

The Role of Human Altered Landscapes and Predators in the Spatial Overlap Between
Moose, Wolves, and Endangered Caribou

by

Meghan Samantha Anderson

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in
Ecology

Department of Biological Sciences
University of Alberta

© Meghan Samantha Anderson, 2014

Abstract

Human altered landscapes can cause the endangerment or extinction of a species, not only by a direct loss of habitat but by altering predator-prey relationships. Predators can drive prey to extinction when the density of the predator becomes subsidized by another abundant, alternate prey. Such indirect species interactions are termed “apparent competition” and are increasingly being linked to species endangerment. The mechanism behind apparent competition may be differences between the prey species in reproductive success, niche overlap, or differences in ability to escape predation. This study focused on a case of apparent competition between moose (*Alces alces*), wolves (*Canis lupus*), and endangered mountain caribou (*Rangifer tarandus caribou*) in the Columbia Mountains of British Columbia. The southern mountain population of caribou escape predation by residing at high elevations most of the year. However, when moose move into caribou habitat in the summer wolves often follow, exposing caribou to greater predation risk. I examined two hypotheses why moose move into caribou habitat in the summer. First, I examined the hypothesis that human-caused early-seral vegetation available in mountain caribou summer habitat attracts moose. I examined this hypothesis using four predictions: i) moose forage will be more abundant in high-elevation cutblocks compared to other habitats at high and low elevations, ii) moose preferentially select for cutblocks at high elevation relative to low-elevation cutblocks, iii) when moose are at high elevations they will be closer to cutblocks than would be expected by random, iv) the amount of cutblocks at high elevations in a moose home range will be positively related to the amount of time moose spend at high elevations. I found my second prediction was supported; moose did select for cutblocks at high elevations. However, the remaining predictions were not supported: moose forage was not more abundant in high-elevation cutblocks, moose at high elevations were not located closer to cutblocks than would be expected by random, and the proportion of cutblocks in a moose home range at high elevations was not positively related to the amount of time

moose spend at high elevations. While moose highly select for human-caused early-seral habitat, when they are at high elevations moose spend the majority of their time in old-growth forests, suggesting that moose forage in old-growth habitat at high elevations as well as early-seral. Given the mixed results and overall lack of support for the hypothesis I conclude that human-caused early-seral vegetation available in caribou summer habitat does not attract moose to high elevations in the summer. Next I examined the hypothesis that in the summer, moose are exposed to less predation risk at high elevations and that moose move into mountain caribou habitat in response to predation risk. I examined this hypothesis using three predictions: i) the spatial overlap between wolves and moose will decrease during the summer, ii) moose will be exposed to lower predation risk at high elevations compared to low elevations in their home ranges, iii) moose will select for areas of low predation risk. Two of my predictions were supported and one received partial support. Moose were able to distance themselves from wolves in the summer by moving upslope and as a result reduced their exposure to predation risk. Moose exposure to wolf predation was most effectively reduced in the early summer when wolves were constrained to valley bottoms because of denning activities. Finally, moose selected areas of intermediate predation risk and avoided areas of high predation risk. Areas of low predation risk, such as, the alpine, provide little food and cover and were avoided by moose. The results support the hypothesis that moose move into mountain caribou habitat in the summer to avoid predation. I conclude that the basis of mountain caribou recovery will continue to be practices aimed at reducing predator populations and the amount of early-seral vegetation to reduce the density of moose.

Acknowledgements

A graduate thesis is a product of team work and as such I have many people to thank. First and foremost I would like to thank Bruce McLellan and Robert Serrouya for the project idea, the support in many different ways, and the guidance. I am in debt to Bruce for never giving up on me and always encouraging me to keep fighting. My supervisor Stan Boutin provided funding and taught me valuable lessons of life. Craig Demars was a gem in providing a listening ear to my various ideas and problems and always providing a solution. My committee member Evelyn Merrill was extremely useful in teaching me how to write scientific papers and I always appreciated her kindness. Scott Nielsen also patiently answered my statistic related question as I tried to learn about the very confusing world of RSF models. For Arc GIS support Charlene Nielsen is an invaluable resource and I felt extremely fortunate for her presence to help with geographic information system help. I would also like to thank Erin Bayne for stepping in last minute to be on the examining committee, when a committee member could no longer attend for health reasons. Erin's presence saved my sanity and a semester's tuition!

