

PLASTICITY IN SELECTION STRATEGIES OF WOODLAND CARIBOU (*RANGIFER*
TARANDUS CARIBOU) DURING WINTER AND CALVING

by

David D. Gustine

B.A., University of Oklahoma, 1994

B.S., Colorado State University, 2000

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

in

NATURAL RESOURCES AND ENVIRONMENTAL STUDIES
(BIOLOGY)

THE UNIVERSITY OF NORTHERN BRITISH COLUMBIA

January 2005

© David D. Gustine, 2005

ABSTRACT

Woodland caribou may be an important 'indicator' or focal species for management agencies because they require large areas to persist and are sensitive to both direct and indirect forms of disturbance. Prior to industrial development in northern regions, it is important to acquire baseline information on areas that are important to local 'herds' as well as to identify physiological and ecological mechanisms of resource selection. I used global positioning system (GPS) data from caribou (*Rangifer tarandus caribou*), wolves (*Canis lupus*), and grizzly bears (*Ursus arctos*), and satellite imagery, resource selection functions, and cause-specific mortality data from 50 caribou neonates to define calving and wintering areas of woodland caribou in northern British Columbia. I identified scale-dependant mechanisms of selection relative to predation risk (calving, summer, winter, and late winter) and forage availability (calving and summer), and energetic costs of movement (winter and late winter) at 2 spatial scales, and quantified the variation in responses to these mechanisms among individual caribou. In all seasons, caribou selected habitats in a hierarchical fashion, and exhibited high variation among individuals. Three unique calving areas, or calving strategies, were defined for the Greater Besa Prophet area; each calving area had different attributes of risk and forage. During calving, spatial separation from areas of high wolf risk was important to parturient females as was access to areas of high vegetative change (i.e., forage quality); animals made trade-off decisions between minimizing the risk of predation and securing forage to address the high nutritional demands of lactation. Calf survival through the first 2 months of life ranged from 54% in 2002 to 79% in 2003.

A total of 19 of 50 neonates died during the summers, of which 17 were by predation: wolverines (age of calves <14 d) and wolves (age of calves >18 d) each killed 5 calves. Movements away from calving sites (>1 km) peaked during the third week of life and increased the odds of a neonate surviving by 196%. These movements coincided with a change in vegetative phenology and the high energetic demands of lactation. During winter and late winter, minimizing the energetic costs of movement was the most important parameter in the selection of resources at a smaller spatial scale defined by seasonal movement, whereas individual caribou showed increased sensitivity to the components of risk at a larger scale of the home range. Variation in the selection of resources by individuals was high, but some similarities facilitated using pooled use/availability data to model resource selection. These pooled models, however, collapsed important biological variation in the selection of resources, limiting biological interpretation of selection models. Variation in the selection of resources among individuals (i.e., plasticity) during all times of the year may be an important life-history strategy for woodland caribou to decrease their predictability on the landscape to major predators. Identifying and maintaining this variation within selection strategies is an important step towards determining the ability of caribou populations to persist in the presence of environmental and anthropogenic disturbance.

TABLE OF CONTENTS

ABSTRACT	ii
TABLE OF CONTENTS	iv
LIST OF TABLES	vii
LIST OF FIGURES	xv
ACKNOWLEDGEMENTS	xviii
CHAPTER 1: INTRODUCTION	1
CONTEXT	1
Calving	1
Winter	3
Objectives	6
ORGANIZATION OF THESIS	8
CHAPTER 2: CALVING STRATEGIES AND CALF SURVIVAL OF WOODLAND CARIBOU IN A MULTI-PREDATOR ECOSYSTEM IN NORTHERN BRITISH COLUMBIA.....	9
ABSTRACT	9
INTRODUCTION	10
STUDY AREA	16
METHODS	21
Cow and calf capture	21
Cause-specific mortality and calf survival	23
Small-scale characteristics of calving sites	25
Large-scale characteristics of calving sites and calving areas	27
<i>Components of Predation Risk</i>	27
<i>Analyses of Predation Risk</i>	31
<i>Indices of Forage Biomass and Quality</i>	34
<i>Analyses of Large-Scale Characteristics of Calving Sites and Calving Areas</i>	36
RESULTS	39
Reproductive characteristics	39
Cause-specific mortality and survival	41
Small-scale characteristics of calving sites and calf survival	43
Large-scale characteristics of calving sites and calving areas and calf survival	49
DISCUSSION	58
Hierarchical scales and trade-offs in risk and forage for calving caribou	58
Predictions of calf survival	63

Implications to understanding successful calving strategies	67
CHAPTER 3: INTERPRETING RESOURCE SELECTION BETWEEN	
SCALES AMONG INDIVIDUAL WOODLAND CARIBOU IN	
WINTER.....	74
ABSTRACT	74
INTRODUCTION.....	75
STUDY AREA	79
METHODS	79
Animal capture and locational data	79
Inputs to resource selection models for caribou.....	82
<i>Vegetation, Topography, and Distance to Linear Features</i>	82
<i>Risk of Predation and Distance to Areas of High Predation Risk</i>	83
<i>Estimated Costs of Movement for Caribou</i>	84
Relative importance of covariates and scale	84
Quantifying variation in the selection of resources among individuals	86
RESULTS.....	88
Reproductive condition of caribou, collar performance, and movement	88
Performance of predation risk models	89
Relative importance of covariates and scale	91
Effect of scale on the components of risk in resource selection.....	98
Variation in the selection of resources among caribou	102
<i>Elevation</i>	104
<i>Slope</i>	104
<i>Aspect</i>	105
<i>Vegetation</i>	106
<i>Fragmentation of Vegetation</i>	108
<i>Components of the Risk of Predation</i>	109
DISCUSSION	110
Relative importance of risk, energetic costs of movement, and scale.....	111
Variation in the selection of resources among caribou	114
<i>Elevation</i>	115
<i>Slope</i>	116
<i>Aspect and Fragmentation of Vegetation</i>	116
<i>Vegetation</i>	117
<i>Components of Risk</i>	118
Interpreting resource selection between scales and among individuals	119
CHAPTER 4: MANAGEMENT IMPLICATIONS FOR THE GREATER	
BESA PROPHET AREA.....	124
INTRODUCTION.....	124
IMPLICATIONS	125
Calving and summer	125
Winter and late winter	130
LITERATURE CITED.....	136

Appendix A: Specifications and schematic of the expandable drop-off radiocollar for woodland caribou (<i>Rangifer tarandus caribou</i>) calves that were captured and monitored in the Greater Besa Prophet area, northern British Columbia.	150
Appendix B: Classification of habitats in the Greater Besa Prophet area, northern British Columbia.	153
Appendix C: Defining the risk of predation from grizzly bears (<i>Ursus arctos</i>) and wolves (<i>Canis lupus</i>) for female caribou during the calving and summer seasons in the Greater Besa Prophet area, northern British Columbia.....	157
Appendix D: Modelling the Normalized Difference Vegetation Index during the calving and summer seasons in the Greater Besa Prophet area, northern British Columbia.	171
Appendix E: Data (age, sex, weight, calving area, and method and date of capture) from the capture of neonatal caribou calves in the Greater Besa Prophet area, northern British Columbia, 2002-2003.	176
Appendix F: Summary of vegetative (line-intercept and plot) data at calving sites of woodland caribou in the Greater Besa Prophet area, northern British Columbia, 2002-2003.	179
Appendix G: Evaluating the relationship between percent-cover and biomass of lichens at calving sites of woodland caribou in the Greater Besa Prophet area, northern British Columbia, 2002-2003.	182
Appendix H: Reproductive status and ultrasound measurements of back fat for woodland caribou in the Greater Besa Prophet area, northern British Columbia, winters 2002-2004.	184
Appendix I: Defining the risk of predation from wolves (<i>Canis lupus</i>) for female caribou during winter and late winter in the Greater Besa Prophet area, northern British Columbia, 2001-2002.....	187

LIST OF TABLES

Table 2.1. Reproductive parameters of female woodland caribou and age, weight, sex, and peak calving data from captured calves in the Greater Besa Prophet area, northern British Columbia, 2002-2003.	40
Table 2.2. Small-scale characteristics of calving sites ($\bar{x} \pm SE$) among the Foothills (FTHILLS), Western High Country (WHC), and North Prophet (NP) calving areas in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Characteristics sharing the same letter were not significantly different, as determined by parametric and nonparametric analyses.	45
Table 2.3. Model sets to evaluate the importance of small- and large-scale characteristics of calving sites as predictors of calf survival through calving (25 May-14 June) and summer (15 June-July 31) for woodland caribou in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Models were evaluated within small or large-scale sets; sample size (n), log-likelihood (LL), number of parameters (K), Akaike's Information Criterion for small samples (AIC_c), Akaike weights (w_i), differences in AIC_c (Δ_i), evidence ratios (E_r), and area under the receiver operating characteristic curve (ROC) were used to identify and evaluate the most parsimonious models within a set.	47
Table 2.4. Large-scale characteristics of random points ($\bar{x} \pm SE$) among the Foothills (FTHILLS), Western High Country (WHC), and North Prophet (NP) calving areas in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Characteristics sharing the same letter were not significantly different, as determined by Kruskal-Wallis analysis of variance and multiple comparisons of mean ranks. Large-scale characteristics of calving sites within a calving area were compared to characteristics of random points within that calving area; an asterisk indicates a significant difference ($P < 0.050$), as determined by the Mann-Whitney U-test.	50
Table 2.5. Cost (slope \pm SE) from the linear relationship of predator risk versus forage characteristics of random points within the Foothills	

(FTHILLS), Western High Country (WHC), and North Prophet (NP) calving areas in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Slopes sharing the same letter were not significantly different among calving areas and slopes in the summer marked by an asterisk were different from the calving season; both comparisons were determined by a t-test of slopes with a Bonferroni adjustment for comparisons among calving areas.....	56
Table 3.1. Coefficients of selection (β_i) relating to the energetic cost of movement (kJ/kg/hr) in the final resource selection models at the scale of seasonal movement for 10 adult female caribou during winter (November-February) and late winter (March-April) seasons in the Greater Besa Prophet area, northern British Columbia, 2001-2002. Animals 22 and 25 were not pregnant, as defined by serum progesterone assays.	92
Table 3.2. Sum of the weights for Akaike's Information Criterion corrected for small sample size ($w_+(j)$) where wolf risk and distance to areas of high wolf risk covariates occurred in the model set at the scale of seasonal range for individual caribou by season (winter (November-February) and late winter (March-April)) in the Greater Besa Prophet area, northern British Columbia, 2001-2002. $\overline{w_+(j)}$ denotes the average contribution of information by covariate $_j$ for a season across all individuals.	93
Table 3.3. Final individual and pooled (East (E) and Mountain (M) dwelling caribou) resource selection models at the scale of the seasonal range for 10 female caribou during winter (November-February) in the Greater Besa Prophet area, northern British Columbia, 2001-2002; squared terms include the linear term (e.g., Elevation ² = Elevation (km) + Elevation ² (km)). Statistics are sample size (n), number of parameters (K), log-likelihood (LL), Akaike's Information Criterion corrected for small sample size (AIC _c), Akaike weights (w_i), evidence ratios (E_r), and average ($n = 5$) Spearman's correlation coefficient from the k-fold cross-validation (\bar{r}_s). All P for $\bar{r}_s < 0.050$	94

Table 3.4. Final individual and pooled (East (E) and Mountain (M) dwelling caribou) resource selection models at the scale of the seasonal range for 10 female caribou during late winter (March-April) in the Greater Besa Prophet area, northern British Columbia, 2001-2002; squared terms include the linear term (e.g., $\text{Elevation}^2 = \text{Elevation (km)} + \text{Elevation}^2 \text{ (km)}$). Statistics are sample size (n), number of parameters (K), log-likelihood (LL), Akaike's Information Criterion corrected for small sample size (AIC_c), Akaike weights (w_i), evidence ratios (E_r), and average ($n = 5$) Spearman's correlation coefficient from the k-fold cross-validation (\bar{r}_s). All P for $\bar{r}_s < 0.050$	96
Table 3.5. Change in the Akaike's Information Criterion corrected for small sample size (Δ_i) when wolf risk and distance to areas of high wolf risk were added to the most parsimonious core model for individual caribou by season (winter (November-February) and late winter (March-April)) and scale (seasonal movement and seasonal range) in the Greater Besa Prophet area, northern British Columbia, 2001-2002. $\bar{\Delta}_i$ denotes the average contribution of information by a covariate for a season across all individuals.....	99
Table A.1. Specifications for the expandable drop-off collars for newborn caribou calves (T. Pojar, Colorado Division of Wildlife, pers. comm.); Advanced Telemetry Systems, Isanti, MN, USA) that were used to monitor 50 caribou neonates in the Greater Besa Prophet area, northern British Columbia, 2002-2003.	151
Table B.1. Nine classes of vegetation used for analyses of habitat selection by grizzly bears, wolves, and woodland caribou in the Greater Besa Prophet area, northern British Columbia, 2001.....	154
Table C.1. An ecologically plausible set of models used to define the risk of predation from grizzly bears during the calving and summer seasons in the Greater Besa Prophet area, northern British Columbia, 2002-2003.....	158
Table C.2. Final pooled models of bear risk (based on locations from 15 female grizzly bears) by season and year in the Greater Besa Prophet area, northern British Columbia, 2002-2003 showing	

sample size (n), log-likelihood (LL), number of parameters (K), Akaike's Information Criterion (AIC), change in AIC (Δ_i), Akaike weights (w_i), evidence ratios (E_r), and average ($n = 5$) Spearman's correlation coefficient from k-fold cross-validation (\bar{r}_s) with associated p-values (P).	159
Table C.3. Coefficients of selection (β_i and $\bar{\beta}_i$ for an averaged model from Table C.2) and standard errors (SE) of the covariates for the final pooled models of bear risk by season and year in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Significant parameters are indicated by asterisk(s)	160
Table C.4. An ecologically plausible set of models used to define the risk of predation from wolves in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Models were developed for 5 wolf packs: pack 1 (Dopp-Keily), pack 2 (Lower Besa), pack 3 (Neves), pack 4 (Pocketknife), and pack 5 (Richards-Upper Prophet).....	161
Table C.5. Final pooled models of wolf risk (based on locations from 22 individuals in 5 wolf packs) by season and year in the Greater Besa Prophet area, northern British Columbia, 2002-2003 showing sample size (n), log-likelihood (LL), number of parameters (K), Akaike's Information Criterion (AIC), change in AIC (Δ_i), Akaike weights (w_i), evidence ratios (E_r), and average ($n = 5$) Spearman's correlation coefficient from k-fold cross-validation (\bar{r}_s) with associated p-values (P).	162
Table C.6. Coefficients of selection (β_i for models from Table C.5) and standard errors (SE) of the covariates for the final pooled models of wolf risk across packs by season and year in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Significant parameters are indicated by asterisk(s).....	163
Table C.7. Final pack models of wolf risk (based on locations from 22 individuals in 5 wolf packs) by season in the Greater Besa Prophet area, northern British Columbia, 2002 showing sample size (n), log-likelihood (LL), number of parameters (K), Akaike's Information Criterion (AIC), change in AIC (Δ_i), Akaike weights (w_i), evidence	

ratios (E_r), and average ($n = 5$) Spearman's correlation coefficient from k-fold cross-validation (\bar{r}_s) with associated p-values (P).	164
Table C.8. Final pack models of wolf risk (based on locations from 22 individuals in 5 wolf packs) by season in the Greater Besa Prophet area, northern British Columbia, 2003 showing sample size (n), log-likelihood (LL), number of parameters (K), Akaike's Information Criterion (AIC), change in AIC (Δ_i), Akaike weights (w_i), evidence ratios (E_r), and average ($n = 5$) Spearman's correlation coefficient from k-fold cross-validation (\bar{r}_s) with associated p-values (P).	165
Table C.9. Coefficients of selection (β_i and $\bar{\beta}_i$ for an averaged model from Tables C.7, C.8) and standard errors (SE) of the covariates for the final risk models for wolf pack 1 (Dopp-Keily) by season and year in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Significant parameters are indicated by asterisk(s).....	166
Table C.10. Coefficients of selection (β_i and $\bar{\beta}_i$ for an averaged model from Tables C.7, C.8) and standard errors (SE) of the covariates for the final risk models for wolf pack 2 (Lower Besa) by season and year in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Significant parameters are indicated by asterisk(s).	167
Table C.11. Coefficients of selection (β_i for models from Tables C.7, C.8) and standard errors (SE) of the covariates for the final risk models for wolf pack 3 (Neves) by season and year in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Significant parameters are indicated by asterisk(s).....	168
Table C.12. Coefficients of selection (β_i and $\bar{\beta}_i$ for an averaged model from Tables C.7, C.8) and standard errors (SE) of the covariates for the final risk models for wolf pack 4 (Pocketknife) by season and year in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Significant parameters are indicated by asterisk(s).	169
Table C.13. Coefficients of selection (β_i and $\bar{\beta}_i$ for an averaged model from Tables C.7, C.8) and standard errors (SE) of the covariates for the final risk models for wolf pack 5 (Richards-Upper Prophet) by	

season and year in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Significant parameters are indicated by asterisk(s).....	170
Table D.1. A model set used to estimate the Normalized Difference Vegetation Index during the calving and summer seasons in the Greater Besa Prophet area, northern British Columbia, 2001.....	172
Table D.2. The R^2 values of the final models used to estimate the Normalized Difference Vegetation Index during the calving and summer seasons in the Greater Besa Prophet area, northern British Columbia, 2001.....	173
Table D.3. Coefficients of selection (β_i for a model from Table D.2) and standard errors (SE) of the covariates of the multiple regression models for each Landsat image to estimate the Normalized Difference Vegetation Index during the calving and summer seasons in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Significant parameters are indicated by asterisk(s).....	174
Table E.1. Animal identification (ID), date of capture, sex (male (M) and female (F)), and estimates for the date of birth (DOB), age (days), and weight (kg) of newborn caribou calves captured by hand and by net-gun in the Foothills (FTHILLS), Western High Country (WHC), and North Prophet (NP) calving areas within the Greater Besa Prophet area, northern British Columbia, 2002-2003.....	177
Table F.1. Percent cover and density of vegetation by functional group and species and biomass of lichens ($\bar{x} \pm SE$) using line-intercept and plot data at calving sites of woodland caribou in the Greater Besa Prophet area, northern British Columbia, 2002-2003.....	180
Table H.1. Reproductive status and ultrasound estimates of back fat for female woodland in the Greater Besa Prophet area in northern British Columbia, 2002-2004; pregnancy for 38A was confirmed via necropsy and A = adult and Y = yearling.	185

Table I.1. Final pooled models of wolf risk by season in the Greater Besa Prophet area, northern British Columbia, 2001-2002 showing sample size (n), log-likelihood (LL), number of parameters (K), Akaike's Information Criterion (AIC), change in AIC (Δ_i), Akaike weights (w_i), evidence ratios (E_r), and average ($n = 5$) Spearman's correlation coefficient from k-fold cross-validation (\bar{r}_s) with associated p-values (P).	188
Table I.2. Coefficients of selection (β_i from Table I.1) and standard errors (SE) of the covariates for the final pooled models of wolf risk by season in the Greater Besa Prophet area, northern British Columbia, 2001-2002. Significant parameters are indicated by asterisk(s).	189
Table I.3. Final pack models of wolf risk during winter (November-February) in the Greater Besa Prophet area, northern British Columbia, 2001-2002 showing sample size (n), log-likelihood (LL), number of parameters (K), Akaike's Information Criterion (AIC), change in AIC (Δ_i), Akaike weights (w_i), evidence ratios (E_r), and average ($n = 5$) Spearman's correlation coefficient from k-fold cross-validation (\bar{r}_s) with associated p-values (P).	190
Table I.4. Final pack models of wolf risk during late winter (March-April) in the Greater Besa Prophet area, northern British Columbia, 2001-2002 showing sample size (n), log-likelihood (LL), number of parameters (K), Akaike's Information Criterion (AIC), change in AIC (Δ_i), Akaike weights (w_i), evidence ratios (E_r), and average ($n = 5$) Spearman's correlation coefficient from k-fold cross-validation (\bar{r}_s) with associated p-values (P).	191
Table I.5. Coefficients of selection ($\bar{\beta}_i$ for an averaged model from Tables I.4) and standard errors (SE) of the covariates for the final risk models for wolf pack 1 (Dopp-Keily) during late winter in the Greater Besa Prophet area, northern British Columbia, 2001-2002. Significant parameters are indicated by asterisk(s).	192
Table I.6. Coefficients of selection (β_i and $\bar{\beta}_i$ for an averaged model from Tables I.3, I.4) and standard errors (SE) of the covariates for the final risk models for wolf pack 2 (Lower Besa) by season in the	

Greater Besa Prophet area, northern British Columbia, 2001-2002. Significant parameters are indicated by asterisk(s).	193
Table I.7. Coefficients of selection ($\bar{\beta}_i$ for an averaged model from Tables I.4) and standard errors (SE) of the covariates for the final risk models for wolf pack 3 (Neves) during late winter in the Greater Besa Prophet area, northern British Columbia, 2001-2002. Significant parameters are indicated by asterisk(s).	194
Table I.8. Coefficients of selection (β_i and $\bar{\beta}_i$ for an averaged model from Tables I.3, I.4) and standard errors (SE) of the covariates for the final risk models for wolf pack 4 (Pocketknife) by season in the Greater Besa Prophet area, northern British Columbia, 2001-2002. Significant parameters are indicated by asterisk(s).	195
Table I.9. Coefficients of selection ($\bar{\beta}_i$ for an averaged model from Tables I.4) and standard errors (SE) of the covariates for the final risk models for wolf pack 4 (Richards-Upper Prophet) by season in the Greater Besa Prophet area, northern British Columbia, 2001-2002. Significant parameters are indicated by asterisk(s).	196
Table I.10. Coefficients of selection (β_i and $\bar{\beta}_i$ for an averaged model from Tables I.3, I.4) and standard errors (SE) of the covariates for the final risk models for wolf pack 4 (Withrow) by season in the Greater Besa Prophet area, northern British Columbia, 2001-2002. Significant parameters are indicated by asterisk(s).	197

LIST OF FIGURES

Figure 2.1. The Greater Besa Prophet area of the Muskwa-Kechika Management Area in northern British Columbia, Canada, 2004.....	18
Figure 2.2. The Foothills, North Prophet, and Western High Country calving areas and calving sites for woodland caribou and linear features of the Greater Besa Prophet area, northern British Columbia, 2004.....	20
Figure 2.3. Timing of calf movements (>1 km) by age away from caribou calving sites compared with mortality (i.e., number of animals that died by the end of week _x divided by the number of animals alive at the beginning of week _x) during the first two months of life (a) and timing of predation-caused mortalities of collared caribou calves (b) in the Greater Besa Prophet area, northern British Columbia, 2002 and 2003.....	42
Figure 2.4. Kaplan-Meier estimates of survival rate at a given age (days) for woodland caribou neonates in a) 2002 and 2003 and b) by calving area (Foothills (FTHILLS), Western High Country (WHC), and North Prophet (NP)) using pooled data for both years, in the Greater Besa Prophet area, northern British Columbia.	44
Figure 2.5. The change in characteristics of predation risk and forage biomass ($\bar{x} \pm SE$) from calving (●) to summer seasons (○) for random points within the Foothills (FTHILLS), Western High Country (WHC), and North Prophet (NP) calving areas and in the Greater Besa Prophet area (LAND) in northern British Columbia, 2002-2003. Significant differences between seasons, as determined by the Mann-Whitney U-test, are indicated by an asterisk.....	53
Figure 3.1. Movement rates (m/hr, $\bar{x} \pm SE$) of 10 adult female caribou averaged within a month by individual and then averaged across individuals, during winter (November-February) and late winter (March-April) months in the Greater Besa Prophet area, northern British Columbia, 2001-2002.....	90

- Figure 3.2. Frequency distributions of wolf risk and distance to areas of high risk from availability data for female woodland caribou at two scales (seasonal movement and seasonal range) in winter (November-February, top graphs) and late winter (March-April, lower graphs) in the Greater Besa Prophet area, northern British Columbia, 2001-2002. 101
- Figure 3.3. Relative likelihood of female caribou selecting elevations (a, b), slopes (c, d), and distances to areas of high risk (e, f) during winter (November-February) and late winter (March-April) assuming other covariates are constant in the final resource selection models for individual caribou (light shading) and pooled models (heavy shading) for animals living in the East (○) and Mountain (▽) regions of the Greater Besa Prophet area, northern British Columbia, 2001-2002. Resource selection functions were scaled 0-1 (RSF_{0-1}) as in Boyce and McDonald (1999) to evaluate selection of resources among individuals and pooled models. Slope was not included in the final pooled East model in the winter (c). 103
- Figure 3.4. Number of GPS collared caribou that selected or avoided a vegetation class (left axes) and the strength of significant ($P < 0.050$) coefficients of selection for the pooled models of animals living in the eastern (East, $n = 2$) and mountainous (Mountain, $n = 8$) portions of the Greater Besa Prophet area during winter (November-February) and late winter (March-April), in northern British Columbia, 2001-2002..... 107
- Figure 4.1. Areas important to GPS-collared female woodland caribou in winter and late winter in the Greater Besa Prophet, northern British Columbia, 2001-2002. 132
- Figure A.1. Schematic of the expandable drop-off collar for neonatal caribou calves (T. Pojar, Colorado Division of Wildlife, pers. comm.; Advanced Telemetry Systems, Isanti, MN, USA) that was used to monitor 50 neonates in the Greater Besa Prophet area, northern British Columbia, 2002-2003..... 152

Figure B.1. Nine habitats, as defined using a vegetation classification from an August 15, 2001 Landsat TM image (see Table B.1), in the Greater Besa Prophet area, northern British Columbia. 156

Figure G.1. Relationship between ocular estimates of percent cover and measured samples of air-dried biomass for a) all lichen species and b) *Cladina* spp. at calving sites of woodland caribou in the Greater Besa Prophet area, northern British Columbia, 2002-2003. 183

ACKNOWLEDGEMENTS

The Muskwa-Kechika Trust Fund and the UNBC Northern Land Use Institute provided essential funding for this research, and R. Backmeyer of the Ministry of Water, Land, and Air Protection was quick to purchase several satellite images. The University of Northern British Columbia made my life easier in Prince George through scholarships.

Kathy Parker, Mike Gillingham, and Doug Heard have been, and will continue to be, a fundamental part of my education as a young professional in wildlife science. I've learned the importance and power of objectivity in science, as well as to never forget about the animals we study; Kathy, Mike, and Doug have created an environment designed to all but guarantee success of their students. Kathy's patience, guidance, friendship, and constant selflessness no doubt will continue to shape my personal and professional life. The only problem with working for Kathy these past few years is that now I have to go and work for someone else; her example and skills as a supervisor, mentor, and teacher will be impossible to match. Mike's impact on this research was immediate. His eagerness and enthusiasm for problem solving and tackling difficult questions, both biological and technical, and his ability to truly answer a question with a question is unparalleled. I've already found myself asking, "what is your question?" of other graduate students. Doug knows caribou and I was lucky to have him share with me his almost endless experiences with these truly unique animals. More importantly, working with Doug showed me that the excitement and novelty of being in the field never goes away.

Field work was rewarding and challenging and I will never forget my summers on the Besa, Thanksgivings at Keily, or visits to the Hammett's. I owe thanks to the Williams Family for taking us into their outfit and treating us like family. The success of this project was directly linked to the technical skill and knowledge of the net-gunners and pilots. Rob Woods and Brad Culling are unique in their ability to safely capture animals both big and small, although Rob's skills as a cribbage player are questionable. Greg Williams is an exceptional bush pilot and good friend; my experience with him has redefined what it means to have a coffee break. I thank A. Moore, N. Mavin, and O. Amar for their excellent flying skills and companionship. J. Ayotte, E. Jones, R. Lay, B. Milakovic, J. Psyllakis, and A. Walker are good friends and, no matter what the task, were always eager to help. C. Johnson was instrumental in getting me through resource selection and logistic regression; his research continues to strongly influence my work. M. Shook completed the mundane task of sorting lichens and made it look easy. S. Emmons was generous with his time working me through GIS and UNIX. I also need to acknowledge the animals whose lives we intruded on in effort to understand and protect them.

R. Wheate and N. Alexander took it upon themselves to take care of my best friend when I was away. W. Alldredge, W. Andelt, D. Benson, W. Gilgert, and T. Pojar helped prepare me for success in graduate school by challenging me as an undergraduate student and technician. The Clarkson and Olson families welcomed me into their home for my last few months in town and treated me like family and helped me finish in the process. Bobbi, JB, and Indy have been my constant companions through it all, thank you. For their extraordinary support, I share this

success with my parents (David and Bobbie Gustine), and my siblings (James and Sarah) and their significant others (Jamie and Bobby). Nicole's understanding, love, and support were influential; I couldn't have done it without her. I would like to dedicate this humble work to my uncle, Richard Gustine, who past away suddenly 4 December 2004, and his 3 children and their families. Dick will be greatly missed.

CHAPTER 1: INTRODUCTION

CONTEXT

The northern ecotype of woodland caribou (*Rangifer tarandus caribou*) is blue-listed as a species of concern in British Columbia and is listed as threatened in Canada (Committee on the Status of Endangered Wildlife 2002). Recent literature, regional data, and anecdotal evidence suggest that many caribou populations are at low levels and are either stable or declining in most of Canada (Seip and Cichowski 1996; Bergerud and Elliot 1998; Heard and Vagt 1998; Mahoney and Virgl 2003; McLoughlin et al. 2003). The resiliency of caribou to endure stochastic events (e.g., extreme winters or forest fires), changes in predator densities, and large-scale human disturbances (i.e., habitat alteration) is, therefore, a source of concern for land managers and users. Woodland caribou are essentially an indicator of landscape or ecosystem health because of their large landscape requirements and sensitivity to human (Murphy and Curatolo 1987; Bradshaw et al. 1997; Stuart-Smith et al. 1997) and environmental disturbance throughout the year (Schaefer and Pruitt 1991). Caribou may be most susceptible to disturbances during 'critical' times of the year (e.g., calving and winter) (Nellemann and Cameron 1998; Dyer et al. 2002), and identifying calving and wintering areas is an important step towards maintaining population persistence.

Calving

Relative to other North American ungulates, woodland caribou occur at lower

densities and use larger areas to meet seasonal demands for calving (spring and summer), breeding (fall), and over-wintering (Cumming 1992; Seip 1992).

Distribution over large areas appears to minimize predation from wolves and may play a significant role in calving success (Bergerud and Page 1987; Seip 1992; Barten et al. 2001). I define dispersal as in Bergerud et al. (1984), Bergerud and Page (1987), and Seip (1992), as increasing the distance between both parturient and non-parturient caribou, other prey species (e.g., moose (*Alces alces*)), and predators; this increases search time and lowers encounter rates for predators (Bergerud et al. 1984; Bergerud and Page 1987; Bergerud 1992; Barten et al. 2001). Calf survival may be related to the ability of parturient caribou to segregate themselves from wolf (*Canis lupus*) and/or moose populations (Bergerud et al. 1984; Seip 1992), as wolf predation appears to be the main source of mortality for neonates (Gasaway et al. 1983; Bergerud and Elliot 1986; Bergerud and Page 1987; Seip 1992; Adams et al. 1995; Wittmer 2004). Other causes of mortality, however, also may be important (e.g., bear (*Ursus* spp.) and golden eagle predation (*Aquila chrysaetos*), insect harassment, malnourishment) (Dale et al. 1994; Griffith et al. 2002; Mahoney and Virgl 2003).

Because of the importance of predation on neonatal survival, parturient females likely select calving areas lower in predation risk (Bergerud et al. 1990; Bergerud 1996; Cumming et al. 1996; Heard et al. 1996; Barten et al. 2001). Often these low-risk areas are in alpine environments with decreased forage abundance in early summer (Bergerud et al. 1984; Seip 1992; Poole et al. 2000; Barten et al. 2001). It is also during this time that lactating females experience high nutritional

demands (White and Luick 1984; Parker et al. 1990) and are at their worst body condition of the year (approx. 3 weeks after parturition) (Chan-McLeod et al. 1999). These nutritional demands of lactation cannot be met through intake of forage in areas with low primary productivity, and therefore, females must use body reserves (White et al. 1981). Post and Klein (1999) emphasized the importance of maternal condition and subsequent nutritional demands and suggested that the productivity of early summer range may have direct effects on perinatal mortality, especially in areas with low lichen productivity in the winter. Access to forage during the calving and summer season also may affect the probability of pregnancy and timing of estrus in fall (Cameron et al. 1993; Adams and Dale 1998*a,b*), which could then affect the mass (Reimers et al. 1983) and subsequent survival of the next year's calf as heavier calves appear to have higher survival than those born at lighter weights (Cameron et al. 1993; Adams et al. 1995). Therefore, to enhance reproductive fitness, females with young must make compromises, or 'trade-offs' between increased access to forage and minimizing the risk of predation (Bowyer et al. 1998; Rachlow and Bowyer 1998; Bowyer et al. 1999).

Winter

In British Columbia, northern woodland caribou use a variety of habitats (i.e., combinations of biotic and abiotic factors) during winter. Low elevation pine-lichen woodlands when snow depths are low (Johnson 2000), windswept alpine ridges (Cichowski 1993; Wood 1996), and spruce-fir forests (Poole et al. 2000) are all wintering habitats for various woodland caribou herds or, possibly, for the same herd

at different times of winter or in different years. Variation in the use of resources among populations is likely due to differences in the availability of habitats to these herds and/or management/industrial activities that have altered availability of particular habitats directly (e.g., destruction of forage) or indirectly (e.g., created more favorable habitat characteristics for other ungulates and/or predators).

Sensitivity of woodland caribou to anthropogenic and environmental disturbances, particularly during winter, is well documented and an important consideration in establishing a population's resiliency (Bradshaw et al. 1997; Stuart-Smith et al. 1997; James and Stuart-Smith 2000; Dyer et al. 2001, 2002; Dzuz 2001; Weclaw and Hudson 2004). Loss of functional winter habitat because of strong spatial avoidance of industrial developments is a significant factor in the decline of woodland caribou in Alberta (Weclaw and Hudson 2004). Avoidance of industrial developments may be a secondary result from an increased risk of predation. For example, linear corridors associated with industrial development tended to increase wolf predation rates on caribou (James and Stuart-Smith 2000). Industrial activity, including seismic exploration, may increase energetic costs for caribou by increasing movements and/or decrease foraging times during times of high nutritional stress in the winter (Bradshaw et al. 1997).

Prescribed burning and its effects also may influence caribou-wolf ecology. Historically, moose and elk (*Cervus elaphus*) were either absent (elk) or occurred in low densities (moose) in northern British Columbia (Bergerud and Elliot 1986; Bergerud and Page 1987; Seip 1991; Bergerud 1996). Prescribed burning between 1950 and the mid-1990s greatly increased the abundance of early seral habitats that

avored expansion of moose and elk populations (Bergerud 1974; Peck and Peek 1991; Bergerud 1996; Seip and Cichowski 1996). Bergerud's (1983) prey-switching theory postulated that an increase in moose densities has caused wolves to switch from caribou as a primary food source to moose as an additional alternative. This switch effectively eliminated the functional response between caribou and wolf populations (Bergerud 1983; Seip 1991). Furthermore, the expansion of elk in northern British Columbia provided an additional prey source that enhanced wolf populations. Increasing wolf numbers are suspected to be a significant factor in declining caribou herds (Bergerud 1974; Bergerud et al. 1984; Bergerud and Elliot 1986; Bergerud and Page 1987; Seip 1991).

The introduction of disturbance to wintering and calving areas coupled with low reproductive potential (relative to other cervids) could have short and long-term deleterious effects on populations of woodland caribou. These effects include loss of actual (Joly et al. 2003) and functional habitat (Dyer et al. 2001; Weclaw and Hudson 2004), and/or elevated predation risk (James and Stuart-Smith 2000; Dyer et al. 2001, 2002). An increase in applications for petroleum exploration in northern British Columbia accentuates the need for research to identify wintering and calving areas to ensure industrial access can be designed to minimize impacts. Quantitative evaluation of predation risk and its influence on selection of resources, and identification of 'trade-off' mechanisms between the risk of predation and forage availability are needed. The following objectives were addressed to identify processes and areas on the landscape that are important to the resiliency of woodland caribou populations in northern British Columbia and to provide insights

into the importance of predation risk and nutrition in the selection of calving strategies.

Objectives

1) To determine relationships among calving strategies, calf survival, and cause-specific mortality.

Wolf predation appears to be the primary source of mortality for caribou calves (Gasaway et al. 1983; Bergerud and Elliot 1986; Seip 1991; Adams et al. 1995), but other factors also contribute to rates of neonatal mortality (Downes et al. 1986; Ballard 1994; Griffith et al. 2002). Caribou may select calving areas and/or calving sites in response to predation risk (Bergerud and Page 1987; Seip 1992; Barten et al. 2001). In my study, I collared 50 neonatal caribou, determined sources and timing of mortality, modelled the risk of predation to caribou neonates from grizzly bears and wolves, and examined the relationship between the risk of predation and neonatal survival.

2) To assess the roles of predation risk and forage availability at different scales in determining successful calving strategies of northern woodland caribou.

Studies suggest that predation risk is a driving factor in selection of calving habitat(s), and that parturient caribou use an alternate foraging strategy to non-parturient caribou (Bergerud and Page 1987; Barten et al. 2001). Because calving caribou use body reserves during early lactation (White and Luick 1984; Chan-McLeod et al. 1999), nutritional demands may be an important component in the

selection of resources. Calving areas should provide for this nutritional need, while minimizing the level of predation risk. Identifying possible relationships among the risk of predation, spacing out from areas of high predation risk, and characteristics of forage (quantity and quality) during calving and summer should provide insights into whether calving caribou exhibit trade-off 'decisions' in response to predation risk. In my study, I used large- and small-scale characteristics (i.e., predation risk and characteristics of vegetation) of the landscape, calving strategies, and calving sites to examine hierarchical responses of woodland caribou to the risk of predation and forage availability.

3) To model resource selection by woodland caribou in the winter and late winter seasons in the Greater Besa Prophet area of northern British Columbia.

The confounding influence of scale and variation in selection among individuals within a population can make biological interpretation of the mechanisms of selection difficult (Wiens 1989; Levin 1992; Aebischer et al. 1993). The importance of environmental and ecological components of selection is likely to vary across scales (Johnson 1980; Johnson 2000; Rettie and Messier 2000). To adequately define resource selection for caribou in winter and late winter in the Greater Besa Prophet area of northern British Columbia, I identified the role of body condition relative to the importance of energetic cost of movement, risk of predation, and distance to areas of high risk in the selection of resources at a relatively small spatial scale; identified the importance of the components of risk at 2 spatial scales; quantified the variation in resource selection among individual caribou; and

qualitatively evaluated the utility of resource selection models pooled across individuals compared to individual models for collared caribou.

ORGANIZATION OF THESIS

I organized this thesis as 2 separate chapters to be submitted for journal publication, followed by a chapter on implications for management. The portion of my research that addresses calf survival, cause-specific mortality and the risk-forage trade-off (objectives 1 and 2) is presented in Chapter 2 (*Calving strategies and calf survival of woodland caribou in a multi-predator ecosystem in northern British Columbia*). Chapter 3 (*Interpreting resource selection between scales among individual woodland caribou in winter*) presents methods, results, and discussion for addressing objective 3. The last chapter (*Management implications for the Greater Besa Prophet area*) summarizes important considerations for managing woodland caribou in the Greater Besa Prophet area in northern British Columbia.

CHAPTER 2: CALVING STRATEGIES AND CALF SURVIVAL OF WOODLAND CARIBOU IN A MULTI-PREDATOR ECOSYSTEM IN NORTHERN BRITISH COLUMBIA¹

ABSTRACT

The proximate role of predation in limiting caribou (*Rangifer tarandus*) populations is well documented, but the long-term effects of predation pressure on selection of calving habitats and the subsequent impacts to calving success remain unclear. We examined the relationships among calf survival, predation risk, and forage characteristics among 3 calving areas and across spatial scales in the Besa Prophet River drainage of northern British Columbia. Fifty woodland caribou (*R. t. tarandus*) neonates were collared and monitored twice daily for the first month and once weekly during the second month of life over the summers of 2002 and 2003. Predation risk for 2002-2003 was determined using resource selection functions (RSFs) from global positioning system (GPS) locations of 15 grizzly bears (*Ursus arctos*) and 5 wolf (*Canis lupus*) packs. The Normalized Difference Vegetation Index (NDVI) derived from Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper (ETM) data was used to quantify indices of large-scale characteristics of forage (i.e., vegetation vigor and an index of forage quality). We incorporated small- and large-scale characteristics (i.e., risk, forage, and movement of caribou calves) of neonatal calving sites into logistic regression models to predict survival for the

¹A version of this chapter will be submitted for publication with the following authorship: Gustine, D. D., K. L. Parker, R. J. Lay, M. P. Gillingham, and D. C. Heard.

calving (25 May-14 June) and summer (15 June-15 August) seasons. Risk and forage characteristics were highly variable among calving areas and calving sites, and parturient caribou responded to these characteristics at different scales. Minimizing wolf risk and selecting against areas of high biomass were important at large scales; avoidance of areas with high biomass was likely associated with an increased risk of predation. Calving in areas high in forage quality was important across scales, as parturient caribou 'took' higher levels of risk for access to areas of high vegetative change. Models using small-scale characteristics of calving sites to predict survival performed better in the calving than summer season; large-scale characteristics predicted survival of caribou neonates better in summer than in the calving season. Wolverines and wolves were the main cause of mortality during the calving and summer seasons, respectively. Movement away from calving sites was an important covariate in the calf survival models and appeared to be in response to increased access to forage during the peak demands of lactation and/or minimizing the risk of wolf predation in the summer. High variation in risk and forage attributes among calving areas and at calving sites within calving areas, with no differences in calf mortality related to that variation, illustrates the importance of plasticity as a life-history strategy for woodland caribou.

INTRODUCTION

Risk of predation is an important component in understanding foraging strategies and habitat selection (Lima and Dill 1990; Sweitzer 1996; Rachlow and Bowyer 1998; Kie 1999; Grand 2002; Ben-David et al. 2004). For animals to

maximize reproductive success, they must make trade-off 'decisions' between the risk of predation and securing adequate forage to meet nutritional demands (Sweitzer 1996; Bowyer et al. 1998; Rachlow and Bowyer 1998; White et al. 2001; Ben-David et al. 2004). Trade-offs are dependant on various biological (e.g., nutritional condition, reproductive status, age; Berger and Cunningham 1988; Sweitzer 1996; Rachlow and Bowyer 1998; Barten et al. 2001; White et al. 2001; Ben-David et al. 2004), environmental (e.g., heterogeneity of vegetation on the landscape, densities and/or distribution of other prey species and predators; Bergerud et al. 1984; Seip 1991; Kie 1999; Altendorf et al. 2001), and/or social variables (e.g., group size, gregariousness, status; Lima and Dill 1990; Molvar and Bowyer 1994; Hebblewhite and Pletscher 2002; Miller 2002). Actual or perceived risk may alter species-specific foraging strategies (Krebs 1980; Lima and Dill 1990). Reproductive females within a species may be the most sensitive to foraging in high-risk habitats due to the susceptibility of neonates to predators (Bergerud et al. 1984; Lima and Dill 1990; Bowyer et al. 1998; Rachlow and Bowyer 1998; Miller 2002; Ben-David et al. 2004). Both sexes of a species must ensure that body reserves are sufficient for breeding and over-winter survival, but females must also secure adequate energy and protein inputs to meet the additional demands of gestation and lactation, and minimize the risk of predation to themselves and their offspring. Costs of foraging decisions, in the form of increased risk, are likely to vary spatially and temporally, but depend on the relationship between the risk of predation and forage characteristic(s) (Bowyer et al. 1998; Bowyer et al. 1999).

Studies have evaluated the behavioral response(s) of reproductive female

cervids in response to variation in the relationship between small-scale risk and forage characteristics (e.g., vegetative characteristics of birth sites; Molvar and Bowyer 1994; Bowyer et al. 1998; Bowyer et al. 1999; Barten et al. 2001; White and Berger 2001; White et al. 2001), but rarely has the risk-forage relationship been investigated at larger scales (Heard et al. 1996; Griffith et al. 2002). The advent of GPS and remote-sensing technologies offer unique opportunities to quantify risk and forage characteristics over large, diverse landscapes (Boyce and McDonald 1999; Griffith et al. 2002; Boyce et al. 2003; Nielsen et al. 2003; Johnson et al. 2004). Woodland caribou are an excellent species to examine trade-off 'decisions' at large-scales because individuals use large areas to meet their seasonal demands, generally have low reproductive potential, and are demographically sensitive to predation. Caribou are also notable among ungulates in that their protein balance may be negative for much of the year (Gerhart et al. 1996). This may increase the importance of access, particularly to spring forage, to meet high nitrogen demands following winters on low protein diets and, therefore, the predation risk-foraging 'trade-off' may be more obvious than in other species.

