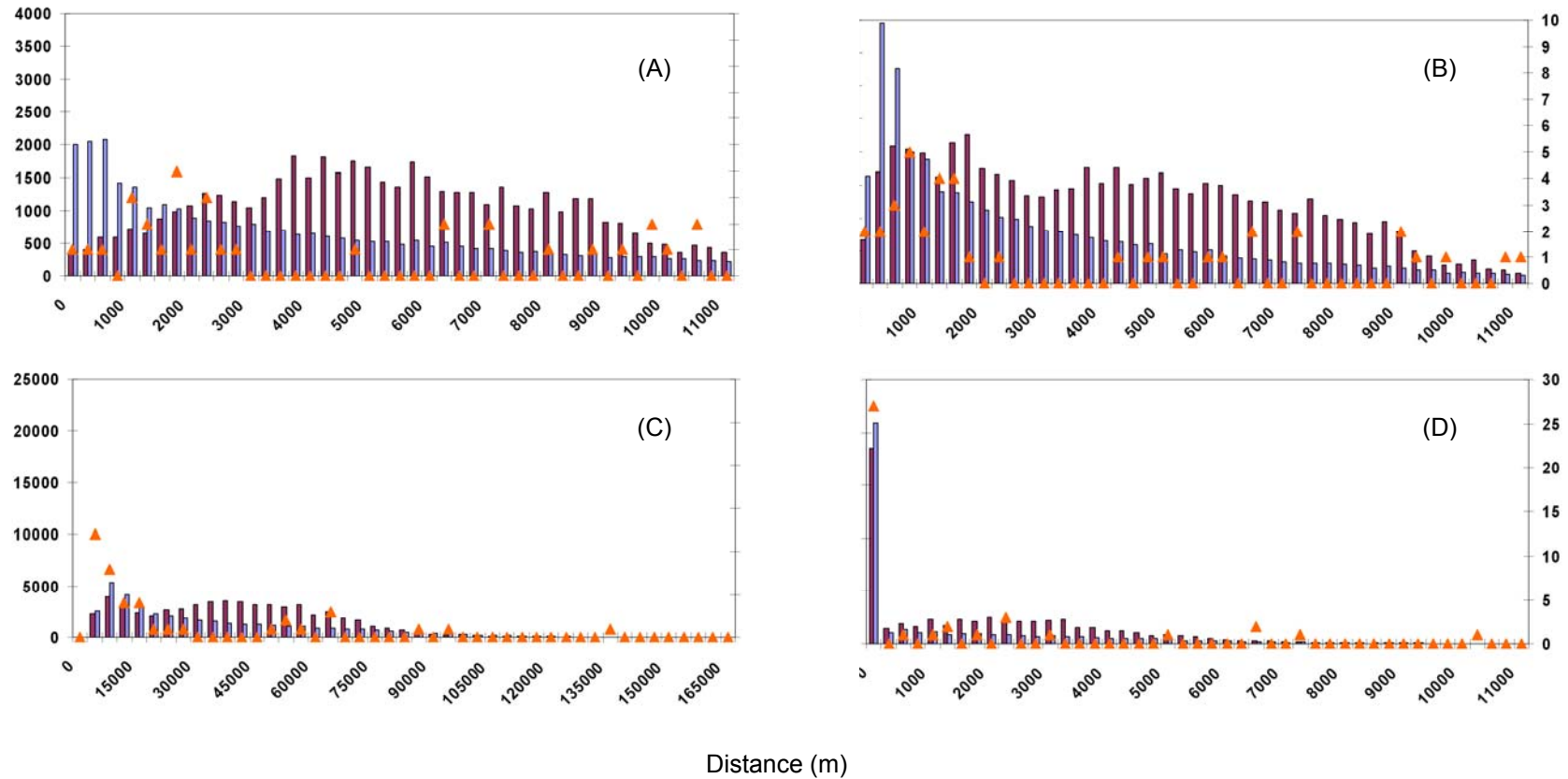


Figure 2. Frequency of observations (purple bars - caribou relocations, blue bars – random locations, orange triangles – caribou killed by wolves) and the shortest, straight-line distances to (A) early-seral forests, (B) roads, (C) modeled risk of predation (Logistic), and (D) modeled risk of predation (Bayesian). Distances to predation risk for the Logistic model was a weighted index calculated following methods of Johnson et al. (2002). The Bayesian model was calculated following methods of (McNay et al. 2006).

(Table 4) and although there was a large amount of use in the Bayesian-predicted high risk zone, more use was made of the area outside that zone (Figure 2).

#### ***4.2 Discriminating Kill Sites from Caribou Relocations***

All independent factors except sex ( $df = 2$ , Wald  $\chi^2 = 2.14$ ,  $P = 0.3427$ ) contributed to  $P(KS)$  as discriminated against relocations of radio-tagged caribou. Subsequent model comparison was therefore restricted to the 19 models without sex. The model ASBa, based on caribou age class at death, season, and the Bayesian risk model (Figure 3) had the lowest AICc and was tied for the highest AUC with a two-factor model based on caribou age class and the Logistic risk model; the latter of which ranked fourth overall (Table 5). However, the odds ratio of the Bayesian model in ASBa was low (Table 6) indicating only weak contribution to prediction of  $P(KS)$  (Figure 4). The Logistic model of risk (Lg, Table 5) ranked as the best single predictor of caribou deaths. All factors remained significant ( $P < 0.0500$ ) in the reduced models. Based on the ASBa model (Table 6), parameter estimates for  $P(KS)$  indicated that wolf kill sites were more likely to be for calves than adults, that they would occur in winter or during the spring migration, and were least likely to occur outside the modeled zones of predation risk.