Other graduate students Nick Pilford, Devin Lyons, Barry Robinson, Stephanie Peacock, Kim Dawe, and Marie Auger-Méthé who are all very bright biologist, were great resources, and very helpful. I also need to thank my field assistant, Liam Harrap, for never complaining, even when "short" days turned into miserable, mosquito infested, rainy, 13 hour days. The summer would never have been the same without his recounts of *Seinfeld*. As well "The Columbia Mountain Caribou Project" crew either collected data or were in charge of data management used in this research (Shannon Stotyn, Gary Pavan, Mandy Kellner, Dave Mair, and more) and need credit.

My parents deserve a great big thank you for their unwavering moral and financial support through my 9 years of post-secondary education- I promise to stop being a student and get a job after this- after I travel for a bit first. I would not be here were it not for the

moral support and encouragement over the long and drawn out years from my dear friends Britt, Marie-Hélèn, Mel, and Jen. My sister and brother in-law, Alexandria Sjöman and Carlos de Vera also found time in their very busy lives as corporate lawyers in the UK and parents of a 3 year old child to proofread my thesis. My friend Ben also proof read sections of this document. Staff members at the Ministry of Forests, Lands, and Natural Resource Operations (FLNRO) in Revelstoke were wonderful in providing field support, safety check ins, office space, and providing rides to the cross-country ski trails so I could get away from thesis writing on lunch hours.

I was supported by a Natural Sciences and Engineering Research Council (NSERC) scholarship during my studies. The project also received funding from the Alpine Club of Canada and a large portion of the telemetry collars were provided by the Selkirk College Geospatial Research Centre. I would finally like to thank the Alberta Cooperative Conservation Research Unit (ACCRU) for providing a truck rental.

Table of Contents

Abstract	ii
Acknowledgements	iv
Table of Contents	vi
List of Tables	ix
List of Figures	x
CHAPTER 1 Apparent Competition and the Decline of Mountain Caribou.....	1
THESIS OBJECTIVES	7
WORKS CITED	10
CHAPTER 2 Does High-Elevation Logging Attract Moose and thus Wolves into Endangered Mountain Caribou Habitat?.....	18
ABSTRACT	18
INTRODUCTION.....	19
STUDY AREA	22
METHODS.....	24
Animal Collaring and Telemetry data	24
Diet and Vegetation	27
Resource Selection.....	30
Home ranges and availability.....	31
Old growth forests as cover.....	33
Availability of cutblocks	33
RESULTS	34

Telemetry data	34
Diet and Vegetation	34
Resource selection	37
Old-growth forests as cover	41
Availability of human-seral habitat and time spent in caribou habitat.....	41
DISCUSSION.....	43
MANAGEMENT IMPLICATIONS	48
WORKS CITED.....	50
CHAPTER 3 Do Moose Move into Mountain Caribou Habitat in Response to Summer Wolf	
Predation Risk?	59
ABSTRACT	59
INTRODUCTION.....	60
STUDY AREA	63
METHODS	63
Telemetry data	63
Spatial overlap	64
Predation Risk	64
Wolf Habitat use	65
Pack size.....	66
Broad scale predation risk.....	67
Fine scale predation risk	68
Moose habitat use model	69

RESULTS	72
DISCUSSION.....	77
WORKS CITED.....	83
CHAPTER 4 Discussion and Conclusion	94
INTRODUCTION.....	94
FINDINGS.....	95
FUTURE DIRECTIONS	98
WORKS CITED.....	100