Woodland caribou have low rates of recruitment even though pregnancy rates range from 90-100% (Cumming 1992; Seip and Cichowski 1996; Rettie and Messier 1998; Mahoney and Virgl 2003; McLoughlin et al. 2003). Precise estimates of parturition for woodland caribou are unavailable, but estimates for barren-ground caribou (*R. t. groenlandicus*) among years range from 71-92% (\bar{x} = 81%, Griffith et al. 2002). Low recruitment rates appear to be related to high calf mortality by wolf predation during the early neonatal period (Gasaway et al. 1983; Bergerud and Elliot

1986; Bergerud and Page 1987; Seip 1992; Adams et al. 1995; Wittmer 2004), but other causes of death such as predation from bears (*Ursus* spp.) (Ballard 1994; Young and McCabe 1997; Mahoney and Virgl 2003), golden eagles (*Aquila chrysaetos*) (Dale et al. 1994; Adams et al. 1995; Griffith et al. 2002), and lynx (*Lynx canadensis*) (Bergerud 1983), congenital defects, insect harassment, sickness and/or disease, malnourishment, and exposure may play important roles in calf mortality (Seip 1991; Dale et al. 1994; Bergerud 1996; Heard et al. 1996). In some populations, mortality rates through the first winter of life appear to be as important to recruitment as mortality through the early neonatal period. Over-winter calf mortality rates in British Columbia range between 20-40% and in declining caribou populations, 60% of calves observed in late June died during their first winter (Seip and Cichowski 1996).

Selection of calving areas is likely influenced by the level(s) of predation risk in adjacent habitats (Bergerud et al. 1990; Bergerud 1996; Cumming et al. 1996; Heard et al. 1996; Barten et al. 2001). Calving areas for woodland caribou are often in rugged mountainous areas in the alpine or shrub-krummholz zones (Oosenbrug and Theberge 1980; Barten et al. 2001). Calving success can be higher for females that calve in alpine areas, presumably due to a decreased exposure to predation (Bergerud et al. 1984; Seip 1992; Poole et al. 2000; Barten et al. 2001). Bergerud and Page (1987) proposed that calving caribou maximize distance from predators and alternate prey species regardless of vegetative phenology. The ability of calving caribou to disperse across the landscape may decrease calf mortality (Seip 1992) because the dispersal by parturient females increases the search time and lowers

the encounter rates of predators, thereby decreasing hunting efficiency (Bergerud and Page 1987; Bergerud 1992; Barten et al. 2001). Bergerud (1996) hypothesized that for caribou, “forage selection will occur in the summer, but only within the options provided by low predation risk habitats.” Indeed, calving caribou in Alaska used sites with fewer predators and a lower abundance of forage when compared to non-parturient caribou; forage quality, however, was not compromised (Barten et al. 2001).

Although predation risk appears to play a role in selection of habitat(s) for successful calving, other factors, such as forage characteristics and/or snow cover at large scales, may play equally important roles (Eastland et al. 1989; Barten et al. 2001; Griffith et al. 2002). Maternal condition has a direct impact on fetal viability and subsequent calf survival, primarily resulting from available resources (i.e., energy and protein) of the dam towards calf production, birth weight, and weight gain (Cameron et al. 1993; Adams and Dale 1998*a,b*; Russell et al. 1998). Heavier calves have higher rates of survival than those born at lighter weights (Cameron et al. 1993), but survival also depends on maternal condition at parturition (Post and Klein 1999). Selection of productive early summer range has direct effects on perinatal mortality (Post and Klein 1999) because physiological demands of lactation are highest during the first 3 weeks following calving (White and Luick 1984; Parker et al. 1990); parturient caribou experience their lowest condition of the year during this time (Chan-McLeod et al. 1999). The importance of forage characteristics has been documented for arctic caribou where the relative amount of forage available on the calving grounds, as indexed by the NDVI, was the best predictor of early calf

survival (Griffith et al. 2002). A plausible explanation for discrepancies on the importance of predation and nutrition in limiting caribou populations is that the relative importance of predation risk and/or forage availability may be area- or herd-specific, vary within an area or herd, or more likely, be a 'trade-off' between the 2 factors. This 'trade-off' may vary across spatial and temporal scales (Wiens 1989; Levin 1992).

Caribou in mountainous environments in winter use multiple strategies to accommodate a predictable food source, varying snow depths, and predation risk from wolves (Johnson et al. 2000; Johnson et al. 2001). Such strategies could be a product of a heterogeneous environment and/or a response to a dynamic risk 'landscape', where variation in use of resources (i.e., plasticity) by caribou may make them less predictable in space and time. Indeed, plasticity among individuals and populations appears high for woodland caribou in British Columbia (Johnson et al. 2002*a,b*; Johnson et al. 2004; see Chapter 3), and as in other cervids (Bowyer et al. 1999), this plasticity may extend to other important times of the year (i.e., calving). In addition to spatial separation from non-parturient caribou, parturient caribou may use different strategies to cope with varying costs of risk across a diverse landscape to meet the demands of lactation and calf survival (Bergerud et al. 1984; Bergerud and Page 1987; Barten et al. 2001).

The goal of this study was to compare risk and forage characteristics among and within 3 different calving areas (i.e., calving strategies) within the Greater Besa Prophet area of northern British Columbia. We examined risk and forage characteristics and calf survival by calving strategy. If predation risk 'drives' the

selection of calving strategies, then risk within each of the calving strategies should be lower than the landscape as a whole. Alternatively, if nutrient acquisition 'drives' the selection of calving strategies, then forage characteristics for all calving strategies should be relatively higher than for the landscape. If trade-offs are occurring, then relative risk and forage characteristics could vary among calving strategies. Within any single calving strategy, however, there may be a smaller scale-dependant response to risk and forage characteristics and/or the trade-off between them. In these cases, risk and forage characteristics at calving sites within each calving strategy would differ from what was available within that strategy. If risk is limiting, then calf survival should be lower in 'riskier' calving strategies. Alternatively, if forage is limiting, calf survival should be higher in strategies with higher relative forage quantity and/or quality. The following hypotheses were evaluated: 1) calf survival and cause-specific mortality differ among calving strategies, 2) calving occurs at high elevations, 3) calving occurs in areas with the lowest risk of predation, 4) calving occurs in areas with the highest nutritional value, and 5) forage characteristics affect the level of risk that caribou take within a calving strategy. Therefore, we assessed the roles of predation risk and forage availability at different scales in determining successful calving strategies of northern woodland caribou.

STUDY AREA

The Greater Besa Prophet area (GBPA) encompasses 740,800 ha, the majority of which is within the 6.2 million-ha Muskwa-Kechika Management Area in

northern British Columbia (Fig. 2.1). The GBPA is located between 57°11' and 57°15' N latitude, and 121°51' and 124°31' W longitude. Elevations range from 700-2,200 m, with treeline occurring between 1,450-1,600 m. Valleys in the GBPA are often covered with hybrid (*Picea glauca x engelmanni*) and/or black spruce (*Picea mariana*), quaking aspen (*Populus tremuloides*), and poorly drained willow-birch (*Salix* spp., *Betula glandulosa*) communities with infrequent white spruce (*Picea glauca*). Mature lodgepole pine (*Pinus contorta*) is uncommon. Dominant understory species are soapberry (*Shepherdia canadensis*), Labrador tea (*Ledum groenlandicum*), sedges (*Carex* spp.), horsetail (*Equisetum* spp.), crowberry (*Empetrum nigrum*), alder (*Alnus* spp.), and various mosses with few lichens. Alpine areas consist of permanent snowfields, glaciers, barren rock with sparse or mat vegetation, and grasslands with trees in krummholz form (Demarchi 1996). Common alpine species are mountain avens (*Dryas integrifolia*), northern rough or altai fescue (*Festuca altaica*), arctic white heather (*Cassiope tetragona*), moss campion (*Silene acaulis*), and a variety of terrestrial lichens and mosses.

The area is characterized by repeated east-west drainages with south-facing slopes that support one of the most diverse ungulate predator-prey ecosystems in North America. Large mammals found in the GBPA are elk (*Cervus elaphus*), moose (*Alces alces*), woodland caribou, white-tailed (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*), Stone's sheep (*Ovis dalli stonei*), mountain goat (*Oreamnos americanus*), bison (*Bison bison*), wolf, grizzly and black bear (*U. americanus*), coyote (*Canis latrans*), lynx, and wolverine (*Gulo gulo*).

The GBPA is currently unaffected by large-scale industrial activity, but

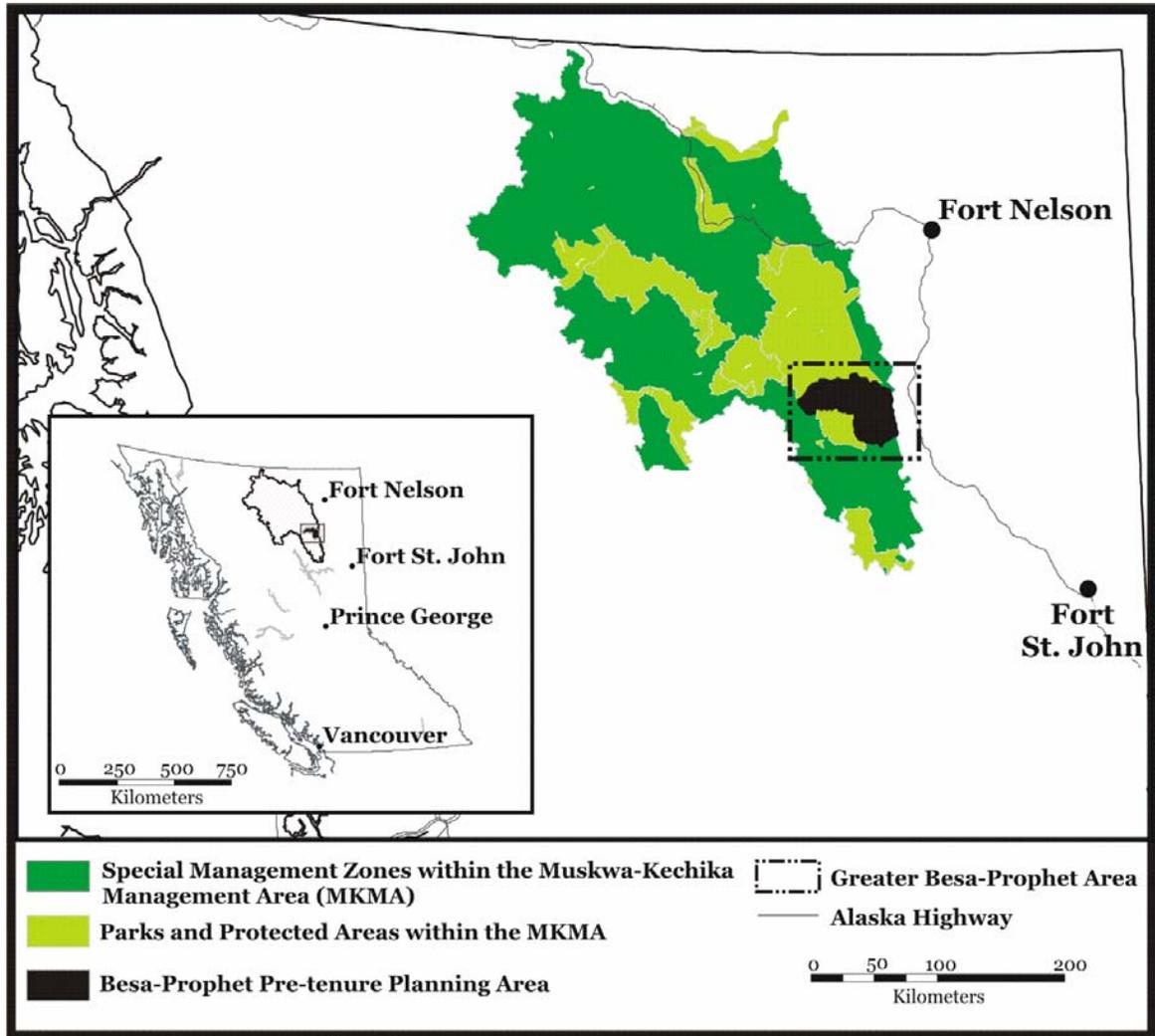


Figure 2.1. The Greater Besa Prophet area of the Muskwa-Kechika Management Area in northern British Columbia, Canada, 2004.

historical and current human activities include hunting and prescribed burning. Terrestrial access is restricted except for low all-terrain vehicle/snowmobile activity in the southern portion of the study area. Moose, deer, elk, caribou, Stone's sheep, mountain goat, grizzly bear, and wolf hunting occur throughout the area. Seismic oil exploration has been infrequent in the mountainous portions of the GBPA (Fig. 2.2), but applications for oil and gas exploration have increased. The Besa Prophet pre-tenure planning area within the GBPA is designated as a special management zone of the Muskwa-Kechika Management Area (Fig. 2.1). This designation allows exploration and/or extraction of natural resources if concerns for wildlife populations are addressed prior to development.

There are 3 general calving areas for caribou in the GBPA as defined by differences in small- and large-scale vegetation characteristics, elevation, topography, geographic location, and presence of adult female caribou and calves during May-July 2002 and 2003 (Fig. 2.2). These calving areas are the Foothills, Western High Country, and North Prophet. The Foothills area on the eastern front of the Rocky Mountains, with elevations ranging from 1,000-2,000 m, is defined by timbered valleys and steep, vegetated mountains. Vegetation types are heterogeneous with spruce-lined valleys transitioning into shrubby subalpine and alpine habitats with little non-vegetated cover and no permanent snowfields. The Western High Country area west of the Foothills ranges from 1,400-2,500 m and is characterized by rugged and steep mountains with little vegetative cover and narrow valleys. Rock, permanent snowfields, and glaciers dominate this area with vegetative cover in the form of spruce-lined river bottoms, and subalpine and alpine

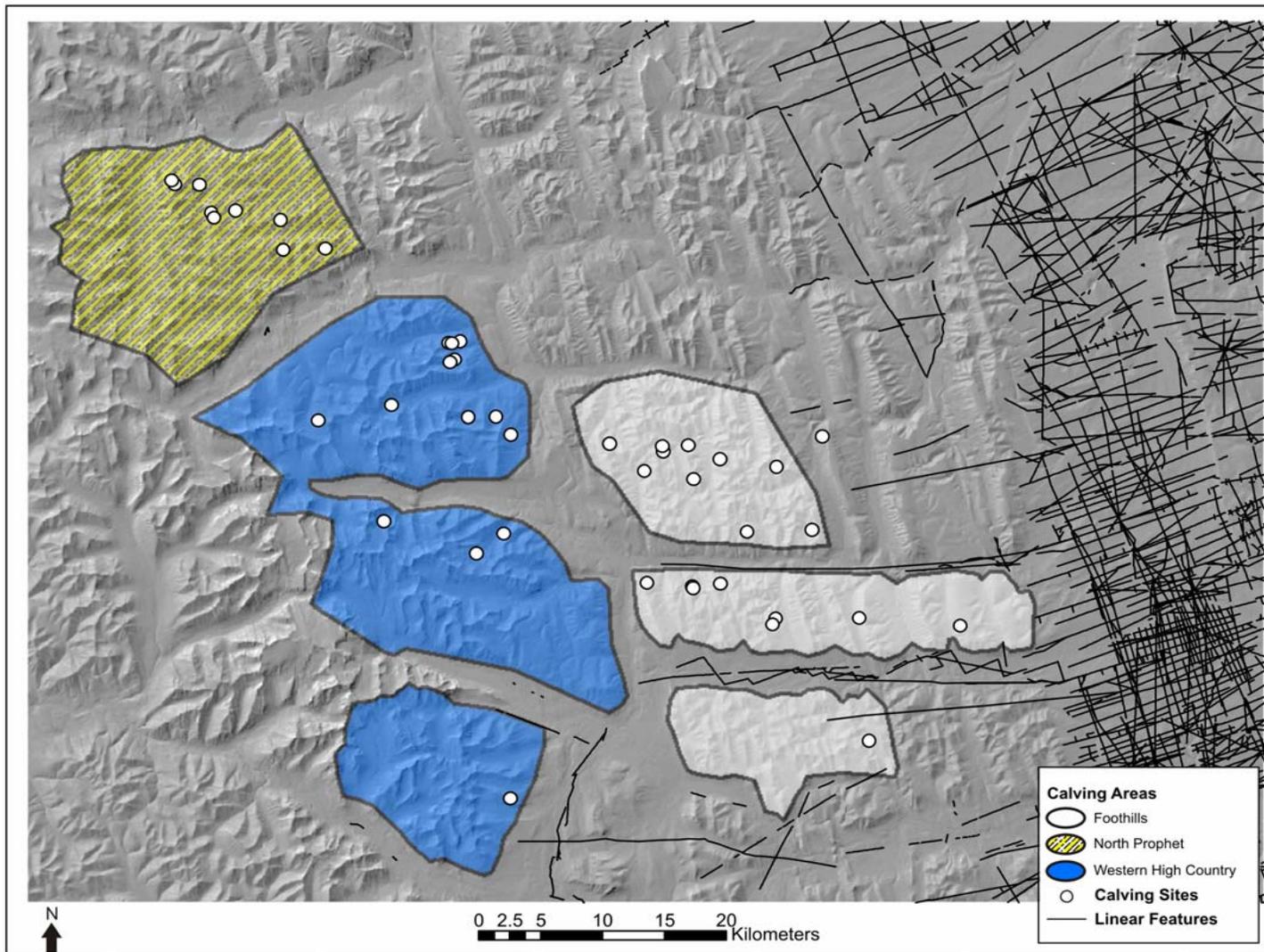


Figure 2.2. The Foothills, North Prophet, and Western High Country calving areas and calving sites for woodland caribou and linear features of the Greater Besa Prophet area, northern British Columbia, 2004.

habitats in the north- and south-facing hanging valleys. The North Prophet is north of the Western High Country and northwest of the Foothills with elevations ranging from 1,200-2,400 m. This area is characterized by wide valleys with no forest cover, and rugged and steep mountains. Subalpine-shrub and subalpine habitats in the valley bottoms grade into alpine habitats on mountainsides. Permanent snowfields and talus and scree fields are common at high elevations.

METHODS

Cow and calf capture

Forty-eight female caribou were captured and fit with GPS collars (Simplex, Televilt, Lindesberg, Sweden) during the winters of 2001/2002 and 2002/2003. We took blood samples to determine reproductive condition via serum progesterone concentrations (Prairie Diagnostics Services, Saskatoon, SK, Canada). Animals were monitored from fixed-wing aircraft (Piper Super Cub 18A) twice daily to identify calving areas, onset of parturition, and parturition rates. Collared individuals were determined to be parturient or non-parturient by calf-at-heel. Once parturition began, calf captures were by helicopter (Bell 206).

We captured 25 caribou neonates during each of the summers of 2002 and 2003. Calves from collared caribou were targeted for capture, but we captured other calves if the capture of these 'targeted' calves was not possible. A two-person capture crew, net-gunner, and helicopter pilot canvassed calving areas of collared females for calves that were old enough for processing (>24 h) (Adams et al. 1995).

We captured calves by hand or by net-gun. To capture calves by hand, one member of the capture crew was dropped from the helicopter close to and below the cow-calf pair, while the other member was dropped above the pair; calves were then pursued on foot. For net-gun capture, we deployed a light-weight 3.7-m² net with 10.2-cm mesh and a tensile strength of 77.3 kg (model 5608.19, Coda Enterprises, Inc., Mesa, AZ, USA) from the helicopter.

During processing, the crew wore clean latex gloves for each capture to minimize scent transfer among calves and humans (Adams et al. 1995; T. Pojar, Colorado Division of Wildlife, pers. comm.). Calves were sexed by the presence or absence of a vulva (Bergerud 1961). We weighed calves using a disposable cotton sling (approx. 33-cm diameter) and a 20-kg hand-held spring scale. Coordination and hoof and umbilicus condition were examined to estimate age (days) from birth (Haugen and Speake 1958). General examinations included notations on presence of diarrhea, and/or injuries.

Each calf was fitted with a drop-off radio-collar weighing approx. 120 g (approx. 1.3% of the average body mass of a captured calf). Collars consisted of a leather-belted and elastic (1:1.5 expansion ratio) neckband with a weather- and impact-resistant motion-sensitive transmitter (Advanced Telemetry Systems, Isanti, MN; as designed by T. Pojar, Colorado Division of Wildlife, pers. comm.; Appendix A: Table A.1, Fig. A.1); the pulse rate of the transmitter increased from 60 to 90 pulses/min if stationary for >2 h. The manufacturer-supplied collar was cut across the leather belting and reattached with 2 lengths of surgical tubing approx. 57 mm long (7 mm inner and 10 mm outer diameters) (Appendix A). The combination of

surgical tubing and elastic ensured that the collars would accommodate calf growth. Surgical tubing is sensitive to exposure from ultra-violet radiation and collars were expected to drop off in 4-5 months.

For subsequent analyses, the calving site was defined as the site where the cow-calf pair was first observed, and was marked as a GPS location. We used a t-test to assess differences between birth weights of male and female caribou calves (estimated from weight at capture (a) and age in days (x), where $y = a - 0.571x$; Parker 1989). We used analysis of variance (ANOVA) to examine birth weights among calving areas, and Tukey's honest significant difference was employed for unequal sample sizes for multiple comparisons (Zar 1998). Annual and pooled sex ratios of captured calves were compared using chi-squared (χ^2) analyses (Zar 1998).

Cause-specific mortality and calf survival

Collared calves were monitored by fixed-wing aircraft (Piper Super Cub 18A) twice daily (0700-1100 and 1800-2300), weather permitting, for 28 d after captures and then once weekly until the end of July per field season. To quantify monitoring frequency during 28 d post capture, we randomly selected an animal and averaged the time (hrs) between relocations. General locations of all adult female caribou and calves observed during monitoring flights were counted and recorded. A movement event was defined as the movement of a calf >1 km from its calving site. In the case of movement events that occurred over more than 1 d, the day the calf left the calving site was defined as the day of the movement. After detecting a mortality signal, the mortality site was visited by helicopter as soon as possible (<16 hrs). A

GPS location was taken on the ground where the collar was found.

At each mortality site, photos were taken, whole or partial carcasses recovered, and/or any evidence (e.g., scat, tracks, and hairs) recorded. If possible, we conducted partial necropsies of predation mortalities to identify timing of wounds. Whole carcasses were weighed, and then frozen for subsequent analysis. Cause-specific mortality was assigned, as outlined by Acorn and Dorrance (1998), to one of the following causes of death: 1) accident/abandonment, or predation by 2) bear, 3) eagle, 4) wolverine, 5) wolf, or 6) unknown predator.

Observed versus expected frequencies of cause-specific mortalities (annual, pooled over 2 yrs, and by calving area) and sex ratios of calves that died were compared using χ^2 analyses. Identified predation-specific mortality among the 3 calving areas was examined using observed ($n_{\text{Foothills}} = 6$, $n_{\text{Western High Country}} = 6$, and $n_{\text{North Prophet}} = 2$) and expected ($n = 14$) frequencies of identified mortalities from predation. The probability of calf survival from predation for a specific time period was determined using the Kaplan-Meier (KM) estimator on an annual and pooled basis (Pollock et al. 1989). Non-predation mortalities were censored from the survival estimate at the time of death. Survival rates by age were determined in days for the first 28 d and in weeks for the next 28 d. Mortality rate was estimated by week and defined as the number of animals that died by the end of week_x divided by the number of animals alive at the beginning of week_x. Survival for each calving area was calculated using pooled survival data. Survival curves across years were compared using the log-rank test with a conservative estimate of variance (Pollock et al. 1989). To increase sample size, we pooled data across years and defined 2

seasons of survival for small- and large-scale models: survival to the end of calving (25 May-14 June) and through summer (15 June-15 August). Survival was compared between these seasons and among calving areas, with a Bonferroni adjustment, using the difference in proportions test (Zar 1998). The number of animals at risk at the beginning of season_x was defined as the sample size for season_x, except for calving when sample size was determined at the termination of capture effort ($n = 48$). Survival for season_x was equal to the KM estimate of survival at the end of season_x.

Small-scale characteristics of calving sites

We collected small-scale habitat information at calving sites in the first week of July during 2002 and 2003. A 100-m cloth tape was placed on the ground at a random bearing with the calving site as the center point. We noted general vegetation community types within 100 m of each calving site. The line-intercept method was used to calculate absolute cover of trees, shrubs, and dwarf shrubs by species, and rocks/soil and cliffs (Higgins et al. 1996). If a transect extended over a cliff, the intercept value was noted, and the survey was terminated.

Five plots (50 x 50 cm) were placed randomly on either side of the transect at 25-m intervals. We recorded the number of individual plants for each graminoid, lichen, and forb species within the plots to estimate plant density. Percent cover by each species, and rocks/soil was estimated visually with the aid of laminated cardboard circle with an area approx. 1% of the plot (0.0025 m²). To evaluate the relationship between percent cover of lichens and lichen biomass (g/m²), we

sampled lichen biomass by removing a 20 x 20-cm sample of soil and vegetation from a randomly chosen corner of each plot. The first 7 transects were not sampled for biomass, as the decision to evaluate the percent cover-biomass relationship was made in the first field season after we started collected calving site data. Biomass samples were air-dried in paper bags and subsequently sorted, identified to genus, and weighed to the nearest 0.001 g. The Shannon-Wiener index of diversity (H') for lichen biomass and herbaceous species at each calving site was calculated as in Krebs (1989).

Each calving site characteristic (as measured above) was compared for calves that lived and died using t-tests, for both the calving and summer seasons, after testing for normality (Levene's test) and employing a Mann-Whitney U-test if the assumption of normality was violated (Siegel 1956; Zar 1998). The relationship between lichen biomass and percent-cover of lichens for total biomass and biomass by genus was evaluated using linear regression. Vegetation characteristics (including lichen biomass), slope ($^{\circ}$), and elevation (m) of calving sites were compared across calving areas using ANOVA and Tukey's test for unequal sample sizes for all post-hoc analyses (Zar 1998). In cases of non-normality, we used the Kruskal-Wallis ANOVA of ranks and a multiple comparisons of mean ranks for post-hoc analyses (Siegel 1956; Siegel and Castellan 1988).

The relationships between small-scale characteristics of calving sites and calf survival to the end of calving and during summer were evaluated using logistic regression. Twelve ecologically plausible models were derived from small-scale characteristics (i.e., grass/grass-like cover (%), forb cover (%), total herbaceous

cover (%), density of herbaceous vegetation (plants per m²), lichen biomass (g/m²), lichen diversity (H'), herbaceous diversity (H'), shrub intercept (%), dwarf shrub intercept (%), cliff intercept (%), and rocks/soil intercept (%)) to predict calf survival. All model inputs for logistic regression analyses were assessed for collinearity and multicollinearity using tolerance scores. In both cases, if tolerance scores were <0.20, covariates were not included in the same model (Menard 2002). The most parsimonious models were identified using Akaike's Information Criterion (AIC) values corrected for small sample size (AIC_c), the difference in AIC_c (Δ_i), Akaike weights (w_i), and evidence ratios (E_r) (Burnham and Anderson 2002). Models were validated using areas under the receiver operating characteristic curves (ROC) (Boyce et al. 2002). A ROC of >0.70 was considered to have an acceptable level of discrimination (Manel et al. 2001; Boyce et al. 2002). Robust estimations of variance for the odds ratios (e^{β_i}) were obtained using the Huber-White sandwich estimator (Stata Corporation, College Station, TX, USA). Transects without lichen biomass data ($n = 7$) were excluded from analyses.

Significance for all tests was assumed at $\alpha = 0.05$. Statistica 6.1 (Statsoft, Inc., Tulsa, OK, USA) was used for all tests; Stata 7 and 8 (Stata Corporation, College Station, TX, USA) were used for all model development, evaluation, and validation. The phrase 'no difference' is used in place of 'means were similar'.

Large-scale characteristics of calving sites and calving areas

Components of Predation Risk

Predation risk to caribou was quantified using logistic regression to form

RSFs that identified habitats selected by grizzly bears and wolves in the GBPA from 14 May to 15 August in 2002 and 2003. The models incorporated bear and wolf GPS data, vegetation class as determined from Landsat TM and ETM imagery, distance to linear features (e.g., seismic lines, roads, and pipelines), an index of vegetation fragmentation, and topographical features (i.e., slope, elevation, and aspect). Risk of predation was defined as the probability of being killed during a season (Lima and Dill 1990). We assumed that the components of predation risk (as in Lima and Dill 1990) were directly related to the relative selection of habitats by predators as defined by RSFs, and these components of risk could be assessed by caribou (Kats and Dill 1998); assumptions for RSFs were as outlined in Boyce and McDonald (1999).

Locations of GPS-collared predators were determined for 15 female grizzly bears and 22 wolves from 5 packs that were being monitored in a concurrent study (B. Milakovic, University of Northern British Columbia, unpublished data). Collars had been programmed to acquire locations every 6 hrs for approx. 2 yrs. Data were recovered via remote download or by retrieving the collar. Bear and wolf data were divided into 2 caribou seasons: calving (15 May-14 June) and summer (14 June-15 August), as defined by field observations of calving caribou, estimates of early calving, and changes in environmental conditions. GPS data were divided into season and year subsets for individual bears, and pack, season, and year subsets for wolves. All but one of duplicate wolf locations (i.e., same date and time) within a pack were randomly selected and removed to address issues of independence. We used 100% minimum convex polygons (MCP) to define areas of resource availability

for each individual bear and wolf pack by caribou season and year (Mohr 1947; Hooge et al. 1999). After MCPs were identified, any GPS data that fell outside of the GBPA were 'clipped' to the boundaries of the GBPA. Five availability points per use point were randomly selected within each MCP for individual bears and wolf packs using the random point generator extension (Jenness 2003) in Arcview 3.2 (Environmental Systems Research Institute, Redlands, CA, USA).

Covariates in the resource selection models for bears and wolves were 25-m resolution raster geographic information system (GIS) data. A digital elevation model was obtained from the 1:20,000 British Columbia Terrain and Resource Inventory Management program (Ministry of Crown Lands 1990); this dataset was used to create the aspect and slope layers. Vegetation classes were identified using an August 2001 Landsat ETM image (R. Lay, University of Northern British Columbia, unpublished data). Fifteen vegetation classes with a minimum mapping unit of 75 x 75 m were combined into 9 classes to address concerns with accuracy and complete separation in logistic regression models while maintaining biologically important differences for wolves and bears (Appendix B: Table B.1, Fig. B.1). These classes were spruce, shrubs, subalpine, *Carex* spp., non-vegetated, pine, riparian spruce, alpine, and burned/disturbed. Aspect was categorized into north (316-45°), east (46-135°), south (136-225°), and west (226-315°) directions to address problems with northerly values having the same aspect but different values (0° and 360°). Pixels with slope $\leq 1^\circ$ were assigned no aspect.

Because linear features can be associated with a higher risk of wolf predation (James and Stuart-Smith 2000), we created a distance to linear features layer using

existing 1997-2000 databases (G. Haines, British Columbia Oil and Gas Commission, pers. comm.). Age, level of use, and type of linear features, such as seismic line, pipeline, and road, were not distinguished. Accuracy of linear features was assessed using orthophotographs (2000) and Landsat ETM panchromatic images (2001) of the GBPA; linear features were added as necessary using ArcGIS 8.3 (Environmental Systems Research Institute, Redlands, CA, USA). All linear features were rasterized and buffered by 10 m to address locational error and resolution limitations of topographical data. A distance surface (25-m cell size) was generated based on the perpendicular distance (m) to the edge of linear features.

An index of vegetation fragmentation was created using Idrisi32 (Clark Labs, Worcester, MA, USA) from 15 vegetation classes (see Appendix B: Table B.1) that were grouped according to coarse vegetation cover type (CVCT) to represent fragmentation as open or closed cover types (R. Lay, University of Northern British Columbia, unpublished data). Open cover types included open-water (gravel bar and water classes), open-rock (rocks and rock-crustose classes), and open-alpine (dry and wet alpine classes). The closed coniferous cover type incorporated pine, spruce, and riparian spruce classes. The snow/glacier, subalpine spruce, burned/disturbed, *Carex*, shrub, and low productivity spruce classes were considered as separate cover types. The raster layer of linear features was incorporated into the CVCT classification as a shrub component, so contiguous vegetation polygons were bisected by these shrub-dominated linear features. This new linear-shrub class was used only in the fragmentation index, and not as a new class in the vegetation classification. The index of vegetation fragmentation (F_i)

used a moving window or kernel to classify each pixel and was defined by the following:

$$F_i = \frac{(b-1)}{(c-1)},$$

where b is the number of CVCTs in a 175 x 175-m kernel and c is the number of 25 x 25-m pixels (49) in that kernel. F_i values ranged from 0.00 to 0.50. These values were categorized into 3 classes (low fragmentation = 0.00-0.01, medium = 0.02-0.04, and high >0.04) based on the frequency distribution of the data.

Analyses of Predation Risk

A suite of ecologically plausible RSF models was developed to define predation risk and distance to areas with a high risk of predation by grizzly bears and wolf pack by season and year (Appendix C: Tables C.1, C.4). Coefficients of selection (i.e., beta coefficients, β_i) were calculated using logistic regression (Manly et al. 2002), and robust estimates of variance for these coefficients were obtained using the Huber-White sandwich estimator (Stata Corporation, College Station, TX, USA). The most parsimonious models were identified using AIC or AIC_c (Burnham and Anderson 2002) and validated using the k-fold cross validation (Boyce et al. 2002) and an averaged Spearman's rank correlation coefficient (\bar{r}_s) (Siegel 1956). The most parsimonious model(s) was selected based on w_i , and $E_r < 2$ for bears and $E_r < 10$ for wolves (Burnham and Anderson 2002). Models were averaged if a less parsimonious model performed better in the k-fold cross-validation or if the most parsimonious model did not perform well ($\bar{r}_s < 0.64$, $P > 0.050$) (Appendix C: Tables

C.2, C.7, C.8). Estimates of averaged coefficients and variance were calculated as outlined in Burnham and Anderson (2002:150, 162).

All model inputs were assessed for collinearity and multicollinearity as in analyses of calving site characteristics, except if tolerance scores were <0.40 , then collinear and multicollinear covariates were not included. This conservative threshold, which was lower than Menard's (2002) recommendation of 0.20, was set to minimize any unknown effects of collinearity or multicollinearity because model predictions were inputs for other models and subsequent analyses. Slope ($^{\circ}$), distance to linear features (km), and elevation (km) were maintained as continuous variables. Elevation and distance to linear features (km) were entered as quadratic terms unless selection for covariates was clearly linear (i.e., coefficients of both terms of the quadratic were the same sign). Vegetation and aspect categories that were rare or did not occur (i.e., near-perfect or perfect separation) in use and/or available data were not included in analyses. Deviation contrasts were used to code all categorical variables (i.e., vegetation, aspect, and fragmentation) (Menard 2002).

Bear data were pooled by season and year because there was little or no social exclusion of individual bears and a high degree of overlap occurred among MCPs (B. Milakovic, University of Northern British Columbia, unpublished data). Consequently, 4 RSFs defined the risk of predation to caribou from grizzly bears (Appendix C: Tables C.2, C.3). In contrast to bears, RSFs were developed for each wolf pack in the GBPA because wolf packs specifically prey on different prey items at different times of the year, and selection of habitat features likely varies (B. Milakovic, University of Northern British Columbia, unpublished data). Twenty-two

RSFs were formed to define risk by wolf pack, season, and year (Appendix C: Tables C.7-C.13). Because MCPs of wolf packs did not provide full coverage of the GBPA in any season or year, and because there was at least one other known uncollared pack in the GBPA, we used pooled RSFs to predict wolf occurrence for those areas without data (Appendix C: Tables C.5, C.6). Selection, validation, and averaging of wolf models was identical to that of the bear models, except that the E_r criteria for averaging pack models was increased from <2 to <10 because model performance for some packs and seasons was lower than bear models, and in some cases, no pack models performed well for a season or year (Appendix C: Tables C.7, C.8). In these cases, models were averaged (Burnham and Anderson 2002).

Risk landscapes for caribou from bears and wolves by season and year were developed from the β_i in the logistic regression models using a raster GIS (PCI Imageworks 9.1, Richmond Hill, ON, Canada) and the following log-linear model (Boyce and McDonald 1999; Manly et al. 2002):

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_i x_i)$$

where x_1, x_2, \dots, x_i are the raster data layers (e.g., elevation, slope, vegetation); this model estimated the relative probability of use by a predator for each 25 x 25-m pixel in the GBPA. We used the SCALE command in XPACE (PCI 9.1, Richmond Hill, ON, Canada) to scale the data from 0-1. Bear RSFs by season and year were applied to the GBPA, whereas wolf RSFs were applied to each pack's MCP for that season and year. The pack and pooled wolf RSF values were combined into one risk landscape for each season and year. In areas where pack boundaries overlapped within a season and year, the lower RSF value was assigned to that

pixel, due to likely decreased vigilance by pack members in those areas and, subsequently, a lower risk of predation (Mech 1977; Rogers et al. 1980; Mech 1994). For all risk layers, a mask for snow/glaciers (i.e., areas >2,400 m in rugged mountains to the west) and water (i.e., large bodies of water in the west and west-central portion of the GBPA) was created where the likelihood of encountering predators was rare, and those areas were given RSF values of zero. Risk surfaces were smoothed using a 75 x 75-m median filter. Risk values were binned into quartiles to create distance surfaces to high risk predator habitats (i.e., the perpendicular distance (km) to the third quartile RSF value for each season and year layer) using Idrisi32 (Clark Labs, Worcester, MA, USA). GIS layers for change in wolf risk and change in bear risk were created for each season and year. Change in risk was equal to the summer risk layer subtracted from the calving risk layer for that species, season, and year.

Indices of Forage Biomass and Quality

NDVI data from partial Landsat TM and ETM images acquired on 4 June (TM), 22 July (TM), and 15 August 2001 (ETM) were used to model NDVI and the changes in NDVI for the GBPA. Our assumptions were that 1) NDVI was correlated with above-ground net primary productivity and leaf area index (i.e., biomass) (Tucker and Sellers 1986; Ruimy et al. 1994), 2) change in NDVI was an index of the amount of plant growth that occurred within a pixel (Griffith et al. 2002; Oindo 2002), and 3) the timing of change important to caribou was likely to occur between 4 June and 22 July (the dates of TM image data) in 2002 and 2003 (R. Lay and D. Gustine,

University of Northern British Columbia, unpublished data).

All images were geocorrected (root mean squared error < 0.50), and raw imagery was converted to spectral radiance to address differences in sensor calibration (Chander and Markum 2003; R. Lay and D. Gustine, University of Northern British Columbia, unpublished data). NDVI was modelled for each image ($n = 2062$, the number of pixels equal to 0.01% of the smallest Landsat data set) using multiple regression with slope ($^{\circ}$), categorized aspect, vegetation, elevation (km), and/or incidence (i.e., the angle the sun strikes the surface of the ground at the time the image was recorded) as independent variables in a suite of models (Appendix D: Table D.1). All model inputs for multiple regression analyses were assessed for collinearity and multicollinearity, and categorical variables were coded as in analyses of calving site characteristics.

Models were selected using the highest adjusted R^2 values and validated with a resampling procedure and pixel-to-pixel rectification with the original NDVI data (Appendix D: Table D.2). Models that were within 0.05 of the best model's adjusted R^2 value were included in validation procedures. A new random sample without replacement ($n = 2062$) was drawn from each set of image data for validation. Predicted NDVI values from the original models were regressed on actual NDVI values from this new data set. Final models were those with the highest average adjusted R^2 values; if 2 models explained the same variation within 0.1%, the more efficient model (i.e., model with fewest parameters) was selected.

NDVI models were used to create large-scale data layers in a raster GIS (PCI Imageworks 9.1, Richmond Hill, ON, Canada) that estimated indices of biomass and

relative forage quality across the GBPA. These layers were created using techniques identical to the risk models, except that we used the coefficients of the multiple regression models (Appendix D: Table D.3) as weighting factors and added those to the intercept to estimate NDVI per pixel as an index of biomass in the GBPA for that image date. Actual NDVI values were regressed against modelled NDVI for cloud-free areas on a pixel-to-pixel basis for a final validation of modelled data (R. Lay and D. Gustine, University of Northern British Columbia, unpublished data) (Appendix D: Table D.1, D.2). Change in modelled NDVI values as an index of quality was calculated by subtracting the 4 June image from the 22 July image. Change was not calculated for non-vegetated cover types that had negative NDVI values throughout the summer (Oindo 2002). The change in NDVI (quality) modelled data were scaled (0-1) as for the risk models; NDVI modelled data (biomass) were left as modelled NDVI values.

Continuous and binned data were used in analyses. Biomass and quality surfaces were smoothed and categorized and distance surfaces to high-biomass and high-quality areas were generated as for the risk surfaces.

Analyses of Large-Scale Characteristics of Calving Sites and Calving Areas

We sampled the modelled risk, quality, and biomass data for 3 scales of analyses pooled across years to compare 1) characteristics among calving strategies (i.e., the 3 calving areas) and the landscape (i.e., the GBPA), 2) characteristics of calving sites in a calving strategy versus characteristics of random points in that calving strategy, and 3) characteristics of calving sites versus random

points on the landscape. The number of random points within each calving strategy was set at 10 times the number of calves captured within an area ($n_{\text{Foothills}} = 200$, $n_{\text{Western High Country}} = 180$, and $n_{\text{North Prophet}} = 100$) and was directly proportional to size of the calving areas. The sample size for random points on the landscape was equal to the total number of data points across calving areas ($n = 480$). Random points were distributed using the random point generator extension (Jenness 2003) in Arcview 3.2 (Environmental Systems Research Institute, Redlands, CA, USA). A raster GIS (PCI 9.1 XPACE, Richmond Hill, ON, Canada) was used to query modelled risk (by season and year) and forage (by season) data for all random points and calving sites.

Logistic regression and an ecologically plausible set of models for calving and summer seasons were used to determine the importance of risk, forage characteristics, and movement towards the survival of calves in 2002 and 2003. Bear risk, distance to areas of high bear risk (km), wolf risk, distance to areas of high wolf risk (km), biomass, quality, and calving area were covariates. Movement was added *a posteriori* to models in the summer to evaluate the importance of movement towards calf survival. Movement was not used to predict calf survival during the calving season because movement events were rare in calves that died. We then developed a model set with forage and risk characteristics and calving area as covariates to predict movement events through the summer season and added 4 new covariates: change in wolf risk and change in bear risk between seasons, and distance to high biomass and distance to high quality forage. Model covariates were assessed for collinearity and multicollinearity; models were selected, validated, and

estimates of variance were calculated as in small-scale analyses of calving site characteristics.

Nonparametric tests were used for all analyses of risk and forage attributes among calving areas, the landscape, and calving sites because preliminary analyses suggested violation of the homogeneity of variances assumption (Siegel 1956). The Mann-Whitney U-test (Siegel 1956) was used to examine risk attributes between years by calving area and the landscape, risk and forage characteristics (pooled across years) at calving sites versus characteristics of that calving area, risk and forage characteristics of all calving sites versus random points on the landscape, and the independent effects of risk and forage characteristics towards survival and movement. To evaluate the differences in forage and risk attributes, slope ($^{\circ}$), and elevation (m) among calving areas and the landscape, we used Kruskal-Wallis ANOVA by ranks with multiple comparisons of mean ranks for post-hoc analyses (Siegel and Castellan 1988). Changes in risk and forage characteristics (pooled across years) within calving areas and the landscape between seasons were evaluated with the Wilcoxon matched pairs test (Siegel 1956).

The trade-off, or cost, of foraging in areas of higher relative quality or biomass was determined by evaluating the relationship between risk and forage characteristics with linear regression (Bowyer et al. 1998; Bowyer et al. 1999). Cost by season was defined as the change in predator-specific risk (y) as biomass or quality (x) increased (i.e., slope of the regression). We assumed that animals experience a cost to foraging if there is a positive relationship between risk and forage characteristics (i.e., slopes > 0), whereas no cost in risk is incurred if there is

no relationship or a negative one (i.e., slopes ≤ 0) (Bowyer et al. 1998; Bowyer et al. 1999). We used a t-test with a Bonferroni adjustment to compare confidence intervals of slopes $\neq 0$ among calving areas and the landscape within and between seasons by predator (Sokal and Rohlf 1995).

RESULTS

Reproductive characteristics

Blood samples were obtained from 47 of the 48 adult female caribou collared during the winters of 2001/2002 and 2002/2003. Forty-three of those animals ($91.5 \pm 4.1\%$, $\bar{x} \pm \text{binomial SE}$) were pregnant, with similar estimates between years (Table 2.1). We were not able to determine reproductive rates for all these animals because the GPS data loggers for 44 of the collars (22 per yr) failed prior to calving. By observing animals for which the very high frequency (VHF) signals on GPS collars continued to function to calving, we determined that 15 of 22 pregnant adult females ($68.2 \pm 10.2\%$, $\bar{x} \pm \text{binomial SE}$) had their calves in the summers of 2002 and 2003. Parturition rates were varied with small sample sizes and high estimates of standard error for both years (Table 2.1). Calving dates ranged from 25 May to 10 June, including observations of many non-collared caribou, with peak calving occurring on 28 May ± 0.3 d ($\bar{x} \pm \text{SE}$).

Twenty-one, 19, and 10 calves were captured in the Foothills, Western High Country, and North Prophet calving areas, respectively (Appendix E: Table E.1). Only 10 calves were with collared adult females (5 per yr). More captures were by

Table 2.1. Reproductive parameters of female woodland caribou and age, weight, sex, and peak calving data from captured calves in the Greater Besa Prophet area, northern British Columbia, 2002-2003.