#### ***4.3 Discriminating Kill Sites from Random Locations***

Age class and sex never contributed significantly (Wald  $\chi^2 < 1.00$ ,  $P > 0.1000$ ) to  $P(KS)$  as discriminated against stratified random locations. The subsequent model comparison was therefore restricted to the 9 models without age class. The model based on season and distance to roads had the lowest AICc (Table 5) but the model based on the Logistic prediction of risk by itself had the highest AUC although it ranked 6<sup>th</sup> in AICc (Table 5). Many of the models were characterized by relatively low AUCs indicating poor model fit when using random nonrepondent data (Table 5). Only the Logistic risk model was comparable in performance to the tests using caribou relocations as the nonrespondent data. The odds ratio for this model using random nonrepondent data indicated that for every 100 interval of the weighted distance away from risk, the intercept for  $P(KS)$  would reduce by 0.03 (Table 6).

## **5.0 DISCUSSION**

The spatial estimator of predation risk based on the Johnson et al. (2002) Logistic model performed better than any other single, spatial estimator in discriminating kill sites from other

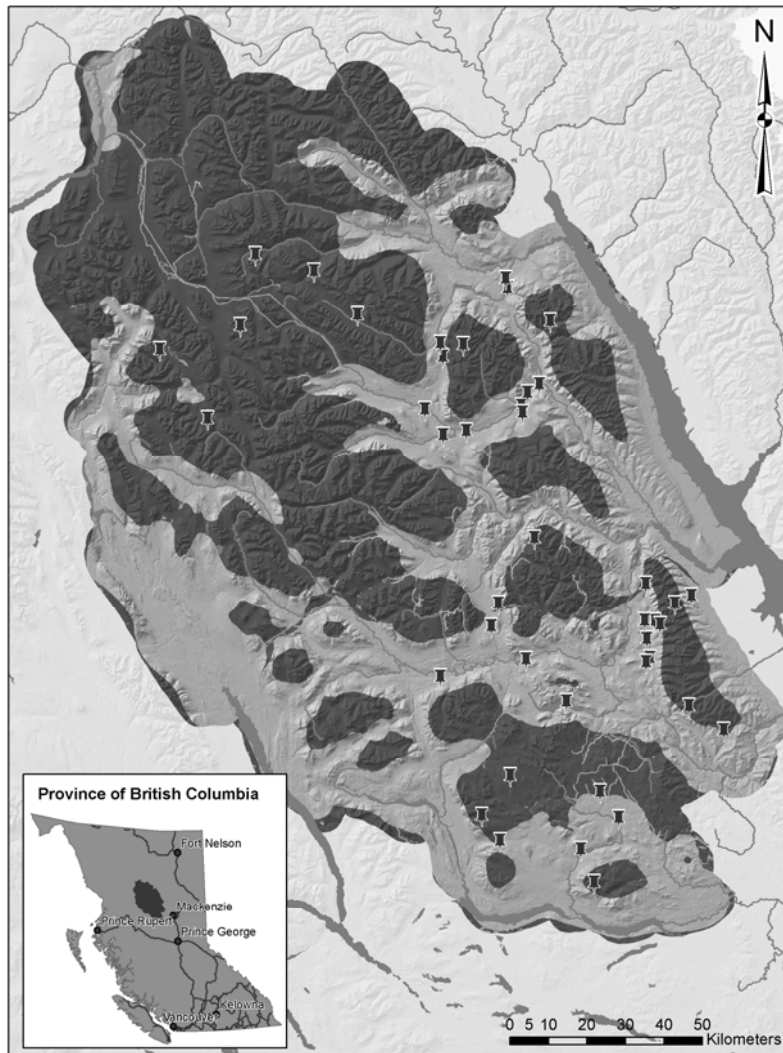


Figure 3. Sites where radio-tagged caribou were killed by wolves (black pins, 1991-2006, north-central British Columbia), in relation to an area of predicted low predation risk (darker shade) modeled with a Bayesian Belief Network (McNay et al. 2006).

sites used by radio-tagged caribou. Using similar logistic methods and random locations as nonrespondents, Gustine et al. (2006) were also able to distinguish areas of lower risk of wolf predation from other places on the landscape. These models essentially characterize risky (conversely, relatively safe) parts of the landscape. However, discriminating sites at which radio-tagged caribou were killed by wolves was more often successful (i.e., more acceptable and better fitting models) when I used caribou relocations as the nonrespondent data rather than stratified random locations. In general, these caribou relocation-based nonrespondent models performed better likely because caribou spend disproportionately less time at low elevations

Table 5. Comparison of logistic regression models used to discriminate sites where radio-tagged woodland caribou were killed by wolves in north-central British Columbia from other sites used while caribou were alive or from random sites on the landscape. Nonrespondent data (NRD) were referred to as caribou relocations or random locations, respectively. Decreasing model rank was assessed using Akaike's information criterion for small sample sizes (AICc), AICc difference from the model with lowest AICc ( $\Delta_n$ ), AIC weight (Wm), area under the receiver operating characteristics curve (AUC), Wald  $\chi^2$ , and number of independent parameters estimated (df). All models had significance levels (P) <0.001.