List of Tables

Table 2.1 The number of active GPS collars on moose each year in the Columbia Mountains, southeastern British Columbia.	34
Table 2.2 Results from the microhistological fecal diet analysis for moose in the Columbia Mountains during the summer of 2011 from June to early September. High elevation fecal samples were collected above 1400m and low elevation samples are those collected below 1400m. Low elevation sample was a composite sample of 21 fecal samples and high elevation sample was a composite of 32 fecal samples.	35
Table 2.3 Results of model selection from the mixed effect model predicting the relative resource selection of moose. The second model was the top model based on model log-likelihood (LL), AIC, delta AIC, and model weight. Predictor variables were <i>h</i> = habitat type, <i>a</i> = aspect, <i>s</i> =slope, <i>e</i> =elevation, and <i>se</i> =sex. Sample size was 36437 used and random locations from 20 GPS collared moose in the Columbia Mountains.	38
Table 2.4 Coefficients from the top mixed effects resource selection model for the summer (May 20-November 17) for moose (n=20) in the Columbia Mountains. The number of used and available locations was 36437. Slope and elevation were standardized before being used in the model. Coefficients in bold were statistically significant.	39
Table 3.1 <i>A priori</i> defined candidate models with binary response variable (use) that were used to model resource selection by moose during the summer from 2005-2010 in the Columbia Mountains.	70
Table 3.2 Comparison of the model results for each <i>a priori</i> model for moose habitat use in the summer. N moose shows the number of individual moose included in the model, N telemetry points shows the number of telemetry points used in the model, AIC _w is the	

Akaike’s model weight, and $\sigma^2_{(r\text{ eff})}$ is the variance of the random component in the GLMM model (Season | Moose id). 76

Table 3.3 Resource use coefficients for moose in the Columbia Mountains (2004-2010) from the predation risk-landscape generalized mixed effects model. Confidence intervals are 95% confidence intervals. The total number of used and available points were 5711 from 20 moose and the AIC score for the model was 6051. 77

List of Figures

Figure 2.1 Study site in the Columbia Mountains of British Columbia, Canada and moose summer minimum convex polygon home ranges (n=20) from 2004 to 2010..... 24

Figure 2.2 Mean and range of elevation for moose (circles) and caribou (triangles) every 14 days. The upper bars are the upper 95th percentiles of the data and the lower bars are the 5th percentiles of the data. The first and last bars that run the entire vertical length of the graph mark the beginning and end of the period defined as summer. Data used consisted of telemetry data for caribou (years 1992-2010), moose (years 2003-2010), and wolves (years 2003-2011) in the Columbia Mountains, British Columbia. 26

Figure 2.3 Mean percent cover of moose forage in the Columbia Mountains in the human-seral above 1200 m (n=44), human-seral below 1200 m (n=28), old-growth above 1200 m (n=115), and old-growth below 1200 m (n=126). Bars represent means and the error bars the standard error of the mean. Moose forage plants represented in this graph are species that had a >5% occurrence in the moose summer diet (*Salix* sp., *Thuja plicata*, *Vaccinium membranaceum*, *Cornus* sp., and lichen)..... 36

Figure 2.4 Mean percent cover of moose summer forage above 1200 m elevation in the Columbia Mountains in human-seral above 1200 m (n=28), natural-seral above 1200 m (n=92), old-growth above 1200 m (n=126). Bars represent means and the error bars the

standard error of the mean. Moose forage plants represented in this graph are species that had a >5% occurrence in the high elevation moose summer diet (*Salix* sp., *Vaccinium membranaceum*, and lichen)..... 37

Figure 2.5 Boxplots of percentage of use (light grey boxes) and available (dark grey boxes) for habitat types within home ranges during the summer in home ranges A) below 1200 m elevation and B) above 1200 m elevation. Squares are the mean percentages. Alp= alpine, H seral= human-seral, N seral= natural-seral, Old= old-growth, Rip= riparian. Percentages were calculated on an individual basis using 20 moose with GPS collars in the Columbia Mountains, 2004 to 2010. The horizontal bars are the median proportions, the top of the box shows the 75th percentile of the data, the bottom of the box shows the 25th percentile of the data, and the whiskers show the maximum and minimum values of the data..... 41

Figure 2.6 Relationship between the proportion of human-seral land cover above 1200 m elevation in summer home range of moose (n=20) and the proportion of telemetry locations above 1200 m elevation of moose monitored during 2004-2010 in the Columbia Mountains, British Columbia, Canada. 42

2.7 Relationship between the proportion of human-seral and natural-seral land cover above 1200 m elevation in summer home range of moose (n=20) and the proportion of telemetry locations above 1200 m elevation of moose monitored during 2004-2010 in the Columbia Mountains, British Columbia, Canada. 43