Parameter	Year	$\bar{x} \pm \text{SE}$	Range	n
Pregnancy (%)	2002	91.7 \pm 5.8		24
	2003	91.3 \pm 6.0		23
Parturition (%)	2002	55.6 \pm 17.6		9
	2003	76.9 \pm 12.2		13
Calving date	2002	30 May \pm 0.4 d	27 May-3 June	25
	2003	26 May \pm 0.2 d	25 May-10 June	25
Sex ratio (F : M)	2002	16 : 9		25
	2003	15 : 10		25
Weight of calves at capture (kg)	2002	9.5 \pm 0.4	6.8-13.5	25
	2003	9.7 \pm 0.5	6.0-19.0	25
Estimated birth weight (kg) [†]	2002	7.7 \pm 0.2	5.6-10.1	25
	2003	8.1 \pm 0.7	5.1-16.1	25
Age of calves at capture (days)	2002	3.1 \pm 0.3	0.5-6.0	25
	2003	2.8 \pm 0.2	1.0-6.0	25

[†] Using the equation $y = a - 0.571x$, where y = estimate of birth weight (kg), a = weight of calf at capture (kg), and x = age in days at capture (from Parker 1989).

net-gun (2002, $n = 11$; 2003, $n = 22$) than by hand (2002, $n = 14$; 2003, $n = 3$). A total of 31 females and 19 males were captured, with no difference in sex ratios across or between years (all $P > 0.090$). Calf weights at capture were similar between years, with an average weight of 9.6 ± 0.3 kg ($\bar{x} \pm SE$). There was no difference in the estimates of birth weights for males and females ($P = 0.604$), or among calves captured in the 3 different calving areas ($F_{(2, 49)} = 2.18$, $P = 0.125$). Age of captured calves ranged from 0.5-6.0 d, with the average age at capture being 3.0 ± 0.2 d. Average handling time per calf was ≤ 2 min, not including pursuit time (in the helicopter or on foot).

Cause-specific mortality and survival

Caribou calves were monitored during the 28 d post-capture once every 16 ± 2.3 hrs ($\bar{x} \pm SE$) and 18 ± 2.2 hrs in 2002 and 2003, respectively. Pooled data by year on animal movements away from calving sites peaked from 15-21 d of age, although movements continued to occur through 22-28 d of age in 2003 (Fig. 2.3a). No calves moved away from calving sites when they were < 8 d of age. Peaks in mortality rate were observed at 8-14 and 29-35 d of age (Fig. 2.3a).

Thirteen female and 6 male calves died in the first 2 months of life during the 2 yrs of the study (Fig. 2.3b). There was no difference in the observed versus expected number of mortalities for males and females ($P = 0.629$). One calf died at 6 d of age probably from abandonment due to handling in 2002 and another calf died at 4 d of age from accidental drowning in 2003. The remainder of mortalities ($n = 17$) were predator-caused (Fig. 2.3b). There was one eagle- and one bear-caused

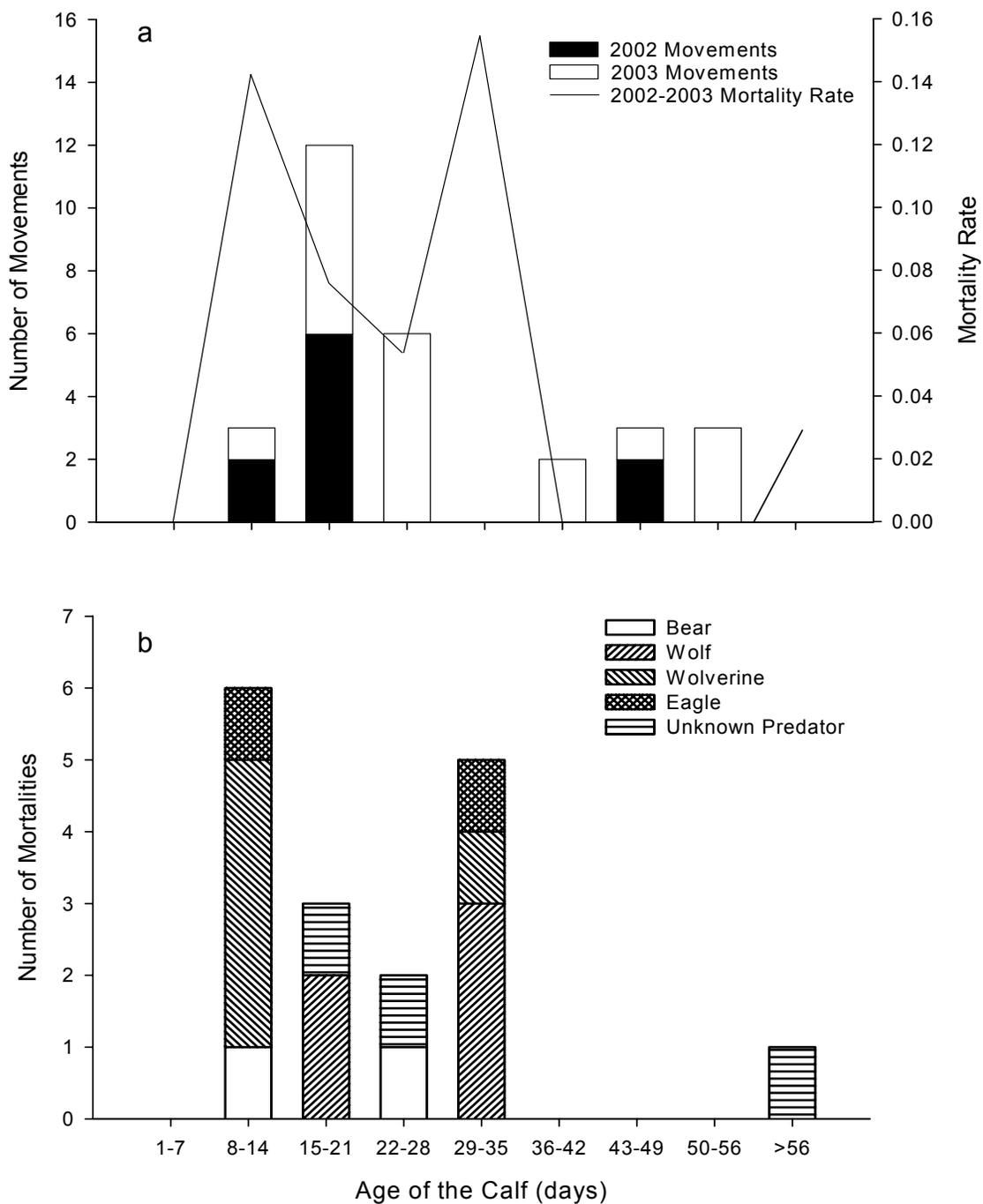


Figure 2.3. Timing of calf movements (>1 km) by age in days away from caribou calving sites compared with mortality (i.e., number of animals that died by the end of week_x divided by the number of animals alive at the beginning of week_x) during the first two months of life (a) and timing of predation-caused mortalities of collared caribou calves (b) in the Greater Besa Prophet area, northern British Columbia, 2002 and 2003.

mortality each year. In 2002, there were 3 mortalities from wolves and 4 mortalities from wolverines; in 2003, there were mortalities from one wolverine and 2 wolves. We were unable to conclusively identify predators in 3 cases (2002, $n = 2$; 2003, $n = 1$). We also recorded mortalities of uncollared caribou calves by a wolverine and eagle at approx. 1 and 2 weeks of age, respectively. Four of the 5 wolverine-caused mortalities of collared calves occurred between 9-15 d of age, whereas all wolf-caused mortalities occurred after calves were 18 d of age (Fig. 2.3b). There were no mortalities <14 d of age in the Foothills and no mortalities by wolves in the North Prophet. There were no differences in observed versus expected frequencies of causes of mortality using all data pooled over 2 yrs or among calving areas (all $P > 0.340$).

Survival through 56 d of life appeared lower, although not significantly, in 2002 than 2003 (0.54 ± 0.11 versus 0.79 ± 0.08 , $P = 0.066$) (Fig. 2.4a). Survival was higher through the calving season (0.88 ± 0.05) than through the summer season (0.69 ± 0.07) ($P = 0.032$). Pooled survival also was not different through 56 d of age among the Foothills (0.65 ± 0.11), Western High Country (0.61 ± 0.12), and North Prophet (0.80 ± 0.13) calving areas (all $P > 0.560$) (Fig. 2.4b).

Small-scale characteristics of calving sites and calf survival

There were no differences in vegetation characteristics of calving sites among calving areas, except for percent intercept of shrubs (Kruskal-Wallis ANOVA, $H_{(2, 48)} = 8.12$) (Table 2.2). Although, not always significant, shrub cover tended to be higher at calving sites in the Foothills than the North Prophet ($P = 0.050$) and the

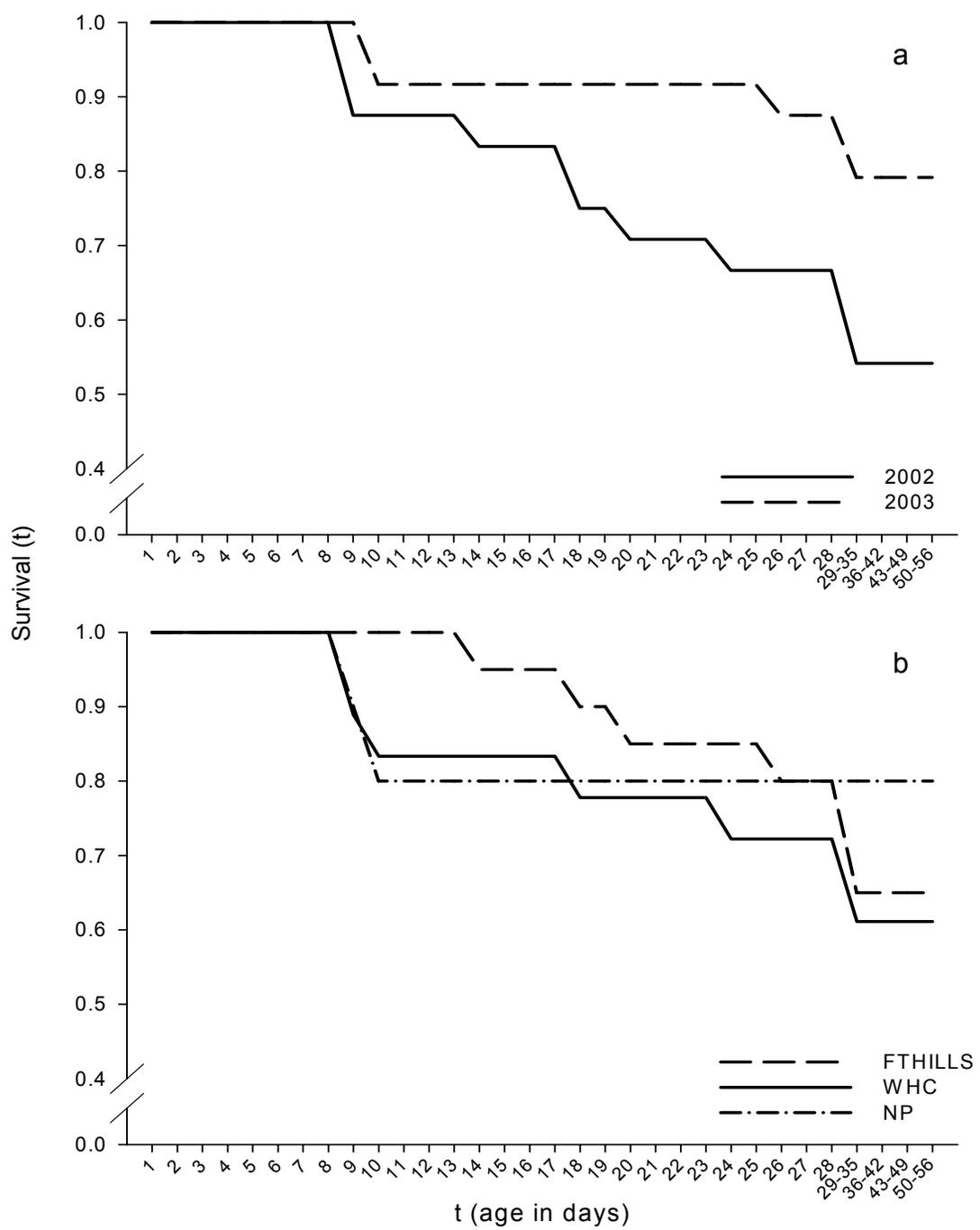


Figure 2.4. Kaplan-Meier estimates of survival rate by time (t) for woodland caribou neonates in a) 2002 and 2003 and b) by calving area (Foothills (FTHILLS), Western High Country (WHC), and North Prophet (NP)) using pooled data for both years, in the Greater Besa Prophet area, northern British Columbia.

Table 2.2. Small-scale characteristics of calving sites ($\bar{x} \pm \text{SE}$) among the Foothills (FTHILLS), Western High Country (WHC), and North Prophet (NP) calving areas in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Characteristics sharing the same letter were not significantly different, as determined by nonparametric ([†]) and parametric analyses ([‡]).

Small-Scale Characteristic	FTHILLS (<i>n</i> = 21)	WHC (<i>n</i> = 19)	NP (<i>n</i> = 10)	<i>P</i>
Shrub Intercept (%)	29.6 ± 6.0 ^a	15.1 ± 5.5 ^{ab}	4.6 ± 1.8 ^b	0.017 [†]
Rock/Soil Intercept (%)	5.8 ± 2.7 ^a	18.6 ± 6.0 ^a	51 ± 10.0 ^b	0.001 [†]
Slope (°)	27.8 ± 1.6 ^a	16.6 ± 1.9 ^b	22.6 ± 2.7 ^{ab}	<0.001 [‡]
Elevation (m)	1767 ± 30 ^a	1783 ± 38 ^a	2033 ± 31 ^b	<0.001 [‡]
Cliff Intercept (%)	2 ± 0.4 ^a	3.8 ± 2.6 ^a	n/a	0.473 [†]
Dwarf Shrub Intercept (%)	22.5 ± 5.2 ^a	36.4 ± 6.3 ^a	19.4 ± 7.4 ^a	0.132 [‡]
Tree Intercept (%)	4.3 ± 1.7 ^a	4.2 ± 3.6 ^a	n/a	0.536 [‡]
Herbaceous Cover (%)	21.2 ± 2.4 ^a	17.6 ± 2.6 ^a	11.9 ± 3.5 ^a	0.097 [‡]
Herbaceous Diversity (<i>H'</i>)	1.63 ± 0.1 ^a	1.29 ± 0.1 ^a	1.21 ± 0.2 ^a	0.070 [‡]
Herbaceous Density (per m ²)	111.3 ± 23.3 ^a	135.5 ± 27.9 ^a	112.6 ± 34.3 ^a	0.773 [‡]
Grass (%)	8.1 ± 2.0 ^a	4.1 ± 1.3 ^a	2.8 ± 1.1 ^a	0.082 [‡]
Grass-likes (%)	3.2 ± 1.04 ^a	6.4 ± 1.71 ^a	2.3 ± 0.9 ^a	0.210 [†]
Forbs (%)	9.9 ± 1.7 ^a	7.1 ± 1.3 ^a	6.8 ± 1.7 ^a	0.300 [‡]
Lichen Biomass (g/m ²)	44.4 ± 8.9 ^a	28.5 ± 7.5 ^a	31.2 ± 10.7 ^a	0.372 [‡]
Lichen Diversity (<i>H'</i>)	1.28 ± 0.10 ^a	1.09 ± 0.17 ^a	1.29 ± 0.23 ^a	0.582 [‡]

[†] Kruskal-Wallis Analysis of variance and multiple comparison of mean ranks

[‡] Analysis of variance and Tukey's honest significant difference for unequal sample sizes

Western High Country ($P = 0.058$). Cover of rocks/soil ($H_{(2, 48)} = 19.25$), slope (ANOVA, $F_{(2, 47)} = 8.90$), and elevation ($F_{(2, 47)} = 13.80$) also differed among calving areas (Table 2.2). Rocks/soil cover was lower at calving sites in the Foothills ($P < 0.001$) and the Western High Country ($P = 0.041$) than the North Prophet. Calving sites in the Western High Country were not as steep as the Foothills sites ($P < 0.001$). The North Prophet calving sites were higher than the Foothills ($P < 0.001$) and Western High Country ($P < 0.001$) sites.

Variation was high within small-scale characteristics at calving sites (Appendix F: F.1); consequently, there were no vegetative differences at sites between calves that lived and died during the calving season or in summer within or between years. Percent cover of lichens was a poor predictor of total lichen biomass ($n = 169$, $r^2 = 0.25$, $P < 0.001$), and within each lichen genus except for *Cladina* spp. ($n = 48$, $r^2 = 0.72$, $P < 0.001$) (Appendix G: Fig. G.1).

Herbaceous cover (%) and shrub intercept (%) at calving sites best predicted survival of caribou calves during calving (Table 2.3). Each 1% increase in herbaceous cover ($e^{\beta_i} \pm SE$, 0.81 ± 0.07 , $P = 0.011$), as determined from plots along the transect, decreased the odds of survival by approx. 19%, whereas a 1% increase in shrub cover from line-intercept data increased the odds of survival by approx. 13% ($e^{\beta_i} \pm SE$, 1.13 ± 0.07 , $P = 0.045$) when the other variable was held constant in both cases. Discrimination of this model was excellent (ROC = 0.946). Models with cliff line-intercept data (%) could not be evaluated during the calving season because no calves died at those calving sites. A model using rocks/soil intercept (%) was the most parsimonious during summer, but discrimination was

Table 2.3. Model sets to evaluate the importance of small- and large-scale characteristics of calving sites as predictors of calf survival through calving (25 May-14 June) and summer (15 June-July 31) for woodland caribou in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Models were evaluated within small or large-scale sets; sample size (n), log-likelihood (LL), number of parameters (K), Akaike's Information Criterion for small samples (AIC_c), differences in AIC_c (Δ_i), Akaike weights (w_i), evidence ratios (E_r), and area under the receiver operating characteristic curve (ROC) were used to identify and evaluate the most parsimonious models within a set.

Model	n	LL	K	AIC_c	Δ_i	w_i	E_r	ROC
Small-Scale Characteristics (Calving)								
Herbaceous Cover (%) + Shrub Intercept (%)	41	-7.015	3	20.355	0.000	0.631	1.00	0.946
Herbaceous Cover (%) + Shrub Intercept (%) + Dwarf Shrub Intercept (%)	41	-6.762	4	22.190	1.835	0.262	2.50	0.953
Herbaceous Cover (%) + Lichen Diversity	41	-9.358	3	25.039	4.685	0.026	10.41	0.845
Grass Cover (%) + Forbs Cover (%) + Shrub Intercept (%)	41	-9.508	4	27.682	7.328	0.017	39.01	0.838
Lichen Biomass (g/m ²) + Shrub Intercept (%)	41	-10.783	3	27.890	7.535	0.015	43.28	0.791
Density (per m ²) + Shrub Intercept (%) + Dwarf Shrub Intercept (%)	41	-10.058	4	28.783	8.428	0.010	67.64	0.865
Rocks-Soil	41	-12.896	2	29.898	9.543	0.006	118.10	0.550
Lichen Biomass (g/m ²) + Density (per m ²)	41	-12.110	3	30.545	10.190	0.004	163.22	0.831
Lichen Diversity + Herbaceous Diversity	41	-12.214	3	30.753	10.398	0.003	181.09	0.703
Rocks-Soil + Lichen Biomass (g/m ²)	41	-12.395	3	31.114	10.759	0.003	216.88	0.669
Large-Scale Characteristics (Summer)								
Movement	48	-25.835	2	55.760	0.000	0.335	1.00	0.740
Movement + Distance to Wolf Risk + Distance to Bear Risk	48	-23.977	4	56.513	0.754	0.230	1.46	0.820
Movement + Wolf Risk	48	-25.742	3	57.756	1.997	0.123	2.71	0.755
Movement + Quality	48	-25.826	3	57.924	2.165	0.113	2.95	0.746
Movement + Biomass + Quality	48	-26.652	3	59.577	3.818	0.050	6.75	0.755
Movement + Biomass + Wolf Risk	48	-25.717	4	59.992	4.233	0.040	8.30	0.748
Movement + Quality + Wolf Risk	48	-25.727	4	60.012	4.253	0.040	8.39	0.742

Table 2.3. Continued.

Model	<i>n</i>	LL	K	AIC_c	Δ_i	w_i	E_r	ROC
Movement + Wolf Risk + Bear Risk	48	-25.740	4	60.039	4.280	0.040	8.50	0.761
Movement + Biomass + Quality + Wolf Risk	48	-26.634	4	61.826	6.066	0.016	20.76	0.751

poor (ROC = 0.685).

Large-scale characteristics of calving sites and calving areas and calf survival

Detailed results on the performance of models defining predation risk by season, year, and predator, and relative forage quality and biomass by season are presented in Appendix C (risk) and Appendix D (forage). Some predation-risk characteristics of calving areas varied between years. The risk of bear predation and the distance to areas of high bear risk did not change from 2002 to 2003 in any calving area or on the landscape during calving or in summer (all $P > 0.115$). Nor did the risk of wolf predation and distance to areas of high wolf risk differ (all $P > 0.205$), except in the Foothills. Risk of wolf predation was higher in 2002 than 2003 in the Foothills only during the calving season ($P = 0.049$). Consequently, because risk appeared to change little across years within calving areas and the landscape, all risk data were pooled across years to facilitate evaluating trends in risk at all scales of analyses.

Risk, forage, and topographical characteristics varied among calving areas in both the calving and summer seasons (all $H_{(3, 958)} > 27.91$, all $P < 0.001$) (Table 2.4). The Foothills area was higher in bear risk and closer to areas of high bear risk than the landscape and the other calving areas (all $P < 0.001$). The North Prophet was lower in bear risk than the landscape and farthest from areas of high bear risk during calving (all $P < 0.001$). Trends in bear risk during summer were similar to calving except the North Prophet did not differ from the Western High Country in the distance to bear risk ($P = 1.000$) (Table 2.4). Between seasons, risk of bear

Table 2.4. Large-scale characteristics of random points ($\bar{x} \pm SE$) among the Foothills (FTHILLS), Western High Country (WHC), and North Prophet (NP) calving areas in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Characteristics sharing the same letter were not significantly different, as determined by Kruskal-Wallis analysis of variance and multiple comparisons of mean ranks. Large-scale characteristics of calving sites within a calving area were compared to characteristics of random points within that calving area; an asterisk (*) indicates a significant difference ($P < 0.050$), as determined by the Mann-Whitney U-test.

Season	Variable	FTHILLS	WHC	NP	Landscape
Random Points					
<i>Calving</i>	Bear Risk	0.63±0.008 ^a	0.49±0.014 ^{bc}	0.47±0.016 ^c	0.52±0.008 ^b
	Distance to Areas of High Bear Risk (m)	175±12.2 ^a	475±36.1 ^{b†}	874±71.1 ^{ct}	1193±120.8 ^{b†}
	Wolf Risk	0.46±0.008 ^a	0.35±0.011 ^b	0.34±0.014 ^b	0.49±0.009 ^a
	Distance to Areas of High Wolf Risk (m)	838±37.4 ^a	1567±85.1 ^b	1910±124.6 ^b	739±41.6 ^c
	Biomass (NDVI)	0.10±0.006 ^a	0.03±0.006 ^b	0.03±0.007 ^b	0.14±0.005 ^c
	Distance to Areas of High Biomass (m)	386±27.0 ^a	666±39.0 ^b	754±52.5 ^b	292±20.2 ^c
<i>Summer</i>	Bear Risk	0.61±0.012 ^a	0.43±0.017 ^b	0.46±0.025 ^b	0.53±0.009 ^c
	Distance to Areas of High Bear Risk (m)	130±10.6 ^a	463±35.4 ^b	386±42.8 ^b	447±33.4 ^b
	Wolf Risk	0.53±0.012 ^a	0.41±0.018 ^b	0.43±0.022 ^{bc}	0.51±0.011 ^{ac}
	Distance to Areas of High Wolf Risk (m)	300±18.9 ^a	536±37.2 ^b	591±58.9 ^b	391±23.8 ^a
	Biomass (NDVI)	0.34±0.007 ^a	0.16±0.014 ^b	0.20±0.019 ^b	0.31±0.008 ^a
	Distance to Areas of High Biomass (m)	123±10.3 ^a	457±35.5 ^b	420.9±45.2 ^b	273±18.2 ^c
<i>n/a</i>	Quality	0.67±0.016 ^a	0.34±0.028 ^b	0.43±0.039 ^{bc}	0.47±0.014 ^c
	Distance to Areas of High Quality (m)	65±8.4 ^a	276±25.9 ^b	173±28.9 ^c	222±14 ^{bc}
	Slope (°)	25±0.7 ^a	26±0.9 ^a	25±1.0 ^a	19±0.6 ^b
	Elevation (m)	1611±14.0 ^a	1857±18.2 ^b	1881±24.8 ^b	1456±18.6 ^c

†The WHC was not different from the landscape in distance to areas of high bear risk; the landscape was consistently ranked closer to areas of high bear risk than the NP.

Table 2.4. Continued.

Season	Variable	FTHILLS	WHC	NP	Landscape
Calving Sites					
<i>Calving</i>	Bear Risk	0.57±0.021*	0.54±0.022	0.38±0.025*	0.52±0.017
	Distance to Areas of High Bear Risk (m)	277±38.1*	425±68.9	920±175.9	466±58.0
	Wolf Risk	0.41±0.024	0.45±0.026*	0.27±0.029	0.39±0.018*
	Distance to Areas of High Wolf Risk (m)	793±82.4	1304±222.7	2532±369.2	1347±149.2*
	Biomass (NDVI)	0.04±0.015*	0.07±0.017*	0.001±0.011	0.04±0.10*
	Distance to Areas of High Biomass (m)	494±56.2*	504.1±109.3	1113±91.2*	627±61.7*
<i>Summer</i>	Bear Risk	0.61±0.039	0.52±0.053	0.29±0.028	0.51±0.031
	Distance to Areas of High Bear Risk (m)	109±23.3	208±69.2*	440±66.9	215±35.3
	Wolf Risk	0.49±0.033	0.54±0.046*	0.34±0.033	0.48±0.025
	Distance to Areas of High Wolf Risk (m)	304±60.5	284±72.4	536±56.3	345±40.8
	Biomass (NDVI)	0.34±0.014	0.28±0.033*	0.14±0.040	0.28±0.019*
	Distance to Areas of High Biomass (m)	139±24.7	242±66.5	508±58.5	254±35.3
<i>n/a</i>	Quality	0.79±0.026	0.60±0.062*	0.42±0.104	0.64±0.039*
	Distance to Areas of High Quality (m)	13±9.2*	116±57.1*	100±36.2	69±23.6*
	Slope (°)	28±1.6	17±1.9*	23±2.7	22±1.3
	Elevation (m)	1767±29.6*	1783±38.3	2033±30.6*	1828±24.9*

predation within calving areas and the landscape did not change (all $P > 0.163$), except in the Western High Country where risk was lower in calving than summer ($P < 0.001$) (Fig. 2.5). The Foothills, the North Prophet, and the landscape were closer to areas of high bear risk in the summer than in calving ($P = 0.043$). At calving sites within each calving area, caribou chose sites in the Foothills ($P = 0.043$) and North Prophet ($P = 0.031$) that were lower in bear risk than what was available within those areas during calving; the calving sites in the Foothills also were farther than random from areas of high bear risk ($P = 0.007$). In summer, the Western High Country calving sites ($P = 0.019$) were closer to areas of high bear risk.

Relative to characteristics of wolf risk, random points within all the calving areas were farther away from areas of high wolf risk than random points on the landscape and were lower in risk than the landscape during calving (all $P < 0.001$) except for the Foothills ($P = 0.176$) (Table 2.4). The Foothills was higher in risk and closer to areas of high risk than the other calving areas (all $P < 0.001$). Trends in risk and distance to high-risk habitats during summer were similar to calving, except the Foothills did not differ from the landscape ($P = 1.000$). Between seasons, risk of wolf predation significantly increased from calving to summer within each calving area (all $P < 0.001$) although risk on the landscape did not change ($P = 0.807$) (Fig. 2.5). Distance to areas of high wolf risk decreased within all calving areas and the landscape from calving to summer (all $P < 0.001$) (Fig. 2.5). At known calving sites, the risk of wolf predation was lower and sites were farther from areas of high wolf risk than random points on the landscape (all $P < 0.001$). The calving sites within the Western High Country were higher in wolf risk than random points within that

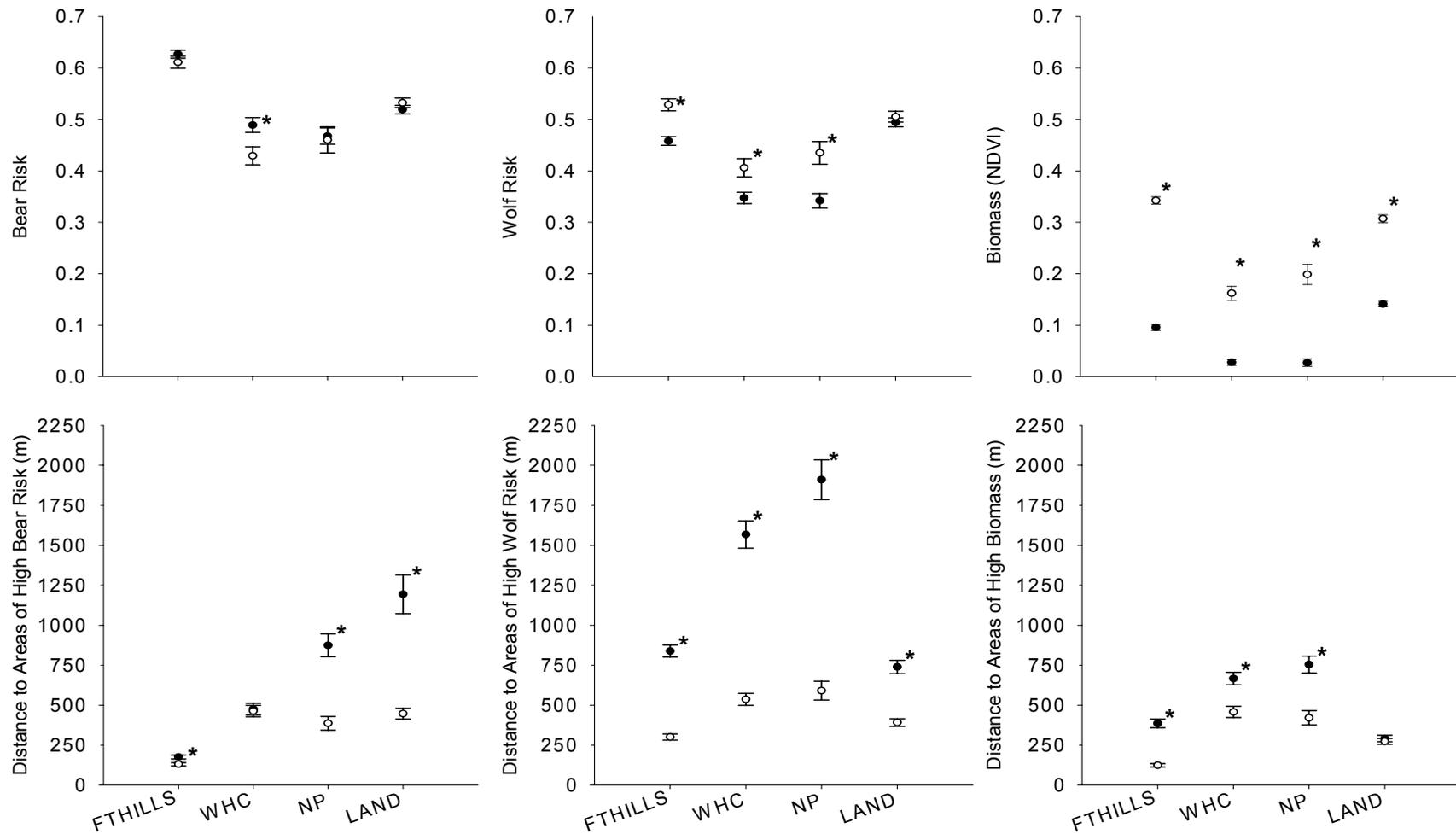


Figure 2.5. The change in characteristics of predation risk and forage biomass ($\bar{x} \pm SE$) from calving (●) to summer seasons (○) for random points within the Foothills (FTHILLS), Western High Country (WHC), and North Prophet (NP) calving areas and in the Greater Besa Prophet landscape (LAND) in northern British Columbia, 2002-2003. Significant differences between seasons, as determined by the Mann-Whitney U-test, are indicated by an asterisk.

calving area during calving ($P = 0.003$) and in summer ($P = 0.008$).

During calving, calving areas had lower biomass and were farther from areas of high biomass than the random points on the landscape ($P < 0.001$) (Table 2.4). Among calving areas, the Foothills had the highest biomass and was closer to areas of high biomass ($P < 0.001$). Trends in summer were similar to calving except there was no difference in biomass between the Foothills and the landscape ($P = 1.000$), and the Foothills was closer to areas of high biomass than the landscape ($P < 0.001$) (Table 2.4). Biomass increased and the distance to areas of high biomass decreased from calving to summer in all the calving areas and the landscape (all $P < 0.001$) (Fig. 2.5). All calving sites had lower biomass than random points on the landscape ($P < 0.001$). Biomass was lower at calving sites than what was available in the Foothills ($P = 0.006$), but higher in the Western High Country in the calving season ($P = 0.032$). All the calving sites were farther from areas of high biomass than what was available in the calving areas ($P < 0.030$). In the summer, all the calving sites ($P = 0.003$) were lower in biomass than random points on the landscape.

Relative to forage quality, the Foothills was higher in quality and closer to areas of high quality than the other calving areas (all $P < 0.019$) and the landscape (all $P < 0.001$) (Table 2.4). In contrast, the Western High Country was lower in quality than the landscape ($P = 0.002$). The North Prophet, with insignificantly higher quality than the Western High Country ($P = 0.086$), was the next closest to areas of high quality forage. All the specific calving sites chosen by caribou were higher in quality and closer to areas of high quality than random points on the

landscape (all $P < 0.001$). Calving sites within the Western High Country were higher in quality ($P = 0.006$) and closer to areas of high quality in that calving area ($P = 0.049$) (Table 2.4). Calving caribou also selected sites closer to areas of high quality than random points in the Foothills calving areas ($P = 0.019$).

Topography varied among calving areas and the landscape and also at calving sites within calving areas and the landscape (Table 2.4). Calving areas were steeper and higher than random points on the landscape, and the Foothills was lower in elevation than the other calving areas (all $P < 0.001$). Within the calving areas, slopes at the Western High Country calving sites were not as steep as random points ($P = 0.001$). Except for the Western High Country ($P = 0.299$), calving sites compared to the calving areas (Foothills, $P < 0.001$; North Prophet, $P = 0.025$) and all calving sites compared to the landscape were higher in elevation ($P < 0.001$).

Forage and risk characteristics were positively related, with few exceptions, in all seasons for all calving areas and the landscape (all $P < 0.030$) (Table 2.5). Exceptions were in the Foothills, where there was no relationship between quality and bear risk ($P = 0.583$) and a negative relationship between quality and wolf risk during calving ($P = 0.011$). Cost (i.e., the slope of the relationship between predator risk and a forage characteristic) varied among predators, forage characteristics, calving areas, and seasons (Table 2.5). During calving, predation cost in bear and wolf risk associated with biomass was lower in the Foothills than the Western High Country and the North Prophet; the North Prophet was the highest in cost for bear risk (all $P < 0.009$). For both calving and summer, the cost in wolf risk per unit

Table 2.5. Cost (slope \pm SE) from the linear relationship of predator risk versus forage characteristics of random points within the Foothills (FTHILLS), Western High Country (WHC), and North Prophet (NP) calving areas in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Slopes sharing the same letter were not significantly different among calving areas and slopes in the summer marked by an asterisk were different from the calving season; both comparisons were determined by a t-test of slopes with a Bonferroni adjustment for comparisons among calving areas.

Season	Risk v. Forage Characteristic	FTHILLS	WHC	NP	Landscape
<i>Calving</i>	Bear Risk v. Biomass	0.24 \pm 0.09 ^a	1.79 \pm 0.08 ^b	1.35 \pm 0.17 ^b	0.25 \pm 0.07 ^a
	Wolf Risk v. Biomass	0.86 \pm 0.08 ^a	1.47 \pm 0.10 ^{bc}	1.31 \pm 0.14 ^{ac}	1.05 \pm 0.06 ^a
	Bear Risk v. Quality	<i>No relationship</i>	0.30 \pm 0.03 ^a	0.24 \pm 0.03 ^a	0.28 \pm 0.02 ^a
	Wolf Risk v. Quality	-0.09 \pm 0.04 ^a	0.23 \pm 0.02 ^b	0.22 \pm 0.03 ^b	0.24 \pm 0.03 ^b
<i>Summer</i>	Bear Risk v. Biomass	1.33 \pm 0.07 ^{a*}	1.17 \pm 0.04 ^{ab*}	1.21 \pm 0.05 ^{ab}	1.01 \pm 0.03 ^{b*}
	Wolf Risk v. Biomass	1.16 \pm 0.08 ^{ab}	1.31 \pm 0.05 ^b	0.99 \pm 0.06	0.93 \pm 0.05 ^a
	Bear Risk v. Quality	0.47 \pm 0.04 ^{a*}	0.53 \pm 0.02 ^{a*}	0.54 \pm 0.04 ^{a*}	0.55 \pm 0.02 ^{a*}
	Wolf Risk v. Quality	0.33 \pm 0.05 ^{a*}	0.52 \pm 0.03 ^{a*}	0.46 \pm 0.03 ^{a*}	0.38 \pm 0.03 ^a

biomass was higher in the Western High Country than the landscape (all $P < 0.009$). In the summer, the cost in bear risk per unit biomass was higher in the Foothills than the landscape ($P < 0.009$). The cost in risk per unit quality usually did not differ among calving areas and the landscape during calving and summer for bears or wolves (Table 2.5). The exception was in the Foothills, where cost in wolf risk was lower than the other calving areas and the landscape (all $P < 0.009$). From calving to summer, cost in bear risk per unit biomass increased in the Foothills and on the landscape, and decreased in the Western High Country (all $P < 0.050$). Cost in risk for both bears and wolves per unit quality increased in every calving area for both bears and wolves (all $P < 0.050$) (Table 2.5).

Models using large-scale characteristics (predation risk, biomass, and quality) to predict survival of calves through calving and summer showed poor discrimination (all ROC < 0.657) when movement was not included. All summer models improved, as indexed by decreased AIC_c (3.00-9.14) and increased discrimination (0.06-0.23), when movement was added as a covariate (Table 2.3). The most parsimonious models (i.e., $E_r < 2.00$) were Movement (ROC = 0.740) and Movement + Distance to High Wolf Risk + Distance to High Bear Risk (ROC = 0.820). These models were averaged, and the odds ratios for the distance to wolf and bear risk covariates did not differ from 1.00; the odds ratio for caribou calves that stayed at the calving site ($e^{\beta_i} \pm SE$, 0.34 ± 0.12 , $P = 0.002$) or moved away ($e^{\beta_i} \pm SE$, 2.96 ± 0.12 , $P = 0.002$) during the summer was $\neq 1.00$. If a calf remained at its calving site to the end of summer, assuming distances to areas of high wolf and bear risk were held constant, the odds of survival decreased by approx. 66%. Models using large-scale

characteristics to predict movement of caribou calves from calving sites during the calving and summer seasons had poor discrimination (all ROC < 0.660). There were no differences in the independent effects of risk and forage characteristics on survival of calves and movement events during any season (all $P > 0.082$).

DISCUSSION

Plasticity in life-history strategies may enable animals to decrease predictability to large predators in space and time (Bowyer et al. 1999; Mitchell and Lima 2002). Calving strategies of woodland caribou in the GBPA offered parturient animals a landscape dynamic in both risk avoidance and forage acquisition. This diversity provided options for female caribou that may increase the likelihood of persistence under dynamic environmental and ecological conditions.

Hierarchical scales and trade-offs in risk and forage for calving caribou

The importance of predation risk in the selection of calving strategies and calving sites by woodland caribou varied by predator and the scale of analyses. Minimizing bear risk was important in the selection of calving sites within calving areas, but not at the scale of the calving area (i.e., calving strategy). Caribou calved in areas with bear risk no different or higher than what was available in 2 of the 3 calving areas. The Foothills was the 'riskiest' area to calve and remain during the summer, as bear risk was higher and random locations within this area were closer to areas of high bear risk in both seasons. Within this high bear-risk strategy and in the North Prophet, however, calving caribou minimized the risk of bear predation by

selecting low-risk, high-elevation sites that increased the distance between calving sites and areas of high risk (Table 2.4). Although the risk of bear predation to caribou neonates has not been previously reported at the scale of the calving site or calving area, bears have been documented to be effective predators of caribou neonates (Ballard 1994; Adams et al. 1995; Young and McCabe 1997; Mahoney and Virgl 2003).

Components of wolf risk, in contrast, were generally important in the selection of calving strategies (Bergerud et al. 1984; Bergerud 1992), but not in selecting calving sites within those strategies. Calving strategies (except for the Foothills) were lower in wolf risk than what was found on the landscape, and all calving strategies were further than random to areas of high wolf risk during calving. Again, the Foothills was the 'riskiest' strategy, as it was higher in risk and closer to areas of high wolf risk than the other calving strategies during calving and summer. Our findings are consistent with previous research regarding the importance of minimizing the risk of wolf predation by woodland caribou (Bergerud et al. 1984; Bergerud and Page 1987; Seip 1991; Bergerud 1992; Bergerud 1996; Rettie and Messier 2000) and other ungulates (Bowyer et al. 1999) at larger scales. There was considerable variation, however, in wolf risk and distances to areas of high wolf risk (approx. 800-2,000 m) among calving strategies (Table 2.4); no calving sites within any calving strategy maximized distance from areas of high wolf risk within that strategy.

The importance of nutrient acquisition in the selection of calving strategies by caribou varied by forage characteristic and the scale of analyses. Avoiding areas of

high biomass appeared to be most important (Barten et al. 2001; Griffith et al. 2002). Caribou calved in areas low in biomass that increased their distance from areas of high biomass during calving and summer. The Foothills was higher in biomass and closer to areas of high biomass (approx. 400 m) than the other calving areas, and in some cases much closer (i.e., North Prophet, approx. 750 m) (Table 2.4). Within calving strategies, however, response to different levels of biomass was variable. Calving sites in the high-biomass strategy (i.e., Foothills) were relatively lower in biomass, while sites in a lower biomass strategy (e.g., Western High Country) were higher in biomass. The contribution of forage quality to the selection of calving strategies and calving sites was variable. The Foothills was higher in quality and closer to areas of high quality than the other calving strategies and the landscape. Conversely, the Western High Country was lower in relative quality and farther away from areas of high quality than random points on the landscape. The importance of relative quality was more apparent in the selection of calving sites (Griffith et al. 2002), which were higher in quality and closer to areas of higher quality than what was available in both low- and high-quality calving areas.

Calving caribou may have used topography to minimize risk or increase access to forage, as evidenced by the selection of certain topographical features of calving strategies and calving sites. Topography may increase separation (e.g., altitudinal separation) from predation and/or serve as a form of escape terrain (e.g., steep slopes) (Bergerud et al. 1984; Bergerud and Page 1987; Bergerud et al. 1990; Barten et al. 2001). Terrain in all the calving areas of our study was steeper and higher in elevation than what was available on the landscape, although elevation

varied among calving strategies. The high-risk strategy (i.e., Foothills) was lower (approx. 1,600 m) than the other calving strategies (approx. 1,870 m) (Table 2.4). Within the high-risk strategy, caribou selected calving sites higher in elevation than what was available within this strategy, whereas caribou in the lower risk areas showed no selection for higher elevations. In addition, variation in topography may have provided better micro-site characteristics for vegetation (Barten et al. 2001) because calving caribou in the Western High Country selected for gentler slopes than what was found within this strategy.

Variation and trends in the large-scale components of bear and wolf risk, topographical features, biomass, and relative forage quality among calving strategies and calving sites suggest that trade-off 'decisions' were made by caribou at several spatial scales. Avoidance of high biomass within calving strategies (Whitten and Cameron 1980; Bergerud et al. 1984; Heard et al. 1996), and selection for areas and calving sites high in relative quality (Bowyer et al. 1999; Barten et al. 2001), suggested that calving caribou foraged selectively in an attempt to address their nutritional requirements (Whitten and Cameron 1980) and minimize their risk (Barten et al. 2001; Griffith et al. 2002). All components of risk and forage were higher in the Foothills than the other calving areas, and based on these data, we assumed animals were taking an increased cost in risk for access to relatively higher biomass and/or quality. Calving caribou that used this strategy, however, did so at a higher risk, but not at a higher cost in risk per unit forage component. The relative cost in both bear and wolf risk per unit biomass was lower in the high-risk strategy than the other calving areas during calving, and there was no cost in increased risk

associated with foraging in areas with high relative quality (Table 2.5). In the high-risk strategy, caribou calved at sites low in biomass that increased the separation from areas of high biomass and this likely decreased the susceptibility of calving caribou and/or their calves to predation, as evidenced by cost in the risk of predation per unit biomass (Bowyer et al. 1998; Bowyer et al. 1999). Non-parturient and male caribou and moose are known to forage in areas higher in biomass and at lower elevations than parturient caribou; avoidance of these areas, therefore, was likely in response to the presence of conspecifics, other ungulates, and/or predators (Bergerud et al. 1984; Bergerud and Page 1987; Seip 1991; Barten et al. 2001). Parturient caribou probably foraged selectively in areas of high quality to address the nutritional requirements of lactation while avoiding areas of high biomass to minimize the risk of predation (Barten et al. 2001; Griffith et al. 2002). The high-risk strategy also increased opportunities for caribou to calve in sites with access to, or that were in, high-quality areas with no increase in risk per unit quality. We recorded no early predation mortalities (<14 d) in this strategy, and our data do not support observations that caribou disperse to calve regardless of vegetative phenology (Bergerud et al. 1984; Bergerud and Page 1987). Alternatively, in the Western High Country, calving caribou selected calving sites that were relatively higher in biomass and quality in a strategy that had the highest cost in wolf risk per unit biomass. Most of this area is unsuitable (i.e., largely non-vegetated with steep and rugged terrain) for large, productive areas of vegetation, so caribou calved at sites in hanging valleys, and did so at a high cost in risk per unit forage component within that calving area. Additionally, in the North Prophet, calving caribou did not select sites lower in

biomass or wolf risk even though cost in risk for biomass was high; rather, caribou selected non-vegetated, high-elevation calving sites that were low in bear risk and that increased separation from areas of high biomass. In this area, minimizing the risk of bear predation appeared to be more important than minimizing wolf risk; our models may actually have underestimated bear risk because this area was at the northern extent of the bear GPS data.