NRD	Model <sup>a</sup>	AIC	$\Delta_n$	Wm	AUC	Wald $\chi^2$	Df
Caribou relocations	ASBa	428.3	0.0	0.92	0.783	92.5	7
	ASLg	433.1	4.8	0.08	0.760	86.0	7
	ASRd	464.6	36.3	<.0001	0.665	75.4	7
	ALg	466.3	38.1	<.0001	0.783	78.6	2
	ASBI	486.3	58.0	<.0001	0.622	67.5	7
	SLg	491.3	63.0	<.0001	0.714	70.0	6
	ABa	496.0	67.8	<.0001	0.742	73.5	2
	SRd	505.8	77.5	<.0001	0.592	54.5	6
	AS	509.2	81.0	<.0001	0.655	65.5	6
	SBI	511.2	82.9	<.0001	0.582	53.3	6
	SBa	520.6	92.4	<.0001	0.725	66.7	6
	Lg	523.5	95.2	<.0001	0.728	66.9	1
	ARd	535.4	107.1	<.0001	0.650	46.8	2
	S	556.7	128.4	<.0001	0.574	37.0	5
	Rd	558.0	129.7	<.0001	0.596	33.0	1
	Ba	567.9	139.6	<.0001	0.678	57.7	1
	ABI	597.1	168.8	<.0001	0.669	8.3	2
	BI	602.6	174.3	<.0001	0.450	1.0	1
	A	614.6	186.4	<.0001	0.611	14.3	1
Random	SRd	503.1	0.0	0.7006	0.570	60.5	6
	SLg	504.8	1.7	0.2994	0.617	62.5	6
	SBk	532.2	29.1	<.0001	0.543	44.3	6
	SBa	538.3	35.2	<.0001	0.604	51.6	6
	S	547.7	44.6	<.0001	0.555	42.5	5
	Lg	575.6	72.5	<.0001	0.668	37.1	1
	Rd	579.9	76.8	<.0001	0.537	28.3	1
	Bk	619.1	116.0	<.0001	0.549	2.0	1
	Ba	619.4	116.3	<.0001	0.573	19.3	1

a – model factors were: A – Caribou age at death (calf, adult), G – Caribou sex (male, female, unknown), S – Season (winter, spring migration, calving, summer-rut, post-rut, fall migration), Rd – shortest, straight-line distance to nearest road, BI – shortest, straight-line distance to early-seral (<20 years old) forest, Lg – weighted distance to predation risk predicted using logistic regression methods described by Johnson et al. (2002), and Ba – position relative to polygons of predation risk (inside or outside) predicted using a Bayesian Belief Network described by McNay et al. (2006).



Table 6. Logistic regression models used to discriminate sites where radio-tagged woodland caribou were killed by wolves in north-central British Columbia, from other sites used while they were alive or from other random sites on the landscape. Nonrespondent data (NRD) were referred to as caribou relocations or random locations, respectively. Caribou relocation, nonrespondent data led to the selected model based on age class of caribou at death, season, and a previously constructed Bayesian Belief Network (McNay et al. 2006), the latter used to predict zones of high predation risk (n = 57,748, Wald  $\chi^2$  = 92.51, P<0.001, AUC = 0.783). Random location, nonrespondent data led to the selected model based on the Logistic prediction of predation risk (n = 39,564, Wald  $\chi^2$  = 37.11, P<0.001, AUC = 0.668). See text for variable and model descriptions.

NRD	Variable	Parameter	Parameter Estimate	SE	Wald $\chi^2$	P	Odds Ratio
Caribou relocations	Intercept	Alive	-3.86	1.28	9.12	0.0025	
		Kill Site	Reference				
	Age Class	Calves	3.29	0.42	60.59	<0.0001	26.97
		Adults	Reference				
	Season	Fall migration	2.74	1.32	4.33	0.0375	15.54
		Winter	5.44	1.31	17.29	<0.0001	231.51
		Spring migration	5.05	1.30	15.21	<0.0001	156.76
		Calving	3.63	1.29	7.89	0.0050	37.94
		Summer/rut	4.47	1.31	11.73	0.0006	87.81
		Post-rut	Reference				
	Bayesian Predation Risk	Out of zone	-2.91	0.39	56.82	<0.0001	0.054
		In zone	Reference				
Random	Intercept	Alive	0.86	0.14	38.63	<0.0001	
		Kill Site	Reference				
	Logistic	Distance	-0.00003	.00003	37.11	<0.0001	1.00