Figure 3.1 Mean and range of elevation for moose (circles), wolves (triangles), and caribou (squares) every 14 days. The upper bars are the upper 95th percentile of the data and the lower bars are the 5th percentile of the data. The first and last bars that run the entire vertical length of the graph mark the beginning and end of the period defined as summer. Data used consisted of telemetry data for caribou (years 1992-2010), moose

(years 2003-2010), and wolves (years 2003-2011) in the Columbia Mountains, British Columbia, Canada. 73

Figure 3.2 Bar graph of the mean predation risk in moose home ranges below 1200 m elevation versus moose home ranges above 1200 m in early summer (20 May-28 July), mid-summer (29 July-29 September), and late summer (30 September-17 November). Error bars are standard errors of the mean. Predation risk calculated for 10 moose in the Columbia Mountains for years 2004-2010. There was a significant difference between predation risk below 1200 m elevation and predation risk above 1200 m elevation in all three seasons (Wilcoxon rank sum paired test, $\alpha=0.01$). 74

Figure 3.3 Linear model fits of the mean predation risk within moose home ranges at moose telemetry locations in early summer (20 May-28 July), mid-summer (29 July-29 September), and late summer (30 September-17 November). Predation risk calculated for 7 moose in the Columbia Mountains for years 2004-2009..... 75

CHAPTER 1 Apparent Competition and the Decline of Mountain Caribou

Human disturbance of habitat is considered one of the top causes of species population decline and extirpation (Caughley 1994, Wilcove et al. 1998, Sih et al. 2000). The mechanism can include but not be limited to direct habitat loss, loss of food, or altered predator-prey systems (Holt 1977, DeCesare et al. 2010). Human disturbance can initiate apparent competition, which is increasingly being recognized as a mechanism behind the decline of numerous prey species (DeCesare et al. 2009). For example, the landscape may be altered to allow the introduction of a new species, which may in turn disrupt the interaction between native prey and their predators. Apparent competition occurs when one or more species indirectly cause a reduction in the population density of another species via a shared common predator(s) (Holt 1977). This differs from direct competition whereby two species compete for a limited resource (Holt 1977, Bonsall and Hassell 1997).

In simple one prey-one predator systems the density of a food limited predator is maintained at an equilibrium by the availability of prey (Holt 1977). The predator cannot depress the number of prey too severely without depressing its own density. When a second prey species is introduced the density of the predator can increase as total prey availability increases (Holt 1977). The original prey can suffer lower densities as the density of predators increases (Holt 1977). When prey differ in reproductive output or survival they can differentially affect the predators' density and each other's densities (Holt 1977, Bonsall and Hassell 1997). As a result, a predators' population growth may no longer be limited by the availability of the original prey species and therefore can drive the prey population to extirpation; this can lead to an inverse density dependent relationship between the predator and the prey species.

Apparent competition can occur in one prey-one predator, or multi prey-one predator, or multi prey-multi predator systems (Holt 1977) so long as the density of one prey species is negatively affected by the presence of an alternate prey and predation is the main cause of population decline. The prey species may not be able to coexist due to differences in i) growth rate of each prey species, ii) the ability of each species to reproduce given the resources available, and iii) the ability of each species to escape predation (Holt 1977).

Apparent competition can be mistaken as competition for resources but the mechanism of population decline is predation and not a lack of habitat or food. However, apparent competition does not exclude the presence of direct competition; some communities that display apparent competition may still have weak forms of direct competition but apparent competition primarily structures the community (Holt 1977). Most communities are likely structured by a mixture of direct competition and apparent competition (Holt 1977, Johnson et al. 2013).

Woodland caribou (*Rangifer tarandus caribou*) populations have declined across North America (Bergerud 1974, Wittmer et al. 2010, Festa-Bianchet et al. 2011). Woodland caribou in western Canada are an example of a species declining primarily because of changes in apparent competition caused by a shift in a multi-prey predator system (Bergerud and Elliot 1986, Seip 1992, James et al. 2004, McLoughlin et al. 2005, Wittmer et al. 2005b). Caribou declines were previously believed to be due to lack of habitat and forage but a growing body of evidence suggests that changes in the abundance of deer and moose have increased wolf density to the detriment of caribou (Seip 1992, Wittmer et al. 2005b, Latham et al. 2011b). The cause of deer and moose increases are varied but there is considerable evidence that it has been influenced by human induced habitat fragmentation and disturbance (Wittmer 2004, Wittmer et al. 2005b, Festa-Bianchet et al. 2011, Boutin et al. 2012, Dawe et al. 2014). Habitat disturbance that results in early-seral vegetation (e.g. timber harvesting, forest fires) facilitates predation through apparent

competition or ease of travel for predators (Rettie and Messier 1998, James 1999, James and Stuart-Smith 2000).