Predictions of calf survival

Despite the spatial variation in the risk of predation, forage, and cost characteristics, survival of caribou calves and cause-specific mortality did not differ among calving strategies. There appears to be no proximate benefit(s) (i.e., higher birth weights, and/or increased survival through summer) of calving in one strategy over another. Models using small- and large-scale characteristics of calving sites, however, performed well in predicting survival of calves during calving and summer, respectively.

Herbaceous and shrub cover were excellent predictors of early calf survival, with cover of shrubs increasing the odds of survival (approx. 13% per 1% increase in shrub cover) through the calving season (Table 2.3). Deciduous shrubs, primarily in the form of willow and bog birch, could obscure neonates from the view of predators (Bowyer et al. 1998; Bowyer et al. 1999; White and Berger 2001) and/or be an important spring forage for parturient caribou (Boertje 1984; Ferguson et al. 1988; Crête et al. 1990a). The role of herbaceous cover in decreasing the survival of caribou calves was less clear. Herbaceous and shrub cover were inversely

correlated, but this relationship may have been confounded by measurements at different scales (i.e., plot versus line-intercept data). It is possible that the influence of shrubs on calf survival was an effect of calving strategy, because the Foothills had higher cover of shrubs than the other calving strategies and only one mortality during calving (age of calf = 14 d); the large-scale model with calving area as a covariate, however, did not perform well in predicting survival of calves for any season. Cliffs may be important refugia for calving caribou from terrestrial predators, but models with cliff-intercept data could not be evaluated because no mortalities occurred at sites near (<50 m) these topographical features. The poor model performance of small-scale characteristics in predicting calf survival through summer suggested that either the importance of small-scale characteristics of calving sites in calf survival diminished during the summer and/or that other factors (e.g., movement away from calving sites) became more important for calf survival.

Large-scale characteristics of calving sites were not good predictors of caribou calf survival; this is not surprising given the cause-specific mortality data. Calving strategies appeared to have a high risk of wolverine predation during calving, as the first increase in mortality was caused by wolverines with eagles and bears to a lesser extent (see Fig. 2.3a and 2.3b). Consequently, the influence of bear and wolf risk was not important in our models predicting early calf survival. Wolverines are known to range over large areas, use a variety of habitats (Whitman et al. 1986), and commonly feed on reindeer (*Rangifer tarandus*) during the denning period in Norway (Landa et al. 1997; Vangen et al. 2001). Although data on densities and diets of wolverines in the northern Canadian Rockies are currently

lacking, anecdotal evidence from the GBPA suggested that it was productive wolverine habitat.

Movement was an important variable in our models to predict survival of calves in the summer. Twenty-one cow-calf pairs left the calving sites when calves were 2-4 weeks of age (Fig. 2.3a). Movement away from calving sites significantly increased the odds of calf survival (approx. 196% when other covariates were held constant). The reasons for these movements were not clear, but the timing of movements suggested that caribou may have responded to changes in vegetation, nutritional demands, and/or risk at smaller temporal scales than those measured in our risk and forage models. Greening of vegetation and timing of change in vegetative phenology are important attributes of forage quality for parturient caribou (Oosenbrug and Theberge 1980; Post and Klein 1999; Griffith et al. 2002; Post et al. 2003). The first peak of movement followed an increase in mortality (Fig. 2.3a and 2.3b) that corresponded with the time of high nutritional demands for lactation (White and Luick 1984) and the time when lactating females experience their worst condition of the year (Chan-McLeod et al. 1999), and, therefore, movement may have been in response to changes in vegetation within calving areas. In a mountainous environment, vegetative change is likely to vary both spatially and temporally among vegetation types, aspects, and elevations (Reed et al. 1994). Our index of forage quality was based on areas of vegetation that experienced the largest amount of growth from the calving to summer season, but we can offer no estimate as to the rate or timing of that growth; the relationship of the change in NDVI and forage quality at smaller temporal scales remains an open area for

research (R. Lay and D. Gustine, University of Northern British Columbia, unpublished data). Caribou likely responded to the change in vegetative phenology as it happened (i.e., at a temporal scale smaller than the seasonal scale) (Oosenbrug and Theberge 1980; Post and Klein 1999; Barten et al. 2001; Griffith et al. 2002; Post et al. 2003). Nonetheless, caribou calved in areas (Foothills) or at sites (i.e., Foothills, Western High Country) near, or in, these areas of high vegetative change between seasons.

A second extended peak in movement (i.e., 8 cow-calf pairs left the calving site) occurred during weeks 5-7 (Fig. 2.3a and 2.3b) following an increase in caribou calf mortality. This timing appeared to coincide with the ability of wolves to leave the dens and, subsequently, a possible change in prey species in the diet (B. Milakovic, University of Northern British Columbia, unpublished data). Indeed, survival for caribou calves was higher through calving than summer; wolves were responsible for 5 of the 8 identified mortalities in the summer season (Fig. 2.3b). The risk of wolf predation increased and the distance to areas of high wolf risk decreased in all the calving areas from the calving to summer season. Nonetheless, calving strategies of woodland caribou were relatively successful in minimizing losses of neonates to wolves during calving compared to other predators even though risk of wolf predation was dynamic in the GBPA. Wolf predation has been identified as an important factor in survival of caribou calves, particularly for neonates (Gasaway et al. 1983; Bergerud et al. 1984; Bergerud and Elliot 1986; Bergerud and Page 1987; Seip 1992; Adams et al. 1995).

Caribou started to form post-calving aggregations (approx. 20-40 cows and

calves) in the Foothills and North Prophet calving areas at the end of June; this grouping behavior is contrary to observations by Poole et al. (2000), but similar to Bergerud et al. (1984). Concurrently, there was an increase in the cost in both bear and wolf risk associated with forage quality in all calving strategies from the calving to summer season (Table 2.5), which suggested that wolves and bears could be responding to caribou as a more predictable prey item (i.e., larger groups) (Hebblewhite and Pletscher 2002) or were actively searching these areas of high vegetative change for other prey. Bears may be feeding on vegetation in these areas of high change (Nielsen et al. 2003), so this relationship was less clear; nevertheless, cost in bear predation per unit forage quality increased for caribou foraging in areas with high relative quality. Alternatively, the gregariousness of caribou in late June could be a social response to the increased risk of wolf predation within the calving areas (Bøving and Post 1997; Barten et al. 2001; Hebblewhite and Pletscher 2002), as a caribou with a calf could minimize the risk of predation by decreasing the chances of being selected from the group (Hamilton 1971), while simultaneously foraging in areas with higher forage biomass and/or relative forage quality (Molvar and Bowyer 1994; Bowyer et al. 1999; Kie 1999).

Implications to understanding successful calving strategies

The interpretation of our data was dependant on the spatial scale of analyses. Analyses of characteristics of all calving sites versus characteristics of random points on the landscape provided some information on large-scale processes that caribou may have responded to, but more often, these pooled analyses collapsed

important variation in risk and forage characteristics. Conclusions from analyses at the 'landscape' scale would have failed to provide insights into how animals responded to risk, forage, and topography in a hierarchical fashion at smaller spatial scales. Our definitions of the 'landscape' and calving areas may have confounded analyses. We acknowledge that processes important to life-history requirements of caribou and their predators are not constrained within the boundaries of the GBPA and/or our 'defined' calving areas. Indeed, a few collared bears and a collared caribou calf did leave the study area; collared caribou, wolves, and bears moved among calving areas. Historical telemetry data (adult caribou, wolves, and bears) and 2 yrs of extensive observations (calving caribou), however, provided good information on the distribution and social structure of animals in the GBPA, and these data were used to identify important areas for capturing and collaring efforts.

The assumption that bear and wolf GPS data were representative samples of animal locations has some limitations. Fix-rate bias in GPS data has been reported for areas with varied topography or cover types (Dussault et al. 1999; D. Heard, British Columbia Ministry of Water, Land, and Air Protection, unpublished data), particularly when fix rates are low (<90%). This bias may have led to an under- or overestimate in the selection of any individual resource by wolves and bears, which would subsequently increase Type I (overestimated selection) and/or II (underestimated selection) error rates (Frair et al. 2004). Our ability to detect whether risk was actually 'the same' between years was reduced because fix rates for wolves and bears were <90%. The responses of calving caribou to modelled risk, however, were similar, with some exceptions, to what has been observed,

quantified, or postulated in other studies (Bergerud et al. 1984; Bergerud and Page 1987; Bergerud et al. 1990; Bergerud 1992; Seip 1992; Barten et al. 2001). The timing of calf mortality coincided with an increase in modelled wolf risk in all of our calving areas. Our results suggest that modelling risk with RSFs is a valid technique in evaluating predator-prey interactions at large spatial scales, and may become more useful as bias in GPS fix rate is identified and corrected.

Low power was also a concern in the use of nonparametric tests, because these tests usually have lower power than their parametric counterparts (Siegel 1956); this reduced discussion of the 'indifferences' in the attributes of risk and forage among calving strategies and at calving sites within calving strategies. Transformation of the data was a possibility, but we wanted to avoid further manipulation of modelled data. The conservative nature of nonparametric tests (i.e., higher P) may have helped to address some concerns of cumulative error throughout the modelling process, although error terms for RSFs integrated with raster and vector GIS and GPS data are difficult to quantify and remain a topic for future research (Corsi et al. 2000).

We may have misinterpreted the responses of parturient caribou to modelled risk. As in Johnson (2000), we can estimate animals' responses only to actual and/or perceived risk (Lima and Dill 1990). Additionally, what we perceived as responses to predation risk may have been responses to the primary prey of wolves and/or bears (Johnson 2000). We submit that our models of risk tracked relative risk in the GBPA at the seasonal scale, but, how caribou 'measured' this risk is uncertain. We do not know if caribou were actively reducing their risk of predation or

simply experiencing a reduced risk (Johnson 2000). Responses to risk may be a product of social learning (Lima and Dill 1990; Caro 1994; Byers 1997; Miller 2002), individual experience (Lima and Dill 1990), visual and/or chemical cues (Kats and Dill 1998), and/or 'luck'. Nonetheless, the predictable fashion in how animals responded to components of risk within calving areas (e.g., minimized bear risk in an area with high bear risk) and on the landscape suggested calving caribou were sensitive to parameters of risk among spatial scales.

Despite these concerns, our results confirm the importance of predation and forage characteristics on the distribution of calving caribou. Parturient caribou generally selected for areas high in relative quality (i.e., vegetated areas with high change in NDVI) and data were consistent with research that has examined the importance of forage quality at large (Griffith et al. 2002) and small scales (Barten et al. 2001). Lowering wolf risk and the ability of caribou to 'space out' from wolves was important in selection of all calving strategies (Bergerud et al. 1984), although variation in the components of risk was high among strategies. In all calving areas, caribou used small-scale features (e.g., cliffs, shrub-cover, steeper slopes), movement, and/or possibly gregariousness (Molvar and Bowyer 1994) to minimize the risk of predation and 'cope' with the increase in wolf risk from calving to summer. Small-scale features and movement had prominent effects on calf survival through calving and summer, respectively. A more precise measure of movement combined with measures of risk and forage characteristics at smaller temporal scales could provide further insights into important mechanisms defining woodland caribou-wolf interactions in a multi-predator multi-prey system.

Plasticity by caribou was high among calving strategies, and although our data showed no proximate benefits to any one calving strategy, there may be factors that maximize reproductive fitness. Characteristics of forage affected the level of risk that caribou 'took' within a calving strategy. The high-risk strategy offered caribou more opportunities to forage in areas of high quality, and possibly high biomass later in the summer. These characteristics could have increased the rate of weight gain in calves through the summer and allowed the dam to replenish body reserves (Reimers et al. 1983; Crête et al. 1990*b*), following the nutritional demands of lactation, necessary for breeding and over-winter survival. Consequently, an improved condition in autumn could have direct effects on reproductive fitness and possibly increase calf survival through winter (Dauphiné 1976; Cameron et al. 1993; Adams and Dale 1998*a,b*; Cook et al. 2003). Benefits of the lower risk strategies were less apparent, as survival did not differ from the high-risk area. The persistence of these strategies, however, suggests that these areas could become more important as ecological conditions change (e.g., changes in ungulate and/or predator distributions and densities) (Bergerud 1983; Bergerud et al. 1984; Bergerud and Elliot 1986; Dale et al. 1994; Bergerud and Elliott 1998).

Diversity of vegetation, topography, and large mammals in the GBPA offered caribou a diversity of 'choices' among scales. Mechanisms (e.g., social learning, (Caro 1994; Byers 1997), nutritional condition (Lima 1988; Boertje 1990; Clark 1994; Sweitzer 1996)) that may, or may not, 'drive' selection of a risk-averse or risk-prone calving strategy (Stephens and Krebs 1986) remains an important area for research. In particular, there is a need to identify the effect(s) of a calving strategy on

physiological parameters of calving caribou and their offspring as well as on calf survival through winter. Current technologies and methodologies (e.g., remotely sensed data and indices of vegetative change, GPS telemetry, RSFs, ultrasound estimates of body fat, stable isotope ecology) are likely to improve and may assist in identifying physiological and/or ecological conditions that 'drive' woodland caribou to 'select' areas to calve, and the subsequent effects on reproductive fitness.

Plasticity as a life-history strategy during calving and summer is likely to be successful as long as caribou have 'choices' on the landscape. If woodland caribou have fewer choices at large scales, they may become more predictable in space and time for their main predators and have difficulty meeting nutritional requirements, with possible consequences to survival, reproductive success, and, ultimately, population persistence. 'Choices' available to woodland caribou at large scales appear to have a direct impact on how animals use smaller scale features to maximize access to forage and/or minimize risk (Rettie and Messier 2000; Johnson et al. 2001; Johnson et al. 2002a,b). Sensitivity of woodland caribou to the direct and indirect effects of anthropogenic (Bradshaw et al. 1997; Stuart-Smith et al. 1997; James and Stuart-Smith 2000; Dyer et al. 2001; Weclaw and Hudson 2004) and environmental disturbances (Schaefer and Pruitt 1991; Joly et al. 2003) has been well documented. Management or industrial activities that alter the distribution of caribou during calving and summer should be avoided until they can be evaluated for possible long-term effects on population productivity. This will become increasingly important as weather patterns, which may affect the availability of forage (e.g., altering the timing of spring snows and/or greening of vegetation; Post

and Klein 1999; Lenart et al. 2002; Weladji and Holand 2003; R. Farnell, Yukon Government, Department of Environment, pers. comm.) and/or the ability of calving caribou to disperse from areas of high risk (Bergerud et al. 1984; Bergerud and Page 1987; Bergerud et al. 1990; Seip 1991), become more unpredictable and could have direct and indirect consequences to the survival of woodland caribou neonates.

CHAPTER 3: INTERPRETING RESOURCE SELECTION BETWEEN SCALES AMONG INDIVIDUAL WOODLAND CARIBOU IN WINTER¹

ABSTRACT

Resource selection functions (RSFs) are commonly used to identify areas and/or mechanisms important to large herbivores. Defining availability of resources is scale-dependant and may limit inference on biological mechanisms of selection, particularly if variation in selection of resources among individuals within a population is high. We used logistic regression, the information-theoretic approach, and global position systems (GPS) data from 10 woodland caribou (*Rangifer tarandus caribou*) and 5 wolf (*Canis lupus*) packs to model resource selection by individual animals in the winter and late winter seasons. We evaluated the influence of spatial scale on the relative importance of cost of movement and components of predation risk. We examined the attributes of the risk of wolf predation within availability data at 2 spatial scales, and quantified variation in resource selection among individual caribou to determine the appropriateness of using selection models from data pooled across individuals. Energetic cost of movement was the most important covariate for all caribou at a spatial scale defined by seasonal movement, whereas increasing distance to areas of high wolf risk was more important at the larger spatial scale of home range. Variation was high in the

¹A version of this chapter will be submitted for publication with the following authorship: Gustine, D. D., K. L. Parker, M. P. Gillingham, and D. C. Heard.

selection of resources among caribou, although commonalities among individuals facilitated pooling use/available data into 2 selection strategies. We caution that using pooled models to define areas important to large herbivores and to infer biological mechanisms for selection should be done only after variation among individuals is quantified.

INTRODUCTION

Evaluating mechanisms in ecological processes may be confounded by the influence of both spatial and temporal scales (Johnson 1980; Wiens 1989; Levin 1992). Animals typically respond to environmental factors in a hierarchical fashion (Johnson 1980; Senft et al. 1987; Schaefer and Messier 1995; Johnson 2000; McLoughlin et al. 2002), and therefore, inferences on ecological mechanisms are likely to vary with the scale of analyses (Wiens 1989; Danell et al. 1991; Johnson 2000). Problems that add further complexity to the issue of scale are that the selection of resources may vary among individuals by age (Nielsen et al. 2002), sex (McLoughlin et al. 2002), and/or reproductive condition (Rachlow and Bowyer 1998) within a population (Aebischer et al. 1993; Garshelis 2000; Nielsen et al. 2002) and that the variation in the selection of habitats among individuals (i.e., plasticity) may be an important life-history trait for the species (see Chapter 1; Bowyer et al. 1999). Factors that influence selection of habitats by ungulates include year (Wood 1996), time of year (i.e., season, Apps et al. 2001), forage abundance and/or availability (Schaefer and Messier 1995), cover (Boyce et al. 2003), anthropogenic disturbance (Nellemens and Cameron 1998), energetic cost of movement (Johnson 2000), and/or

the risk of predation (Lima and Dill 1990; Bowyer et al. 1998; Kie 1999). Factors may vary in relative importance across scales (Wiens 1989) with those most limiting to individual fitness possibly important at coarser scales (Rettie and Messier 2000).

Resource selection functions have been used to identify and model characteristics of areas that are selected and inferred as important to ungulate populations at a variety of scales (Schaefer and Messier 1995; Poole et al. 2000; Rettie and Messier 2000; Apps et al. 2001; Boyce et al. 2003; Johnson et al. 2004). The RSFs are often defined using logistic regression in use versus availability designs (Boyce and McDonald 1999; Boyce et al. 2002; Manly et al. 2002). Because availability is commonly limited to the study area (McClellan et al. 1998) or home range(s) of a population (Johnson 1980), inferences are typically made relative to the selection of resources by a population, and rarely on the selection of resources by individuals (Aebischer et al. 1993) within that population (i.e., Type I or II versus Type III design, Thomas and Taylor 1990), particularly for large mammals (Nielsen et al. 2002). Defining availability as the study area, or as the sum of the availabilities of individual animals, to model selection across animals may provide good predictive models of animal distribution (Boyce et al. 2003), but could be limited in delineating mechanisms of resource use, particularly if variation in resource selection is high among individuals (Aebischer et al. 1993; Manly et al. 2002; Nielsen et al. 2002). Johnson et al. (2002a,b) suggested using parameters of movement to define availability for woodland caribou because movement events (i.e., migration, and intra- and inter-patch movements) could provide insights into scale-dependant mechanisms of selection and future research should be conducted

at multiple scales to identify important habitats. Management agencies, however, frequently have limited resources and/or locational data to conduct multi-scale analyses, and therefore, recent research has attempted to ascertain the 'best' scale of analysis in predicting habitats important to large herbivores (Apps et al. 2001; Boyce et al. 2003). Although a 'best' scale is unlikely to exist for examining mechanisms that underlie selection behavior(s) (Wiens 1989), some scales, particularly the patch scale (i.e., Johnson's (1980) third order of selection), and corresponding definitions of availability (i.e., home ranges) may be more appropriate and/or useful to managers. Woodland caribou are an excellent species to evaluate the importance of different covariates in resource selection at different scales, the interaction between scale and definitions of availability, and the variation in the selection of resources among individuals. Caribou require large areas to over-winter (Cumming 1992; Zimmerman et al. 2002), exhibit scale-dependant responses to habitat factors (Apps et al. 2001; Johnson 2000; Poole et al. 2000; Rettie and Messier 2000; Mosnier et al. 2003), and appear sensitive to physiological (e.g., energetic costs of movement, Gerhart et al. 1996; Johnson et al. 2002a) and ecological parameters (i.e., risk of predation; Bergerud et al. 1984; Bergerud and Elliot 1986; Seip 1991, 1992; Bergerud 1992; Johnson et al. 2002a).

Woodland caribou move on the landscape to capitalize on habitat components that provide welfare factors (Cumming 1992). The northern ecotype of woodland caribou in British Columbia (Heard and Vagt 1998) over-winters in wind-swept alpine areas (Cichowski 1993; Wood 1996), low elevation pine-lichen stands when snow depths are low (Johnson 2000; Zimmerman et al. 2002), or intermediate

to high-elevation spruce-fir forests (Cichowski 1993; Poole et al. 2000). Sizes of winter home ranges and movement rates vary among regions and individuals, and are largely dependant on the types of available habitats and the scale of analyses (Wood 1996; Poole et al. 2000; Johnson et al. 2002*a,b*). Minimizing energetic costs in winter may be important for female caribou moving among patches, often in areas with a high risk of predation (Johnson 2000). The importance of minimizing costs may be influenced by body condition. Data show that non-pregnant females have lower fat reserves than pregnant animals (Dauphiné 1976; Appendix H); this difference in body condition may affect movement rates and the availability of resources, and, subsequently, resource selection.

Woodland caribou appear sensitive to distribution of other ungulates and wolves during the winter (Bergerud 1992; Seip 1992; Cumming et al. 1996; James 1999; James and Stuart-Smith 2000; Johnson et al. 2002*a*). Increased densities of caribou often stimulate a functional response in wolf populations (Bergerud and Elliot 1986; Seip 1991; Bergerud 1992; Dale et al. 1994). Dispersal by caribou over large areas is thought to be an effective life-history strategy against wolf predation during all times of the year (Bergerud 1992; James 1999), and may play a role in survival (Seip 1992; Wittmer 2004). By increasing the distance between conspecifics, other ungulates (e.g., moose (*Alces alces*)), and wolves, dispersal by individuals increases search time and lowers encounter rates for wolves, therefore decreasing hunting efficiency (Bergerud et al. 1984; Bergerud and Page 1987; Cumming et al. 1996; James 1999; Barten et al. 2001).

The goal of this study was to identify habitats and ecological parameters

important to female woodland caribou during the winter (November-February) and late-winter seasons (March-April) in a multi-predator multi-prey ecosystem in north-central British Columbia. Our objectives were 1) to identify the relative importance of the cost of movement, the risk of predation, and the distance to areas of high risk for pregnant and non-pregnant animals at a relatively small spatial scale defined by seasonal movement, 2) to identify the consequences of defining availability at the scale of seasonal movements versus the relatively large seasonal home range on the importance of the components of predation risk, 3) to quantify the variation in the selection of resources among individual caribou at the management-oriented scale of the seasonal home range, and identify common selection strategies among individuals, and 4) to qualitatively evaluate the utility of resource selection models pooled across individuals compared to individual models for collared caribou.

STUDY AREA

The Greater Besa Prophet area (GBPA) (approximately 741,000 ha) is part of the 6.2 million-ha Muskwa-Kechika Management Area in northern British Columbia and is located between 57°11' and 57°15' N latitude, and 121°51' and 124°31' W longitude. A detailed description is provided in Chapter 2:16 (see Fig. 2.1).

METHODS

Animal capture and locational data

Twenty-five adult female caribou and 23 wolves from 6 packs were captured

and fitted with GPS collars (Simplex, Televilt, Lindesberg, Sweden) in November-December 2001. Collars were programmed to acquire locations every 6 hrs for 2 yrs. Previous telemetry data on wintering areas of female caribou and territories of wolf packs in the GBPA were used to target areas for animal capture. Caribou were captured from a helicopter (Bell 206) using a net-gun. We took blood samples to determine reproductive condition of caribou via serum progesterone concentrations (Prairie Diagnostics Services, Saskatoon, SK, Canada).

GPS data were recovered via remote download or by collar retrieval. Data on individual caribou were included in analyses if there were locational data from the date of capture to the date of download. All GPS data were screened for erroneous easting and/or northing coordinates (i.e., points beyond realistic animal movement between successive locations as defined by biological and/or statistical significance (D'Eon 2002) and dilution of precision >25) which were removed from analysis using a spatial analysis program (M. Gillingham, University of Northern British Columbia). Fix rate per caribou (i.e., per GPS collar) was defined as the number of quality fixes (i.e., fixes that met aforementioned criteria) acquired from capture to the end of the late winter season divided by the total number of possible fixes within that time period. Caribou locations acquired on the day of and after capture were not included in analyses because preliminary analyses suggested movement rates immediately post capture tended to be atypical.

Movement rates (m/hrr) of caribou and changes in environmental conditions from November to April were used to define 2 caribou seasons: winter (November-February) and late winter (March-April). Movement rates per individual (i.e.,

distance between consecutive 6-hr fixes) were averaged by month and then averaged across individuals for a pooled estimate of monthly movement rate; n for the SE was the number of caribou.

We used movement rates and seasonal home ranges to define availability of resources for individual caribou and wolf packs. Availability was defined at 2 scales for caribou, both within Johnson's (1980) third order of selection: seasonal movement and seasonal range. Seasonal movement was an individual caribou's potential for movement within a season. Movement potential was a circle, centered on each use point (i.e., a GPS location), with a radius equal to the distance determined from the 95th percentile movement rate for 6-hr fixes; 5 points for availability locations were randomly selected within this distance from the use point. A seasonal range was the home range, as defined by a 100% minimum convex polygon (MCP) (Mohr 1947), of an individual caribou for that season, 'buffered' by the movement potential distance. Resource availability for each wolf pack was also defined using 100% MCPs for each pack by caribou season (i.e., winter and late winter). MCPs were estimated using the animal movement extension (Hooge et al. 1999) in Arcview 3.2 (Environmental Systems Research Institute, Redlands, CA, USA) and MCPs and GPS data were 'clipped' to the boundaries of the GBPA. All but one of duplicate wolf locations (i.e., same date and time) within a pack were randomly removed to address issues of independence. Five availability points per use point were randomly selected within each MCP for each wolf pack and individual caribou using the random point generator extension (Jenness 2003) in Arcview 3.2 (Environmental Systems Research Institute, Redlands, CA, USA).

Inputs to resource selection models for caribou

Vegetation, Topography, and Distance to Linear Features

Vegetative and topographical covariates in resource selection model sets for caribou and wolves were 25-m resolution raster geographic information system (GIS) data. A digital elevation model (DEM) was obtained from the 1:20,000 British Columbia Terrain and Resource Inventory Management program (Ministry of Crown Lands 1990); this dataset was used to create the slope ($^{\circ}$) and aspect layers. For wolves, aspect was categorized into north ($316-45^{\circ}$), east ($46-135^{\circ}$), south ($136-225^{\circ}$), and west ($226-315^{\circ}$) directions to address problems with northerly values having the same aspect but different values (0° and 360°); pixels with slope $\leq 1^{\circ}$ were assigned no aspect. For caribou, aspect was maintained as 2 continuous variables to minimize issues of perfect separation; these were northness (i.e., $\cos(\text{aspect})$) and eastness (i.e., $\sin(\text{aspect})$) (Palmer 1993). Northness values of 1.00 and -1.00 suggest selection for north and south aspects, respectively, while values near 0.00 suggest selection for east and west aspects. Eastness values show selection for east (i.e., 1.00) and west (i.e., -1.00) aspects; values of 0.00 show selection for northern/southern exposures (Palmer 1993). Vegetation classes were identified using an August 2001 Landsat Enhanced Thematic Mapper image (R. Lay, University of Northern British Columbia, unpublished data). Fifteen vegetation classes with a minimum mapping unit of 75 x 75 m were combined into 9 classes to allow for accuracy levels $>80\%$ and complete separation in logistic regression models, while maintaining biologically important differences (Appendix B: Table B.1, Fig. B.1). These classes were spruce, shrubs, subalpine, *Carex* spp., non-

vegetated, pine, riparian spruce, alpine, and burned/disturbed. Measures of vegetative diversity or juxtaposition also may be an important component of resource selection (Johnson 2000). Therefore, we created an index of vegetation fragmentation from grouped vegetation cover types representing fragmentation as closed, open, or unique cover types as in Chapter 2:30-31. Because linear features may be important travel routes for wolves in winter (James and Stuart-Smith 2000), we created a distance to linear features layer as in Chapter 2:30.

Risk of Predation and Distance to Areas of High Predation Risk

Predation risk to caribou was quantified using logistic regression to form resource selection functions that identified habitats important to wolves in the GBPA from 1 November 2001 to 30 April 2002. The models incorporated wolf GPS data, elevation (km), categorized aspect, slope ($^{\circ}$), vegetation, distance to linear features (km), and the index of fragmentation. Risk of predation was defined as the probability of being killed during a season (Lima and Dill 1990); assumptions were as in Chapter 2:28. Ecologically plausible RSF risk models (Appendix C.4) were developed to define predation risk and distance to habitats with a high risk of predation from each wolf pack by season. We calculated coefficients of selection (i.e., beta coefficients, β_i) using logistic regression (Manly et al. 2002), and identified the most parsimonious models, as in Chapter 2:31-32. Nine RSFs were formed to define risk by wolf pack and season (winter and late winter).

Estimated Costs of Movement for Caribou

We used the change in elevation and the distance between use and available points to model the energetic cost of movement (kJ/kg/hr) by female caribou across variable terrain (Johnson et al. 2002a). Cost of movement was estimated from equations developed by Fancy and White (1987), ignoring snow depth or slope because the time between fixes (i.e., 6 hrs) probably allowed access to numerous microsite conditions. Therefore, these equations underestimate actual cost because topography and snow depths are extremely variable across the GBPA. The DEM (Ministry of Crown Lands 1990) was used to determine if a caribou moved uphill, horizontal, or downhill from one location to another; therefore, 'use' cost was from use location_x to use location_{x+1}, and 'available' costs were from use point_x to each of the 5 available points within the potential for movement distance around use point_x. The cost of locomotion for moving uphill (3.640 kJ/kg/km), on a horizontal surface (1.722 kJ/kg/km), or downhill (1.293 kJ/kg/km) was multiplied by the distance (km) between points divided by the duration of time between GPS fixes to give an estimate per unit time (kJ/kg/hr).

Relative importance of covariates and scale

Logistic regression and Akaike's Information Criterion for small sample sizes (AIC_c) were used to form RSFs that identified habitats important to individual female caribou in the GBPA from 1 November 2001 to 30 April 2002. All variable coding, and model estimation, selection, averaging, and assessments of inputs were as in the predation risk models, except for a stricter evidence ratio (E_r) criterion (<2) and

less stringent tolerance score threshold (<0.20) (Burnham and Anderson 2002; Menard 2002). For all caribou, elevation (km) and the risk of wolf predation were entered as quadratic (i.e., linear and squared terms) and linear terms, respectively. The effects (i.e., linear versus Gaussian or bell-shaped) of slope ($^{\circ}$) and the distance to areas of high wolf risk (km) were evaluated for each individual caribou by examining the change in AIC_c after adding or removing the squared term of the quadratic; if the addition of the quadratic term to the saturated model decreased AIC_c , then the variable was entered as a squared term. Vegetation classes that were rare or did not occur in use and/or available data were not included in model formulation.

We evaluated the relative importance of the risk and cost covariates at the scale of seasonal movement and the risk covariates at the scale of the seasonal range by examining Akaike weights (w_i) after the addition of these covariates to a core model set (Burnham and Anderson 2002). High w_i (i.e., the likelihood of the model given the data and other models in the set) and a lower AIC_c suggest the model 'improved' by the additional information provided by the covariate(s), whereas a lower w_i and higher AIC_c suggest the information from the covariate(s) was redundant (Burnham and Anderson 2002). We evaluated 9 ecologically plausible 'core' models that included elevation (km), aspect (i.e., northness and eastness), slope, vegetation, and the index of fragmentation. The risk of predation, distance to areas of high wolf risk (km), and cost of movement (kJ/kg/hr) covariates were added individually to each model in the core set for each caribou by season. At the scale of seasonal range, we added only the risk covariates, as cost could not be evaluated

effectively at this scale. The complete model set (core models plus the cost, risk, and distance to areas of high risk covariates) for each caribou, season, and scale was evaluated in the same manner as the predation risk models. We estimated the relative importance of covariate_{*j*} (i.e., cost, risk, or distance to areas of high risk) by summing the w_i across all models for individual caribou by season where covariate_{*j*} was included in the model ($w_+(j)$, Burnham and Anderson:168); the larger the $w_+(j)$, the more important covariate_{*j*} was relative to the other covariates (Burnham and Anderson 2002:168). We averaged $w_+(j)$ across caribou by season ($\overline{w_+(j)}$) to evaluate the relative importance of covariate_{*j*} among all caribou.

To examine the importance of the risk components at both scales in reference to the core model set, we calculated the change in AIC_c (Δ_i) when covariate_{*j*} was added to the 'best' core model for each caribou by season and scale; we then averaged the Δ_i when covariate_{*j*} was included in the model across animals within a season and scale ($\overline{\Delta_i}$). We used frequency histograms and t-tests (Zar 1998) to compare the attributes of the available risk and distance to areas of high risk data between scales (i.e., seasonal range and seasonal movement) by season for each individual caribou.

Quantifying variation in the selection of resources among individuals

Resource selection by individual caribou was determined from the most parsimonious models that performed the 'best' at the scale of the seasonal range (i.e., defined by the \bar{r}_s from the k-fold cross-validation for each individual caribou by season (Boyce et al. 2002)). We used the scale of seasonal range because 1) this

is the scale most commonly used by management agencies, 2) all covariates can be easily transferred to habitat maps, and 3) selection at larger spatial scales is typically easier to detect (McClellan et al. 1998; Apps et al. 2001); therefore, models at the larger scale (i.e., without energetic cost) should enable easier classification of resource selection strategies among individuals. The Wald's statistic was used to determine if the β_i differed from zero, which identified significant selection ($\beta_i > 0$) or avoidance ($\beta_i < 0$) of a resource (Boyce and McDonald 1999; Manly et al. 2002); we defined avoidance as negatively selecting a resource. Selection coefficients of the 'best' model(s) that differed from zero were evaluated graphically for similarities (i.e., value and sign of β_i) among caribou within and between seasons. We used a log-linear model, as in predation risk, to estimate RSFs for each individual caribou by season. To facilitate comparisons among caribou, however, we scaled the RSFs from 0-1 using the following equation:

$$RSF_{0-1} = \frac{RSF_i - RSF_{min}}{RSF_{max} - RSF_{min}}$$

where RSF_i is the product of the log-linear model, and RSF_{min} and RSF_{max} are the smallest and largest RSF values (Boyce and McDonald 1999). Values approaching 1.0 indicated a greater likelihood of selection of a resource by caribou, while values nearing 0.0 indicated avoidance. RSF_{0-1} values were plotted as a function of use data for continuous covariates (i.e., elevation, slope, and distance to areas of high risk) using the 'best' model for each caribou by season while other covariates in the model were held constant. We qualitatively compared β_i s different from zero among caribou and pooled models by season for aspect and fragmentation.

Selection and avoidance of vegetation classes were examined graphically among animals by counting the number of animals that showed significant selection or avoidance of a vegetation class; avoidance included classes of vegetation with >30 available points and no use data (i.e., classes that were not included in resource selection models due to concerns of complete separation). If selection or avoidance of resources was similar among animals within a season, use and availability data were pooled (Nielsen et al. 2002) and models were re-evaluated (i.e., most parsimonious models identified, selected, validated, and averaged if necessary). Pooled models were validated with the k-fold cross-validation (Boyce et al. 2002), and covariates from the 'best' model(s) were compared graphically to individual models by season; all variables, other than vegetation, were evaluated as outlined above, while β_i s from the pooled model(s) for vegetation were compared with the number of animals that showed significant selection or avoidance of a vegetation class. Significance of all tests was assumed at $\alpha = 0.05$, and Stata 7.0 was used for all statistical procedures (Stata Corporation, College Station, TX, USA).

RESULTS

Reproductive condition of caribou, collar performance, and movement

Of the 25 animals captured and collared, 24 were adults; 22 of 24 adult caribou were pregnant ($91.7 \pm 5.8\%$, $\bar{x} \pm \text{binomial SE}$). Eleven of the 25 GPS collars on female caribou functioned as programmed from date of capture to 30 April 2002, but because >90% of the locations for one animal was east of the GBPA, we used data for 10 individuals in our analyses; the 2 non-pregnant individuals were in

that sample. After screening the GPS data for quality of locations, 3,254 (552 for non-pregnant animals) and 2,123 (452 for non-pregnant animals) data points were analyzed for female caribou during winter and late winter, respectively. Fix rates were high ($91.3 \pm 2.1\%$, $\bar{x} \pm SE$) with 7 collars acquiring fixes $>92\%$ of the time and 3 collars $>80\%$.

Movement rates were highly variable within and among individuals at all temporal scales (i.e., day, week, and month). Pooled monthly movement rates and variation in rates declined from approximately 100 m/hr in November to 40 m/hr in April (Fig. 3.1).

Performance of predation-risk models

Most models for risk by wolf pack and season performed adequately (all $\bar{r}_s > 0.70$, all $P < 0.024$) in the k-fold cross-validation, with few exceptions (Appendix I: Tables I.1, I.3, and I.4). Variation was high in the use of resources among packs. Most packs selected for shrubs (all $\beta_i > 0.821$, all $P \leq 0.001$) and/or burned/disturbed habitats (all $\beta_i > 0.605$, all $P \leq 0.004$), and avoided pine (all $\beta_i < -0.743$, all $P \leq 0.027$) and spruce stands (all $\beta_i < -0.407$, all $P \leq 0.031$); trends in the selection coefficients of the pooled models were similar (Appendix I: Tables I.2 and I.5-I.10). There were no 2001 winter wolf data for packs in the west-central portion of the GBPA, and, therefore, we pooled the wolf GPS data from all the packs to estimate risk in this area.

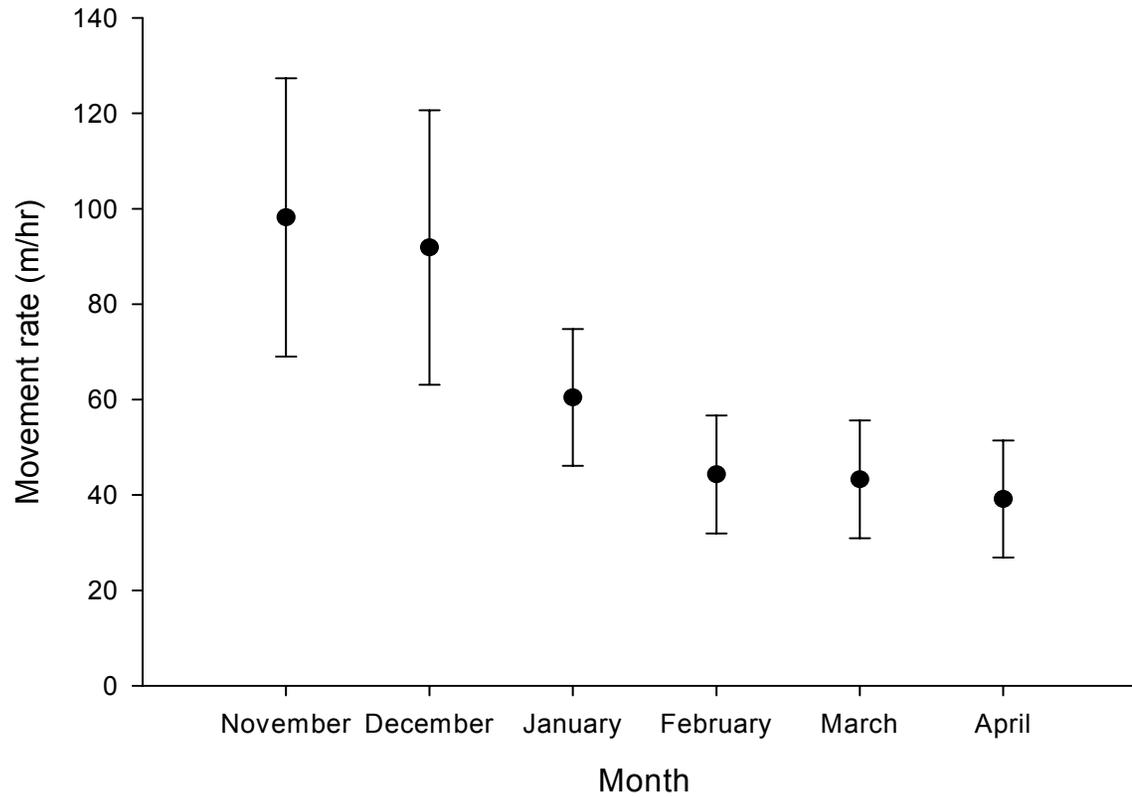


Figure 3.1. Movement rates (m/hr, $\bar{x} \pm SE$) of 10 adult female caribou averaged within a month by individual and then averaged across individuals, during winter (November-February) and late winter (March-April) months in the Greater Besa Prophet area, northern British Columbia, 2001-2002.

Relative importance of covariates and scale

At the scale of seasonal movement, wolf risk and distance to areas of high wolf risk contributed little information to the core model set as explanatory covariates (all $\overline{w_+(j)} < 0.059$). Risk was not a parameter in any of the selected models (i.e., the most parsimonious) for any caribou in either season. Distance to areas of high risk was important in one model for one animal (caribou 17, $w_i = 0.589$), but the β_i s for both the linear ($P = 0.179$) and squared ($P = 0.503$) terms of the quadratic were not different from zero. At the scale of seasonal movement, cost of movement (kJ/kg/hr) contributed the most information as an explanatory covariate in both seasons for all (all $\overline{w_+(j)} > 0.912$) but one caribou (caribou 17 in late winter). Most individuals strongly minimized the cost of locomotion in winter and late winter, with non-pregnant animals showing a stronger avoidance of high-cost movements than most pregnant animals (except caribou 10, Table 3.1). In the late winter, our models suggested that non-pregnant caribou continued to strongly minimize their cost of movement, whereas the importance of minimizing the cost of locomotion varied for pregnant animals (caribou 10 was the most sensitive to minimizing cost, Table 3.1).

At the scale of seasonal range, the relative importance of wolf risk varied among individuals, but generally contributed little information to the core model set as an explanatory covariate during winter or late winter (all $\overline{w_+(j)} \leq 0.282$, Table 3.2); risk was included in the final models for only 3 animals in both seasons (Tables 3.3, 3.4). Conversely, distance to areas of high wolf risk was more important, with

Table 3.1. Coefficients of selection (β_i) relating to the energetic cost of movement (kJ/kg/hr) in the final resource selection models at the scale of seasonal movement for 10 adult female caribou during winter (November-February) and late winter (March-April) seasons in the Greater Besa Prophet area, northern British Columbia, 2001-2002. Animals 22 and 25 were not pregnant, as defined by serum progesterone assays.

Caribou	Winter	Late Winter
	$\beta_i \pm \text{SE}$	$\beta_i \pm \text{SE}$
2	-0.544 \pm 0.092**†	-0.918 \pm 0.428*†
6	-0.691 \pm 0.169**†	-1.524 \pm 0.710*
10	-1.203 \pm 0.235**	-2.133 \pm 0.366**†
11	-0.523 \pm 0.141**	-0.459 \pm 0.155*
16	-0.523 \pm 0.128**	-1.091 \pm 0.306**
17	-0.392 \pm 0.091**	
20	-0.513 \pm 0.156*	-0.849 \pm 0.228**
22	-0.857 \pm 0.282*	-1.921 \pm 0.441**
23	-0.677 \pm 0.365	-1.124 \pm 0.406**†
25	-1.410 \pm 0.291**	-1.687 \pm 0.393**†

* $P < 0.050$

** $P < 0.001$

† β_i is from an averaged model

Table 3.2. The relative importance of each variable as shown as the sum of the weights for Akaike's Information Criterion corrected for small sample size ($w_+(j)$) where wolf risk and distance to areas of high wolf risk covariates occurred in the model set at the scale of seasonal range for individual caribou by season (winter (November-February) and late winter (March-April)) in the Greater Besa Prophet area, northern British Columbia, 2001-2002. $\overline{w_+(j)}$ denotes the average contribution of information by covariate $_j$ for a season across all individuals.

Caribou	$w_+(j)$ (Core Models)		$w_+(j)$ (Core Models + Wolf Risk)		$w_+(j)$ (Core Models + Distance to Areas of High Wolf Risk (km))	
	Winter	Late Winter	Winter	Late Winter	Winter	Late Winter
2	0.000	0.000	0.000	0.000	1.000	1.000
6	0.000	0.112	0.000	0.284	1.000	0.604
10	0.000	0.000	0.000	0.001	1.000	0.999
11	0.116	0.220	0.828	0.160	0.056	0.620
16	0.000	0.000	0.000	0.000	1.000	1.000
17	0.000	0.000	1.000	1.000	0.000	0.000
20	0.000	0.000	0.984	1.000	0.016	0.000
22	0.000	0.000	0.000	0.000	1.000	1.000
23	0.000	0.000	0.000	0.000	1.000	1.000
25	0.007	0.000	0.005	0.000	0.989	1.000
$\overline{w_+(j)}$	0.012	0.033	0.282	0.244	0.706	0.722

Table 3.3. Final individual and pooled (East (E) and Mountain (M) dwelling caribou) resource selection models at the scale of the seasonal range for 10 female caribou during winter (November-February) in the Greater Besa Prophet area, northern British Columbia, 2001-2002; squared terms include the linear term (e.g., Elevation² = Elevation (km) + Elevation² (km)). Statistics are sample size (*n*), number of parameters (*K*), log-likelihood (LL), Akaike's Information Criterion corrected for small sample size (AIC_c), Akaike weights (*w_i*), evidence ratios (*E_r*), and average (*n* = 5) Spearman's correlation coefficient from the k-fold cross-validation (\bar{r}_s). All *P* for $\bar{r}_s < 0.050$.