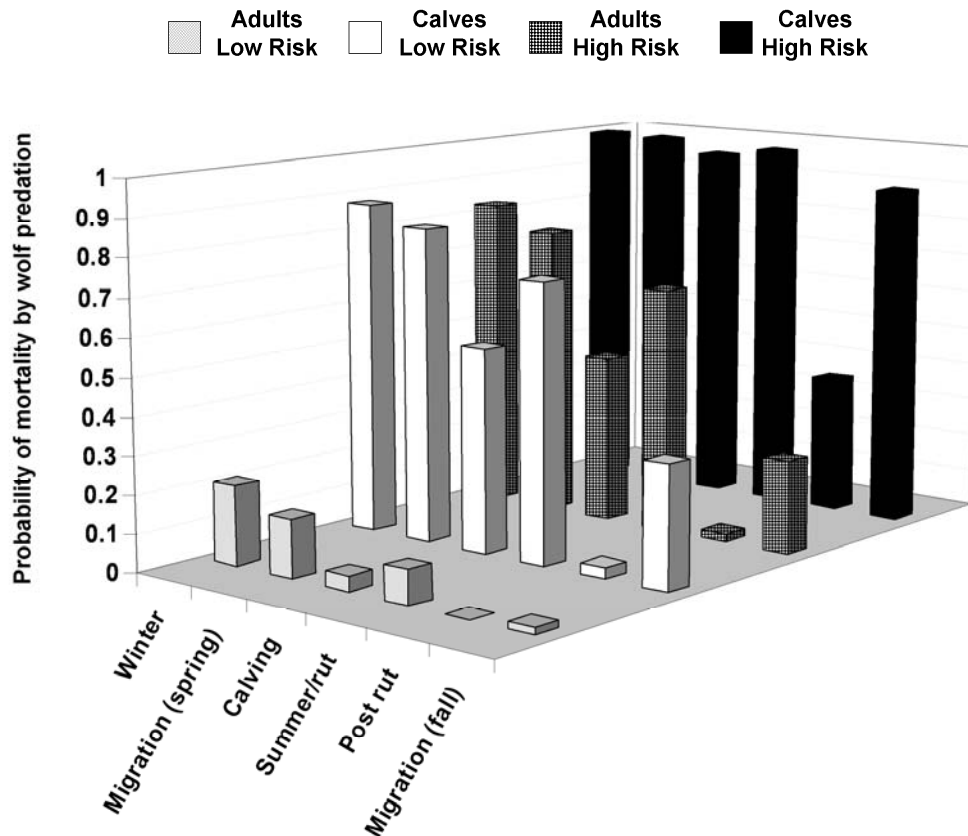


Figure 4. Probability of a kill site due to mortality by wolf predation for radio-tagged caribou calves and adults during specific seasons, within two zones of predation risk (High and Low) in north-central British Columbia, 1991-2006. Risk zones were previously modeled using a Bayesian Belief Network (McNay et al. 2006).

where risk of predation is normally considered to be relatively high (Seip 1992). It would have therefore been relatively more likely, compared to using stratified-random nonrespondents, to discriminate sites where radio-tagged caribou were killed by wolves. The results indicate that radio-tagged caribou survival was correlated with habitat selection; at least at relatively high levels of scalar, habitat choice (i.e., seasonal range selection). Gustine et al. (2006) concluded this for the selection of calving ranges by woodland caribou and I conclude that caribou generally select for safer habitat than otherwise. However, our common conclusion does not answer whether caribou actively select for low-risk habitats rather than simply be eliminated from high-risk habitats since the result would apparently be the same in either case. Courtois et al. (2008) documented eventual spatial shift in use of habitat by caribou due to persistent and long-lasting changes to their landscape (i.e., timber harvest); so did Shaffer and Mahoney (2007). By comparison to this behavioural adaptation, caribou mortality can also be significantly higher

in disturbed landscapes (Courtois et al. 2007). These study results imply both behavioural and demographic factors manifest in the apparent selection of low-risk habitats by caribou.

Both previously published risk models that I evaluated (Bayesian and Logistic), performed well when caribou relocations were used as the nonrespondents and both were complemented by supplementary information about the kill sites (i.e., seasons and caribou age class in particular). It is not surprising that these models performed better than the simpler models based on distance to roads or distance to early-seral forest. Both factors apparently contribute to caribou mortality (James and Stuart Smith 2000, Courtois et al. 2008) and the models of predation risk incorporated these factors either directly (McNay et al. 2006) or by association (Johnson et al. 2002). The negative parameter estimate for distance to roads indicated the probability of a kill site from predation by wolves was more likely further away from roads; contrary to expectations based on conclusion from James and Stuart Smith (2000). Roads and other linear corridors in the Wolverine and Chase herd areas are fewer, and caribou are located on average 10-fold further from roads, compared to the study by James and Stuart Smith. The difference in the study results reflects a difference in availability of roads. Where caribou live in areas of relatively high road density, it's possible that a wolf kill site will be closer to a road than otherwise; particularly if predators tend to favour the use of roads as they apparently did in the James and Stuart Smith study. In an area of relatively low road density, it's not necessarily the case that caribou deaths would be close to roads even if predators favoured using roads. Despite the fact that caribou chose their general range closer to roads than expected (Table 4), there was lower use of the 1-km area around roads than would be expected based on random locations.

The low odds ratio for the Bayesian factor in the ASBa model likely resulted due to leverage from 12 mortalities that occurred  $>1,350$  m asl (Appendix A) and outside the Bayesian-predicted high risk polygon (Figure 2). The Bayesian model underestimates risk of predation in at least two ways that could have influenced these mortalities and, had they been considered, would likely have improved model performance: first, predation risk was only considered to exist  $\leq 100$  m from roads (McNay et al. 2006) where perhaps this parameter should be much greater (James and Stuart Smith 2000) and second, rivers were not considered to be linear corridors yet wolves frequently seek large rivers as travel corridors, especially during winter (Kunkel and Pletscher 2001, Mech and Boitani 2003). An even more compelling reason for the low odds ratio was that wolves were likely accessing the modeled low-risk zone just prior to and during calving specifically to hunt caribou calves. In general, the odds ratio (Table 6) for age class implied that caribou kill sites were more likely to be calves than adults; in fact the probability of a calf kill site remained relatively high for most seasons except post-rut and regardless of the risk of

predation by wolves (Figure 3). However, of the total 10 calf deaths, 6 occurred > 1,350 m asl (Appendix A); half of the observed deaths in the Bayesian-predicted low risk zone. Five of the 6 calf kills in that zone occurred during calving or just prior to calving when the probability of a caribou kill site being an adult was relatively low (Figure 3). Only two of the caribou kills that occurred >1,350 m asl were in summer months (Appendix A). Although the Bayesian risk model was able to discriminate kill sites, it probably cannot do so accurately during the calving season and summer when access to the higher-elevation caribou range is not restricted by snow.