Woodland caribou in Western Canada are divided into populations or regions. The southern mountain population, which is a subpopulation of woodland caribou, is the population that is the focus of this thesis. The southern mountain population has shown some of the steepest declines (Wittmer et al. 2005a) and is designated as endangered (BC Conservation Data Centre 2010, COSEWIC 2014). The range of the southern mountain caribou population is also incidentally where the greatest amount of habitat disturbance and alternate prey are found (Wittmer et al. 2005a). The southern mountain population of caribou lives in the high-snowfall area of southeastern British Columbia and is characterized by seasonal, elevational migrations and forage on arboreal lichen in the winter (The Mountain Caribou Technical Advisory Committee 2002). These caribou are often referred to as mountain caribou.

Unless effective management can take place to reduce rates of predation, the majority southern mountains populations of caribou are likely to go extinct (Wittmer et al. 2010, Festa-Bianchet et al. 2011). In a recent population viability analysis of 10 populations of mountain caribou, one population was predicted to go extinct in 50 years and all others were predicted to go extinct in < 200 years (Wittmer et al. 2010). Beyond those ten populations studied by Wittmer et al (2010) two populations have already become extinct since 2004; and two other populations now have < 10 animals (Hatter 2006, Serrouya and Wittmer 2010). To conserve mountain caribou we need to better understand the complexities of apparent competition relationships involving caribou.

The predators and alternate prey found interacting with caribou varies by location. Shared predators include wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), black bears (*U. americanus*), and cougars (*Felis concolor*) (Seip 1992, Flaa and McLellan 2000, Kinley and Apps 2001, James et al. 2004, Wittmer et al. 2005a). Black bears and grizzly bears are important predators of caribou neonates (Adams et al. 1995, Rettie and Messier 1998) but

at the calf stage (10 days +), wolves may play an increasingly important role; in northern BC wolves accounted for 30% of calf mortalities (Gustine et al. 2006). In the Columbia Mountains grizzly and black bears are the primary predators of adult caribou (Stotyn 2008). However, wolf predation has increased from 0% (before 2000) to 21% (2000-2006) (Stotyn 2008). As the wolf population increases in size in response to moose and deer population increases, wolves may begin to have an increased impact on caribou survival (Stotyn 2008, Latham et al. 2011b). Furthermore, the majority of bears in woodland caribou habitat are herbivorous (Hobson et al. 2000) and are unlikely to demonstrate a strong functional response to prey such as moose or caribou. As a result wolves are likely becoming increasingly important predators of caribou in the Columbia Mountains.

Species that share common predators with caribou primarily include moose, deer (*Odocoileus spp.*), and elk (*Cervus elaphus*) (Seip 1992, Latham et al. 2011b). Of particular concern are species that are capable of driving a functional response in predators, such as moose and wolves. Wolves tend to prefer moose over caribou (James et al. 2004, Serrouya 2013) due to the greater amount of energy obtained per kill and lower search times (Bergerud et al. 1984, Adams et al. 1995, Hayes and Harestad 2000b, Lessard et al. 2005). Woodland caribou are unlikely to be the primary prey of most predators due to their low population levels (Wittmer et al. 2005b). When caribou predation does occur it is likely an incidental event (Wittmer et al. 2005b). In the Columbia Mountains the diet of wolves from spring to fall consists primarily of moose (on average 95% of the diet), followed by deer and caribou (1.3% on average), and a small amount of beaver (Stotyn 2008). However, this shifts seasonally and in the fall the proportion of caribou in the diet of wolves showed signs of increasing to an average of 22% of the diet (Stotyn 2008). Overall, the majority of caribou predation by wolves occurs in summer (Seip 1992) and fall/early winter (Seip 1992, Stotyn 2008).