Animal(s)	Model	<i>n</i>	<i>K</i>	LL	AIC _c	<i>w_i</i>	<i>E_r</i>	$\bar{r}_s \pm SE$
2 (E) ^a	Distance to Areas of High Wolf Risk ² (km) + Vegetation + Elevation ² (km)	2156	12	-832.143	1688.408	0.291	1.000	0.711 ± 0.060
	Distance to Areas of High Wolf Risk ² (km) + Vegetation + Elevation ² (km) + Fragmentation	2156	14	-830.214	1688.598	0.265	1.100	0.696 ± 0.052
	Distance to Areas of High Wolf Risk ² (km) + Vegetation + Aspect + Elevation ² (km)	2156	14	-830.404	1688.979	0.219	1.330	0.756 ± 0.060
6 (E)	Distance to Areas of High Wolf Risk ² (km) + Vegetation + Aspect + Elevation ² (km) + Slope (°) + Fragmentation	1872	16	-624.109	1280.476	0.952	1.000	0.790 ± 0.037
10 (M) ^a	Distance to Areas of High Wolf Risk ² (km) + Vegetation + Elevation ² (km) + Slope (°)	2322	14	-720.714	1469.586	0.574	1.000	0.939 ± 0.012
	Distance to Areas of High Wolf Risk ² (km) + Vegetation + Aspect + Elevation ² (km) + Slope (°) + Fragmentation	2322	18	-716.958	1470.182	0.426	1.347	0.895 ± 0.023
11 (M)	Risk + Vegetation + Elevation ² (km) + Slope ² (°)	2166	13	-814.734	1655.614	0.772	1.000	0.905 ± 0.030
16 (M)	Distance to Areas of High Wolf Risk ² (km) + Vegetation + Elevation ² (km) + Fragmentation	1992	15	-703.248	1436.708	0.519	1.000	0.937 ± 0.023
17 (M)	Risk + Vegetation + Elevation ² (km) + Slope ² (°)	2295	13	-848.505	1723.146	0.873	1.000	0.863 ± 0.035

Table 3.3. Continued.

Animal(s)	Model	<i>n</i>	K	LL	AIC_c	<i>w_i</i>	<i>E_r</i>	$\bar{r}_s \pm SE$
20 (M)	Risk + Vegetation + Aspect + Elevation ² (km) + Slope (°) + Fragmentation	1686	18	-638.172	1312.711	0.948	1.000	0.908 ± 0.017
22 (M)	Distance to Areas of High Wolf Risk ² (km)+ Vegetation + Aspect + Elevation ² (km) + Slope (°) + Fragmentation	1227	17	-466.876	968.201	0.907	1.000	0.781 ± 0.050
23 (M) ^a	Distance to Areas of High Wolf Risk ² (km)+ Vegetation + Aspect + Elevation ² (km)	1470	13	-472.176	970.566	0.386	1.000	0.800 ± 0.049
	Distance to Areas of High Wolf Risk ² (km)+ Vegetation + Aspect + Elevation ² (km) + Slope (°) + Fragmentation	1470	17	-468.727	971.829	0.205	1.880	0.772 ± 0.050
25 (M)	Distance to Areas of High Wolf Risk ² (km)+ Vegetation + Aspect + Elevation ² (km) + Slope ² (°) + Fragmentation	1569	17	-526.407	1087.165	0.912	1.000	0.890 ± 0.035
East ^a	Distance to Areas of High Wolf Risk ² (km) + Vegetation + Elevation ² (km) + Fragmentation	4071	14	-1536.44	3100.979	0.289	1.000	0.840 ± 0.020
	Distance to Areas of High Wolf Risk ² (km) + Vegetation + Elevation ² (km)	4071	12	-1538.56	3101.192	0.260	1.112	0.840 ± 0.050
Mountain	Distance to Areas of High Wolf Risk ² (km) + Vegetation + Aspect + Elevation ² (km) + Slope (°) + Fragmentation	15384	18	-6108.040	12252.120	0.505	1.000	0.980 ± 0.010

^aThese models were averaged within an individual or pooled model as in Burnham and Anderson (2002:150, 162).

Table 3.4. Final individual and pooled (East (E) and Mountain (M) dwelling caribou) resource selection models at the scale of the seasonal range for 10 female caribou during late winter (March-April) in the Greater Besa Prophet area, northern British Columbia, 2001-2002; squared terms include the linear term (e.g., Elevation² = Elevation (km) + Elevation² (km)). Statistics are sample size (*n*), number of parameters (*K*), log-likelihood (*LL*), Akaike's Information Criterion corrected for small sample size (*AIC_c*), Akaike weights (*w_i*), evidence ratios (*E_r*), and average (*n* = 5) Spearman's correlation coefficient from the k-fold cross-validation (\bar{r}_s). All *P* for $\bar{r}_s < 0.050$.

Animal(s)	Model	<i>n</i>	<i>K</i>	<i>LL</i>	<i>AIC_c</i>	<i>w_i</i>	<i>E_r</i>	$\bar{r}_s \pm SE$
2 (E)	Distance to Areas of High Wolf Risk ² (km)+ Vegetation + Aspect + Elevation ² (km) + Slope (°) + Fragmentation	1272	14	-421.591	871.471	0.631	1.000	0.726 ± 0.051
6 (E) ^a	Distance to Areas of High Wolf Risk ² (km)+ Vegetation + Elevation ² (km) + Fragmentation	1092	10	-463.276	946.719	0.322	1.000	0.734 ± 0.030
	Risk + Vegetation + Elevation ² (km) + Fragmentation	1092	9	-464.946	948.025	0.168	1.921	0.765 ± 0.061
10 (M)	Distance to Areas of High Wolf Risk ² (km)+ Vegetation + Aspect + Elevation ² (km) + Slope (°) + Fragmentation	1368	17	-406.006	846.415	0.798	1.000	0.688 ± 0.067
11 (M)	Distance to Areas of High Wolf Risk ² (km)+ Vegetation + Aspect + Elevation ² (km) + Slope (°) + Fragmentation	1395	18	-395.458	827.360	0.482	1.000	0.823 ± 0.044
16 (M)	Distance to Areas of High Wolf Risk ² (km)+ Vegetation + Aspect + Elevation ² (km) + Slope (°) + Fragmentation	1260	18	-434.685	905.863	0.936	1.000	0.703 ± 0.030
17 (M)	Risk + Vegetation + Aspect + Elevation ² (km) + Slope ² (°) + Fragmentation	1293	13	-460.648	947.541	1.000	1.000	n/a ^b

Table 3.4. Continued.

Animal(s)	Model	<i>n</i>	<i>K</i>	LL	AIC_c	<i>w_i</i>	<i>E_r</i>	$\bar{r}_s \pm SE$
20 (M)	Risk + Vegetation + Aspect + Elevation ² (km) + Slope ² (°) + Fragmentation	1038	12	-422.748	869.753	1.000	1.000	0.706 ± 0.041
22 (M) ^a	Distance to Areas of High Wolf Risk ² (km)+ Vegetation + Elevation ² (km) + Slope (°)	1038	9	-380.220	778.580	0.454	1.000	n/a ^b
	Distance to Areas of High Wolf Risk ² (km)+ Vegetation + Aspect + Elevation ² (km) + Slope (°) + Fragmentation	1038	13	-376.336	778.977	0.372	1.219	n/a ^b
23 (M)	Distance to Areas of High Wolf Risk ² (km)+ Vegetation + Aspect + Elevation ² (km) + Slope (°) + Fragmentation	832	17	-269.484	573.637	0.961	1.000	0.778 ± 0.051
25 (M) ^a	Distance to Areas of High Wolf Risk ² (km)+ Vegetation + Aspect + Elevation ² (km) + Slope ² (°) + Fragmentation	1222	14	-479.877	988.056	0.613	1.000	0.908 ± 0.041
	Distance to Areas of High Wolf Risk ² (km)+ Vegetation + Elevation ² (km) + Slope ² (°)	1222	10	-484.457	989.063	0.371	1.654	0.897 ± 0.027
East	Distance to Areas of High Wolf Risk ² (km)+ Vegetation + Elevation ² (km) + Slope (°)	2381	10	-944.630	1909.335	0.889	1.000	0.790 ± 0.040
Mountain	Distance to Areas of High Wolf Risk ² (km)+ Vegetation + Elevation ² (km) + Slope (°)	1029	14	-4297.110	8622.251	0.637	1.000	0.960 ± 0.010

^aThese models were averaged within an individual or pooled model as in Burnham and Anderson (2002:150, 162).

^bPerfect separation within training and testing data sets precluded estimating $\bar{r}_s \pm SE$.

few exceptions, in models for most caribou in both seasons (all $\overline{w_+}(j) \geq 0.706$, Table 3.2). Distance to areas of high risk was a covariate in the final models for 7 and 8 of the 10 animals in winter and late winter, respectively (Tables 3.3, 3.4).

Effect of scale on the components of risk in resource selection

Wolf risk marginally improved the core models in winter and late winter (all $\overline{\Delta}_i > -1.574$) at the scale of seasonal movement, but increased the AIC_c for 6 animals in each season (Table 3.5). At the scale of seasonal range, risk (with few exceptions) generally improved the core models in winter ($\overline{\Delta}_i = -38.687$) and late winter ($\overline{\Delta}_i = -3.783$), but also increased AIC_c for 5 animals in late winter (Table 3.5). Distance to areas of high wolf risk generally improved the 'best' core model for each caribou and season at the scale of seasonal movement (all $\overline{\Delta}_i < -2.935$), but may have provided redundant information (higher AIC_c) for 3 animals in late winter (Table 3.5). At the scale of seasonal range, the distance covariate, with few exceptions, improved the core models in winter ($\overline{\Delta}_i = -54.424$) and late winter ($\overline{\Delta}_i = -17.301$), but again marginally increased AIC_c for one animal in winter and 2 in late winter (Table 3.5).

Availability data for the components of risk (i.e., wolf risk and the distance to areas of high risk) varied with the definition of scale. In both seasons, the distribution of available points for wolf risk at the scale of seasonal movement was shifted to the left (i.e., consistently lower in risk) of available points in the seasonal range; conversely, the distribution of available points for the distance to areas of high wolf risk was shifted to the right (i.e., farther from areas of high risk) (Fig. 3.2). Available points for 7 of the 10 caribou at the seasonal movement scale were lower

Table 3.5. Change in the Akaike's Information Criterion corrected for small sample size (Δ_i) when wolf risk and distance to areas of high wolf risk were added to the most parsimonious core model for individual caribou by season (winter (November-February) and late winter (March-April)) and scale (seasonal movement and seasonal range) in the Greater Besa Prophet area, northern British Columbia, 2001-2002. $\bar{\Delta}_i$ denotes the average contribution of information by a covariate for a season across all individuals.

Season	Caribou	Δ_i (Core Models + Wolf Risk)		Δ_i (Core Models + Distance to Areas of High Wolf Risk (km))	
		Seasonal Movement	Seasonal Range	Seasonal Movement	Seasonal Range
<i>Winter</i>	2	1.553	-69.052	-8.558	-48.073
	6	-2.358	-3.510	-13.091	-121.435
	10	-11.347	-25.091	-24.010	-32.439
	11	-0.744	-3.594	-1.714	1.422
	16	1.923	-32.329	-8.639	-115.103
	17	4.641	-2.346	-2.506	-9.000
	20	0.729	-72.601	-3.842	-18.166
	22	0.749	-122.963	-5.406	-98.040
	23	1.740	-23.851	-7.101	-93.582
	25	-0.575	-31.535	-0.693	-9.823
	$\bar{\Delta}_i$	-0.369	-38.687	-7.556	-54.424

Table 3.5. Continued.

Season	Caribou	Δ_i (Core Models + Wolf Risk)		Δ_i (Core Models + Distance to Areas of High Wolf Risk (km))	
		Seasonal Movement	Seasonal Range	Seasonal Movement	Seasonal Range
<i>Late Winter</i>	2	0.126	0.901	-10.192	-14.473
	6	-3.079	-1.812	1.477	-71.670
	10	-5.572	-11.667	-3.257	-8.077
	11	0.063	0.732	-12.849	-3.880
	16	1.903	3.391	-4.301	-21.433
	17	0.969	0.699	-1.540	-32.995
	20	-7.112	-4.090	-0.037	-10.024
	22	1.814	-27.296	1.776	1.167
	23	0.830	-0.513	1.013	-9.627
	25	-5.687	1.825	-1.444	0.699
		$\bar{\Delta}_i$	-1.574	-3.783	-2.935

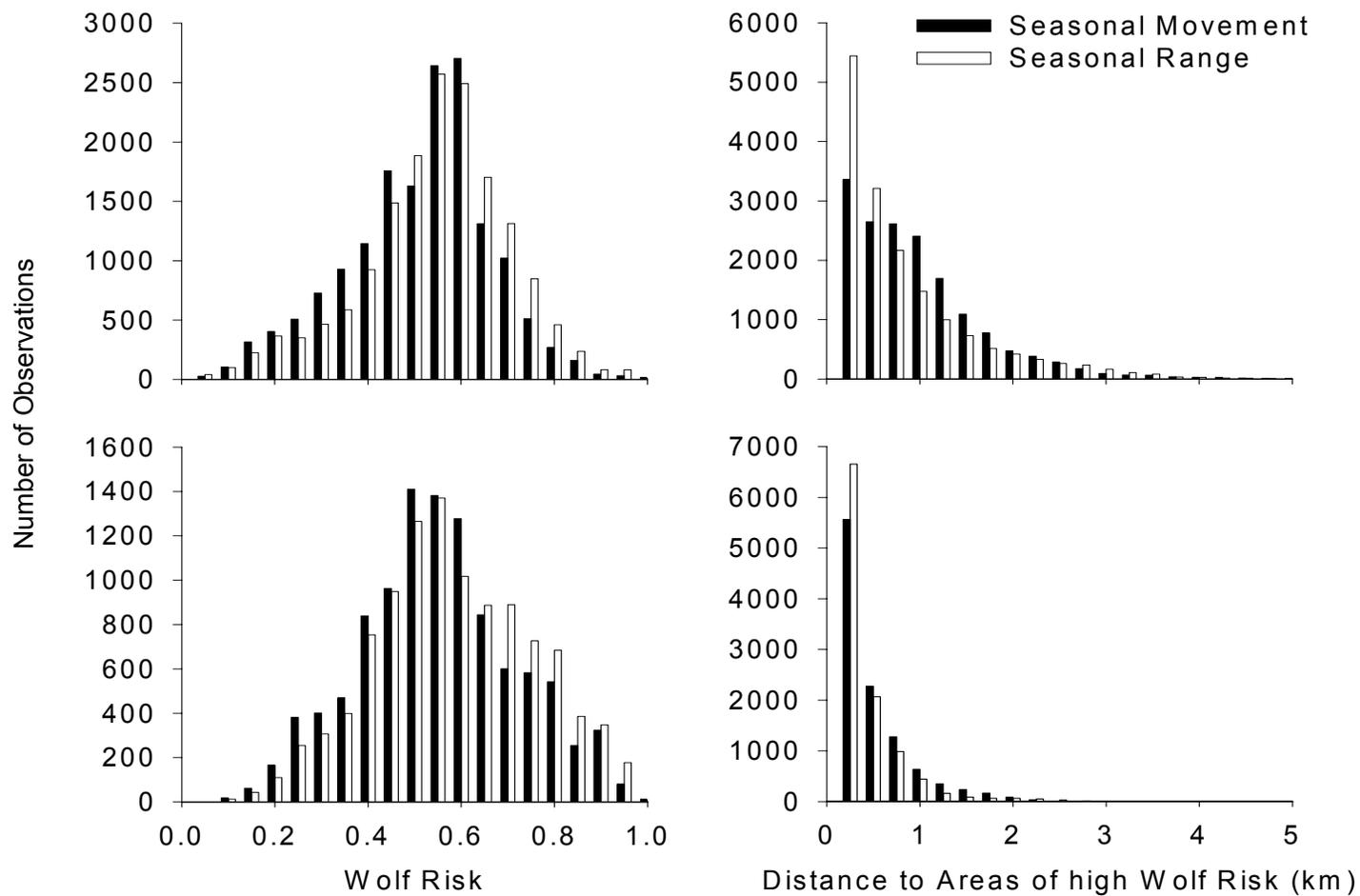


Figure 3.2. Frequency distributions of wolf risk and distance to areas of high risk from availability data for female woodland caribou at two scales (seasonal movement and seasonal range) in winter (November-February, top graphs) and late winter (March-April, lower graphs) in the Greater Besa Prophet area, northern British Columbia, 2001-2002.

in risk than the scale of seasonal range in both the winter and late winter seasons (all $P < 0.026$). In winter, risk did not differ between scales for 2 animals (all $P < 0.103$), and was higher at the scale of seasonal movement for caribou 22 (all $P < 0.001$); during late winter, risk did not differ between scales for 3 animals (all $P > 0.075$). Relative to the distance to high-risk areas, available points at the scale of seasonal movement were farther away than at the scale of seasonal range for 7 and 5 caribou in the winter (all $P < 0.002$) and late winter (all $P < 0.001$) seasons, respectively. In both seasons, the distance to areas of high risk did not differ for 2 caribou (all $P > 0.122$), while during winter, the available points for caribou 16 were closer ($P = 0.001$) at the scale of seasonal movement than the scale of seasonal range. In the late winter, the available points for 3 caribou were closer at the scale of seasonal movement than at the scale of seasonal range (all $P < 0.040$).

Variation in the selection of resources among caribou

Variation was high among individuals in the selection for topographic variables and components of risk at the scale of seasonal range (Fig. 3.3). We noted similar patterns in the selection of elevations (i.e., the direction of the quadratic form as determined by the signs (+ or -) of the squared and linear terms) and, to a lesser extent, slopes (Tables 3.3, 3.4); therefore, we pooled use and available data into 2 groups (animals that resided in the eastern (East, $n = 2$) and mountainous portions (Mountain, $n = 8$) of the GBPA). There also were some consistencies in selection of vegetation classes among all caribou. In winter, all individual models could be validated with the k-fold cross-validation with an average

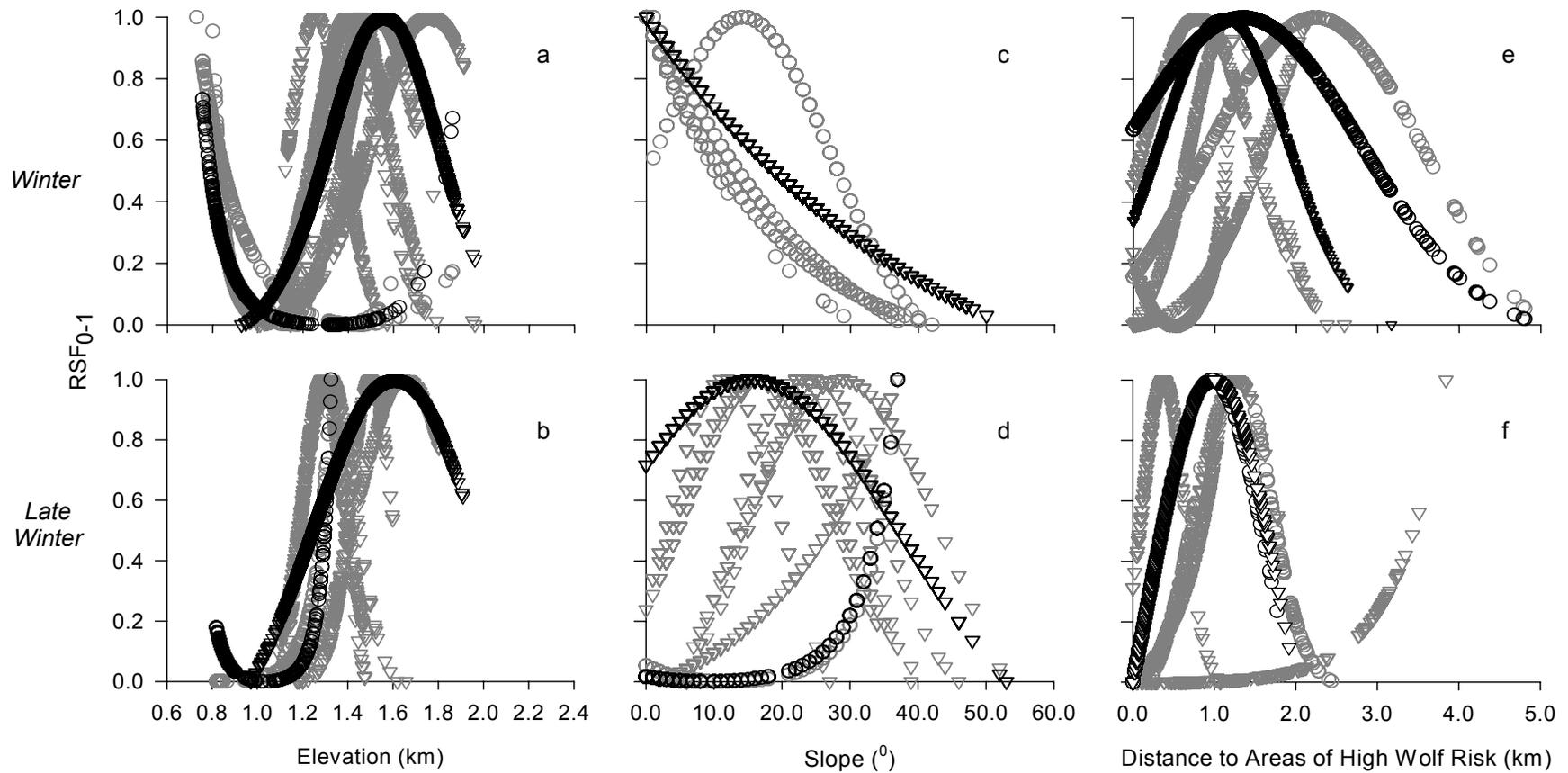


Figure 3.3. Relative likelihood of female caribou selecting elevations (a, b), slopes (c, d), and distances to areas of high risk (e, f) during winter (November-February) and late winter (March-April) assuming other covariates are constant in the final resource selection models for individual caribou (light shading) and pooled models (heavy shading) for animals living in the East (○) and Mountain (▽) regions of the Greater Besa Prophet area, northern British Columbia, 2001-2002. Resource selection functions were scaled 0-1 (RSF₀₋₁) as in Boyce and McDonald (1999) to evaluate selection of resources among individuals and pooled models. Slope was not included in the final pooled East model in the winter (c); points are data from GPS locations.

\bar{r}_s of 0.832 ± 0.026 (\pm SE) across individuals; pooled models also performed well (East, $P = 0.002$; Mountain, $P < 0.001$, average $\bar{r}_s = 0.887 \pm 0.047$). In late winter, individual models had an average \bar{r}_s of 0.773 ± 0.025 and pooled models (East, $P = 0.007$; Mountain, $P < 0.001$) an average of 0.875 ± 0.085 (Table 3.4).

Elevation

Elevation was an important parameter in the selection models for all individual caribou in both seasons (Tables 3.3, 3.4). In winter, both the linear and squared terms of the quadratic were significantly different from zero (all $P < 0.008$) for every model; in late winter, either one or both terms of the quadratic (all $P < 0.004$) were significant for 7 caribou. During winter, both caribou that resided in the east showed low variation in the selection of elevations and the β_i s of elevation in the East model were similar to individual models (Fig. 3.3a). Conversely, in both seasons mountain-dwelling individuals showed high variation in the selection of elevation with some individuals choosing moderate ($n = 3$, 1,200-1,400 m) to high elevations ($n = 2$, 1,400-1,600 m and 1,500-1,800 m); the Mountain model collapsed all of this variation into selection for elevations ranging from approximately 1,400-1,750 m (Fig. 3.3a). In late winter, using the East model, caribou showed selection for elevations $>1,200$ m, but only one caribou had β_i s different from zero (Fig. 3.3b).

Slope

Slope helped define habitat selection for 8 and 9 caribou in winter and late winter, respectively (Tables 3.3, 3.4). In the winter, however, slope was only

significant for 4 animals (all $P < 0.038$), whereas in late winter, slope was a stronger factor in the selection of resources ($\beta_i \neq 0$ for 8 caribou; all $P < 0.029$). During winter, slope did not enter the East model for 2 individuals because one caribou showed a decreasing linear avoidance of steeper slopes and slope did not enter the final model for the other caribou (Fig. 3.3c). Individuals in the mountains also showed a similar response to steep slopes (also reflected in the Mountain model), although one individual selected for slopes between approximately 10-25° (Fig. 3.3c). In late winter, selection for slopes by caribou fit the Gaussian function (i.e., selected for middle slopes from what was available), with one exception. That individual, from the east, selected for slopes $>30^\circ$, and the East model displayed a similar trend (Fig. 3.3d). Caribou in the mountains showed selection for gentle to steep slopes, but avoided flat ($<5^\circ$) and steep areas ($>40^\circ$), with high variation among individuals (Fig. 3.3d). The Mountain model indicated selection for slopes from approximately 5-30° (Fig. 3.3d).

Aspect

Aspect was important in selection models by 6 and 7 caribou in winter and late winter, respectively (Tables 3.3, 3.4). The selection coefficient was significant, however, only for 2 animals (all $P < 0.004$) in winter, and 3 caribou in late winter (all $P < 0.014$). In both seasons, caribou 6 selected for north and westerly aspects and caribou 20 selected for north and eastern aspects. In late winter, another animal (caribou 16) selected for eastern exposures. Aspect entered the Mountain model only in winter, but northness and eastness did not differ from zero (all $P > 0.097$).

Vegetation

Vegetation was an important parameter in habitat selection by all caribou in both seasons (Tables 3.3, 3.4). Selection coefficients were significant for at least one vegetation class for all (all $P < 0.046$) but 2 individuals in late winter (caribou 2 and 22, all $P > 0.134$). In the winter, caribou generally selected riparian spruce (all $\beta_i > 0.859$, all $P < 0.001$) and spruce (all $\beta_i > 0.488$, all $P < 0.006$) classes and avoided the shrub ($n = 5$, all $\beta_i > 0.697$, all $P < 0.033$) and subalpine shrub ($n = 3$, all $\beta_i > 0.832$, all $P < 0.001$) classes; one animal, however, did avoid spruce ($\beta_i = -0.795 \pm 0.184$, $\beta_i \pm SE$, $P < 0.001$) (Fig. 3.4). In the east, both caribou showed strong selection for *Carex* spp. (all $\beta_i > 0.924$, all $P < 0.004$); in the mountains, 4 caribou strongly avoided burned/disturbed areas (all $\beta_i > -1.232$, all $P < 0.001$) and 3 caribou selected alpine areas (all $\beta_i > 0.979$, all $P < 0.001$) (Fig. 3.4). The selection coefficients for vegetation classes in the East and Mountain models generally tracked the number of individual animals that selected or avoided these vegetation classes (Fig. 3.4). The East model showed selection for the *Carex* spp. class ($P < 0.001$) and avoidance of the non-vegetated and alpine areas (all $P < 0.040$). The Mountain model showed strong selection for *Carex* spp. ($P < 0.001$) and avoidance of subalpine shrub areas ($P < 0.001$) (Fig. 3.4). During late winter, trends were less similar in the selection of vegetation among individuals. One caribou in the east showed significant selection for shrub areas ($\beta_i = 0.506$, $P = 0.040$). In the mountains, some caribou selected for spruce ($n = 4$, all $\beta_i > 0.712$, all $P < 0.004$), some animals strongly selected against pine ($n = 2$, all $\beta_i < -1.192$, all P

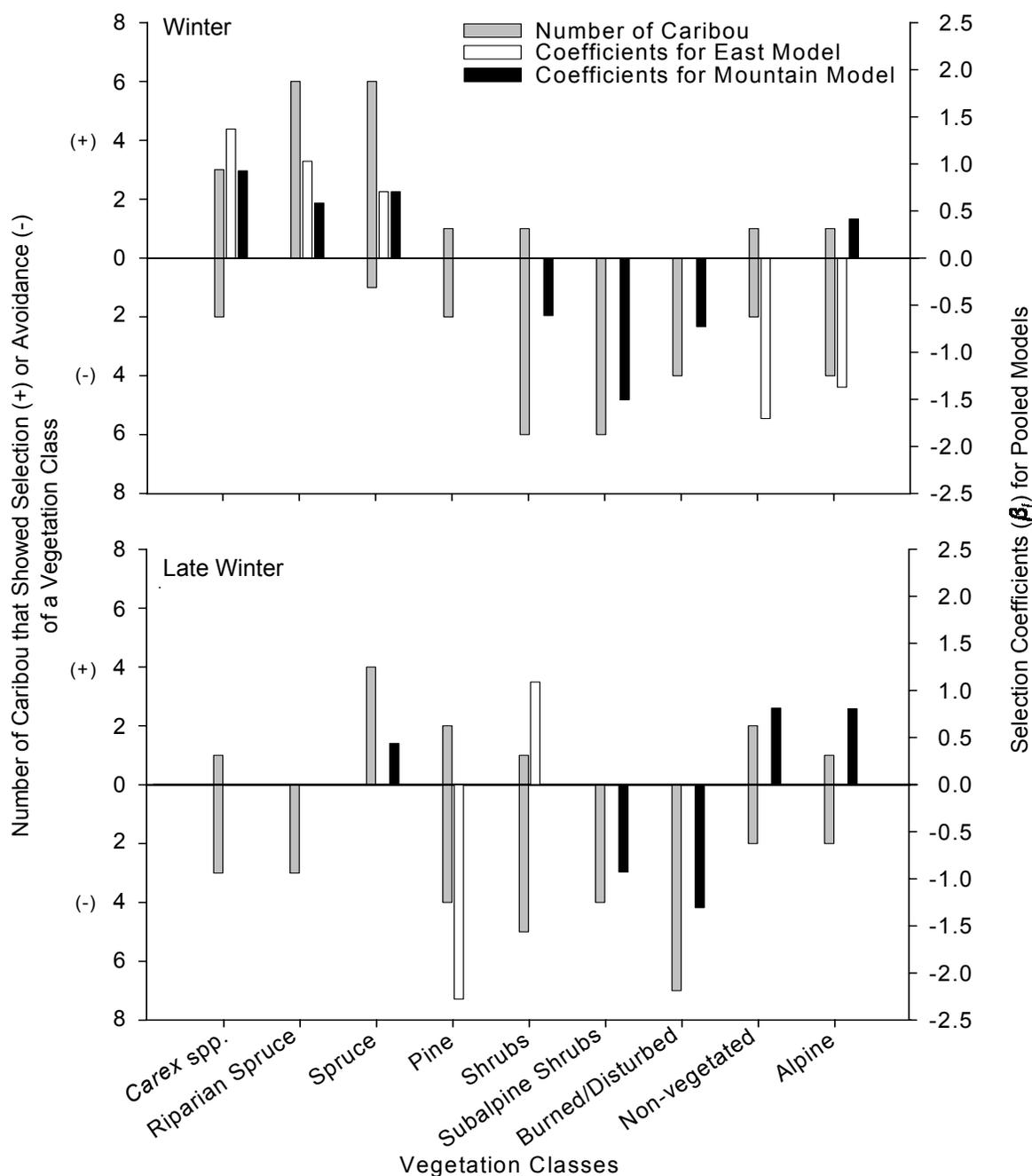


Figure 3.4. Number of GPS-collared caribou that selected or avoided a vegetation class (left axes) and the strength of significant ($P < 0.050$) coefficients of selection for the pooled models of animals living in the eastern (East, $n = 2$) and mountainous (Mountain, $n = 8$) portions of the Greater Besa Prophet area during winter (November-February) and late winter (March-April), in northern British Columbia, 2001-2002.

< 0.001) and some selected for non-vegetated habitats ($n = 2$, all $\beta_i > 0.651$, all $P < 0.024$); for half of the mountain dwelling caribou ($n = 4$), animals strongly avoided the burned/disturbed class (all $\beta_i < -1.192$, all $P < 0.001$) (Fig. 3.4). The East model showed selection for the shrub class ($P < 0.001$) and a very strong avoidance of pine ($P < 0.004$); the Mountain model showed selection for the non-vegetated and alpine areas with strong avoidance of the burned and disturbed class (all $P < 0.001$) (Fig. 3.4).

Fragmentation of Vegetation

Fragmentation helped define resource selection by 8 and 10 of the 10 caribou in the winter and late winter seasons, respectively (Tables 3.3, 3.4). At least one category of fragmentation was significantly selected for by 5 animals in winter (all $P < 0.024$) and 6 caribou in late winter (all $P < 0.043$). During the winter, one caribou in the east avoided low fragmented habitats (-0.458 ± 0.154 , $\beta_i \pm SE$, $P = 0.003$) and selected for highly fragmented areas (0.253 ± 0.112 , $P = 0.024$), and although fragmentation entered the model for the other caribou and the East model, the β_i s did not differ from zero (all $P > 0.150$). Caribou in the mountains generally selected for areas with low fragmentation ($n = 3$, all $\beta_i > 0.255$, all $P < 0.016$) and avoided highly fragmented areas ($n = 3$, all $\beta_i < -0.231$, all $P < 0.020$), with one exception (caribou 20) that selected against low fragmentation (-0.295 ± 0.126 , $P = 0.020$). In the Mountain model, caribou avoided areas of high fragmentation (-0.074 ± 0.032 , $P = 0.022$). In late winter, a caribou in the east avoided areas with low fragmentation (-0.468 ± 0.149 , $P = 0.002$); β_i s for fragmentation were not different from zero for

the other caribou in the east, and subsequently, fragmentation did not enter the East model. For animals in the mountains, response to the fragmentation covariate in late winter was varied. Two caribou avoided areas low in fragmentation ($\beta_i < -0.473$, all $P < 0.015$) and selected highly fragmented areas (all $\beta_i > 0.530$, all $P < 0.002$), while 2 other caribou avoided highly fragmented areas (all $\beta_i < -0.467$, all $P < 0.004$) and selected for areas low in fragmentation (all $\beta_i > 0.984$, all $P < 0.001$); fragmentation did not enter the Mountain model.

Components of the Risk of Predation

Risk was not a significant parameter in the final individual or pooled models for caribou that lived in the eastern portion of the study area during winter. In the mountains, responses to risk were variable for individuals with risk as a covariate in their final models (Table 3.2). In winter, caribou 11 minimized risk (-0.201 ± 0.092 , $\beta_i \pm SE$, $P = 0.028$) whereas caribou 17 ($\beta_i = 0.660 \pm 0.100$, $P < 0.001$) and 20 ($\beta_i = 0.341 \pm 0.080$, $P < 0.001$) were at a higher risk in their selection of resources; consequently, the risk parameter was not important in the Mountain model. In late winter, the risk β_i for the averaged model for caribou 6 in the east was not different from zero ($P = 0.656$); risk did not enter the pooled East model. In the mountains, caribou 17 continued to select resources at a high risk ($\beta_i = 0.794 \pm 0.158$, $P < 0.001$), whereas caribou 20 was at a lower risk ($\beta_i = -0.721 \pm 0.139$, $P < 0.001$); risk did not enter the Mountain model.

Specific responses to distance to high-risk areas varied among animals, but

generally followed a Gaussian function in both seasons, with 2 exceptions in late winter (Fig. 3.3e, 3.3f). In the winter, one caribou in the east selected for distances approximately 1.25-3.00 km away from high-risk areas; the East model showed selection for distances from 0.50-2.25 km (Fig. 3.3e). Mountain-dwelling animals showed selection for a range of distances from areas of high risk (e.g., 0.25-1.25 km, 1.00-1.50 km) with caribou showing initial avoidance of distances <0.40 km from areas of high risk and strong selection for distances >0.75 km, and another individual showing similar selection, but in an almost linear fashion, for distances >0.75 km (Fig. 3.3e). The Mountain model indicated selection for distances of approximately 0.50-1.50 km from high wolf risk (Fig. 3.3e). In late winter, the East and Mountain models also both indicated selection for distances approximately 0.50-1.50 km from high risk (Fig. 3.3f). In the east, one caribou selected for distances from approximately 1.00-1.75 km. In the mountains, 2 caribou selected for distances approximately 1.00-1.75 km from areas of high risk, and 2 individuals showed selection for increasing the distance to areas of high risk (caribou 10, 2.121 ± 0.354 , $\beta_i \pm SE$, $P < 0.001$; caribou 16, 1.742 ± 0.292 , $P < 0.001$) (Fig. 3.3f).

DISCUSSION

Our interpretation of habitat selection and the relative importance of different factors contributing to resource selection by female caribou was scale-dependant (Wiens 1989) and complicated by high variation in selection among individuals (Aebischer et al. 1993; Garshelis 2000). Although this individual variation may pose technical difficulties in modelling resource selection, identifying variation is an

important step in interpreting these data biologically (Aebischer et al. 1993; Nielsen et al. 2002). Use of resources by western woodland caribou populations typically varies among regions (Cichowski 1993; Wood 1996; Johnson 2000; Poole et al. 2000) and this may be due, in part, to differential availability of resources (Garshelis 2000) and/or distributions of predators among regions (e.g., elevation gradients and slopes, and/or human activities that may have shaped vegetative patterns and distributions of other ungulates and wolves (Seip 1998)). Therefore, in a highly diverse area such as the Greater Besa Prophet in northern British Columbia, high variation among individuals should be expected.

Relative importance of risk, energetic costs of movement, and scale

Caribou generally did not respond to the components of risk at the scale of seasonal movement. Risk was not a significant parameter for any individual, and the distance to areas of high wolf risk was important only for one animal (and the selection coefficients in that model did not differ from zero). Conversely, all individuals except one in both seasons strongly minimized the energetic costs of movement (Table 3.1). Minimizing the costs of movement was identified previously as the most important parameter in selection models for adult female caribou during inter-patch movements at several temporal scales in winter (Johnson 2000). In our study, non-pregnant individuals appeared to be more sensitive to minimizing costs in winter and possibly late winter than the pregnant animals, although our sample size was low for non-pregnant animals ($n = 2$). The one animal (caribou 10) that minimized the cost of movement more than the 2 non-pregnant individuals was killed

by a grizzly bear (*Ursus arctos*) on 7 May 2002. Data from ultrasound measurements of back fat from animals in the GBPA (Appendix H) and from Dauphiné (1976) show that non-pregnant caribou have less fat than pregnant individuals in winter. High mobility has high energetic costs associated with snow depth (Parker et al. 1984; Fancy and White 1987). Females in poorer condition might attempt to minimize energetic costs earlier in winter than animals with higher fat reserves, but, in doing so, may be unable to capitalize on food resources distributed over large areas (Barrett 1982). An increased sensitivity to minimizing energetic costs of movement and the trend towards reduced movement rates in late winter (Fig. 3.1) may be in response to changes in snow depth (Stuart-Smith et al. 1997), low or declining body condition (Dauphiné 1976), and/or reduced movement rates of wolves (B. Milakovic, University of Northern British Columbia, unpublished data). Our measure of the energetic costs of movement is conservative because we did not incorporate snow depths and steepness of slopes in the equations for cost. In rare cases when animal movements were beyond the 95th percentile movement, the random distances 'chosen' for available points would be relatively short, and therefore provide lower estimates of energetic costs. Therefore, given that we likely underestimated costs, the actual importance of minimizing energetic costs of movement in selection of resources by female woodland caribou in winter and late winter is even higher.

At the scale of seasonal range, spacing out from areas of high risk was an important parameter for female woodland caribou in both seasons. With few exceptions, the distance to high-risk areas contributed substantial information to final

resource-selection models. Risk per se provided little additional information to the core model set in winter, although its importance increased in late winter. These data support the importance of increasing the distance to high-risk areas at larger scales (Bergerud 1992; Seip 1992; Cumming et al. 1996; James 1999; Rettie and Messier 2000). The impracticality of defining the energetic costs of movement at such a larger scale precludes a conclusion on which parameter was more important.

Because the spatial scale of availability had a prominent effect on the importance of the components of risk in the selection of resources by female caribou, it should be considered when evaluating any inferences from RSFs (McClellan et al. 1998). Caribou made selection 'decisions' in a hierarchical fashion (Johnson 1980; Johnson et al. 2001), with increased sensitivity to components of risk at the larger scale (Bergerud 1996; Johnson 2000; Rettie and Messier 2000). The distributions of availability data were sensitive to scale (Fig. 3.2), suggesting that at the scale of seasonal movement, caribou had already 'selected' areas lower in risk and farther from areas of high risk within the seasonal range (Bergerud and Page 1987; Bergerud 1996; Rettie and Messier 2000). There were some inconsistencies in attributes of availability between scales among individuals, suggesting further individuals may respond variably to risk at different spatial scales. Differential responses to risk could be due, in part, to body condition because females in poorer condition may 'take' a higher risk in their wintering foraging strategy to slow the depletion of body reserves throughout the winter (Lima 1988; Skogland 1991; Clark 1994; Sweitzer 1996). A female with more body reserves could 'afford' to have reduced intake in a relatively 'safer' area. Finer scale data on

body condition (e.g., change in body reserves throughout the winter months) and predation risk are needed to evaluate the 'asset protection' hypothesis (Clark 1994).

Variation in the selection of resources among caribou

Specific comparisons to patterns in the selection of habitat factors by woodland caribou in areas with less topographic relief east of the Rocky Mountains (e.g., Gaspé Peninsula, Mosnier et al. 2003) and/or increased industrial disturbance (e.g., northern Alberta, James and Stuart-Smith 2000) are difficult because of dissimilarities in topography, vegetation, and/or land management activities that have altered distributions of other ungulates and large carnivores. Historic industrial activity in the eastern portion of the GBPA may have affected selection of habitats by caribou but we assumed this would take the form of higher risk (i.e., distance to linear features in risk models; James and Stuart-Smith 2000). Currently, the GBPA is mostly free of industrial activity during winter, and therefore, distance to anthropogenic edge was not included in selection models for caribou. We primarily compared our results with the few studies that have examined both biotic and abiotic factors in the selection of resources in the winter by the northern ecotype of woodland caribou in British Columbia (Cichowski 1993; Johnson 2000; Poole et al. 2000; Wood 1996; Zimmerman et al. 2002).

Pooled models in our study had better predictive capacity, as defined by the k-fold cross-validation, but collapsed possibly important biological variation in the selection of resources among caribou. Generally, the East model offered a good estimate of resource selection in both seasons, and this is probably due to the low

number of animals it represented ($n = 2$) as well as a less diverse landscape, both in topography and vegetation, in the eastern portion of the GBPA. The Mountain model, which pooled use/available data from 8 animals, collapsed the variation within a season.

Elevation

Selection of elevations was more variable among individual caribou in areas with greater topographic diversity (i.e., the mountains) for both seasons, as noted for other cervids (Kie et al. 2002; Lingle 2002). In winter, caribou in the east exhibited similar patterns in the selection of elevations, as this area has relatively little topographical relief (approximately 700-1,100 m). It is difficult to comment on variation between the 2 individuals in the east in late winter as the β_i s for elevation were only different from zero for one animal. Selection for these lower elevations is similar to some caribou in the Tweedsmuir-Entiako herd, as individuals in that herd wintered in either lower (approx. 1,000 m) or upper (approx. 1,600 m) elevations (Cichowski 1993). Alternatively, in the mountains, variation in selection of elevations was lower in late winter than winter, and the range in elevations selected by elevations was much greater in both seasons than individuals in the east. In both seasons, the Mountain models collapsed this variation into a range of elevations that was not common among animals (Fig. 3.3a, 3.3b). The large variation in elevational range among individuals makes it difficult to compare with other herds, but estimates from the Mountain model appear similar to caribou near Takla Lake (Poole et al. 2000) and to the Tweedsmuir-Entiako, Itcha-Ilgachuz, and Rainbow herds

(Cichowski 1993).

Slope

Caribou in the GBPA exhibited considerable variation in the selection of slopes and the form of that selection (i.e., linear versus quadratic), which also may be related to high topographic diversity (Kie et al. 2002; Lingle 2002). The East model seemed to provide a representative estimate of selection in late winter when slope was an important parameter (Fig. 3.4c). The Mountain model did not really represent selection of slopes among individuals in either season, particularly in late winter. In late winter, the Mountain model 'stretched' the quadratic over a range of slopes (approximately 5-30°) that some animals clearly did not select, thereby generalizing selection when some animals were being quite selective of slopes within their home ranges (Fig. 3.4d). Selection of slopes from the Mountain model were similar to the slopes used by caribou near Takla Lake (Poole et al. 2000).

Aspect and Fragmentation of Vegetation

The components of aspect and fragmentation were difficult to interpret, because the selection coefficients in the final individual models often were not different from zero, particularly for aspect. Variation in the responses to fragmentation increased in late winter, making it difficult to generalize among caribou. Individuals living in the mountains generally displayed the more typical response to fragmentation of vegetation in the winter (i.e., selecting less fragmented areas and/or avoiding areas with high fragmentation) (Seip 1998; Zimmerman et al.

2002); this may be in response to the risk of predation (Seip 1991) and/or abundance or availability of winter forage in less fragmented vegetation types (e.g., large spruce stands) (Zimmerman et al. 2002).