A comparison of the odds ratios (Table 6) for seasonal variation implied that caribou kill sites were correctly classified best during winter and spring migration (Figure 3). Although kill sites were more likely discriminated by the winter season, much of the predation in winter occurred late (March and April) near the onset of migration (Appendix A). This migration was when caribou moved away from winter ranges to seek either calving range (adult females) or lower elevation spring range (males) (Unpublished data, Wildlife Infometrics Inc., Mackenzie, BC). By migrating away from winter range, caribou were likely reducing their annual risk of predation even though they had to negotiate zones of high predation risk to do so. During migration there was likely a greater tendency for radio-tagged caribou to overlap with moose and wolves and incidental contact alone could thereby have increased predation rates (Wittmer et al. 2005, Sinclair et al. 1998). At this relatively fine spatial resolution (i.e., site selection during migration), caribou undertake risk of predation to presumably position themselves for relatively greater net gain (i.e., either lower risk of predation, greater forage resources, or both) in the subsequent season. The distinction in scalar habitat was also noted by Hebblewhite and Merrill (2007) in their comparison of risk of migration and the apparent benefits to elk in seeking low risk summer range. Although elk were at higher risk during migration, the benefits apparently led to lower annual mortality (resident versus migrants). Migratory elk that moved through zones of high predation risk, and suffered relatively high mortality, still had lower annual mortality than elk that did not migrate. Similar results were found by McNay and Voller (1995) where migratory black-tailed deer (*Odocoileus hemionus columbianus*) incurred less annual mortality than resident deer.

## **6.0 MANAGEMENT IMPLICATIONS**

The Bayesian risk model has been used elsewhere to inform decisions about recovery of threatened caribou in north-central BC (McNay et al. 2008). My findings support the notion that the model can perform well and can therefore be used to identify spatial locations and seasons of high predation risk for caribou in the Wolverine and Chase caribou herd areas. Furthermore,

based on temporal information about predation by wolves, predictions can be made about when and where this type of caribou mortality is most likely to occur. It's likely the model and conclusions resulting from its application could be extrapolated to adjacent herd areas (e.g., the Takla and Scott herds or quite possibly the Finlay herd) where seasonal weather, forage resources, predators, and primary prey populations are expected to be similar.

Spatial depiction of the risk zone revealed that the southern portion of the study area had larger areas of predation risk than the northern portion (Figure 2). Because the spatial estimator of predation risk is primarily based on the location of early-seral forests, further range disturbances that lead to this forest type are expected to lead to higher predation risk and greater probability of caribou mortality. Areas being harvested for timber or being killed by the recent outbreak of mountain pine beetle (*Dendroctonus ponderosae*) are predominately located at low elevations where caribou migrate between ranges. If the risk of predation in these areas is not mitigated, I expect caribou range will be reduced to "islands" of relative safety as has apparently occurred in the adjacent Takla herd (Poole et al. 2000). Model results for the Chase and Wolverine herds depict where this spatial retraction of caribou range is most likely to occur. Spatially-explicit recovery actions could be undertaken to avoid that outcome. Specifically, migration routes used by caribou should be managed in a manner to minimize use by wolves. Presumably this could be accomplished by avoiding habitat management that yields increased populations of wolves' primary prey, by reducing wolves' primary prey, or by reducing wolf numbers (McNay et al. 2008). Maintenance or recovery of severely declining caribou populations will undoubtedly require multiple recovery actions including the reduction of predation rates. However, broad-scale reduction of wolves is not the objective of recovery as defined by the Species at Risk Act. I suggest that models of predation risk, such as the ones evaluated here, can identify areas where removal of wolves at specific locations may be as effective as a broader, indiscriminate predator reduction policy although research is required to test this notion.

## 7.0 REFERENCES

- Allison, P.D. 1999. Logistic regression using the SAS system: Theory and application. SAS Publishing. Cary, NC 288pp.
- Apps, C.D., and B.N. McLellan. 2006. Factors influencing the dispersion and fragmentation of endangered mountain caribou populations. *Biological Conservation* 130:84-97.

- Bergerud, A.T. 1983. The natural population control of caribou. Pages 14-61 *in* F.L. Bunnell, D.S. Eastman, and J.M. Peek, co-editors. Symposium on natural regulation of wildlife populations. Forest, Wildlife, and Range Experiment Station, University of Idaho, Moscow, Idaho.
- \_\_\_\_\_, A.T., H.E. Butler, and D.R. Miller. 1984. Antipredator tactics of calving caribou: dispersion in mountains. *Canadian Journal of Zoology* 62:1566-1575.
- Bradshaw, C.A., S. Boutin and D.M. Hebert. 1997. Effects of petroleum exploration on woodland caribou in northeastern Alberta. *Journal of Wildlife Management* 61:1127-1133.
- Boertje, R., P. Valkenburg, and M. McNay. 1996. Increases in moose, caribou, and wolves following wolf control in Alaska. *Journal of Wildlife Management* 60:474-489.
- Cheatum, E.L. 1949. Bone marrow as an index of malnutrition in deer. *N.Y. State Conservation* 3:19-22.
- Courtois, R., J-P. Ouellet, L. Breton, and C. Dussault. 2007. Effects of forest disturbance on density, space use, and mortality of woodland caribou. *Ecoscience* 14:491-498.
- \_\_\_\_\_, R., A. Gingras, D. Fortin, A. Sebbane, B. Rochette, and L. Breton. 2008. Demographic and behavioural response of woodland caribou to forest harvesting. *Canadian Journal of Forest Research* 38:2837-2849.
- Dyer, S.J., J.P. O'Neill, S.M. Wasel, and S. Boutin. 2001. Avoidance of industrial development by woodland caribou. *Journal of Wildlife Management* 65:531-542.
- Elliot, J. 1985. Muskwa wolf management project of north-eastern BC: wolf/ungulate management 1984-85 annual report. British Columbia Ministry of Environment, Fort St. John, British Columbia.
- Gustine, D.D., K.L. Parker, R.J. Lay, M.P. Gillingham, and D.C. Heard. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs* No. 165.