Large scale timber harvesting has directly affected moose densities in British Columbia and indirectly affected wolves and caribou. The habitat range of moose has been

slowly expanding in Western North-American since the early 20th century as human disturbance to the landscape increased (increasing moose forage), and the climate became more favourable for moose (Kelsall and Telfer 1974, Telfer 1984, Spalding 1990, Karns 1998, Darimont et al. 2005). When moose first colonized North American 15,000 years ago (Hundertmark et al. 2002) their range was limited by climate and vegetation (Karns 1998). Undisturbed coastal British Columbia and the interior rainforest of British Columbia does not contain vegetation typically considered moose habitat (Telfer 1984) and pre 1900, moose were believed to be rare or absent in southern BC (Hatter 1950, Spalding 1990, Kay 1997). Thus, the current overlap in moose and caribou ranges is a relatively recent event (Darimont et al. 2005, Stotyn 2008). Large scale timber harvesting has increased moose abundance in British Columbia (Darimont et al. 2005, Serrouya et al. 2011) because timber harvesting tends to increase the carrying capacity of an area for moose (Peek 1998). In 2003, the moose population north of Revelstoke was reported to have increased by 100% over a decade (Poole and Serrouya 2003) which was correlated with an increase in early-seral vegetation on the landscape and milder temperatures (Serrouya and D'Eon 2003). As large scale logging continues, moose range and population expansion will continue to be facilitated in British Columbia (Darimont et al. 2005).

While human modification of vegetation has aided moose range and population expansion it has done nothing to directly benefit caribou. Caribou are associated with old growth forests (Apps et al. 2001, Stotyn 2008) and are not associated with early-seral vegetation like moose. Habitat disturbance which favours alternate prey (Festa-Bianchet et al. 2011, Latham et al. 2011*b*, Serrouya et al. 2011) combined with the lower fecundity rate of caribou (Shackleton 1999) leads to an imbalance in between moose and caribou, making it difficult for them to coexist on a landscape when they share a food limited predator. Further complicating the matter for caribou is human alterations of the landscape which have facilitated in caribou predation (James and Stuart-Smith 2000, Latham et al. 2011*a*)

and possibly reduced the spatial separation between caribou and alternate prey and predators (James et al. 2004, Stotyn 2008, Peters et al. 2013).

The southern mountain population of caribou make seasonal altitudinal migrations and spend their winters in deep snow packs to which they are well adapted (Wittmer 2004, Stotyn 2008). These migrations spatially segregate caribou from alternate prey and predators (Bergerud and Page 1987, Seip 1992, Stotyn 2008). The spatial separation between these three species is related to their food and habitat selection. Moose are restricted to the valley bottom in the winter by a heavy snow pack (Stotyn et al. 2007). Typically caribou and moose do not overlap much in habitat type: caribou tend to prefer mature coniferous forests, whereas moose tend to prefer young deciduous forests (Bowman et al. 2010). In the spring mountain caribou descend from high elevation old growth forests to low elevation cedar and hemlock forests and in summer they return to high elevation Englemann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forests to access forbs and deciduous vegetation (Simpson et al. 1987, Rominger et al. 2000, Kinley and Apps 2001). In contrast, moose select riparian habitats in the spring (Telfer 1984, Peek 1998) where they find abundant, high quality forage, and shelter from heat (Peek 1998). In the summer and fall, moose migrate to higher elevation/subalpine forests, and wet meadow complexes that are abundant in forbs and shrubs in the subalpine (Telfer 1984) but moose avoid the alpine in all seasons (Boer 1997). Wolf habitat selection is similar to that of moose because they are spatially associated with moose and the availability of prey (Oakleaf, John et al. 2006) (Cumming and Beange 1993, Kuzyk 2002, Oakleaf, John et al. 2006, Bowman et al. 2010). For example, in Alberta wolves use and select for cutblocks, young forests (Neufeld 2006), and shrubby areas (Kuzyk 2002), which are typical moose habitats.