Vegetation

There was less variation in the selection of vegetation types among caribou than other parameters, and the pooled models appeared to adequately represent selection among individuals. In winter, most caribou selected for sedge (*Carex* spp.) meadows, and riparian spruce and spruce stands (Fig. 3.5a). Selection for these vegetation types was similar to other research conducted on the northern ecotype of woodland caribou (spruce, Poole et al. 2000; riparian spruce and *Carex* spp., Johnson 2000), suggesting that animals may have foraged on arboreal lichens and/or sedges, although we conducted no feeding site investigations and did not observe stands with abundant arboreal lichens in the GBPA. As noted in Johnson (2000), sedges may be an important source of supplemental protein (Skoog 1968) to lichen diets that are typically low in protein and high in digestible energy (Russell et al. 1993). Using the pooled models, mountain-dwelling individuals, with one exception, tended to avoid shrub, subalpine shrub, and burned/disturbed habitats (Fig. 3.5a, 3.5b). Selection against the subalpine shrub and burned/disturbed classes occurred in both seasons and against shrub areas in winter, which was likely in response to the risk of predation, as these vegetation types were consistently selected for by wolf packs in the GBPA. Avoidance of areas burned within 50 yrs has been documented in Alaska (Joly et al. 2003) and Manitoba (Schaefer and Pruitt

1991). In the short term, burns appear to negatively effect population productivity either directly (i.e., loss of forage, Seip 1990) or indirectly (e.g., increases in moose populations and wolves, Bergerud and Elliot 1986; Seip 1991), but fires may benefit caribou in the long term (>100 yrs) (Klein 1982).

In late winter, using the East model, animals strongly avoided the pine vegetation class, which was in contrast to other research on selection of vegetation types in winter for woodland caribou (Cichowski 1993; Wood 1996; Johnson 2000), and showed strong selection for the shrub class. The strong avoidance of the pine cover type may be explained partially by the lack of mature, lichen-producing pine stands in the GBPA; selection for the shrub class likely put these animals at a higher risk in the selection of resources (see above). In the Mountain model, some animals showed selection for alpine and non-vegetated areas in the late winter, whereas other animals avoided these areas. Animals that selected for these areas may have benefited from terrestrial lichens in windswept areas (Cichowski 1993; Wood 1996) and/or a lower risk of predation (Bergerud et al. 1984; Bergerud and Page 1987; Seip 1991, 1992).

Components of Risk

Caribou were not sensitive to modelled risk, but rather animals responded to distances to areas of high wolf risk (James 1999). There was high variation among individuals in the distances that caribou 'spaced away' from areas of high risk, but the form of the response was similar among most caribou. In both seasons animals did not respond to this parameter in a linear fashion, but rather, most selection fit a

Gaussian function (Fig. 3.5e, 3.5f). Distances past a threshold (i.e., the Gaussian function begins to approach zero) were not seen as 'safer'. It is likely that these responses were related to other components of habitat, such as feeding areas, where animals could not disperse themselves far away from areas of high risk all the time. The importance of 'spacing out' from areas of high wolf risk in resource selection at the scale of seasonal range is consistent with other research on caribou (Bergerud and Page 1987; Seip 1991; Bergerud 1992; James 1999; Rettie and Messier 2000).

Interpreting resource selection between scales and among individuals

Modelling resource selection at one scale would have severely limited interpretation of our selection models (Wiens 1989; Levin 1992). Our two definitions of availability were within Johnson's (1980) third order of selection, but still resulted in different interpretations of responses by caribou to biological (i.e., energetic cost of movement) and ecological factors (e.g., the risk of predation). For example, examination of selection at the scale of seasonal movement would have suggested that components of risk were unimportant to female woodland caribou, when at a larger spatial scale, the importance of 'spacing out' from areas of high wolf risk became more apparent (Bergerud and Page 1987; Seip 1991; Bergerud 1992; James 1999). We examined the contribution of the components of risk relative only to biotic (i.e., vegetation) and abiotic (e.g., elevation) habitat factors; future research should incorporate other factors such as age, sex, and reproductive status at various scales (Lima and Dill 1990; Molvar and Bowyer 1994; Bowyer et al. 1998; Bowyer et

al. 1999; Nielsen et al. 2002). Our findings that the risk of predation becomes more important at larger spatial scales are similar to those of Rettie and Messier (2000), but they also identify the importance of minimizing the energetic costs of movement by female woodland caribou in a mountainous environment in the winter and late winter months (as in Johnson 2000).

Interpreting the importance of modelled risk was difficult, particularly in the framework of the information-theoretic approach. We modelled risk using the same covariates that were included in the model set to determine resource selection for caribou, and although no variables were strongly collinear, if risk was important, the continuous risk covariate would have contributed little information to the suite of covariates already in the model (i.e., if animals selected against risk, a suite of habitat factors within the most parsimonious models may have already provided this refugia from predation) (Burnham and Anderson 2002). Models for all individuals with risk as the only covariate, however, were never selected from the model set as the most parsimonious.

Prior to pooling use/availability data, researchers should quantify variation in the selection of resources among individuals (Thomas and Taylor 1990; White and Garrott 1990; Aebischer et al. 1993; Garshelis 2000; Manly et al. 2002). Our justification for pooling models was based on large-scale geographic differences in abiotic factors, and, to a lesser extent, similarities in the selection of biotic and abiotic factors, not in the use (i.e., percent of locations) of these factors. By grouping animals, we placed subjective constraints on what appeared to be a selection 'strategy', but not identifying commonalities in selection among groups of

individuals likely would have provided a model with little biological and/or possibly predictive value (Aebischer et al. 1993; Nielsen et al. 2002). Animals that resided in the 'flatter' eastern portion of the GBPA clearly responded to abiotic factors quite differently than animals living in the mountainous region. Intuitively, individual models should have higher predictive capacity than pooled models, as selection coefficients within each model are specific to an individual's selection behavior. Results from the k-fold cross-validation, however, did not support this assertion. This may possibly result from lower variation in biotic and abiotic factors in use/availability data for individuals (i.e., spatial autocorrelation; Apps et al. 2001; Nielsen et al. 2002; Boyce et al. 2003), rare cases of categorical covariates (e.g., vegetation; Menard 2002), smaller data sets, and/or individual animals responding to unidentified habitat factors at finer scales (Johnson 2000). Spatial autocorrelation could be an artifact of restrictive definitions of availability (e.g., reduced movement would lead to smaller areas of availability). These issues may become more clear with possible solutions as more researchers model resource selection for individual animals.

Perfect or near-perfect separation (i.e., zero or very low cell values) within individual models is a technical problem that may interfere with biological interpretation (Menard 2002). We had several cases where use of a vegetation class was rare or did not occur, but the vegetation class was abundant in availability data, and most often, these occurred in classes selected by wolf packs. Vegetation classes that were not used, however, were biologically significant, because animals avoided these cover types. We attempted to account for this by counting the

animals that clearly avoided certain vegetation classes. Issues of separation will continue to cause problems in modelling selection among individuals with categorical covariates. One potential technical solution may be to buffer GPS points by locational error and sample areas of vegetation rather than discrete points (G. Pendleton, Alaska Department of Fish and Game, pers. comm.).

We acknowledge that interpreting selection among individuals graphically could be overly simplistic. Evaluating selection coefficients while holding other covariates in the model constant may not be an accurate representation of selection, because selection likely occurs for combinations of biotic and abiotic factors (Boyce et al. 2003). Quantifying variation among individual animals, however, is an important first step in modelling resource selection for a population (White and Garrott 1990; Aebischer et al. 1993; Garshelis 2000; Nielsen et al. 2002) and this offers a simple technique to do so. Research efforts should be directed towards more rigorous methods that quantify variation in selection among individuals using RSFs. Other concerns for interpreting model results include bias in locational data which may lead to an increase in Type I (overestimate selection) or Type II (underestimate selection) error rates (Friar et al. 2004; D. Heard, British Columbia Ministry of Water, Land, and Air Protection, unpublished data). Our fix rates were high ($\bar{x} = 91.3\%$), which suggested low bias (Friar et al. 2004), although some locational bias was likely present for individuals with lower fix rates.

Variation in resource selection among individual caribou is a source of concern relative to the utility of pooled models, particularly in the context of interpreting biological mechanisms behind selection (Aebischer et al. 1993; Nielsen

et al. 2002; Boyce et al. 2003). One of the benefits of RSFs is that researchers can examine variation in selection among individuals within a particular time period, yet Type III designs (Thomas and Taylor 1990) for large mammals are rarely conducted and/or rarely published (Nielsen et al. 2002). Models from pooled data are essentially an 'average' animal, but prior to pooling, we should identify whether an 'average' animal properly represents the population in question (White and Garrott 1990; Aebischer et al. 1993). We recommend that even with some of the above concerns, future studies should interpret selection for environmental and ecological factors within and across individuals at multiple scales (Wiens 1989; Aebischer et al. 1993). Scale-dependant responses among individuals are most likely to help us understand the mechanisms behind selection of resources (Wiens 1989; Danell et al. 1991).

CHAPTER 4: MANAGEMENT IMPLICATIONS FOR THE GREATER BESA PROPHET AREA

INTRODUCTION

Management agencies most often want to know where and when animals select areas within a management's jurisdiction, and why animals use these areas. This research illustrates concerns that should be addressed prior to examining the where, when, and why of predicting distributions of animals. Models of where and when can be generated if managers and researchers quantify variation among individuals (Nielsen et al. 2002) and seasons (Wood 1996; Apps et al. 2001). I agree with Nielsen et al. (2002) that if similarities in resource selection exist within groups of animals within a season, it may be technically feasible and biological appropriate to pool data into selection 'strategies', as this may address limited sample sizes as well as other technical concerns (e.g., complete separation, validation procedures, etc.). If variation is high among individuals and, therefore, pooling data is unjustified, unique approaches may be required to map selection of resources by a population that maintains individual selection strategies or the spatial scale of investigation should be adjusted for better predictive capacity (i.e., decrease resolution and/or increase extent; McClean et al. 1998; M. Boyce, University of Alberta, pers. comm.). The latter approach assumes that larger scale models maintain habitat factors that are important to animals among scales, but appropriate validation procedures must be used to qualify this assertion. Albeit time intensive, these precautions should help provide products (e.g., maps) that more precisely

portray a species' selection of resources within an area. As to why animals select particular areas within a landscape, it should be expected that large herbivores respond to habitat factors in a hierarchical fashion (Johnson 1980; Senft et al. 1987; Schaefer and Messier 1995; Johnson 2000; Apps et al. 2001; Boyce et al. 2003). Consequently, multi-scale analyses (Schaefer and Messier 1995; Johnson 2000; Apps et al. 2001; Boyce et al. 2003) with varied definitions of availability (McClellan et al. 1998; Meyer et al. 1998) are necessary to identify mechanisms of selection (Wiens 1989), particularly if covariates include ecological factors such as predation risk. I offer the following recommendations on where and when woodland caribou select resources, reasons as to why they may select or avoid these areas, as well as concerns for current and future management of caribou in the Greater Besa Prophet area (GBPA).

IMPLICATIONS

Calving and summer

Reproductive parameters for female woodland caribou in the GBPA were generally typical (Table 2.1), but more research is needed for better estimates of parturition rates. Pregnancy rates of caribou in the GBPA ($91.5 \pm 4.1\%$, $\bar{x} \pm SE$) were within previously observed estimates (90-100%) of woodland (Seip and Cichowski 1996; Mahoney and Virgl 2003; McLoughlin et al. 2003) and barren ground caribou (Griffith et al. 2002). Estimates of parturition were highly variable between years (2002, $n = 9$, $55.6 \pm 17.6\%$, $\bar{x} \pm SE$; 2003, $n = 13$, $76.9 \pm 12.2\%$) and were probably related to small sample sizes as 44 of the 48 global positioning

system collars (GPS) (22 per yr) failed prior to calving. These estimates, however, did not differ from the 81% (range = 71-92%) documented for barren ground caribou in Alaska (Griffith et al. 2002). Low parturition rates may be an indication of poor quality winter and/or summer range because fetal adsorption and abortion, although rare (Dauphiné 1976; Cameron and Ver Hoef 1994), likely result from poor body condition (Russell et al. 1998). Therefore, more precise estimates of parturition would be useful in the GBPA to assist in monitoring population condition and trends.

Calving peaked on 28 May with observations of caribou with neonates ranging from 25 May-10 June; these estimates are similar to calving dates of other woodland caribou herds (Oosenbrug and Theberge 1980; Vik Stronen 2000). Caribou possibly calved earlier than 25 May, as early to late calving can last up to 4 weeks (Adams et al. 1995). Consequently, the extent of calving may have ranged from 14 May-11 June (Oosenbrug and Theberge 1980).

I identified 3 distinct calving areas in the GBPA: the Foothills, Western High Country, and North Prophet (Fig 2.2). Delineation of these areas was based on two summers of intensive monitoring and distributions of parturient caribou, and geographic, vegetative, and topographic differences (see Chapter 2). Each of these calving areas may provide calving caribou a unique combination of habitat factors that are likely to vary in importance among years as environmental and ecological conditions change. Caribou calved in areas away from linear features (e.g., seismic lines) that were steeper and higher than random (i.e., moved into the mountains to calve) (Fig. 2.2). The Foothills area provides large areas of highly productive alpine and subalpine vegetation types in close proximity to steep terrain that may be used

as escape cover for caribou with calves (Bergerud et al. 1984). This area appeared to 'green up' earlier than the other calving areas, which may provide nutritious forage for lactating females (Barten et al. 2001; Griffith et al. 2002; Oosenbrug and Theberge 1980) that reach their lowest body condition of the year during the 3 weeks after calving (White and Luick 1984; Chan-McLeod et al. 1999). Although high in wolf and bear risk, the Foothills is so productive vegetatively that parturient females can calve in a variety of habitats that allow them to forage in high-quality areas without an increased cost (i.e., increase in risk per unit of forage) in risk (see Chapter 2). Conversely, the Western High Country provides areas lower in the risk of predation, but also lower in forage biomass and quality. In this area, caribou calved in hanging valleys (e.g., valleys running north-south near the head of Keily Creek or Richards Creek) or on ridges between valleys (e.g., ridge to the north of Colledge Lake). Animals that calve in these areas, however, may become more predictable prey for predators (i.e., higher cost in risk per unit of forage) that reside in adjacent areas. Caribou typically calved in the vegetated portions of these valleys that offer few options to evade predation (see Chapter 2). The importance of this area may vary annually and/or with changes in ungulate densities, particularly moose and elk, because these areas are unlikely calving habitats for moose and elk. As moose and elk densities increase, predators may respond to and concentrate on areas with more abundant neonatal prey items to minimize search times and increase encounter rates (Bergerud 1983); this could increase neonatal survival of calves born in the Western High Country. The North Prophet is a unique area of the GBPA in that it is generally free of forest cover, provides large areas of subalpine

and alpine vegetation, and has access to steep, rocky terrain. Caribou calved in high-elevation talus fields or moist-alpine sites; this area likely offers benefits of both abundant and productive alpine/subalpine vegetation that may 'green-up' relatively soon and access to steep terrain that may act as escape cover for caribou with young. For these same reasons, the North Prophet may be attractive to grizzly bears (*Ursus arctos*) in early summer (Nielsen et al 2002; Nielsen et al. 2003). Minimizing the risk of bear predation was an important factor in the selection of calving sites within the North Prophet (see Chapter 2). Caribou in the North Prophet generally calved in larger groups than the other areas, with as many as 10-15 adult females. Regardless of the differences in environmental and ecological conditions among calving areas, calf mortality did not differ among areas (see Chapter 2). The persistence of these calving areas may be important because calf production in an area is likely to vary with changing environmental (e.g., timing of late spring snows) and/or ecological conditions (e.g., changes in ungulate and predator densities). During calving, calving areas should be free of anthropogenic disturbance that may alter distributions of parturient female caribou, other ungulates, and/or predators; caribou are sensitive to these types of disturbances (Bradshaw et al. 1997; Nellemann and Cameron 1998; James and Stuart Smith 2000; Dyer et al. 2001; Weclaw and Hudson 2004).

The Foothills and North Prophet calving areas are important summer (15 June-15 August) range for woodland caribou in the GBPA. Large aggregations of caribou (approx. 20-40) started to form during the third week after calving (i.e., approximately the second to third week in June) in these two calving areas; there

was another increase in movement towards these areas in the second week in July. Five cows with collared calves left the Western High Country the third week of June; of this sample, three pairs went to the Foothills, one pair went to the North Prophet, and another pair went to the Akie drainage to the west (outside of the GBPA), and no pairs moved to the Western High Country. Twenty-nine cow-calf pairs left their calving sites by the end of July, and this movement had obvious impacts to calf survival. Calves that remained at their calving sites through the end of summer decreased their odds of survival by 66%. Formation of large groups of caribou may be an important social response to simultaneously minimize the risk of wolf predation (Bøving and Post 1997; Barten et al. 2001; Hebblewhite and Pletscher 2002) and forage in more productive areas within a calving area to address the nutritional demands of lactation (White and Luick 1984; Barten et al. 2001). High-quality summer range could have direct impacts to population productivity from the potential increase in mass by parturient females and neonates and the subsequent impacts to survival and reproductive condition (Cameron et al. 1993; Cameron and Ver Hoef 1994; Post and Klein 1999; Adams and Dale 1998a,b; Cook et al. 2003). Because of its relatively easier access, the Foothills area is most susceptible to anthropogenic activity; cow-calf pairs should have choices in routes to this area to form post-calving aggregations that are important to calf survival. Any disturbance during either times of movement or formation of post-calving aggregations may have significant direct (e.g., increased predation) and/or indirect consequences (e.g., displacement to lower quality summer range) to calf survival and population productivity. In addition, the Foothills and North Prophet calving areas also provide

areas where snow persists through summer. Woodland caribou in the GBPA and the Yukon likely use snowfields as refugia from insect harassment and/or provide thermal cover on warm summer days (R. Farnell, Yukon Government, Department of Environment, pers. comm.).

Wolverines and wolves were important sources of mortality for calves <14 and >18 d, respectively. Observations and anecdotal evidence suggest the GBPA is productive wolverine habitat. Wolverines can be effective predators of reindeer and caribou neonates (Landa et al. 1997; Vangen et al. 2001). Activating traplines north of the Sikanni River may decrease mortality from wolverines and wolves during calving and summer, although calf survival was relatively high during the calving season ($88 \pm 5.0\%$, $\bar{x} \pm SE$). Based on this study, there are no additional recommendations for lowering the rate of calf mortality from wolf predation since wolves were regularly trapped in the Sikanni drainage. Adult wolf mortality within the GBPA appeared high (11 of 27 GPS collared wolves, approx. 41%) throughout the duration of the 2-yr study (B. Milakovic, University of Northern British Columbia, unpublished data). Additionally, there were likely unsanctioned efforts to 'control' wolf populations occurring in the Upper Prophet River watershed; this unsanctioned activity probably occurred during the 2002-2003 winter and may partially explain the increase in caribou calf survival that year ($54 \pm 1.1\%$ in 2002 vs. $79 \pm 8.0\%$ in 2003).

Winter and late winter

Adult female caribou exhibited considerable variation in the selection of resources in winter (November-February) and late winter (March-April) of 2001-

2002. To define areas important for each individual caribou ($n = 10$), I used a raster geographic information system (GIS) (PCI 9.1, Richmond Hill, ON, Canada), seasonal home ranges for individual caribou, and resource selection functions (RSFs) developed from logistic regression and the log-linear model (Boyce and McDonald 1999; Manly et al. 2002) were used (Fig. 4.1). To maintain variation in the selection of resources among individuals, I used the maximum RSF value, scaled (0-1) (Manly et al. 2002) for each pixel from among the individual models. For example, if 3 caribou models overlapped a single pixel, and RSFs for caribou A, B, and C were equal to 0.25, 0.50, and 0.75 respectively, the highest value (0.75) was assigned to that pixel. RSF values were then divided in 5 quantiles (i.e., 20th, 40th, 60th, 80th, and 100th percentile values) representing low to high relative probabilities of female caribou occupying a pixel. For areas where I had no estimates of use for individuals (i.e., a vegetation class did not occur in the use data for a season), data were 'filled in' using estimates of selection from either the East or Mountain models (see Chapter 3). I did not estimate relative selection for the entire GBPA because our technique to define availability (i.e., 100% minimum convex polygons buffered by the movement potential of an individual caribou within a season, see Chapter 3) did not cover the study area. Because selection is likely to change with availability, RSF models applied to areas outside the definitions of availability are likely to provide unreliable estimates of selection (Garshelis 2000). For all caribou, selection for late winter habitats was within areas selected during winter; therefore, I provide one map of areas important to female woodland caribou over winter (Fig. 4.1). These areas were not the only areas selected by caribou in

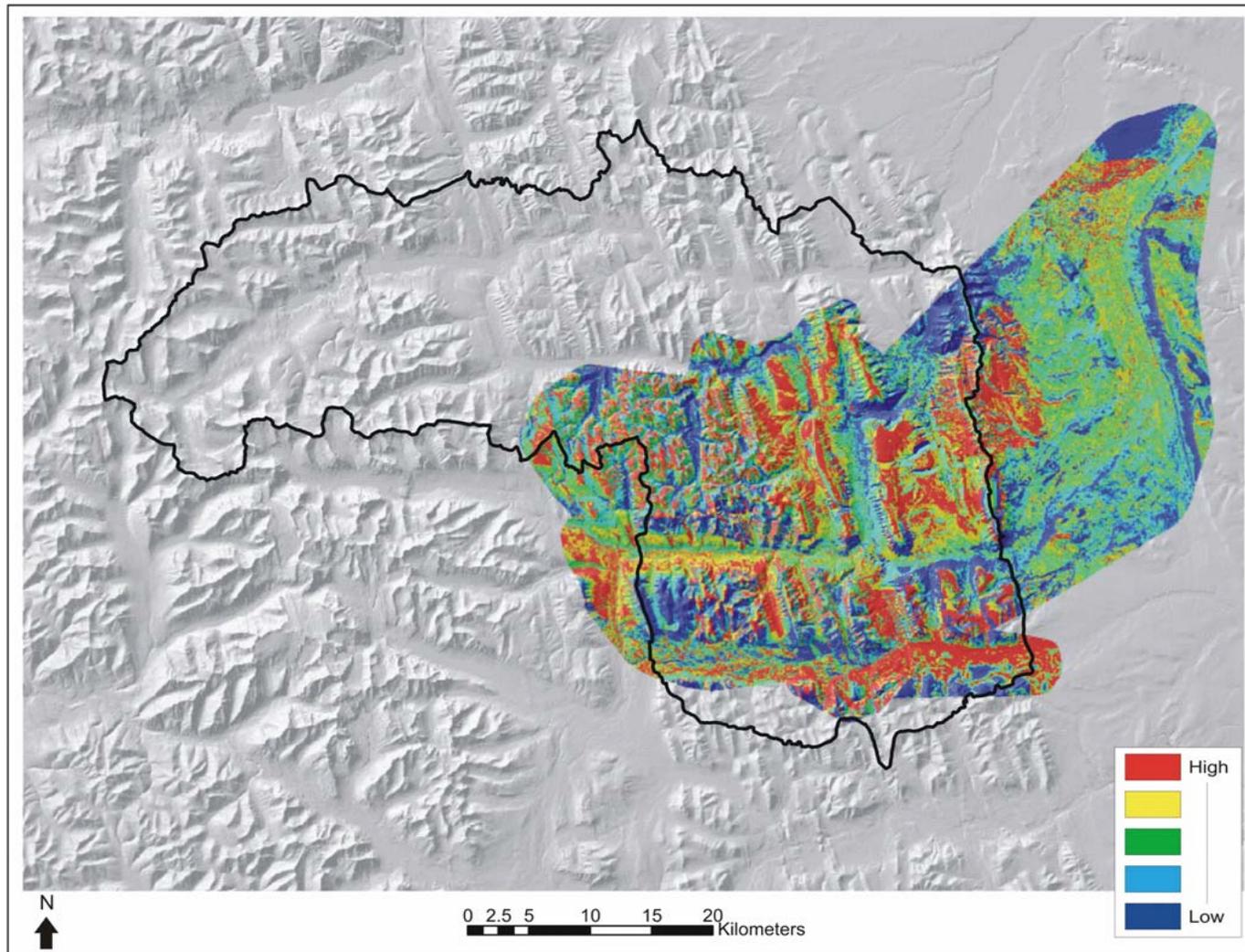


Figure 4.1. Areas selected by GPS-collared female woodland caribou in winter and late winter in the Greater Besa Prophet, northern British Columbia, 2001-2002.

the GBPA because observations, telemetry data from 1998-2000 (R. Woods, Ministry of Water, Land, and Air Protection, unpublished data), and Zimmerman et al. (2002) indicated that animals also were wintering near Hewan Creek, and Mounts Dopp and Trimble. Additional locational data from 19 GPS collars that were deployed in January 2004 will be available in January 2005, and used to update Fig. 4.1.

Current management actions and historic and future industrial development may negatively affect caribou in the GBPA. Prescribed burning is a common management activity in the GBPA to enhance Stone's sheep populations, but it may adversely affect the caribou population by increasing numbers of moose and elk, which provides more abundant prey for wolves and bears (Gasaway et al. 1983; Bergerud and Elliot 1986; Seip 1991, 1992; Ballard et al. 2000), and by reducing the amount of forage for caribou (Klein 1982; Seip 1990; Schaefer and Pruitt 1991; Thomas 1998). Preliminary selection models suggest moose (K. Parker and M. Gillingham, University of Northern British Columbia, unpublished data), Stone's sheep (A. Walker, University of Northern British Columbia, unpublished data), grizzly bears, and wolves (B. Milakovic, University of Northern British Columbia, unpublished data) select for burned/disturbed areas at some time during the year in the GBPA; elk in the area are likely benefiting from burns (Peck and Peek 1991). Assuming this activity is increasing numbers of moose and elk, the wolf population may also be increasing (Gasaway et al. 1983; Gasaway et al. 1992; Ballard et al. 2000). Grizzly bears may also benefit from burning, as they feed on early seral vegetation typical of recent burns (Nielsen et al. 2003) as well as the ungulates that

are attracted to these areas (B. Milakovic, University of Northern British Columbia, unpublished data). Caribou in Alaska (Joly et al. 2003) and Manitoba (Schaefer and Pruitt 1991) avoided burns <50 yrs old; individuals in the Beverly herd did not use burned areas until approx. 40-60 yrs post-burn (Thomas 1998). Fires may benefit populations in the long term (>100 yrs) (Klein 1982; Thomas 1998), but the recovery of lichens after a fire is slow (Schaefer and Pruitt 1991). Four of the 8 caribou in the mountains strongly avoided burned/disturbed areas while the others tended to avoid these areas (see Chapter 3).

Linear corridors in the eastern section of the GBPA could be negatively affecting the woodland caribou population. Assuming the average width for lines that can be observed from aerial photography or satellite imagery is 5 m, there are approx. 6,000 ha of the GBPA covered by linear features as of December 2003 (Fig. 2.2); most of these linear features have been converted from spruce (*Picea* spp.) to shrub species, primarily in the form of willow (*Salix* spp.). With the development of linear corridors, there is often increased recreational use of all-terrain vehicles and snowmobiles. Linear developments and seismic activity during the winter months in Alberta have been linked to increased predation from wolves that use the corridors to increase encounter rates with prey (James 1999; James and Stuart-Smith 2000). Woodland caribou in the GBPA are sensitive to distances to areas of high risk in winter and late winter (see Chapter 3) and linear corridors are associated with a higher risk of predation (Dyer et al. 2001, 2002; McLoughlin et al. 2003). Indeed, wolves from the Pocketknife pack used linear features disproportionately to their availability in the GBPA from November-April in 2002 and 2003.

The impact of current and historic industrial development on the loss of habitat appears to be the largest factor in the decline of woodland caribou in Alberta (Weclaw and Hudson 2004). Nellemen and Cameron (1998), Dyer et al. (2001), and Weclaw and Hudson (2004) noted that the impact of industrial complexes on caribou exceeded the area of the actual 'footprint' of development (e.g., area of well sites and roads) because animals tended to avoid well sites by approx. 1.0 km and roads by 0.25 km; this avoidance was strongest during late winter and calving (Dyer et al. 2002). Linear corridors and industrial activity have been associated with higher movement rates (Murphy and Curatolo 1987) and decreased foraging activity in caribou (Bradshaw et al. 1997). Woodland caribou in the GBPA are sensitive to minimizing the energetic costs of movement, particularly during late winter (see Chapter 3). The cumulative effects of increased energetic costs from increased movement (Murphy and Curatolo 1987), reduced foraging times (Bradshaw et al. 1997), the increased risk of predation (James and Stuart-Smith 2000), and loss of functional habitat due to anthropogenic disturbance (Dyer et al. 2001; Weclaw and Hudson 2004) would likely decrease productivity of the population(s) of caribou in the GBPA. As proposals for seismic developments increase, all efforts should be made to minimize the aforementioned effects of access associated with seismic and industrial activity increases in the mountainous regions of GBPA. These cautions are strongly advised if caribou are to remain in perpetuity in the GBPA, and to avoid the declines in numbers that have resulted as a consequence of industrial development in other areas (Dzuz 2001; McLoughlin et al. 2003; Weclaw and Hudson 2004).

LITERATURE CITED

- Acorn, R. S., and M. J. Dorrance. 1998. Methods of investigating predation of livestock. Alberta Agriculture, Food and Rural Development, Edmonton, Alberta.
- Adams, L. G., and B. W. Dale. 1998a. Reproductive performance of female Alaskan caribou. *Journal of Wildlife Management* 62:1184-1195.
- Adams, L. G., and B. W. Dale. 1998b. Timing and synchrony of parturition in Alaskan caribou. *Journal of Mammalogy* 79:287-294.
- Adams, L. G., F. J. Singer, and B. W. Dale. 1995. Caribou calf mortality in Denali, National Park, Alaska. *Journal of Wildlife Management* 59:584-594.
- Aebischer, N. J., P. A. Robertson, and K. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313-1325.
- Altendorf, K. B., J. W. Laundré, C. A. Lopez Gonzales, and J. S. Brown. 2001. Assessing effects of predation risk on foraging behavior of mule deer. *Journal of Mammalogy* 82:430-439.
- Apps, C. D., B. N. McLellan, T. A. Kinley, and J. P. Flaa. 2001. Scale-dependant habitat selection by mountain caribou, Columbia Mountains, British Columbia. *Journal of Wildlife Management* 65:65-77.
- Ballard, W. B. 1994. Effects of black bear predation on caribou--a review. *Alces* 30:25-35.
- Ballard, W. B., P. R. Krausman, S. Boe, S. Cunningham, and H. A. Whitlaw. 2000. Short-term response of gray wolves (*Canis lupis*) to wildfire in northwestern Alaska. *Canadian Field-Naturalist* 114:241-247.
- Barrett, G. W. 1982. Distribution, behavior, and mortality of pronghorns during a severe winter in Alberta. *Journal of Wildlife Management* 46:991-1002.
- Barten, N. L., R. T. Bowyer, and K. J. Jenkins. 2001. Habitat use by female caribou: tradeoffs associated with parturition. *Journal of Wildlife Management* 65:77-92.
- Ben-David, M., K. Titus, and L. R. Beier. 2004. Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? *Oecologia* 138:465-474.
- Berger, J., and C. Cunningham. 1988. Size-related effects on search times in North American grassland female ungulates. *Ecology* 69:177-183.

- Bergerud, A. T. 1961. Sex determination of caribou calves. *Journal of Wildlife Management* 25:199.
- Bergerud, A. T. 1974. Decline of caribou in North America following settlement. *Journal of Wildlife Management* 38:757-770.
- Bergerud, A. T. 1983. Prey switching in a simple ecosystem. *Scientific American* 249:130-136.
- Bergerud, A. T. 1992. Rareness as an antipredator strategy to reduce the risk of predation for moose and caribou. Pages 1008-1021 *in* D. R. McCullough and R. H. Barrett, editors. *Wildlife 2001: Populations*. Elsevier, London, U.K.
- Bergerud, A. T. 1996. Evolving perspectives on caribou population dynamics, have we got it right yet? *Rangifer*, Special Issue No. 9:95-115.
- Bergerud, A. T., H. E. Butler, and D. R. Miller. 1984. Antipredator tactics of calving caribou: dispersion in mountains. *Canadian Journal of Zoology* 62:1566-1575.
- Bergerud, A. T., R. Ferguson, and H. E. Butler. 1990. Spring migration and dispersion of woodland caribou at calving. *Animal Behaviour* 39:360-368.
- Bergerud, A. T., and J. P. Elliot. 1986. Dynamics of caribou and wolves in British Columbia. *Canadian Journal of Zoology* 64:1515-1529.
- Bergerud, A. T., and J. P. Elliott. 1998. Wolf predation in a multiple-ungulate system in northern British Columbia. *Canadian Journal of Zoology* 76:1551-1569.
- Bergerud, A. T., and R. E. Page. 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. *Canadian Journal of Zoology* 65:1597-1606.
- Boertje, R. D. 1984. Seasonal diets of the Denali Caribou Herd, Alaska. *Arctic* 37:161-165.
- Bøving, P. S., and E. Post. 1997. Vigilance and foraging behavior of female caribou in relation to predation risk. *Rangifer* 17:55-63.
- Bowyer, R. T., J. G. Kie, and V. Van Ballenberghe. 1998. Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? *Journal of Mammalogy* 79:415-425.
- Bowyer, R. T., V. Van Ballenberghe, J. G. Kie, and J. A. Maier. 1999. Birth-site selection by Alaskan moose: maternal strategies for coping with a risky environment. *Journal of Mammalogy* 80:1070-1083.

- Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience* 10:421-431.
- Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. *Trends in Ecology and Evolution* 14:268-272.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281-300.
- Bradshaw, C.J., S. Boutin, and D.M. Hebert. 1997. Effects of petroleum exploration on woodland caribou in northeastern Alberta. *Journal of Wildlife Management* 61:1127-1133.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York.
- Byers J. A. 1997. American pronghorn: social adaptations and the ghosts of predators past. University of Chicago Press, Chicago, IL.
- Cameron, R. D., W. T. Smith, S. G. Fancy, K. L. Gerhart., and R. G. White. 1993. Calving success of female caribou in relation to body weight. *Canadian Journal of Zoology* 71:480-486.
- Cameron, R. D., and J. M. Ver Hoef. 1994. Predicting parturition rate of caribou from autumn body mass. *Journal of Wildlife Management* 58:674-679.
- Caro, T. M. 1994. Ungulate antipredator behaviour: preliminary and comparative data from African bonds. *Behaviour* 128:189-228.
- Chander, G., and B. L. Markum. 2003. Revised Landsat-5 TM radiometric calibration procedures, and post-calibration dynamic ranges. *IEEE Transactions on Geoscience and Remote Sensing* 41:2674-2677.
- Chan-McLeod, A. C. A., R. G. White, and D. E. Russell. 1999. Comparative body composition strategies of breeding and non-breeding caribou. *Canadian Journal of Zoology* 77:1901-1907.
- Cichowski, D.B. 1993. Seasonal movements, habitat use, and winter feeding ecology of woodland caribou in west-central British Columbia. British Columbia Ministry of Environment, Lands, and Parks Land Management Report No. 79.
- Clark, C. W. 1994. Antipredator behaviour and the asset-protection principle. *Behavioural Ecology* 5:159-170.

- Crête, M., J. Huot, and L. Gauthier. 1990a. Food selection during early lactation by caribou calving on the tundra in Quebec. *Arctic* 43:60-65.
- Crête, M., J. Huot, R. Nault, and R. Patenaude. 1990b. Reproduction, growth, and body composition of Rivière George caribou in captivity. *Arctic* 46:189-196.
- Committee on the Status of Endangered Wildlife. 2002. Summary of the full list of Canadian species at risk. Canadian Wildlife Service, Environment Canada, Ottawa, Ontario, Canada
- Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2003. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs* 155:1-61.
- Corsi, F., J. de Leeuw, and A. K. Skidmore. 2000. Modeling Species Distribution with GIS. Pages 389-434 in L. Boitani and T. K. Fuller, editors. *Research Techniques in Animal Ecology: Controversies and Consequences*. Columbia University, New York, New York, USA.
- Cumming, H. G. 1992. Woodland caribou: facts for forest managers. *Forestry Chronicle* 68:481-491.
- Cumming, H. G., D. B. Beange, and Lavoie, G. 1996. Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared predation risk. *Rangifer*, Special Issue No. 9:81-94.
- Dale, B. W., L. G. Adams, and R. T. Bowyer. 1994. Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. *Journal of Animal Ecology* 63:644-652.
- Danell, K., L. Edehuis, and P. Lundberg. 1991. Herbivory and tree stand composition: moose patch use in winter. *Ecology* 72:1350-1357.
- Dauphiné, T. C. 1976. Biology of the Kaminuriak population of barren-ground caribou. Part 4: Growth, reproduction, and energy reserves. Canadian Wildlife Service Report Series No. 38.
- Demarchi, D. A. 1996. Introduction to the Ecoregions of British Columbia. British Columbia Wildlife Branch, Ministry of Environment, Lands and Parks, Victoria, British Columbia, Canada.
- D'Eon, R. G., R. Serrouya, G. Smith, and C. O. Kochanny. 2002. GPS radiotelemetry error and bias in mountainous terrain. *Wildlife Society Bulletin* 30:430-439.
- Downes, C. M., J. B. Theborge, and S. M. Smith. 1986. The influence of insects on the distribution, microhabitat choice, and behavior of the Burwash caribou herd. *Canadian Journal of Zoology* 64:622-629.

- Dussault, C., R. Courtois, J. P. Ouellet, and J. Huot. 1999. Evaluation of GPS telemetry collar performance for habitat studies in the boreal forest. *Wildlife Society Bulletin* 27:965-972.
- Dyer, S. J., O'Neill, J. P., S. M. Wasel, and S. Boutin. 2001. Avoidance of industrial development by woodland caribou. *Journal of Wildlife management* 65:531-542.
- Dyer, S. J., O'Neill, J. P., S. M. Wasel, and S. Boutin. 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. *Canadian Journal of Zoology* 80:839-845.
- Dzus, E. 2001. Status of the Woodland Caribou (*Rangifer tarandus caribou*) in Alberta. Alberta Environment, Fisheries and Wildlife Management Division, and Alberta Conservation Association, Wildlife Status Report No. 30, Edmonton, Alberta, Canada.
- Eastland, W. G., R. T. Bowyer, and S. G. Fancy. 1989. Effects of snow cover on selection of calving sites by caribou. *Journal of Mammalogy* 70:824-828.
- Fancy, S. G., and R. G. White. 1987. Energy expenditures for locomotion by barren-ground caribou. *Canadian Journal of Zoology* 65:122-128.
- Ferguson, S. H., A. T. Bergerud, and R. Ferguson. 1988. Predation risk and habitat selection in the persistence of a remnant caribou population. *Oecologia* 76:236-245.
- Frair, J. L., S. E. Nielsen, E. H. Merrill, S. R. Lele, M. S. Boyce, R. H. Munro, G. B. Stenhouse, and H. L. Beyer. 2004. Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology* 41:201-212.
- Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pages 111-164 *in* L. Boitani and T. K. Fuller, editors. *Research Techniques in Animal Ecology: Controversies and Consequences*. Columbia University, New York, New York, USA.
- Gasaway, W. C., R. D. Boertje, D. V. Grangaard, D. G. Kelleyhouse, R. O. Stephenson, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildlife Monographs* 120.
- Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelations of wolves, prey, and man in interior Alaska. *Journal of Wildlife Management* 47:1-50.
- Gerhart, K. L., R. G. White, R. D. Cameron, and D. E. Russell. 1996. Body

- composition and nutrient reserves of arctic caribou. *Canadian Journal of Zoology* 74:136-146.
- Grand, T. C. 2002. Alternative forms of competition and predation dramatically affect habitat selection under foraging-predation risk trade-offs. *Behavioural Ecology* 13:280-290.
- Griffith, B., D. C. Douglas, N. E. Walsh, D. D. Young, T. R. McCabe, D. E. Russell, R. G. White, R. D. Cameron, and K. R. Whitten. 2002. The Porcupine caribou herd. Pages 8-37 *in* Arctic Refuge coastal plain terrestrial wildlife research summaries. U.S. Geological Survey, Biological Resources Division, Biological Science Report USGS/BRD/BSR-2002-0001.
- Hamilton, W. D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31:295-311.
- Haugen, A. O., and D. W. Speake. 1958. Determining age of young fawn white-tailed deer. *Journal of Wildlife Management* 22:319-321.
- Heard, D. C., and K. L. Vagt. 1998. Caribou in British Columbia: a 1996 status report. *Rangifer*, Special Issue No. 10:117-123.
- Heard, D. C., T. M. Williams, and D. A. Melton. 1996. The relationship between food intake and predation risk in migratory caribou and implications to caribou and wolf population dynamics. *Rangifer*, Special Issue No. 9:37-44.
- Hebblewhite, M., and D. H. Pletscher. 2002. Effects of elk group size on predation by wolves. *Canadian Journal of Zoology* 80:800-809.
- Higgins, K. F., J. L. Oldemeyer, K. J. Jenkins, G. K. Clambey, and R. F. Harlow. 1996. Vegetation sampling and measurement. Pages 567-591 *in* T. A. Bookhout, editor. Research and management techniques for wildlife and habitats. The Wildlife Society, Bethesda, Maryland.
- Hooge, P. N., W. Eichenlaub, and E. K. Solomon. 1999. The animal movement program, v. 2.0. Available for review and download from the U.S. Geologic Survey at the Alaska Biological Center at <http://www.absc.usgs.gov/glba/gistools/index.htm>
- James A. R. C. 1999. Effects of industrial development on the predator-prey relationship between wolves and caribou in northeastern Alberta. PhD Dissertation, University of Alberta, Edmonton, Alberta, Canada.
- 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.

- Jenness, J. 2003. Random Point Generator, v. 1.27. Available for review and download at http://www.jennessent.com/arcview/random_points.htm
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- Johnson, C. J. 2000. A multi-scale approach to understanding the movements of woodland caribou. PhD Dissertation, University of Northern British Columbia, Prince George, British Columbia, Canada.
- Johnson, C. J., K. L. Parker, and D. C. Heard. 2000. Feeding site selection by woodland caribou in north-central British Columbia. *Rangifer*, Special Issue No. 12:159-172.
- Johnson, C. J., K. L. Parker, and D. C. Heard. 2001. Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. *Oecologia* 127:590-602.
- Johnson, C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002a. Movement parameters of ungulates and scale-specific responses to the environment. *Journal of Animal Ecology* 71:225-235.
- Johnson, C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002b. A multiscale behavioral approach to understanding the movements of woodland caribou. *Ecological Applications* 12:1840-1860.
- Johnson, C. J., D. R. Seip, and M. S. Boyce. 2004. Characterizing woodland caribou habitat in sub-boreal and boreal forests. *Journal of Applied Ecology* 41:238-251.
- Joly, K., B. W. Dale, W. B. Collins, and L. G. Adams. 2003. Winter habitat use by female caribou in relation to wildland fires in interior Alaska. *Canadian Journal of Zoology* 81:1192-1201.
- Kats, L. B., and Dill, L. M. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. *Ecoscience* 5:361-394.
- Kie, J. G. 1999. Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. *Journal of Mammalogy* 80:1114-1129.
- Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. *Ecology* 83:530-544.
- Klein, D. R. 1982. Fire, lichens, and caribou. *Journal of Range Management* 35:390-395.

- Krebs, C. J. 1989. *Ecological Methodology*. First edition. Harper and Row, New York.
- Krebs, J. R. 1980. Optimal foraging, predation risk, and territory defence. *Ardea* 68:83-90.
- Landa, A., J. Strand, J. E. Swenson, and T. Skogland. 1997. Wolverines and their prey in southern Norway. *Canadian Journal of Zoology* 75:1292-1299.
- Lenart, E. A., R. T. Bowyer, J. Ver Hoef, and R. W. Ruess. 2002. Climate change and caribou: effects of summer weather on forage. *Canadian Journal of Zoology* 80:664-678.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943-1967.
- Lima S. L. 1988. Initiation and termination of daily feeding in dark-eyed juncos: influences of predation risk and energy reserves. *Oikos* 53:3-11.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619-640.
- Lingle, S. 2002. Coyote predation and habitat segregation of white-tailed deer and mule deer. *Ecology* 83:2037-2048.
- Mahoney, S. P., and J. A. Virgl. 2003. Habitat selection and demography of a nonmigratory woodland caribou population in Newfoundland. *Canadian Journal of Zoology* 81:321-334.
- Manel, S., H. C. Williams, and S. J. Ormerod. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* 38:921-931.
- Manly, B. F., L. L. McDonald, and D. L. Thomas. 2002. *Resource selection by animals: statistical design and analysis for field studies*. Second edition. Chapman-Hall, London, U.K.
- McClellan, S. A., M. A. Rumble, R. M. King, and W. L. Baker. 1998. Evaluation of resource selection methods with different definitions of availability. *Journal of Wildlife Management* 62:793-801.
- McLoughlin, P. D., R. L. Case, R. J. Gau, H. D. Cluff, R. Mulders, and F. Messier. 2002. Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. *Oecologia* 132:102-108.
- McLoughlin, P. D., E. Dzuz, B. Wynes, and S. Boutin. 2003. Declines in

- populations of woodland caribou. *Journal of Wildlife Management* 64:755-761.
- Mech, L. D. 1977. Wolf pack buffer zones as prey reservoirs. *Science* 198:320-321.
- Mech, L. D. 1994. Buffer zones of territories of gray wolves as regions of intraspecific strife. *Journal of Mammalogy* 75:199-202.
- Menard, S. 2002. Applied logistic regression analysis. Second edition. Sara Miller McCune, Sage, Thousand Oaks, California, USA.
- Miller, L. E. 2002. Introduction to predator sensitive foraging. Pages 1-17 *in* L. E. Miller, editor. *Eat or be eaten: predator sensitive foraging among primates*. Cambridge University, Cambridge, United Kingdom.
- Ministry of Crown Lands. 1990. Terrain and Resource Inventory Management in British Columbia Specifications and Guidelines for Geomatics: Digital Baseline Mapping at 1:20,000. Ministry of Crown Lands for the Government of British Columbia, Victoria, British Columbia, Canada.
- Mitchell, W. A., and S. L. Lima. 2002. Predator-prey shell games: large-scale movement and its implications for decision-making by prey. *Oikos* 99:249-259.
- Mohr, C. O. 1947. Table of equivalent populations in North American mammals. *The American Midland Naturalist* 37:223-249.
- Molvar, E. M., and R. T. Bowyer. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. *Journal of Mammalogy* 75:621-630.
- Mosnier, A., J. Ouellet, L. Sirois, and N. Fournier. 2003. Habitat selection and home-range dynamics of the Gaspé caribou: a hierarchical analysis. *Canadian Journal of Zoology* 81:1174-1184.
- Murphy, S. M., and J. A. Curatolo . 1987. Activity budgets and movement rates of caribou encountering pipelines, roads, and traffic in northern Alaska. *Canadian Journal of Zoology* 65:2483-2490.
- Nelleman, C., and R. D. Cameron 1998. Cumulative impacts of an evolving oil-field complex on the distribution of calving caribou. *Canadian Journal of Zoology* 76:1425-1430.
- Nielsen, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. M. Munro. 2002. Modelling grizzly bear habitats in the Yellowhead ecosystem of Alberta: taking

autocorrelation seriously. *Ursus* 13:45-56.