- Hanley, J.A. and B.J. McNeil. 1982. The meaning and use of the area under an ROC curve. *Radiology* 143(1):29-36.
- Hatter, J. 1950. The moose of central British Columbia. Dissertation, State College of Washington, Pullman, Washington.
- Hayes, R.D., R. Farnell, R.M.P. Ward, J. Carey, M. Dehn, G.W. Kuzyk, A. M. Baer, C.L. Gardner, and M. O'Donoghue. 2003. Experimental reduction of wolves in the Yukon: ungulate responses and management implications. *Wildlife Monographs* 152.
- Heard, D.C. and K.L. Vagt. 1998. Caribou in British Columbia: a 1996 status report. *Rangifer*, Special Issue No. 10:117-123.
- \_\_\_\_\_, D.C., A.B.D. Walker, J.B. Ayotte, and G.S. Watts. 2008. Using GIS to modify a stratified random block survey design for moose. *Alces* 44:111-116.
- Hebblewhite, M. and E.H. Merrill. 2007. Multiscale wolf predation risk for elk: does migration reduce risk? *Oecologia* 152:377-387.
- Iannacchione, V.G., J.G. Milne, and R.E. Folsom. 1991. Response probability weight adjustments using logistic regression. 151st Annual Meeting of the American Statistical Association, Atlanta, GA August 18-22, 1991.
- Jalkotzy, M.G., P.I. Ross, and M.D. Nasserden. 1997. The effects of linear developments on wildlife: a review of selected scientific literature. Prepared for the Canadian Association of Petroleum Producers. Arc Wildlife Services Ltd., Calgary, Alberta.
- James, A.R.C. and A.K. Stuart Smith. 2000. Distribution of caribou and wolves in relation to linear corridors. *Journal of Wildlife Management* 64:154-159.
- Janz, D. 1989. Wolf-deer interactions on Vancouver Island. *In* Wolf – prey dynamics and management, proceedings of a symposium May 1988, University of British Columbia. BC Ministry of Environment Report No. WR-40, Ministry of Environment, Victoria, BC.
- Johnson, C. J. 2000. A multi-scale behavioural approach to understanding the movements of woodland caribou. Ph.D. thesis. Univ. Northern B.C., Prince George, B.C. 210 p.

- \_\_\_\_\_, C.J., K.L. Parker, D.C. Heard, and M.P. Gillingham. 2002. A multiscale behavioural approach to understanding the movements of woodland caribou. *Ecological Applications* 12:1840-1860.
- \_\_\_\_\_, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- Kunkel, K. and D.H. Pletscher. 2001. Winter hunting patterns of wolves in and near Glacier National Park, Montana. *Journal of Wildlife Management* 65:520-530.
- Lance, A.N. 2002. Caribou Monitoring at Valteau Creek: Caribou Use of the Valteau Creek Watershed, Fort St. James District, 1997-2001. Industrial Forestry Service Ltd. 44 pp. plus appendices.
- Lima, S.L. and D.L.M. Dill. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619-640.
- Macgregor, W. 1985. Provincial and regional caribou plans. Pages 2-8 *in* R. Page, editor. Caribou research and management in British Columbia. British Columbia Ministry of Forests, Research Branch, WHR-27, Victoria, BC.
- McKay, B. 1997. Valteau Creek caribou study. Unpublished Report, British Columbia Ministry of Water, Land, and Air Protection, Prince George, B.C.
- McNay, R.S. and L. Giguere. 2007. Timing and synchronicity of calving in woodland caribou herds of north-central British Columbia. Internal Report, Wildlife Infometrics Report 230. Wildlife Infometrics Inc., Mackenzie, British Columbia, Canada
- \_\_\_\_\_, R.S. and J. Voller. 1995. Mortality causes and survival estimates for adult female Columbian black-tailed deer. *Journal of Wildlife Management* 59:138-146.
- \_\_\_\_\_, R.S. and J. Voller. 2007. Mortality and survival-rate estimates for woodland caribou in north-central British Columbia. Internal Report, Wildlife Infometrics Report No. 236. Wildlife Infometrics Inc., Mackenzie, British Columbia, Canada.



- \_\_\_\_\_, R.S., D. Heard, R. Sulyma, and R. Ellis. 2008. A recovery action plan for northern caribou herds in north-central British Columbia. FORREX 22, Forest Research Extension Partnership, Kamloops, British Columbia.
- \_\_\_\_\_, R.S., B.G. Marcot, V. Brumovsky, and R. Ellis. 2006. A Bayesian approach to evaluating habitat suitability for woodland caribou in north-central British Columbia. *Canadian Journal of Forest Research* 36:3117-3133.
- MCTAC (Mountain Caribou Technical Advisory Committee). 2003. A strategy for the recovery of mountain caribou in British Columbia. British Columbia Ministry of Water, Land, and Air Protection, Victoria, BC.
- Mech, L.D. and L. Boitani. 2000. *Wolves: Behavior, ecology, and conservation*. University of Chicago Press, Chicago. 448pp.
- Messier, F., S. Boutin, and D. Heard. 2004. Revelstoke mountain caribou recovery: an independent review of predator-prey-habitat interactions. Unpublished Report, Revelstoke Caribou Recovery Committee, Revelstoke, British Columbia.
- NRC (National Research Council, Committee on Management of Wolf and Bear Populations in Alaska). 1997. *Wolves, bears, and their prey in Alaska: Biological and social challenges in wildlife management*. National Academy Press, Washington. 224pp.
- Nyberg, B. 1999. An introductory guide to adaptive management for project leaders and participants. British Columbia Ministry of Forests, Forest Practices Branch, Victoria, BC.
- Poole, K.G., D.C. Heard, and G. Mowat. 2000. Habitat use by woodland caribou near Takla Lake in central British Columbia. *Canadian Journal of Zoology* 70:1552-1561.
- Racey, G., A. Harris, L. Gerrish, T. Armstrong, J. McNicol, and J. Baker. 1999. *Forest management guidelines for the conservation of Woodland Caribou: a landscape approach for use in northwestern Ontario*. Version 1.0 Ontario Ministry of Natural Resources, Thunder Bay, Ontario. 69pp.