As caribou and moose change their pattern of habitat use by season the spatial overlap between them and wolves changes. Spatial separation between moose and caribou is the greatest during spring and calving seasons and is low during summer and early winter (Stotyn 2008). For wolves and caribou the spatial separation is lowest in the spring and

calving season when young calves are vulnerable to predation. In summer, when moose are closer to caribou, spatial separation is moderate and in winter when the wolves are constrained to the valley bottoms by deep snow packs the spatial separation between wolves and caribou is the greatest (Stotyn 2008).

The spatial separation behaviour caribou employ to reduce predation may no longer be sufficient to reduce predation. Apparent competition is precipitated by either human disturbance which favors the fitness of one prey species over another or increases the spatial overlap between two prey species (DeCesare et al. 2009). It has been suggested that timber harvesting at high elevations has allowed the summer range of moose to expand upslope and into caribou habitat (Seip 1992, Wittmer et al. 2005a), thus increasing the spatial overlap between caribou, alternate prey and their shared predators. When moose move to higher elevation habitat in the summer wolves follow. Summer is when the rates of caribou predation are the highest (Wittmer et al. 2005a) and when the spatial separation between moose and caribou is the lowest (Stotyn 2008). However, it may be that moose have historically used high elevation habitats in the summer before large scale forest harvesting at high elevations. For example, Tefler (1984) noted that moose migrate to higher elevations to subalpine forests and shrub lands above the timberline to use naturally occurring wet meadow complexes in summer and fall. However, little is known about moose habitat use and selection in mountain habitats in the summer to know what may be causing them to move to higher elevations and thus spatially overlap with mountain caribou.

THESIS OBJECTIVES

The primary goal of this thesis was to better understand why moose move up mountain slopes to higher elevations where they spatially overlap with mountain caribou. To better understand the complexities of apparent competition it is important to understand the ecology of the species involved. By better understanding moose habitat and forage selection

we may be better able to manage the landscape and moose populations for the conservation of mountain caribou.

The chapters of this thesis have been written in manuscript format and therefore there is overlap between the introduction, study area, and methods descriptions between each data chapter. In chapter two I used a series of predictions to examine a dominant, but untested, hypothesis that high elevation timber harvesting is the mechanism behind the increased spatial overlap between moose, caribou, and wolves. First, I predicted that the percent cover of moose forage species would be greater in high-elevation cutblocks compared to other habitats at high and low elevations. Disturbed habitats generally produce more forage for moose than late succession forest (Peek et al. 1976, Wolff 1978), however, it is unknown how this changes with elevation. For moose to make the effort to move to high elevation cutblocks I predicted there would need to be a benefit that outweighs the energy cost involved. If moose are moving upslope to forage in high elevation cutblocks then I expected there would be a greater availability of forage compared to both habitats at low elevations and other habitats at high elevations. Second, I predicted that moose would select for cutblocks at high elevations. Moose select for cutblocks in the summer (Peek et al. 1976), however, it is unknown how moose selection of cutblocks changes with elevation. If moose selection for cutblocks is lower at high elevations compared to low elevations then moose are not undertaking energetic movements into caribou habitat for cutblocks at high elevations. Third, I predicted that when moose were in old growth forests at high elevations they would be closer to cutblocks than would be expected by random. When moose forage in open disturbed areas they require forests to use as cover or shelter to be close (Eastman 1974, Wixleman et al. 1998). Thus I predicted that when moose were using old growth habitat at high elevations they were using it primarily as cover. Finally, I predicted that moose with a greater amount of cutblocks in their home-range would spend a greater amount of time at high elevations. Cutblocks generally produce moose forage and moose select for these habitats, thus I expect that the limiting factor to moose spending more time

at high elevations is the availability of early-seral vegetation produced in disturbed habitats. To test these predictions I used a combination of telemetry data for moose and caribou, moose fecal analyses, and vegetation surveys. The goal was to better understand what habitat types moose were using and selecting in relation to caribou habitat and how their diet may be related to different habitats they use.