- Nielsen, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. Munro. 2003. Development and testing of phenologically driven grizzly bear habitat models. *Ecoscience* 10:1-10.
- Oindo, B. 2002. Predicting Mammal Species Richness and Abundance Using Multi-temporal NDVI. *Photogrammetric Engineering and Remote Sensing* 68:623-629.
- Oosenbrug, S. M., and J. B. Theberge. 1980. Altitudinal movements and summer habitat preferences of woodland caribou in the Kluane Ranges, Yukon Territory. *Arctic* 33:59-72.
- Palmer, M. W. 1993. Putting things in even better order: the advances of canonical correspondence analysis. *Ecology* 74:2215-2230.
- Parker, K. L. 1989. Growth rates and morphological measurements of caribou calves. *Rangifer* 9:9-13.
- Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. *Journal of Wildlife Management* 48:474-488.
- Parker, K. L., R. G. White, M. P. Gillingham, and D. F. Holleman. 1990. Comparison of energy metabolism in relation to daily activity and milk consumption by caribou and muskox neonates. *Canadian Journal of Zoology* 68:106-114.
- Peck, R., and J. M. Peek. 1991. Elk (*Cervus elaphus*) habitat use related to prescribed fire, Tuchodi River, British Columbia. *Canadian Field-Naturalist* 105:354-362.
- Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53:7-15.
- Poole, K. G., D. C. Heard, and G. Mowat. 2000. Habitat use by woodland caribou near Takla Lake in central British Columbia. *Canadian Journal of Zoology* 78:1552-1561.
- Post, E., P. S. Bøving, C. Pederson, and M. A. MacArthur. 2003. Synchrony between caribou calving and plant phenology in depredated and non-depredated populations. *Canadian Journal of Zoology* 81:1709-1714.
- Post, E., and D. R. Klein. 1999. Caribou calf production and seasonal range quality during a population decline. *Journal of Wildlife Management* 63:335-345.

- Rachlow, J. L., and R. T. Bowyer. 1998. Habitat selection by Dall's sheep (*Ovis dalli*): maternal trade-offs. *Journal of Zoology* 245:457-465.
- Reed, B. C., J. F. Brown, D. Vander Zee, T. R. Loveland, J. W. Merchant, and D. O. Ohlen. 1994. Measuring the phenological variability from satellite imagery. *Journal of Vegetation Science* 5:703-714.
- Reimers, E., D. R. Klein, and R. Sørungård. 1983. Calving time, growth rate, and body size of Norwegian reindeer on different ranges. *Alpine Arctic Research* 15:107-118.
- Rettie, W. J., and F. Messier. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. *Canadian Journal of Zoology* 76:251-259.
- Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23:466-478
- Rogers, L. L., L. D. Mech, D. K. Dawson, J. M. Peek, and M. Korb. 1980. Deer distribution in relation to wolf pack territory edges. *Journal of Wildlife Management* 44:253-258.
- Ruimy, A., G. Dedieu, and B. Saugier. 1994. Methodology for the estimation of terrestrial net primary production from remotely sensed data. *Journal of Geophysical Research* 99:5263-5283.
- Russell, D. E., K. L. Gerhart, R. G. White, and D. Van de Wetering. 1998. Detection of early pregnancy in caribou: evidence for embryonic mortality. *Journal of Wildlife Management* 62:1066-1075.
- Russell, D. E., A. M. Martell, and W. A. C. Nixon. 1993. Range ecology of the Porcupine Caribou Herd in Canada. *Rangifer* Special Issue No. 8:1-168.
- Schaefer, J. A., and F. Messier. 1995. Habitat selection as a hierarchy: the spatial scales of winter foraging by muskoxen. *Ecography* 18:333-344.
- Schaefer, J. A., and W. O. Pruitt Jr. 1991. Fire and woodland caribou in southeastern Manitoba. *Wildlife Monographs* 116.
- Seip, D. R. 1990. Ecology of woodland caribou in Wells Gray Provincial Park. *British Columbia Ministry of Environment Wildlife Bulletin* B-68.
- Seip, D. R. 1991. Predation and caribou populations. *Rangifer* 11:46-52.
- Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology* 70:1494-1503.

- Seip, D. R. 1998. Ecosystem management and the conservation of caribou habitat in British Columbia. *Rangifer* Special Issue No. 10:203-212.
- Seip, D. R., and D. B. Cichowski. 1996. Population ecology of caribou in British Columbia. *Rangifer* Special Issue No. 9:73-80.
- Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging ecology and ecological hierarchies. *BioScience* 37:789-791.
- Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. First edition. McGraw-Hill, New York, New York.
- Siegel, S., and N. J. Castellan. 1988. Nonparametric statistics for the behavioral sciences. Second edition. McGraw-Hill, New York, New York.
- Skogland, T. 1991. What are the effects of predators on large ungulate populations. *Oikos* 61:401-410.
- Skoog, R. O. 1968. Ecology of the caribou (*Rangifer tarandus grantii*) in Alaska. PhD Dissertation. University of California, Berkeley, CA, USA.
- Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. Third edition. W. H. Freeman and Co., New York.
- Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. First edition. Princeton University, New Jersey.
- Stuart-Smith, A. K., C. J. A. Bradshaw, S. Boutin, D. M. Hebert, and A. B. Rippin. 1997. Woodland caribou relative to landscape patterns in northeastern Alberta. *Journal of Wildlife Management* 61:622-633.
- Sweitzer, R. A. 1996. Predation or starvation: foraging decisions by porcupines (*Erethizon dorsatum*). *Journal of Mammalogy* 77:1068-1077.
- Thomas, D. C. 1998. Fire caribou relationships: (VII) Fire management on the winter range of the Beverly herd: final conclusions and recommendations. Technical Report Series No. 315. Canadian Wildlife Service, Edmonton, Alberta, Canada.
- Thomas, D. L., and E. J. Taylor. 1990. Study designs and tests for comparing resource use and availability. *Journal of Wildlife Management* 54:322-330.
- Tucker, C. J., and P. J. Sellers. 1986. Satellite remote sensing of primary production. *International Journal of Remote Sensing* 7:1395-1416.

- Vangen, K. M., J. Persson, A. Landa, R. Andersen, and P. Segerström. 2001. Characteristics of dispersal in wolverines. *Canadian Journal of Zoology* 79:1641-1649.
- Vik Stronen, A. 2000. Habitat selection and calf survival in the Telkwa caribou herd, British Columbia 1997-2000. Master of Environmental Design Thesis, University of Calgary, Calgary, Alberta.
- Weclaw, P., and R. J. Hudson. 2004. Simulation of conservation and management of woodland caribou. *Ecological Modelling* 177:75-94.
- Weladji, R. B., and O. Holand. 2003. Global climate change and reindeer: effects of winter weather on the autumn weight and growth of calves. *Oecologia* 136:317-323.
- White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.
- White, K. S., and J. Berger. 2001. Antipredator strategies of Alaskan moose: are maternal trade-offs influenced by offspring activity? *Canadian Journal of Zoology* 79:2055-2062.
- White, K. S., J. W. Testa, and J. Berger. 2001. Behavioral and ecologic effects of differential predation pressure on moose in Alaska. *Journal of Mammalogy* 82:422-429.
- White, R. G., F. L. Bunnell, E. Gaare, T. Skogland, and B. Hubert. 1981. Ungulates on arctic ranges. Pages 397-483 in L. C. Bliss, O. W. Heal, and J. J. Moore, editors. *Tundra ecosystems: a comparative analysis*. International Biological Program 25. Cambridge University, Cambridge, England, U.K.
- White, R. G., and J. R. Luick. 1984. Plasticity and constraints in the lactational strategy of reindeer and caribou. *Symposia of the Zoological Society of London* 51:215-232.
- Whitman, J. S., W. B. Ballard, and C. L. Gardner. 1986. Home range and habitat use by wolverines in south-central Alaska. *Journal of Wildlife Management* 50:460-463.
- Whitten, K. R., and R. D. Cameron. 1980. Nutrient dynamics of caribou forage on Alaska's Arctic slope. *Proceedings of the Second International Reindeer/Caribou Symposium*:159-166.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.
- Wittmer, H. 2004. Mechanisms underlying the decline of mountain caribou in British

Columbia. PhD Dissertation, University of British Columbia, Vancouver, British Columbia, Canada.

- Wood, M. 1996. Seasonal habitat use and movements of woodland caribou in the Omineca Mountains, north central British Columbia, 1991-1993. *Rangifer*, Special Issue No. 9:365-378.
- Young, D. D., and T. R. McCabe. 1997. Grizzly bear predation rates on caribou calves in northeastern Alaska. *Journal of Wildlife Management* 61:1056-1066.
- Zar, J. H. 1998. *Biostatistical analysis*. Fourth edition. Prentice-Hall, New Jersey, USA.
- Zimmerman, K. L., R. S. McNay, L. Gigure, J. J. Joy, K. Schmidt, P. Hengeveld, S. Walshe, G. Keddie, and L. Wilson. 2002. Ecological factors affecting northern caribou in the Omineca Region, British Columbia: 2001. Pacific Slope Consulting, Vancouver, British Columbia, Canada.

Appendix A: Specifications and schematic of the expandable drop-off radiocollar for woodland caribou (*Rangifer tarandus caribou*) calves that were captured and monitored in the Greater Besa Prophet area, northern British Columbia.

Table A.1. Specifications for the expandable drop-off collars for newborn caribou calves (T. Pojar, Colorado Division of Wildlife, pers. comm.); Advanced Telemetry Systems, Isanti, MN, USA) that were used to monitor 50 caribou neonates in the Greater Besa Prophet area, northern British Columbia, 2002-2003.

Specifications
Radio pack attached to 2" wide light weight belting
Belt tab extend 2" beyond radio pack on one side
8" length of 2 " wide elastic attached to opposite side of radio pack
Elastic with 1.5:1 expansion
Incorporate antenna into this length of elastic
4" tab of light weight 2 " wide belting attached to end of elastic opposite the radio pack
Paired holes punched in the belt tab attached to the elastic 3/4" apart at 1/2" intervals
One set of paired holes 3/4 " apart punched in the belt tab attached to the radio pack 1" from radio pack
3/4" fasteners (with nuts) per collar, threaded portion 1/2" long (or may use nylon zip ties for all necessary fastening)
Total weight less than 120 g
Radio life warranted 6 months
Frequency drift \pm 2KHz
Mortality sensor set at 2 hrs
Pulse rate 55-65 ppm
Pulse width 20-30 ms
Identification tag embedded in radio pack
Two lengths of latex surgical tubing 2.54 cm long; 7 mm inner and 10 mm outer diameter; small lengths of heat shrink tape wrapped around ends to keep tubing from tearing prematurely

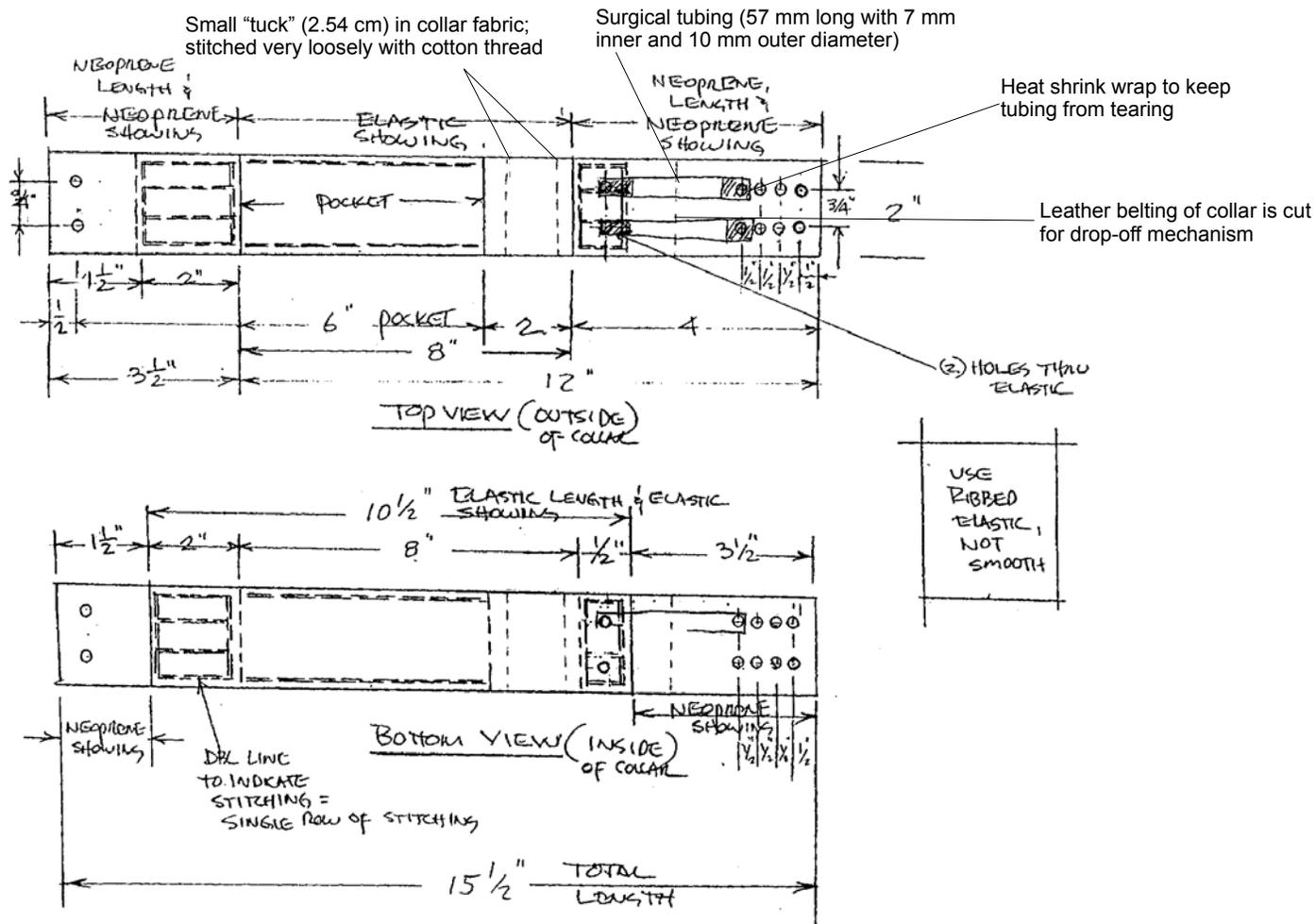


Figure A.1. Schematic of the expandable drop-off collar for neonatal caribou calves (T. Pojar, Colorado Division of Wildlife; Advanced Telemetry Systems, Isanti, MN, USA) that was used to monitor 50 neonates in the Greater Besa Prophet area, northern British Columbia, 2002-2003.

Appendix B: Classification of habitats in the Greater Besa Prophet area, northern British Columbia.

Table B.1. Nine classes of vegetation used for analyses of habitat selection by grizzly bears, wolves, and woodland caribou in the Greater Besa Prophet area, northern British Columbia, 2001.

Vegetation Classes	Users accuracy (%)^a	Producers Accuracy (%)^a	Original 15 Classes^a	Description^a
Spruce	82.4	70.0	Spruce + Low productivity Spruce	White and hybrid spruce (<i>Picea glauca</i> and <i>Picea glauca</i> x <i>engelmanni</i>)-dominated communities
Shrubs	50.0	75.0	Shrubs	Deciduous shrubs < 1600 m dominated by birch (<i>Betula</i> spp.) and willow (<i>Salix</i> spp.), some cinquefoil (<i>Potentilla fruticosa</i>)
Subalpine	87.5	87.5	Shrubs + Subalpine Spruce	Deciduous shrubs > 1599 m; spruce-shrub transition zone at middle to upper elevations (white and hybrid-spruce, and dominated by birch and willow)
<i>Carex</i> spp.	77.8	70.0	<i>Carex</i> spp.	Wetland meadows dominated by sedges (<i>Carex</i> spp.), typically at low elevations
Non-vegetated	92.9	100.0	Rocks, Rock/Crustose Lichens, Snow/Glacier, and Water	Rock; rock habitats with black, crustose lichens; permanent snow-fields or glaciers and water bodies

Table B.1. Continued.

Vegetation Classes	Users accuracy (%)^a	Producers Accuracy (%)^a	Original Classes^a	Description^a
Pine	60.0	60.0	Pine	Lodgepole pine (<i>Pinus contorta</i>)-dominated communities
Riparian Spruce	78.3	90.0	Riparian Spruce and Gravel Bar	Low elevation, wet areas with black (<i>Picea mariana</i>) and hybrid spruce; often with standing water in spring and summer; exposed gravel bars adjacent to rivers and creeks
Alpine	94.1	80.0	Wet and Dry Alpine	Herbaceous alpine vegetation
Burned/ Disturbed	88.9	80.0	Burned/Disturbed	Previously burned areas, grass, deciduous trees, or avalanche chutes
Overall Accuracy	83.9			

^aAs determined by R.J. Lay (University of Northern British Columbia, unpublished data).

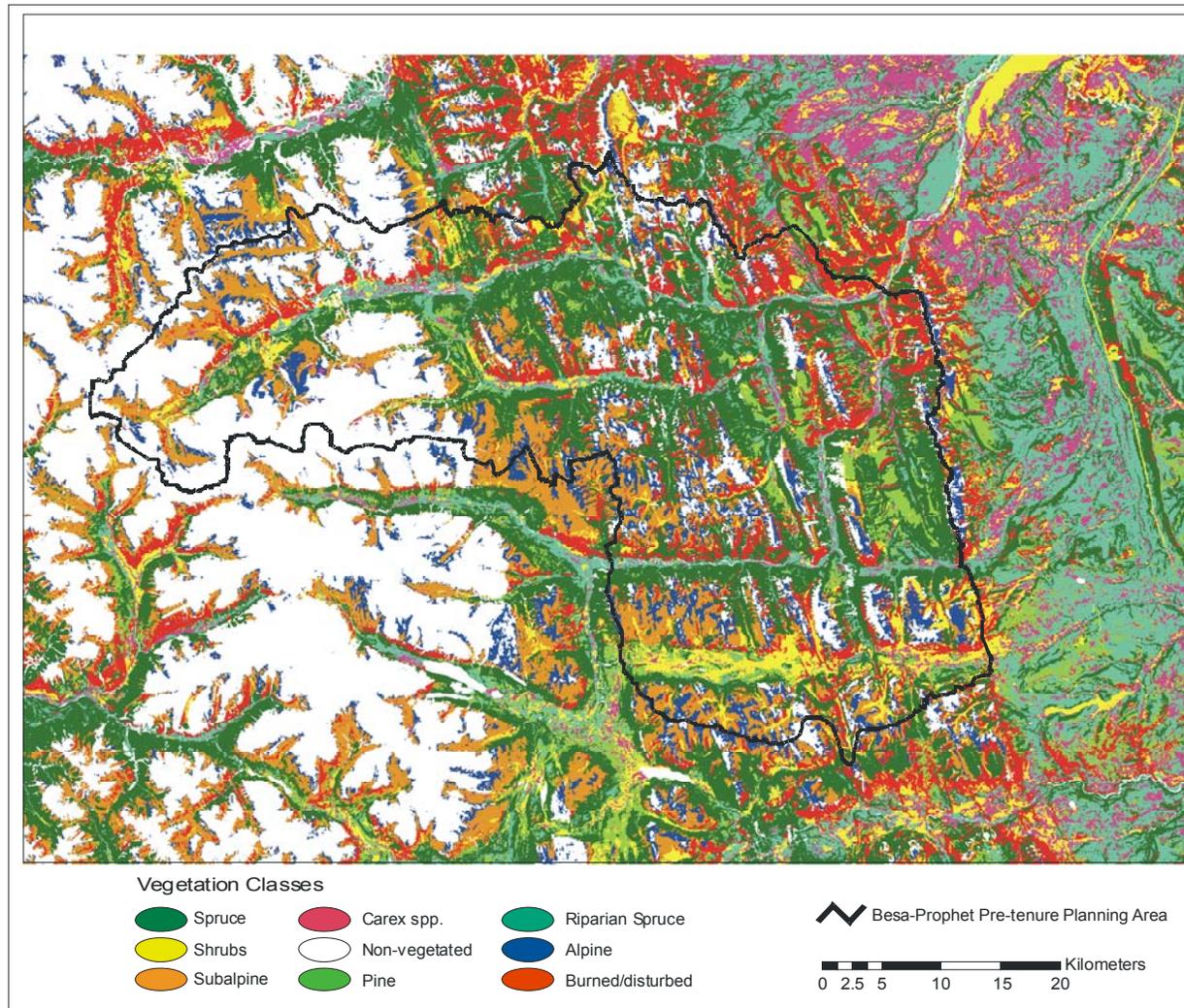


Figure B.1. Nine habitats, as defined using a vegetation classification from an August 15, 2001 Landsat Enhanced Thematic Mapper image (see Table B.1), in the Greater Besa Prophet area, northern British Columbia.

Appendix C: Defining the risk of predation from grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) for female caribou during the calving and summer seasons in the Greater Besa Prophet area, northern British Columbia.

Table C.1. An ecologically plausible set of models used to define the risk of predation from grizzly bears during the calving and summer seasons in the Greater Besa Prophet area, northern British Columbia, 2002-2003.

Models
Vegetation + Aspect + Fragmentation + Elevation + Elevation ²
Vegetation + Aspect + Elevation + Elevation ²
Vegetation + Fragmentation + Elevation + Elevation ²
Vegetation + Fragmentation
Vegetation
Aspect + Fragmentation + Elevation + Elevation ²
Aspect + Elevation + Elevation ²
Elevation + Elevation ² + Fragmentation
Fragmentation + Slope

Table C.2. Final pooled models of bear risk (based on locations from 15 female grizzly bears) by season and year in the Greater Besa Prophet area, northern British Columbia, 2002-2003 showing sample size (n), log-likelihood (LL), number of parameters (K), Akaike's Information Criterion (AIC), change in AIC (Δ_i), Akaike weights (w_i), evidence ratios (E_r), and average ($n = 5$) Spearman's correlation coefficient from k-fold cross-validation (\bar{r}_s) with associated p-values (P).

Year	Season	Model	n	LL	K	AIC	Δ_i^a	w_i^a	E_r^a	\bar{r}_s^{bc}	P^c
2002	Calving	Vegetation + Fragmentation + Elevation + Elevation ²	1986	-824.886	13	1675.773	0.000	0.954	1.00	0.90	< 0.001
	Summer ^d	Vegetation + Fragmentation + Elevation + Elevation ²	6645	-2720.525	13	5467.050	0.000	0.508	1.00	0.95	< 0.001
		Vegetation + Aspect + Fragmentation + Elevation + Elevation ²	6645	-2716.638	17	5467.275	0.226	0.454	1.12	0.97	< 0.001
2003	Calving	Vegetation + Aspect + Fragmentation + Elevation + Elevation ²	4931	-2102.896	17	4239.791	0.000	0.994	1.00	0.91	< 0.001
	Summer	Vegetation + Aspect + Fragmentation + Elevation + Elevation ²	10307	-4220.158	17	8474.316	0.000	0.999	1.00	0.97	< 0.001

^aBurnham and Anderson (2002)

^bBoyce et al. (2002)

^cSiegel (1956)

^dModels were averaged

Table C.3. Coefficients of selection (β_i and $\bar{\beta}_i$ for an averaged model from Table C.2) and standard errors (SE) of the covariates for the final pooled models of bear risk by season and year in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Significant parameters are indicated by asterisk(s).

Covariates	Calving 2002	Summer 2002	Calving 2003	Summer 2003
	$\beta_i \pm \text{SE}$	$\bar{\beta}_i \pm \text{SE}$	$\beta_i \pm \text{SE}$	$\bar{\beta}_i \pm \text{SE}$
Elevation (km)	21.512 ± 5.193**	5.128 ± 1.537**	14.270 ± 2.439**	6.196 ± 1.130**
Elevation ² (km)	-7.088 ± 1.688**	-1.608 ± 0.478**	-4.836 ± 0.757**	-2.238 ± 0.370**
Low fragmentation	-0.336 ± 0.106**	-0.232 ± 0.047**	-0.240 ± 0.066**	-0.178 ± 0.045**
Medium fragmentation	-0.101 ± 0.091	0.037 ± 0.040	0.014 ± 0.056	0.126 ± 0.038**
High fragmentation	0.437 ± 0.088**	0.196 ± 0.041**	0.226 ± 0.057**	0.053 ± 0.041
Slope (°)				
North		0.044 ± 0.036	-0.194 ± 0.101	0.182 ± 0.061*
East		-0.038 ± 0.034	-0.190 ± 0.095*	-0.255 ± 0.059**
South		-0.067 ± 0.039	0.180 ± 0.087*	-0.271 ± 0.059**
West		-0.059 ± 0.043	-0.118 ± 0.104	-0.083 ± 0.069
No aspect (flat)		0.120 ± 0.090	0.323 ± 0.256	0.427 ± 0.137*
Spruce	-0.037 ± 0.153	-0.186 ± 0.075*	-0.094 ± 0.114	-0.453 ± 0.076**
Shrubs	-0.557 ± 0.289	0.322 ± 0.106*	-0.375 ± 0.188*	0.317 ± 0.098**
Subalpine	-0.209 ± 0.175	0.618 ± 0.072**	-0.031 ± 0.119	0.901 ± 0.070**
<i>Carex</i> spp.	1.082 ± 0.439*	0.412 ± 0.186*	-0.384 ± 0.368	-0.026 ± 0.189
Non-vegetated	-0.315 ± 0.209	-1.323 ± 0.140**	0.511 ± 0.122**	-0.879 ± 0.132**
Pine	-1.111 ± 0.478*	-0.165 ± 0.154	-0.472 ± 0.243	-0.314 ± 0.154*
Riparian spruce	1.146 ± 0.299**	0.319 ± 0.137*	0.169 ± 0.239	-0.115 ± 0.134
Alpine	-0.226 ± 0.237	-0.527 ± 0.122**	0.207 ± 0.147	-0.258 ± 0.120*
Burned/disturbed	0.227 ± 0.182	0.530 ± 0.083**	0.468 ± 0.120**	0.825 ± 0.078**

* $P < 0.05$

** $P < 0.001$

Table C.4. An ecologically plausible set of models used to define the risk of predation from wolves in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Models were developed for 5 wolf packs: pack 1 (Dopp-Keily), pack 2 (Lower Besa), pack 3 (Neves), pack 4 (Pocketknife), and pack 5 (Richards-Upper Prophet).

Models
Vegetation + Aspect + Fragmentation + Elevation + Elevation ²
Vegetation + Aspect + Elevation + Elevation ²
Vegetation + Fragmentation + Elevation + Elevation ²
Vegetation + Fragmentation
Vegetation
Aspect + Elevation + Elevation ²
Aspect + Fragmentation
Slope + Aspect
Elevation + Elevation ² + Fragmentation
^a Vegetation + Fragmentation + Distance to Linear Features + Distance to Linear Features ²
^a Linear Distance + Distance to Linear Features + Distance to Linear Features ²
^a Vegetation + Distance to Linear Features + Distance to Linear Features ²
^a Fragmentation + Distance to Linear Features + Distance to Linear Features ²

^aModels evaluated only for pack 4 which occurs on the eastern edge of the study area where linear features are present

Table C.5. Final pooled models of wolf risk (based on locations from 22 individuals in 5 wolf packs) by season and year in the Greater Besa Prophet area, northern British Columbia, 2002-2003 showing sample size (n), log-likelihood (LL), number of parameters (K), Akaike's Information Criterion (AIC), change in AIC (Δ_i), Akaike weights (w_i), evidence ratios (E_r), and average ($n = 5$) Spearman's correlation coefficient from k-fold cross-validation (\bar{r}_s) with associated p-values (P).

Year	Season	Model	n	LL	K	AIC	Δ_i^a	w_i^a	E_r^a	\bar{r}_s^{bc}	P^c
2002	Calving	Vegetation + Aspect + Fragmentation + Elevation + Elevation ²	1891	-751.959	17	1537.917	0.000	0.973	1.00	0.88	< 0.001
	Summer	Slope + Aspect	4321	-1707.875	6	3427.749	0.000	1.000	1.00	0.97	< 0.001
2003	Calving	Vegetation + Aspect + Fragmentation + Elevation + Elevation ²	1791	-866.135	17	1766.269	0.000	0.995	1.00	0.92	< 0.001
	Summer	Vegetation + Aspect + Fragmentation + Elevation + Elevation ²	3052	-1213.817	17	2461.633	0.000	0.491	1.00	0.94	< 0.001

^aBurnham and Anderson (2002)

^bBoyce et al. (2002)

^cSiegel (1956)

Table C.6. Coefficients of selection (β_i for models from Table C.5) and standard errors (SE) of the covariates for the final pooled models of wolf risk across packs by season and year in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Significant parameters are indicated by asterisk(s).

Covariates	Calving 2002	Summer 2002	Calving 2003	Summer 2003
	$\beta_i \pm SE$	$\beta_i \pm SE$	$\beta_i \pm SE$	$\beta_i \pm SE$
Elevation (km)	7.234 ± 2.839*		6.812 ± 1.827**	4.647 ± 1.459**
Elevation ² (km)	-3.090 ± 1.056*		-2.982 ± 0.740**	-1.695 ± 0.566*
Low fragmentation	-0.374 ± 0.117*		-0.368 ± 0.105**	0.001 ± 0.080
Medium fragmentation	0.192 ± 0.092*		0.244 ± 0.082*	-0.156 ± 0.073*
High fragmentation	0.182 ± 0.096		0.124 ± 0.087	0.155 ± 0.073*
Slope (°)		-0.089 ± -0.005**		
North	-0.130 ± 0.128	0.371 ± 0.081**	-0.373 ± 0.120*	0.024 ± 0.098
East	-0.386 ± 0.131*	0.021 ± 0.082	-0.346 ± 0.122*	-0.229 ± 0.104*
South	0.219 ± 0.123	0.234 ± 0.085*	0.269 ± 0.109*	-0.158 ± 0.102
West	-0.546 ± 0.181*	-0.410 ± 0.117**	-0.270 ± 0.135*	-0.018 ± 0.115
No aspect (flat)	0.843 ± 0.168**	-0.216 ± 0.143	0.720 ± 0.177**	0.381 ± 0.164*
Spruce	-0.604 ± 0.184**		-0.152 ± 0.15	-0.140 ± 0.135
Shrubs	0.659 ± 0.188**		0.864 ± 0.166**	1.087 ± 0.147**
Subalpine	-0.158 ± 0.262		0.130 ± 0.221	0.561 ± 0.137**
<i>Carex</i> spp.	0.395 ± 0.234		0.329 ± 0.218	0.524 ± 0.202*
Non-vegetated	0.171 ± 0.272		-0.115 ± 0.273	-1.558 ± 0.310**
Pine	-0.811 ± 0.304*		-0.235 ± 0.265	-0.237 ± 0.224
Riparian spruce	0.215 ± 0.186		0.497 ± 0.182*	0.541 ± 0.173*
Alpine	0.211 ± 0.361		-1.063 ± 0.496*	-0.414 ± 0.259
Burned/disturbed	-0.078 ± 0.193		-0.254 ± 0.195	-0.364 ± 0.209

* $P < 0.05$

** $P < 0.001$

Table C.7. Final pack models of wolf risk (based on locations from 22 individuals in 5 wolf packs) by season in the Greater Besa Prophet area, northern British Columbia, 2002 showing ample size (n), log-likelihood (LL), number of parameters (K), Akaike's Information Criterion (AIC), change in AIC (Δ_i), Akaike weights (w_i), evidence ratios (E_r), and average ($n = 5$) Spearman's correlation coefficient from k-fold cross-validation (\bar{r}_s) with associated p-values (P).

Pack	Season	Model	n	LL	K	AIC	Δ_i^a	w_i^a	E_r^a	\bar{r}_s^{bc}	P^c
1 ^d	Calving	Vegetation + Aspect + Elevation	390	-129.068	14	287.107	0.000	0.753	1.00	0.49	0.151
		Vegetation + Aspect + Fragmentation + Elevation	390	-128.381	16	290.049	2.941	0.173	4.35	0.55	0.100
1	Summer	Slope + Aspect	999	-380.482	6	772.963	0.000	1.000	1.00	0.85	0.002
2	Calving	Elevation + Elevation ² + Fragmentation	169	-66.041	5	142.327	0.000	0.921	1.00	0.62	0.056
2	Summer	Slope + Aspect	720	-248.151	6	508.302	0.000	1.000	1.00	0.83	0.003
3	Calving	Elevation + Elevation ² + Fragmentation	105	-38.078	5	86.561	0.000	0.472	1.00	0.71	0.021
3	Summer	Vegetation + Aspect + Fragmentation + Elevation + Elevation ²	678	-228.694	17	491.388	0.000	0.930	1.00	0.75	0.013
4 ^d	Calving	Vegetation + Aspect + Fragmentation + Elevation + Elevation ²	349	-122.426	15	276.113	0.000	0.733	1.00	0.63	0.051
		Vegetation + Fragmentation + Distance to Linear Features + Distance to Linear Features ²	349	-128.956	11	280.565	4.453	0.079	9.26	0.60	0.067
4	Summer	Vegetation + Fragmentation + Elevation + Elevation ²	840	-326.815	13	679.629	0.000	0.621	1.00	0.80	0.006
5	Calving	Vegetation + Aspect + Elevation	510	-175.829	14	380.394	0.000	0.665	1.00	0.71	0.021
5 ^d	Summer	Vegetation + Aspect + Elevation	964	-343.989	14	715.978	0.000	0.805	1.00	0.80	0.006
		Vegetation + Aspect + Fragmentation + Elevation	964	-343.870	16	719.739	3.761	0.123	6.56	0.88	0.001

^aBurnham and Anderson (2002), ^bBoyce et al. (2002), ^cSiegel (1956), and ^dModels were averaged

Table C.8. Sample size (n), log-likelihood (LL), number of parameters (K), Akaike's Information Criterion (AIC), change in AIC (Δ_i), Akaike weights (w_i), evidence ratios (E_r), and average ($n = 5$) Spearman's correlation coefficient from k-fold cross-validation (\bar{r}_s) with associated p-values (P) for the final pack models of wolf risk (based on locations from 22 individuals in 5 wolf packs) by season in the Greater Besa Prophet area, northern British Columbia, 2003.

Pack	Season	Model	n	LL	K	AIC	Δ_i^a	w_i^a	E_r^a	\bar{r}_s^{bc}	P^c
1	Calving	Vegetation + Aspect + Fragmentation + Elevation	522	-226.110	16	485.171	0.000	0.889	1.00	0.79	0.007
1 ^d	Summer	Vegetation	809	-293.722	9	605.444	0.000	0.573	1.00	0.64	0.046
		Vegetation + Fragmentation + Elevation + Elevation ²	809	-290.788	13	607.576	2.132	0.197	2.90	0.86	0.001
2 ^d	Calving	Vegetation + Aspect + Elevation + Elevation ²	809	-289.257	15	608.513	3.069	0.124	4.64	0.88	0.001
		Vegetation + Aspect + Elevation + Elevation ²	346	-106.841	12	238.475	0.000	0.567	1.00	0.61	0.061
		Vegetation + Fragmentation + Elevation + Elevation ²	346	-108.324	11	239.307	0.966	0.350	1.62	0.64	0.046
		Vegetation + Aspect + Fragmentation + Elevation + Elevation ²	346	-105.782	15	242.837	3.882	0.082	6.97	0.56	0.092
2	Summer	Vegetation + Fragmentation + Elevation	406	-128.960	10	278.375	0.000	0.807	1.00	0.74	0.014
3	Calving	Vegetation + Fragmentation + Elevation + Elevation ²	238	-79.500	13	186.393	0.000	0.812	1.00	0.67	0.034
3	Summer	Vegetation + Aspect + Elevation + Elevation ²	564	-212.066	14	452.794	0.000	0.684	1.00	0.67	0.034
4 ^d	Calving	Vegetation + Aspect + Elevation + Elevation ²	302	-143.091	13	313.265	0.000	0.644	1.00	0.58	0.079
		Vegetation + Aspect + Fragmentation + Elevation + Elevation ²	302	-141.947	15	315.363	1.713	0.274	2.35	0.52	0.123
4	Summer	Fragmentation + Distance to Linear Features + Distance to Linear Features ²	420	-176.011	4	360.080	0.000	0.684	1.00	0.69	0.027
5	Calving	Elevation + Elevation ² + Fragmentation	357	-169.374	5	348.861	0.000	0.962	1.00	0.70	0.024
5	Summer	Vegetation + Fragmentation + Elevation + Elevation ²	779	-283.188	13	592.375	0.000	0.728	1.00	0.85	0.002

^aBurnham and Anderson (2002), ^bBoyce et al. (2002), ^cSiegel (1956), and ^dmodels were averaged

Table C.9. Coefficients of selection (β_i and $\bar{\beta}_i$ for an averaged model from Tables C.7, C.8) and standard errors (SE) of the covariates for the final risk models for wolf pack 1 (Dopp-Keily) by season and year in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Significant parameters are indicated by asterisk(s).

Covariates	Calving 2002	Summer 2002	Calving 2003	Summer 2003
	$\bar{\beta}_i \pm SE$	$\beta_i \pm SE$	$\hat{\beta} \pm SE$	$\beta_i \pm SE$
Elevation (km)	-4.013 ± 1.091**		-2.113 ± 1.154	3.551 ± 2.74
Elevation ² (km)				-1.327 ± 0.91
Low fragmentation	-0.057 ± 0.063		-0.206 ± 0.189	-0.001 ± 0.029
Medium fragmentation	0.012 ± 0.046		0.462 ± 0.164*	-0.006 ± 0.028
High fragmentation	0.045 ± 0.054		-0.255 ± 0.224	0.007 ± 0.032
Slope (°)		-0.095 ± -0.010**		
North	-0.275 ± 0.342	0.613 ± 0.185**	-1.011 ± 0.294**	-0.044 ± 0.044
East	-0.216 ± 0.383	0.451 ± 0.193*	-0.265 ± 0.273	-0.016 ± 0.035
South	0.930 ± 0.307*	0.684 ± 0.182**	0.552 ± 0.209*	-0.001 ± 0.03
West	-1.442 ± 0.612*	-0.950 ± 0.318*	-0.534 ± 0.336	0.041 ± 0.047
No aspect (flat)	1.003 ± 0.367*	-0.797 ± 0.364*	1.257 ± 0.502*	0.020 ± 0.098
Spruce	-0.831 ± 0.389*		1.083 ± 0.292**	0.625 ± 0.193*
Shrubs	-0.393 ± 0.635		-0.729 ± 0.579	0.799 ± 0.340*
Subalpine	0.118 ± 0.495		0.606 ± 0.370	0.655 ± 0.180**
<i>Carex</i> spp.	-0.288 ± 0.461		-0.581 ± 0.996	-0.289 ± 0.534
Non-vegetated	0.471 ± 0.507		-0.821 ± 0.717	-2.575 ± 0.446**
Pine	-1.624 ± 0.678*		0.521 ± 0.545	0.281 ± 0.413
Riparian spruce	1.009 ± 0.417*		0.322 ± 0.507	0.704 ± 0.315*
Alpine	1.108 ± 0.594		-0.708 ± 0.811	-0.230 ± 0.332
Burned/disturbed	0.429 ± 0.443		0.306 ± 0.489	0.030 ± 0.357

* $P < 0.05$

** $P < 0.001$

Table C.10. Coefficients of selection (β_i and $\bar{\beta}_i$ for an averaged model from Tables C.7, C.8) and standard errors (SE) of the covariates for the final risk models for wolf pack 2 (Lower Besa) by season and year in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Significant parameters are indicated by asterisk(s).

Covariates	Calving 2002	Summer 2002	Calving 2003	Summer 2003
	$\beta_i \pm \text{SE}$	$\beta_i \pm \text{SE}$	$\beta_i \pm \text{SE}$	$\bar{\beta}_i \pm \text{SE}$
Elevation (km)	-27.960 \pm 10.267*		-41.949 \pm 7.320**	-8.854 \pm 1.358**
Elevation ² (km)	9.267 \pm 4.230		14.674 \pm 3.044**	
Low fragmentation	-0.315 \pm 0.444		-0.041 \pm 0.160	-0.135 \pm 0.304
Medium fragmentation	-0.537 \pm 0.379		-0.006 \pm 0.114	-0.335 \pm 0.263
High fragmentation	0.852 \pm 0.307*		0.046 \pm 0.120	0.470 \pm 0.214*
Slope (°)		-0.158 \pm 0.021**		
North		-0.239 \pm 0.222	-0.391 \pm 0.234	
East		0.305 \pm 0.195	-0.077 \pm 0.182	
South		0.600 \pm 0.232*	-0.030 \pm 0.236	
West		-0.561 \pm 0.304	0.293 \pm 0.198	
No aspect (flat)		-0.104 \pm 0.346	0.206 \pm 0.232	
Spruce			-0.909 \pm 0.357*	-0.030 \pm 0.347
Shrubs			1.623 \pm 0.566*	1.153 \pm 0.366*
Subalpine				
<i>Carex</i> spp.			-0.478 \pm 0.401	-0.587 \pm 0.408
Non-vegetated			-1.359 \pm 1.156	
Pine			1.359 \pm 0.591*	-0.303 \pm 1.005
Riparian spruce			0.523 \pm 0.385	0.455 \pm 0.353
Alpine				
Burned/disturbed			-0.759 \pm 0.484	-0.688 \pm 0.551

* $P < 0.05$

** $P < 0.001$

Table C.11. Coefficients of selection (β_i for models from Tables C.7, C.8) and standard errors (SE) of the covariates for the final risk models for wolf pack 3 (Neves) by season and year in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Significant parameters are indicated by asterisk(s).

Covariates	Calving 2002	Summer 2002	Calving 2003	Summer 2003
	$\beta_i \pm \text{SE}$	$\beta_i \pm \text{SE}$	$\beta_i \pm \text{SE}$	$\beta_i \pm \text{SE}$
Elevation (km)	-183.927 \pm 32.562	77.485 \pm 39.200*	-31.149 \pm 20.319	17.879 \pm 10.485
Elevation ² (km)	57.321 \pm 10.660**	-25.108 \pm 13.496	7.201 \pm 6.560	-5.391 \pm 3.381
Low fragmentation	0.242 \pm 0.453	0.370 \pm 0.183*	-0.105 \pm 0.347	
Medium fragmentation	-0.133 \pm 0.428	0.196 \pm 0.162	-0.389 \pm 0.298	
High fragmentation	-0.110 \pm 0.446	-0.566 \pm 0.189*	0.493 \pm 0.307	
Slope (°)				
North		1.046 \pm 0.197**		0.647 \pm 0.209*
East		-0.945 \pm 0.315**		-0.558 \pm 0.307
South		-0.864 \pm 0.254**		-0.441 \pm 0.25
West		-0.250 \pm 0.280		0.197 \pm 0.277
No aspect (flat)		1.014 \pm 0.374*		0.155 \pm 0.385
Spruce		-0.867 \pm 0.328*	-1.390 \pm 0.599*	-0.728 \pm 0.312*
Shrubs		1.225 \pm 0.332**	1.445 \pm 0.481*	1.683 \pm 0.297**
Subalpine		-0.988 \pm 0.585	0.127 \pm 1.111	-0.234 \pm 0.370
<i>Carex</i> spp.		-0.604 \pm 1.059	-1.105 \pm 0.691	1.872 \pm 0.496**
Non-vegetated		-0.225 \pm 0.697	0.264 \pm 1.092	-1.457 \pm 0.672*
Pine		0.755 \pm 0.375*	-2.356 \pm 0.967*	0.306 \pm 0.371
Riparian spruce		1.302 \pm 0.474*	-0.791 \pm 0.702	-0.192 \pm 0.607
Alpine		-0.398 \pm 1.072	1.792 \pm 1.317	-1.25 \pm 0.649
Burned/disturbed		-0.201 \pm 0.640	2.014 \pm 0.817	

* $P < 0.05$

** $P < 0.001$

Table C.12. Coefficients of selection (β_i and $\bar{\beta}_i$ for an averaged model from Tables C.7, C.8) and standard errors (SE) of the covariates for the final risk models for wolf pack 4 (Pocketknife) by season and year in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Significant parameters are indicated by asterisk(s).