- Rankin, M.L. and R.S. McNay. 2007. Use of serial dependence to indicate movement decisions by woodland caribou in north-central British Columbia. Wildlife Infometrics Inc. Report No. 235. Wildlife Infometrics Inc., Mackenzie, British Columbia, Canada
- Rempel, R.S., P.C. Elkie, A.R. Rodgers, and M.J. Gluck. 1997. Timber-management and natural-disturbance effects on moose habitat: landscape evaluation. *Journal of Wildlife Management* 61:517-524.
- Rettie, W.J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23:466-478.
- \_\_\_\_\_, W.J., and F. Messier. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. *Canadian Journal of Zoology* 76:251-259.
- Schaefer, J.A. and S.P. Mahoney. 2007. Effects of progressive clearcut logging on Newfoundland caribou. *Journal of Wildlife Management* 71:1753-1757.
- Seip, D. 2005. Recovery implementation plan for threatened woodland caribou (*Rangifer tarandus caribou*) in the Hart and Cariboo Mountains recovery area, British Columbia. Internal Report, Species at Risk Coordination Office, British Columbia Ministry of Agriculture and Land, Victoria, BC.
- \_\_\_\_\_. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology* 70:1494-1503.
- \_\_\_\_\_. 1991. Predation and caribou populations. *Rangifer Special Issue* 7:46-52.
- Sinclair, A.R.E., R.P. Pech, C.R. Dickman, D. Hik, P. Mahon, and A.E. Newsome. 1998. Predicting effects of predation on conservation of endangered prey. *Conservation Biology* 12:564-575.
- Spalding, D.J. 1992. The history of elk (*Cervus elaphus*) in British Columbia. Contributions to Natural Science No. 18, The Royal British Columbia Museum, Victoria, British Columbia.

- \_\_\_\_\_. 1990. The early history of moose (*Alces alces*): distribution and relative abundance in British Columbia. Contributions to Natural Science No. 11, The Royal British Columbia Museum, Victoria, British Columbia.
- Terry, E.L. and M.D. Wood. 1999. Seasonal movements and habitat selection by woodland caribou in the Wolverine herd, north-central British Columbia. Phase 2: 1994-1997. Peace/Williston Fish and Wildlife Compensation Program, Prince George, British Columbia, Canada. 36 p.
- Thomas, D.C. 1995. A review of wolf-caribou relationships and conservation implications in Canada. Pages 261-273 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Proceedings of the Second North American Symposium on Wolves, Edmonton, Alberta, 25-27 August 1992. Occasional Paper No. 35, Canadian Circumpolar Institute, Edmonton, Alberta.
- Thompson, I.D., and R.W. Stewart. 1997. Management of moose habitats. Pp. 377-401. In (A.W. Franzmann and C.C. Schwartz, eds.) Ecology and Management of the North American Moose. Smithsonian Institution Press, Washington.
- Vittinghoff, E. and C.E. McCulloch. 2007. Relaxing the rule of ten events per variable in logistic and cox regression. American Journal of Epidemiology 165(6):710-718.
- Wallmo, O.C. 1969. Response of deer to alternate-strip clearcutting of lodgepole pine and spruce-fir timber in Colorado. USDA Forest Service Research Note RM-141.
- Wittmer, H.U. 2004. Mechanisms underlying the decline of mountain caribou (*Rangifer tarandus caribou*) in British Columbia. Dissertation, University of British Columbia, Vancouver, BC.
- Wittmer, H.U., B.N. McLellan, D.R. Seip, J.A. Young, T.A. Kinley, G.S. Watts, and D. Hamilton. 2005. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. Canadian Journal of Zoology 83:407-418.
- Wood, M.D. and E.L. Terry. 1999. Seasonal Movement and Habitat Selection by Woodland Caribou in the Omineca Mountains, North-Central British Columbia Phase 1: The Chase

And Wolverine Herds (1991-1994). Peace/Williston Fish and Wildlife Compensation Program Report No. 201. 41pp. plus appendices.

Youds, J. and L. Roorda. 2001. Proposal to temporarily reduce wolf population density in the Quesnel Highland-Cariboo Mountains, Cariboo Region. Unpublished Report, Ministry of Water, Land, and Air Protection, Williams Lake, British Columbia.

## 8.0 APPENDIX A

Date, inferred predation cause, and location of mortality for individual, calf (C), yearling (Y), and adult (A) radio-tagged caribou found dead within the Chase (C) and Wolverine (W) caribou herd areas. Inferred cause of predation was due to wolf (*Canis lupus* - CALU), wolverine (*Gulo gulo* – GUGU), Grizzly bear (*Ursus arctos* – URAR), or unknown (PRED).