Covariates	Calving 2002	Summer 2002	Calving 2003	Summer 2003
	$\bar{\beta}_i \pm \text{SE}$	$\beta_i \pm \text{SE}$	$\bar{\beta}_i \pm \text{SE}$	$\beta_i \pm \text{SE}$
Elevation (km)	45.017 ± 21.275*	-3.778 ± 8.080	13.712 ± 8.067	
Elevation ² (km)	-20.024 ± 9.509*	0.802 ± 3.363	-4.854 ± 3.712	
Linear distance (km)	-0.090 ± 0.053			-0.199 ± 0.042**
Linear distance ² (km)	0.048 ± 0.016*			
Low fragmentation	-0.871 ± 0.338*	-1.011 ± 0.227**	-0.086 ± 0.092	-0.669 ± 0.270*
Medium fragmentation	0.297 ± 0.241	0.228 ± 0.157	0.076 ± 0.068	0.191 ± 0.200
High fragmentation	0.616 ± 0.218*	0.782 ± 0.158**	0.010 ± 0.063	0.478 ± 0.196*
Slope (°)				
North	0.128 ± 0.265		0.307 ± 0.250	
East	-0.045 ± 0.239		-0.586 ± 0.304	
South	-0.516 ± 0.370		-0.556 ± 0.329	
West	-1.059 ± 0.429*		-0.143 ± 0.349	
No aspect (flat)	1.536 ± 0.323**		0.978 ± 0.300*	
Spruce	-0.261 ± 0.395	-0.580 ± 0.327	0.775 ± 0.469	
Shrubs	1.527 ± 0.487*	0.834 ± 0.368*	0.873 ± 0.401*	
Subalpine		0.078 ± 1.162		
<i>Carex</i> spp.	0.033 ± 0.450	0.679 ± 0.361	0.988 ± 0.383*	
Non-vegetated	1.086 ± 0.908	-0.979 ± 0.805	-0.204 ± 0.973	
Pine	-1.619 ± 0.807*	-0.241 ± 0.407	0.146 ± 0.554	
Riparian spruce	-0.383 ± 0.345	0.311 ± 0.353	0.625 ± 0.392	
Alpine		0.204 ± 0.855		
Burned/disturbed	-0.529 ± 0.671	-0.307 ± 0.424	-1.654 ± 0.899	

* $P < 0.05$

** $P < 0.001$

Table C.13. Coefficients of selection (β_i and $\bar{\beta}_i$ for an averaged model from Tables C.7, C.8) and standard errors (SE) of the covariates for the final risk models for wolf pack 5 (Richards-Upper Prophet) by season and year in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Significant parameters are indicated by asterisk(s).

Covariates	Calving 2002	Summer 2002	Calving 2003	Summer 2003
	$\beta_i \pm \text{SE}$	$\bar{\beta}_i \pm \text{SE}$	$\bar{\beta}_i \pm \text{SE}$	$\beta_i \pm \text{SE}$
Elevation (km)	-3.800 ± 0.989**	-2.025 ± 0.606**	-5.182 ± 5.938	4.444 ± 7.664
Elevation ² (km)			0.719 ± 1.987	-1.887 ± 2.342
Low fragmentation		0.001 ± 0.020	-0.967 ± 0.307*	0.278 ± 0.164
Medium fragmentation		0.007 ± 0.018	0.415 ± 0.217	-0.298 ± 0.156
High fragmentation		-0.008 ± 0.022	0.552 ± 0.203*	0.021 ± 0.161
Slope (°)				
North	-0.313 ± 0.291	0.568 ± 0.180*		
East	-0.565 ± 0.316	0.107 ± 0.178		
South	0.257 ± 0.266	0.021 ± 0.170		
West	-0.577 ± 0.383	-0.298 ± 0.230		
No aspect (flat)	1.197 ± 0.615	-0.398 ± 0.361		
Spruce	-0.720 ± 0.337*	-1.061 ± 0.232**		-0.688 ± 0.369
Shrubs	1.235 ± 0.434*	1.034 ± 0.285**		0.037 ± 0.392
Subalpine	-0.088 ± 0.420	0.810 ± 0.211**		0.232 ± 0.284
<i>Carex</i> spp.	-0.254 ± 0.681	0.612 ± 0.494		2.151 ± 0.454**
Non-vegetated	-0.163 ± 0.463	-1.404 ± 0.368**		-1.408 ± 0.441**
Pine	-0.861 ± 0.741	-0.957 ± 0.540		-0.716 ± 0.964
Riparian spruce	0.131 ± 0.429	0.984 ± 0.312*		0.469 ± 0.539
Alpine	0.736 ± 0.59	-0.007 ± 0.342		-0.270 ± 0.425
Burned/disturbed	-0.016 ± 0.478	-0.011 ± 0.288		0.194 ± 0.362

* $P < 0.05$

** $P < 0.001$

Appendix D: Modelling the Normalized Difference Vegetation Index during the calving and summer seasons in the Greater Besa Prophet area, northern British Columbia.

Table D.1. A model set to estimate the Normalized Difference Vegetation Index during the calving and summer seasons in the Greater Besa Prophet area, northern British Columbia, 2001.

Models
Vegetation + Slope + Aspect + Elevation
Incidence + Aspect + Elevation
Incidence + Elevation
Vegetation + Aspect + Elevation
Vegetation + Elevation
Slope + Aspect
Vegetation + Incidence
Vegetation
Vegetation + Aspect
Vegetation + Slope + Aspect
Slope + Aspect + Elevation

Table D.2. The R^2 values of the final models used to estimate the Normalized Difference Vegetation Index during the calving and summer seasons in the Greater Besa Prophet area, northern British Columbia, 2001.

Landsat Image	Model	Initial adjusted R^2	Validated adjusted R^2	Final pixel-to-pixel R^2
4 June 01	Vegetation + Slope + Aspect + Elevation	0.623	0.639	0.608
22 July 01	Vegetation + Aspect + Elevation (km)	0.649	0.674	0.689
15 August 01	Vegetation + Elevation (km)	0.850	0.845	0.884

Table D.3. Coefficients of selection (β_i for a model from Table D.2) and standard errors (SE) of the covariates of the multiple regression models for each Landsat image to estimate the Normalized Difference Vegetation Index during the calving and summer seasons in the Greater Besa Prophet area, northern British Columbia, 2002-2003. Significant parameters are indicated by asterisk(s).

Covariates	4 June 2001	22 July 2001	15 August 2001
	$\beta_i \pm \text{SE}$	$\beta_i \pm \text{SE}$	$\beta_i \pm \text{SE}$
Elevation (km)	-0.118 \pm 0.010**	-0.102 \pm 0.008**	-0.054 \pm 0.007**
Slope (°)	-0.002 \pm 0.0002**		
North	-0.038 \pm 0.005**	-0.001 \pm 0.004	
East	0.023 \pm 0.004**	0.008 \pm 0.003*	
South	0.03 \pm 0.005**	0.015 \pm 0.004**	
West	0.004 \pm 0.004	-0.003 \pm 0.004	
No aspect	-0.018 \pm 0.009*	-0.019 \pm 0.006**	
<i>Carex</i> spp.	0.096 \pm 0.011**	0.107 \pm 0.008**	0.134 \pm 0.008**
Shrubs	-0.012 \pm 0.007	0.188 \pm 0.007**	0.222 \pm 0.006**
Low productivity spruce	0.105 \pm 0.010**	0.062 \pm 0.008**	0.061 \pm 0.007**
Gravel bar	-0.216 \pm 0.027**	-0.171 \pm 0.018**	-0.117 \pm 0.020**
Rocks	-0.029 \pm 0.008**	-0.215 \pm 0.009**	-0.243 \pm 0.006**
Rocks/crustose lichens	-0.077 \pm 0.032*	-0.145 \pm 0.034**	-0.162 \pm 0.033**
Snow/glacier	0.140 \pm 0.019**	-0.174 \pm 0.025**	-0.354 \pm 0.015**
Water	-0.302 \pm 0.036**	-0.272 \pm 0.053**	-0.437 \pm 0.022**
Pine	0.116 \pm 0.012**	0.097 \pm 0.009**	0.122 \pm 0.008**
Subalpine spruce	0.04 \pm 0.012**	0.182 \pm 0.014**	0.196 \pm 0.007**
Spruce	0.105 \pm 0.007**	0.058 \pm 0.007**	0.086 \pm 0.005**
Riparian spruce	0.082 \pm 0.009**	0.048 \pm 0.007**	0.071 \pm 0.007**
Dry alpine	-0.019 \pm 0.011	0.090 \pm 0.011**	0.116 \pm 0.009**
Moist alpine	-0.042 \pm 0.017*	0.058 \pm 0.021**	0.112 \pm 0.012**

Table D.3. Continued.

Covariates	4 June 2001	22 July 2001	15 August 2001
	$\beta_i \pm \text{SE}$	$\beta_i \pm \text{SE}$	$\beta_i \pm \text{SE}$
Burned/disturbed	$0.053 \pm 0.008^{**}$	$0.189 \pm 0.007^{**}$	$0.240 \pm 0.006^{**}$
Rock-vegetation transition zone	$-0.041 \pm 0.011^{**}$	$-0.103 \pm 0.012^{**}$	$-0.047 \pm 0.008^{**}$
Intercept	$0.307 \pm 0.014^{**}$	$0.415 \pm 0.012^{**}$	$0.306 \pm 0.011^{**}$

* $P < 0.050$

** $P < 0.001$

Appendix E: Data (age, sex, weight, calving area, and method and date of capture) from the capture of neonatal caribou calves in the Greater Besa Prophet area, northern British Columbia, 2002-2003.

Table E.1. Animal identification (ID), date of capture, sex (male (M) and female (F)), and estimates for the date of birth (DOB), age (days), and weight (kg) of newborn caribou calves captured by hand and by net-gun in the Foothills (FTHILLS), Western High Country (WHC), and North Prophet (NP) calving areas within the Greater Besa Prophet area, northern British Columbia, 2002-2003.

ID	Capture Date	Sex	DOB	Age (days)	Weight (kg)	Capture Method	Calving Area
C01C	31-May-02	F	27-May-02	4.0	10.50	Hand	FTHILLS
C02C	31-May-02	F	29-May-02	2.0	10.00	Hand	FTHILLS
C03C	31-May-02	F	29-May-02	2.0	9.50	Hand	FTHILLS
C04C	1-Jun-02	M	29-May-02	2.5	8.50	Hand	WHC
C05C	1-Jun-02	F	27-May-02	5.0	9.50	Hand	NP
C06C	1-Jun-02	F	30-May-02	2.0	6.75	Hand	WHC
C07C	2-Jun-02	F	30-May-02	3.0	8.50	Hand	FTHILLS
C08C	2-Jun-02	M	1-Jun-02	0.5	7.25	Hand	FTHILLS
C09C	2-Jun-02	M	28-May-02	4.5	10.75	Hand	NP
C10C	2-Jun-02	M	29-May-02	4.0	9.75	Hand	NP
C11C	2-Jun-02	F	1-Jun-02	0.5	6.75	Hand	FTHILLS
C12C	2-Jun-02	F	1-Jun-02	1.0	6.75	Hand	FTHILLS
C13C	2-Jun-02	F	2-Jun-02	0.5	7.25	Hand	FTHILLS
C14C	3-Jun-02	F	31-May-02	2.5	8.75	Hand	WHC
C15C	4-Jun-02	M	29-May-02	6.0	12.75	Net gun	WHC
C16C	4-Jun-02	F	1-Jun-02	3.0	9.00	Net gun	WHC
C17C	4-Jun-02	M	1-Jun-02	3.0	9.00	Net gun	WHC
C18C	4-Jun-02	M	31-May-02	4.0	11.75	Net gun	FTHILLS
C19C	4-Jun-02	F	1-Jun-02	3.0	8.75	Net gun	FTHILLS
C20C	4-Jun-02	F	29-May-02	6.0	13.00	Net gun	FTHILLS
C21C	4-Jun-02	M	31-May-02	3.5	8.50	Net gun	WHC
C22C	4-Jun-02	M	31-May-02	4.0	10.00	Net gun	WHC
C23C	4-Jun-02	F	1-Jun-02	2.5	11.00	Net gun	WHC

Table E.1 . Continued.

ID	Capture Date	Sex	DOB	Age (days)	Weight (kg)	Capture Method	Calving Area
C24C	4-Jun-02	F	29-May-02	6.0	13.50	Net gun	WHC
C25C	4-Jun-02	F	1-Jun-02	3.0	8.75	Net gun	WHC
C26C	28-May-03	M	27-May-03	1.0	7.25	Hand	WHC
C27C	28-May-03	F	25-May-03	2.5	8.75	Net gun	WHC
C28C	28-May-03	F	25-May-03	2.5	10.50	Net gun	WHC
C29C	28-May-03	F	25-May-03	2.5	8.00	Net gun	FTHILLS
C30C	29-May-03	F	25-May-03	4.0	11.00	Net gun	FTHILLS
C31C	29-May-03	F	25-May-03	3.5	8.50	Net gun	FTHILLS
C32C	29-May-03	M	27-May-03	1.5	8.75	Net gun	FTHILLS
C33C	29-May-03	F	25-May-03	3.5	9.75	Net gun	WHC
C34C	29-May-03	M	26-May-03	2.5	9.00	Net gun	WHC
C35C	29-May-03	M	26-May-03	3.0	10.25	Net gun	FTHILLS
C36C	29-May-03	F	26-May-03	3.0	10.25	Net gun	FTHILLS
C37C	29-May-03	M	26-May-03	3.0	13.00	Net gun	FTHILLS
C38C	30-May-03	M	28-May-03	1.5	7.00	Net gun	FTHILLS
C39C	30-May-03	F	27-May-03	2.5	8.00	Net gun	NP
C40C	30-May-03	F	27-May-03	2.5	8.75	Net gun	NP
C41C	30-May-03	F	27-May-03	2.5	7.50	Net gun	NP
C42C	30-May-03	M	28-May-03	1.5	6.00	Net gun	NP
C43C	30-May-03	F	26-May-03	3.5	9.00	Net gun	NP
C44C	30-May-03	M	27-May-03	2.5	9.00	Net gun	NP
C45C	30-May-03	M	27-May-03	2.5	8.75	Hand	NP
C46C	31-May-03	F	27-May-03	4.0	8.75	Net gun	WHC
C47C	31-May-03	F	28-May-03	3.0	9.00	Hand	WHC
C48C	31-May-03	F	29-May-03	2.0	13.50	Net gun	WHC
C49C	31-May-03	F	27-May-03	3.5	13.50	Net gun	FTHILLS
C50C	31-May-03	M	26-May-03	6.0	19.00	Net gun	FTHILLS

Appendix F: Summary of vegetative (line-intercept and plot) data at calving sites of woodland caribou in the Greater Besa Prophet area, northern British Columbia, 2002-2003.

Table F.1. Percent cover and density of vegetation by functional group and species and biomass of lichens ($\bar{x} \pm SE$) using line-intercept and plot data at calving sites of woodland caribou in the Greater Besa Prophet area, northern British Columbia, 2002-2003.

Functional Group	Species	2002		2003	
		Cover (%)	Density (per m ²) or Lichen Biomass (g/m ²)	Cover (%)	Density (per m ²) or Lichen Biomass (g/m ²)
Line-Intercept Data					
Trees	<i>Abies lasiocarpa</i> (krummholz)	0.54 ± 0.54			
	<i>Picea glauca x engelmanni</i>	3.71 ± 2.74		0.14 ± 0.11	
	<i>Picea mariana</i>	0.47 ± 0.25		0.31 ± 0.18	
Shrubs	<i>Alnus</i> spp.			0.10 ± 0.10	
	<i>Betula glandulosa</i>	10.56 ± 4.21		3.10 ± 1.16	
	<i>Betula glandulosa</i> mix (<i>Salix</i> spp. and <i>Juniperus</i> spp.)	0.10 ± 0.10		0.97 ± 0.81	
	<i>Juniperus</i> spp.	0.06 ± 0.06		0.07 ± 0.05	
	<i>Ledum groenlandicum</i>	0.10 ± 0.10		0.30 ± 0.30	
	<i>Salix</i> spp.	5.55 ± 2.70		16.89 ± 4.62	
Dwarf Shrubs	<i>Cassiope mertensiana</i>	1.91 ± 0.71		1.02 ± 0.59	
	<i>Dryas integrifolia</i>	24.44 ± 5.04		15.89 ± 3.97	
	<i>Dryas integrifolia</i> mix (<i>Vaccinium</i> spp. and <i>Salix reticulata</i>)	7.02 ± 4.18		0.27 ± 0.16	
Other		14.67 ± 7.32		36.61 ± 11.09	
Plot Data					
Forbs	<i>Anemone</i> spp.	0.54 ± 0.30	3.12 ± 1.32	0.34 ± 0.16	1.14 ± 0.53
	<i>Antennaria</i> spp.	0.52 ± 0.28	2.49 ± 1.11	0.12 ± 0.06	0.63 ± 0.38
	<i>Astragalus alpinus</i>	0.42 ± 0.28	3.99 ± 2.66	0.04 ± 0.04	0.10 ± 0.07

Table F.1. Continued.

Functional Group	Species	2002		2003	
		Cover (%)	Density (per m ²) or Lichen Biomass (g/m ²)	Cover (%)	Density (per m ²) or Lichen Biomass (g/m ²)
Forbs	<i>Epilobium angustifolium</i>	0.56 ± 0.28	1.10 ± 0.52	0.40 ± 0.32	0.77 ± 0.59
	<i>Hedysarum</i> spp.	0.50 ± 0.38	0.96 ± 0.59	1.28 ± 0.68	1.13 ± 0.45
	<i>Lupinus arcticus</i>	5.14 ± 1.78	3.94 ± 1.16	3.58 ± 1.26	1.60 ± 0.48
	<i>Mertensia paniculata</i>	0.76 ± 0.44	1.78 ± 0.80	0.16 ± 0.10	0.43 ± 0.23
	<i>Oxytropis</i> spp.	0.58 ± 0.42	0.68 ± 0.47	0.74 ± 0.32	1.50 ± 0.60
	<i>Pedicularis</i> spp.	0.98 ± 0.28	9.72 ± 4.16	1.10 ± 0.42	4.10 ± 1.44
	<i>Polemonium</i> spp.	0.54 ± 0.28	1.63 ± 0.70	0.46 ± 0.22	0.80 ± 0.38
	<i>Potentilla</i> spp.	1.42 ± 0.62	4.72 ± 2.23	0.54 ± 0.24	1.47 ± 0.60
	<i>Saxifraga</i> spp.	1.94 ± 1.50	1.32 ± 0.73	0.46 ± 0.24	0.92 ± 0.51
	<i>Silene acaulis</i>	1.30 ± 0.54	1.65 ± 0.59	1.28 ± 0.68	0.67 ± 0.20
	<i>Solidago</i> spp.	0.76 ± 0.42	1.93 ± 0.79	0.28 ± 0.14	0.87 ± 0.36
	Other	0.06 ± 0.06	0.68 ± 0.54	0.18 ± 0.10	1.44 ± 0.78
Grasses and Grass-likes	<i>Carex</i> spp.	5.56 ± 1.36	43.72 ± 13.23	7.3 ± 2.48	42.93 ± 14.08
	<i>Equisetum</i> spp.	1.48 ± 1.04	13.69 ± 9.20	2.40 ± 1.04	41.00 ± 18.50
	<i>Festuca</i> spp.	12.46 ± 3.56	5.56 ± 1.07	7.38 ± 1.98	4.10 ± 0.92
	<i>Poa</i> spp.	1.54 ± 0.94	3.06 ± 0.94	0.06 ± 0.04	0.70 ± 0.44
	Other	0.01 ± 0.01	0.07 ± 0.07	0.58 ± 0.36	2.30 ± 1.14
Lichens	<i>Cladina</i> spp. and <i>Cladonia</i> spp.		0.73 ± 0.14		0.43 ± 0.08
	Other		42.2 ± 4.87		30.47 ± 5.43

Appendix G: Evaluating the relationship between percent cover and biomass of lichens at calving sites of woodland caribou in the Greater Besa Prophet area, northern British Columbia, 2002-2003.

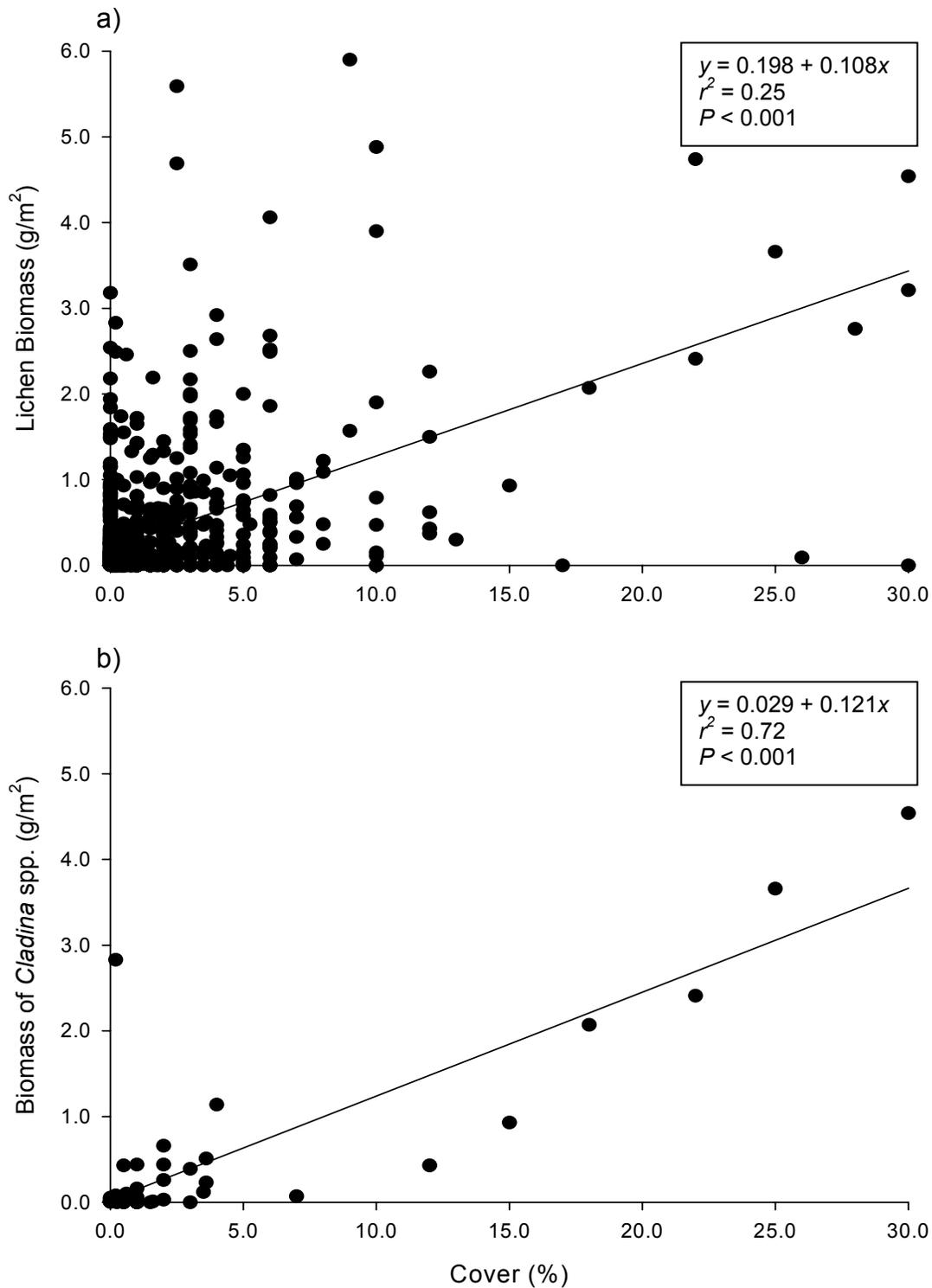


Figure G.1. Relationship between ocular estimates of percent cover and measured samples of air-dried biomass for a) all lichen species and b) *Cladina* spp. at calving sites of woodland caribou in the Greater Besa Prophet area, northern British Columbia, 2002-2003.

Appendix H: Reproductive status and ultrasound measurements of back fat for woodland caribou in the Greater Besa Prophet area, northern British Columbia, winters 2002-2004.

Table H.1. Reproductive status and ultrasound estimates of back fat for female woodland caribou in the Greater Besa Prophet area in northern British Columbia, 2002-2004; pregnancy for 38A was confirmed via necropsy and A = adult and Y = yearling.

Caribou	Capture Date	Progesterone (ng/ml)	Reproductive Status	General Location	Age Class	Back Fat (cm)	Body Fat (%) ^a
26A	10-Feb-03	4.7	Pregnant	Klingzut Mountain	A	0.3	6.44
27A	10-Feb-03	4.3	Pregnant	Besa-Townsley Flat Mountain	A	0.1	5.99
21B	11-Feb-03	3.7	Pregnant	Ten Mile Lake	A	0.5	6.90
25B	11-Feb-03	3.9	Pregnant	Ten Mile Lake	A	0.7	7.35
28A	11-Feb-03	7.3	Pregnant	Ten Mile Lake	A	0.4	6.67
29A	11-Feb-03	4.8	Pregnant	Ten Mile Lake	A	0.2	6.21
30A	11-Feb-03	2.7	Pregnant	Mountain East of Richards Creek	A	0.9	7.80
31A	11-Feb-03	3.8	Pregnant	Mountain East of Richards Creek	A	0.5	6.90
32A	12-Feb-03	5.0	Pregnant	Mountain East of Big Flat	A	1.3	8.71
33A	12-Feb-03	<.2	Not Pregnant	Mountain East of Big Flat	Y	0.1	5.99
34A	12-Feb-03	5.8	Pregnant	Mountain East of Big Flat	A	0.5	6.90
35A	12-Feb-03	3.1	Pregnant	Mountain East of Big Flat	A	1.6	9.39
36A	12-Feb-03	<.2	Not Pregnant	Mid-Klingzut Draw	A	0.1	5.99
37A	12-Feb-03	<.2	Not Pregnant	South of Ten Mile Lake	A	0.1	5.99
38A	13-Feb-03	n/a	Pregnant	Buckinghorse Flats	A	0.4	6.67
39A	13-Feb-03	4.7	Pregnant	Buckinghorse Flats	A	0.3	6.44
40A	13-Feb-03	10.9	Pregnant	Buckinghorse Flats	A	0.7	7.35
41A	14-Feb-03	4.3	Pregnant	Buckinghorse Flats	A	0.9	7.80
42A	14-Feb-03	6.2	Pregnant	Buckinghorse Flats	A	0.2	6.21
43A	14-Feb-03	4.8	Pregnant	Buckinghorse Flats	A	1.7	9.62
44A	20-Jan-04	7.2	Pregnant	Big Flat Mountain	A	0.4	6.67
45A	20-Jan-04	<.2	Not Pregnant	Big Flat Mountain	A	0.2	6.21

Table H.1. Continued.

Caribou	Capture Date	Progesterone (ng/ml)	Reproductive Status	General Location	Age Class	Back Fat (cm)	Body Fat (%)^a
46A	20-Jan-04	3.8	Pregnant	Big Flat Mountain	A	0.5	6.90
47A	20-Jan-04	4.4	Pregnant	Big Flat Mountain	A	0.3	6.44
48A	20-Jan-04	7.8	Pregnant	Big Flat Mountain	A	0.9	7.80
49A	20-Jan-04	<.2	Not Pregnant	Big Flat Mountain	A	0.2	6.21
50A	20-Jan-04	5.7	Pregnant	First Mountain- Pocketknife	A	0.4	6.67
51A	20-Jan-04	4.5	Pregnant	First Mountain- Pocketknife	A	0.2	6.21
52A	20-Jan-04	5.6	Pregnant	First Mountain- Pocketknife	A	0.6	7.12
53A	21-Jan-04	5.0	Pregnant	Klingzut Mountain	A	0.3	6.44
54A	21-Jan-04	4.8	Pregnant	Mid-Klingzut Draw	A	0.5	6.90
55A	21-Jan-04	3.9	Pregnant	Mountain East of Richards Creek	A	0.6	7.12
56A	21-Jan-04	5.4	Pregnant	East of Besa-Townsley Flat Mountain	A	0.2	6.21
57A	21-Jan-04	6.1	Pregnant	East of Besa-Townsley Flat Mountain	A	0.3	6.44
58A	21-Jan-04	12.4	Pregnant	Granger Lick	A	0.3	6.44
59A	21-Jan-04	3.4	Pregnant	Granger Lick	A	0.4	6.67
60A	21-Jan-04	4.8	Pregnant	Granger Lick	A	0.9	7.80
61A	21-Jan-04	5.3	Pregnant	Besa-Townsley Flat Mountain	A	1.1	8.26
62A	21-Jan-04	5.6	Pregnant	Besa-Townsley Flat Mountain	A	0.4	6.67

^aUsing the MAXFAT equation for caribou: $y = 5.76 + 2.27x$, where y = estimate of body fat (%) and x = ultrasound measurement of back fat (cm) (T. Stephenson, California Department of Fish and Game, unpublished data).

Appendix I: Defining the risk of predation from wolves (*Canis lupus*) for female caribou during winter and late winter in the Greater Besa Prophet area, northern British Columbia, 2001-2002.

Table I.1. Final pooled models of wolf risk by season in the Greater Besa Prophet area, northern British Columbia, 2001-2002 showing sample size (n), log-likelihood (LL), number of parameters (K), Akaike's Information Criterion (AIC), change in AIC (Δ_i), Akaike weights (w_i), evidence ratios (E_r), and average ($n = 5$) Spearman's correlation coefficient from k-fold cross-validation (\bar{r}_s) with associated p-values (P).

Season	Model	n	LL	K	AIC	Δ_i^a	w_i^a	E_r^a	\bar{r}_s^{bc}	P^c
Winter	Vegetation + Fragmentation + Elevation + Elevation ²	2424	-1044.911	13	2115.821	0.000	0.681	1.00	0.78	3.53
Late Winter	Vegetation + Aspect + Fragmentation + Elevation + Elevation ²	7854	-3251.704	17	6537.407	0.000	1.000	1.00	0.96	9.70

^aBurnham and Anderson (2002)

^bBoyce et al. (2002)

^cSiegel (1956)

Table I.2. Coefficients of selection (β_i from Table I.1) and standard errors (SE) of the covariates for the final pooled models of wolf risk by season in the Greater Besa Prophet area, northern British Columbia, 2001-2002. Significant parameters are indicated by asterisk(s).

Covariates	Winter $\beta_i \pm \text{SE}$	Late Winter $\beta_i \pm \text{SE}$
Elevation (km)	14.028 \pm 3.411**	11.851 \pm 1.442**
Elevation ² (km)	-5.912 \pm 1.409**	-4.819 \pm 0.551**
Low fragmentation	-0.092 \pm 0.090	0.306 \pm 0.054**
Medium fragmentation	-0.039 \pm 0.078	0.614 \pm 0.044**
High fragmentation	0.131 \pm 0.078	0.092 \pm 0.045*
Slope (°)		
North		-0.472 \pm 0.075**
East		-0.185 \pm 0.063*
South		0.402 \pm 0.057**
West		-0.019 \pm 0.074
No aspect (flat)		0.273 \pm 0.102*
Spruce	-0.448 \pm 0.144*	-0.374 \pm 0.077**
Shrubs	0.629 \pm 0.158**	0.187 \pm 0.099
Subalpine	0.252 \pm 0.398	-0.133 \pm 0.132
<i>Carex</i> spp.	0.191 \pm 0.212	0.287 \pm 0.132*
Non-vegetated	-0.292 \pm 0.306	-0.005 \pm 0.127
Pine	-0.827 \pm 0.247*	-0.837 \pm 0.159**
Riparian spruce	-0.179 \pm 0.175	0.057 \pm 0.095
Alpine	0.428 \pm 0.352	0.482 \pm 0.155*
Burned/disturbed	0.246 \pm 0.150	0.335 \pm 0.076**

* $P < 0.05$

** $P < 0.001$

Table I.3. Final pack models of wolf risk during winter (November-February) in the Greater Besa Prophet area, northern British Columbia, 2001-2002 showing sample size (n), log-likelihood (LL), number of parameters (K), Akaike's Information Criterion (AIC), change in AIC (Δ_i), Akaike weights (w_i), evidence ratios (E_r), and average ($n = 5$) Spearman's correlation coefficient from k-fold cross-validation (\bar{r}_s) with associated p-values (P).

Pack	Model	n	LL	K	AIC	Δ_i^a	w_i^a	E_r^a	\bar{r}_s^{bc}	P^c
1	n/a									
2 ^d	Vegetation + Aspect + Elevation + Elevation ²	428	-165.373	16	363.915	0.000	0.517	1.00	0.59	0.073
	Vegetation + Fragmentation + Elevation + Elevation ²	428	-170.177	12	364.990	1.075	0.302	1.71	0.55	0.100
	Vegetation + Aspect + Fragmentation + Elevation + Elevation ²	428	-168.566	14	366.013	2.098	0.181	2.85	0.53	0.115
3	n/a									
4	Vegetation + Aspect + Elevation + Elevation ²	1079	-448.854	14	925.708	0.000	0.481	1.00	0.75	0.012
5	n/a									
6 ^d	Vegetation + Fragmentation + Elevation + Elevation ²	888	-374.743	13	775.487	0.000	0.553	1.00	0.56	0.092
	Vegetation + Aspect + Elevation + Elevation ²	888	-373.234	15	776.469	0.982	0.339	1.63	0.49	0.151
	Vegetation + Aspect + Fragmentation + Elevation + Elevation ²	888	-372.403	17	778.806	3.319	0.105	5.26	0.53	0.115

^aBurnham and Anderson (2002), ^bBoyce et al. (2002), ^cSiegel (1956), and ^dmodels were averaged

Table I.4. Final pack models of wolf risk during late winter (March-April) in the Greater Besa Prophet area, northern British Columbia, 2001-2002 showing sample size (n), log-likelihood (LL), number of parameters (K), Akaike's Information Criterion (AIC), change in AIC (Δ_i), Akaike weights (w_i), evidence ratios (E_r), and average ($n = 5$) Spearman's correlation coefficient from k-fold cross-validation (\bar{r}_s) with associated p-values (P).

Pack	Model	n	LL	K	AIC	Δ_i^a	w_i^a	E_r^a	\bar{r}_s^{bc}	P^c
1	Vegetation + Aspect + Fragmentation + Elevation + Elevation ²	1542	-578.667	17	1191.334	0.000	1.000	1.00	0.90	<0.001
	Vegetation + Aspect + Elevation + Elevation ²	1308	-482.152	15	994.303	0.000	0.601	1.00	0.83	0.003
2	Vegetation + Aspect + Elevation + Elevation ²	1182	-473.747	17	981.494	0.000	0.510	1.00	0.72	0.019
	Vegetation + Aspect + Fragmentation + Elevation + Elevation ²	1266	-507.279	17	1048.557	0.000	0.759	1.00	0.70	0.024
3	Vegetation + Aspect + Fragmentation + Elevation + Elevation ²	1308	-428.973	16	889.946	0.000	0.491	1.00	0.86	0.001
	Vegetation + Aspect + Elevation	1248	-484.533	17	1003.066	2.231	0.247	3.05	0.69	0.027
4	Vegetation + Aspect + Fragmentation + Elevation + Elevation ²	1248	-484.533	17	1003.066	2.231	0.247	3.05	0.69	0.027
	Vegetation + Aspect + Elevation + Elevation ²	1248	-485.417	15	1000.835	0.000	0.753	1.00	0.69	0.027

^aBurnham and Anderson (2002), ^bBoyce et al. (2002), ^cSiegel (1956), and ^dmodels were averaged

Table I.5. Coefficients of selection ($\bar{\beta}_i$ for an averaged model from Tables I.4) and standard errors (SE) of the covariates for the final risk models for wolf pack 1 (Dopp-Keily) during late winter in the Greater Besa Prophet area, northern British Columbia, 2001-2002. Significant parameters are indicated by asterisk(s).

Covariates	Late Winter $\bar{\beta}_i \pm \text{SE}$
Elevation (km)	38.316 \pm 10.557**
Elevation ² (km)	-13.358 \pm 3.675**
Low fragmentation	-0.599 \pm 0.139**
Medium fragmentation	0.472 \pm 0.104**
High fragmentation	0.127 \pm 0.112
Slope (°)	
North	-0.503 \pm 0.174*
East	-0.587 \pm 0.168**
South	0.129 \pm 0.132
West	0.600 \pm 0.17**
No aspect (flat)	0.361 \pm 0.248
Spruce	-0.055 \pm 0.183
Shrubs	-0.665 \pm 0.424
Subalpine	-0.109 \pm 0.236
<i>Carex</i> spp.	0.400 \pm 0.443
Non-vegetated	0.084 \pm 0.247
Pine	-0.758 \pm 0.374*
Riparian spruce	0.726 \pm 0.243*
Alpine	-0.228 \pm 0.410
Burned/disturbed	0.605 \pm 0.211*

* $P < 0.05$

** $P < 0.001$

Table I.6. Coefficients of selection (β_i and $\bar{\beta}_i$ for an averaged model from Tables I.3, I.4) and standard errors (SE) of the covariates for the final risk models for wolf pack 2 (Lower Besa) by season in the Greater Besa Prophet area, northern British Columbia, 2001-2002. Significant parameters are indicated by asterisk(s).

Covariates	Winter $\beta_i \pm SE$	Late Winter $\bar{\beta}_i \pm SE$
Elevation (km)	39.649 \pm 8.811**	15.181 \pm 5.326*
Elevation ² (km)	-16.990 \pm 3.63**	-7.566 \pm 2.412*
Low fragmentation	-0.107 \pm 0.227	
Medium fragmentation	-0.270 \pm 0.236	
High fragmentation	0.395 \pm 0.197*	
Slope (°)		
North	-0.237 \pm 0.159	-0.621 \pm 0.224*
East	-0.191 \pm 0.167	-0.367 \pm 0.271
South	-0.403 \pm 0.202*	1.279 \pm 0.161**
West	0.278 \pm 0.166	-0.835 \pm 0.281*
No aspect (flat)	-0.387 \pm 0.273	-0.115 \pm 0.257
Spruce	-0.086 \pm 0.397	-1.068 \pm 0.357*
Shrubs	1.389 \pm 0.359**	0.035 \pm 0.283
Subalpine	0.949 \pm 1.025	1.178 \pm 0.746
<i>Carex</i> spp.	-0.073 \pm 0.449	-0.681 \pm 0.337*
Non-vegetated	0.518 \pm 0.489	0.701 \pm 0.351*
Pine	-0.869 \pm 0.563	-1.554 \pm 0.578*
Riparian spruce	0.031 \pm 0.342	0.057 \pm 0.261
Alpine		1.335 \pm 0.751
Burned/disturbed	-0.940 \pm 0.405*	-0.066 \pm 0.235

* $P < 0.05$

** $P < 0.001$

Table I.7. Coefficients of selection ($\bar{\beta}_i$ for an averaged model from Tables I.4) and standard errors (SE) of the covariates for the final risk models for wolf pack 3 (Neves) during late winter in the Greater Besa Prophet area, northern British Columbia, 2001-2002. Significant parameters are indicated by asterisk(s).

Covariates	Late Winter $\bar{\beta}_i \pm \text{SE}$
Elevation (km)	-22.085 \pm 5.642**
Elevation ² (km)	6.151 \pm 1.921*
Low fragmentation	-0.410 \pm 0.147*
Medium fragmentation	0.188 \pm 0.123
High fragmentation	0.222 \pm 0.118
Slope (°)	
North	-0.220 \pm 0.226
East	0.393 \pm 0.2*
South	0.315 \pm 0.198
West	0.221 \pm 0.218
No aspect (flat)	-0.709 \pm 0.568
Spruce	-0.221 \pm 0.207
Shrubs	0.293 \pm 0.245
Subalpine	0.243 \pm 0.295
<i>Carex</i> spp.	-1.167 \pm 0.790
Non-vegetated	0.087 \pm 0.387
Pine	-0.528 \pm 0.385
Riparian spruce	-0.599 \pm 0.370
Alpine	0.865 \pm 0.361*
Burned/disturbed	1.026 \pm 0.237**

* $P < 0.05$

** $P < 0.001$

Table I.8. Coefficients of selection (β_i and $\bar{\beta}_i$ for an averaged model from Tables I.3, I.4) and standard errors (SE) of the covariates for the final risk models for wolf pack 4 (Pocketknife) by season in the Greater Besa Prophet area, northern British Columbia, 2001-2002. Significant parameters are indicated by asterisk(s).

Covariates	Winter $\bar{\beta}_i \pm SE$	Late Winter $\bar{\beta}_i \pm SE$
Elevation (km)	26.354 \pm 5.632**	17.576 \pm 6.293*
Elevation ² (km)	-10.717 \pm 2.372**	-6.562 \pm 2.55*
Low fragmentation		-0.341 \pm 0.144*
Medium fragmentation		0.206 \pm 0.113
High fragmentation		0.135 \pm 0.120
Slope (°)		
North	0.410 \pm 0.169*	-0.415 \pm 0.166*
East	0.098 \pm 0.147	-0.381 \pm 0.146*
South	-0.015 \pm 0.173	0.031 \pm 0.169
West	-0.501 \pm 0.230*	-0.206 \pm 0.207
No aspect (flat)	0.008 \pm 0.237	0.970 \pm 0.184**
Spruce	-0.662 \pm 0.246*	-0.417 \pm 0.263
Shrubs	0.981 \pm 0.267**	0.990 \pm 0.269**
Subalpine		-0.630 \pm 0.978
<i>Carex</i> spp.	0.547 \pm 0.291	1.178 \pm 0.295**
Non-vegetated	-1.449 \pm 0.912	-0.564 \pm 0.540
Pine	-0.743 \pm 0.335*	-1.312 \pm 0.438*
Riparian spruce	-0.149 \pm 0.251	0.297 \pm 0.275
Alpine	1.231 \pm 0.608*	0.357 \pm 0.582
Burned/disturbed	0.244 \pm 0.277	0.100 \pm 0.284

* $P < 0.05$

** $P < 0.001$

Table I.9. Coefficients of selection ($\bar{\beta}_i$ for an averaged model from Tables I.4) and standard errors (SE) of the covariates for the final risk models for wolf pack 4 (Richards-Upper Prophet) by season in the Greater Besa Prophet area, northern British Columbia, 2001-2002. Significant parameters are indicated by asterisk(s).

Covariates	Late Winter $\bar{\beta}_i \pm \text{SE}$
Elevation (km)	-5.893 \pm 0.672**
Elevation ² (km)	
Low fragmentation	-0.100 \pm 0.139
Medium fragmentation	0.272 \pm 0.12*
High fragmentation	-0.172 \pm 0.128
Slope (°)	
North	-0.226 \pm 0.185
East	0.027 \pm 0.179
South	0.220 \pm 0.171
West	0.497 \pm 0.204*
No aspect (flat)	-0.519 \pm 0.328
Spruce	-0.407 \pm 0.184*
Shrubs	0.821 \pm 0.254*
Subalpine	-0.644 \pm 0.442
<i>Carex</i> spp.	0.431 \pm 0.348
Non-vegetated	-0.368 \pm 0.322
Pine	-0.030 \pm 0.336
Riparian spruce	-0.227 \pm 0.263
Alpine	0.490 \pm 0.497
Burned/disturbed	-0.067 \pm 0.248

* $P < 0.05$

** $P < 0.001$

Table I.10. Coefficients of selection (β_i and $\bar{\beta}_i$ for an averaged model from Tables I.3, I.4) and standard errors (SE) of the covariates for the final risk models for wolf pack 4 (Withrow) by season in the Greater Besa Prophet area, northern British Columbia, 2001-2002. Significant parameters are indicated by asterisk(s).

Covariates	Winter	Late Winter
	$\beta_i \pm SE$	$\bar{\beta}_i \pm SE$
Elevation (km)	-15.093 \pm 5.233*	15.982 \pm 6.307*
Elevation ² (km)	4.858 \pm 1.965*	-5.182 \pm 2.34*
Low fragmentation	0.096 \pm 0.086	
Medium fragmentation	-0.005 \pm 0.072	
High fragmentation	-0.092 \pm 0.082	
Slope (°)		
North	-0.022 \pm 0.09	-0.451 \pm 0.252
East	-0.134 \pm 0.100	-0.328 \pm 0.200
South	0.061 \pm 0.082	0.597 \pm 0.167**
West	0.088 \pm 0.092	-0.034 \pm 0.204
No aspect (flat)	0.008 \pm 0.164	0.216 \pm 0.422
Spruce	0.192 \pm 0.205	-0.470 \pm 0.218*
Shrubs	0.401 \pm 0.246	-0.600 \pm 0.335
Subalpine	0.349 \pm 0.388	0.164 \pm 0.333
<i>Carex</i> spp.	-0.227 \pm 0.468	-0.040 \pm 0.479
Non-vegetated	-0.545 \pm 0.491	0.439 \pm 0.300
Pine	-1.080 \pm 0.485*	-0.365 \pm 0.497
Riparian spruce	-0.269 \pm 0.342	-0.378 \pm 0.361
Alpine	0.070 \pm 0.391	0.606 \pm 0.34
Burned/disturbed	1.110 \pm 0.214**	0.643 \pm 0.188*

* $P < 0.05$

** $P < 0.001$