Caribou	Date	Cause	Age	Area	Elevation	Location		Variant
						Zone	Subzone	
CN102C	22/11/2001	CALU	A	C	915	BWBS	dk	1
CN142C	10/01/2002	GUGU	Y	C	1543	ESSF	mv	4
CN517C	09/03/2002	CALU	A	C	843	BWBS	dk	1
CN518W	15/03/2002	CALU	A	W	1091	SBS	mk	1
CN162W	21/04/2002	PRED	A	W	1050	BWBS	dk	1
CN521C	21/04/2002	CALU	A	C	1129	ESSF	mv	3
CN178C	27/04/2002	PRED	C	C	968	BWBS	dk	1
CN025W	03/05/2002	CALU	A	W	961	BWBS	dk	1
CN153C	03/04/2002	GUGU	A	C	991	BWBS	dk	1
CN523C	14/04/2002	CALU	A	C	888	BWBS	dk	1
CN104C	05/04/2002	CALU	A	C	844	BWBS	dk	1
CN175C	10/05/2002	CALU	C	C	753	BWBS	dk	1
CN061C	02/12/1999	CALU	A	C	787	BWBS	dk	1
CN219W	18/07/2002	URAR	C	W	1606	ESSF	mvp	
CN215C	04/08/2002	CALU	C	C	1632			
CN526W	22/11/1998	CALU	C	W	1186	ESSF	mv	3
CN546W	28/04/1999	CALU	C	W	1023	BWBS	dk	1
CN095C	24/06/1999	CALU	C	C	1683	SWB	mks	
CN077W	28/06/1999	URAM	C	W	1428	ESSF	mv	3
CN083C	29/06/1999	CALU	C	C	1576	ESSF	mv	3
CN078C	30/06/1999	CALU	C	C	1655	SWB	mks	
CN086W	17/07/1999	PRED	C	W	1287	ESSF	mv	3
CN062C	17/09/1999	URAR	A	C	1294	ESSF	mv	3
CN029W	30/11/1999	CALU	A	W	1024	BWBS	dk	1
CN038W	09/02/2000	CALU	A	W	1655	ESSF	mvp	
CN044W	25/03/2000	CALU	A	W	1770	BAFA	un	
CN071W	04/05/2000	CALU	A	W	1493	ESSF	mv	3
CN140W	28/06/2000	URAM	C	W	1480	ESSF	mv	3
CN135C	16/08/2000	PRED	C	C	1802	BAFA	un	
CN010C	26/05/2001	CALU	A	C	1490	SWB	mk	
CN192C	17/06/2001	PRED	C	C	1850	ESSF	mvp	
CN005C	28/06/2001	PRED	A	C	892	SBS	mc	2
CN179C	23/06/2001	GUGU	C	C	1659	ESSF	mcp	
CN180C	04/07/2001	CALU	C	C	1589	SWB	mks	

Caribou	Date	Cause	Age	Area	Elevation	Location		Variant
						Zone	Subzone	
CN186W	30/06/2001	PRED	C	W	1711	ESSF	mvp	
CN169C	17/09/2001	URAR	A	C	932	BWBS	dk	1
CN200W	22/08/2001	CALU	C	W	1185	ESSF	mv	3
CN197W	09/09/2001	PRED	C	W	1420	ESSF	mv	3
CN103C	25/01/2003	PRED	A	C	1582	ESSF	mv	3
CN065C	11/02/2003	CALU	A	C	815	BWBS	dk	1
CN221W	02/03/2003	CALU	C	W	1499	ESSF	mv	3
CN591W	02/09/2002	CALU	A	W	760	BWBS	dk	1
CN213C	13/10/2002	GUGU	C	C	1698	ESSF	mvp	
CN916C	16/05/1993	CALU	A	C	943	BWBS	dk	1
CN926W	16/05/1996	CALU	A	W	929	BWBS	dk	1
CN927W	25/05/1996	CALU	A	W	867	BWBS	dk	1
CN002C	26/04/2003	PRED	A	C	1637	ESSF	mvp	
CN034W	19/02/1998	PRED	A	W				
CN919C	12/03/1993	CALU	A	C	1177			
CN922W	11/04/1996	GUGU	A	W				
CN124W	03/04/2004	CALU	A	W	1014	BWBS	dk	1
CN161W	05/04/2004	PRED	A	W	1262	ESSF	mv	3
CN232W	28/04/2004	CALU	A	W	770	BWBS	dk	1
CN043W	22/05/2004	CALU	A	W	1212	ESSF	mv	3
CN067C	08/12/2003	CALU	A	C	1234	ESSF	mv	3
CN001C	07/05/2004	PRED	A	C	928	BWBS	dk	1
CN042W	24/12/2004	CALU	A	W	913	BWBS	dk	1
CN106C	21/11/2004	CALU	A	C	927	BWBS	dk	1
CN228C	19/04/2005	CALU	A	C	1133	BWBS	dk	1
CN123W	18/04/2005	PRED	A	W	1056	BWBS	dk	1
CN012W	30/05/2005	CALU	A	W	1142	ESSF	mv	3
CN063C	15/01/2006	CALU	A	C	971			
CN036W	17/05/2006	CALU	A	W	930			
CN070W	23/02/2006	PRED	A	W				
CN015W	31/05/2005	CALU	A	W	1007			
CN144C	15/05/2005	URAR	A	C				
CN059C	20/05/2006	URAR	A	C				
CN807W	11/10/1998	CALU	A	W	1371	ESSF	mv	3
CN812W	25/05/1996	CALU	A	W	1667	ESSF	mvp	
CN809W	15/06/1996	CALU	A	W	1257	ESSF	mv	3