In chapter three an alternate hypothesis was presented: that moose move into high elevation mountain habitat to avoid predation (Kunkel and Pletscher 2000). In the summer, moose are no longer restricted by deep snow to the valley bottoms and may be able to reduce their exposure to predation risk by spacing out, similar to the strategy of mountain caribou. This hypothesis was examined using three predictions. First, in terms of elevation, the spatial overlap between wolves and moose will decrease. Similar to what others have reported (Stotyn 2008, Peters et al. 2012), it is expected that the spatial overlap between moose and wolves will decrease in the summer and this will be due to shifts in elevation by moose and wolves. Second, moose will be exposed to lower predation risk at high elevations compared to low elevation. It is expected that wolf predation risk will be higher for moose at low elevations because wolves will be constrained to valley bottoms by denning activities in the spring and early summer (Murie 1944, Haber 1977, Mech 1988). Third, it is expected that moose will select for areas of low predation risk, given that moose are limited by wolf predation (Messier 1991, Ballenberghe and Ballard 1994) and wolves are a dominant predator. The primary objective of chapter three was to examine if moose were responding to wolf predation risk by moving to high elevation habitat to reduce their exposure to predation risk. I tested my predictions by modeling predation risk based on the spatial intensity of wolf habitat use and wolf pack numbers. Avoidance of predation risk can occur at multiple spatial scales, I therefore tested the ability of moose to avoid predation risk at both a broad home range level and a finer scale at moose locations (30 m x 30 m). At a broad home range scale, predation risk above and below 1200 m elevation was compared. At the finer scale how predation risk at moose telemetry points changed with elevation was

examined. For the third prediction, how moose responded to wolf predation risk by selecting for areas of low predation risk was tested using a mixed effect model with predation risk and predation risk related landscape variables.

WORKS CITED

Adams, L. G., F. J. Singer, and B. W. Dale. 1995. Caribou Calf Mortality in Denali National Park, Alaska. *The Journal of Wildlife Management* 59:584–594.

Apps, C. D., B. N. McLellan, T. A. Kinley, and J. P. Flaa. 2001. Scale-Dependent Habitat Selection by Mountain Caribou, Columbia Mountains, British Columbia. *The Journal of Wildlife Management* 65:65–77.

Ballenberghe, V. Van, and W. B. Ballard. 1994. Limitation and regulation of moose populations: the role of predation. *Canadian Journal of Zoology* 72:2071–2077.

BC Conservation Data Centre. 2010. <<http://www.env.gov.bc.ca/cdc/>>.

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

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

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.

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

Boer, A. H. 1997. Interspecific relationships. Pages 337–349 in A. W. Franzmann and C. C. Schwartz, editors. *Ecology and management of the North American Moose*. Smithsonian Institution Press, Washington, D.C.

- Bonsall, M. B., and M. P. Hassell. 1997. Apparent competition structures ecological assemblages. *Nature* 388:371–373.
- Boutin, S., M. S. Boyce, M. Hebblewhite, D. Hervieux, K. H. Knopff, M. C. Latham, A. D. M. Latham, J. Nagy, D. Seip, and R. Serrouya. 2012. Why are caribou declining in the oil sands? *Frontiers in Ecology and the Environment* 10:65–67.
- Bowman, J., J. C. Ray, A. J. Magoun, D. S. Johnson, and F. N. Dawson. 2010. Roads, logging, and the large-mammal community of an eastern Canadian boreal forest. 467:454–467.
- Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63:215–244.
- COSEWIC. 2014. Committee on the Status of Endangered Wildlife in Canada. <http://www.cosewic.gc.ca/eng/sct5/index_e.cfm>.
- Cumming, H. G., and D. B. Beange. 1993. Survival of woodland caribou in commercial forests of northern Ontario. *The Forestry Chronicle* 69:579–588. NRC Research Press Ottawa, Canada.
- Darimont, C. T., T. E. Reimchen, P. C. Paquet, and V. Crichton. 2005. Range expansion by moose into coastal temperate rainforests of British Columbia, Canada. *Diversity and Distributions* 11:235–239.
- DeCesare, N. J., M. Hebblewhite, H. S. Robinson, and M. Musiani. 2010. Endangered, apparently: the role of apparent competition in endangered species conservation. *Animal Conservation* 13:353–362.
- Eastman, D. S. 1974. Habitat use by moose of burns, cutovers and forests in northcentral British Columbia. Pages 238–256 *in*. Proceedings of the North American Moose Conference. Volume 10.

- Festa-Bianchet, M., J. C. Ray, S. Boutin, S. D. Côté, and A. Gunn. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. *Canadian Journal of Zoology* 89:419–434.
- Flaa, J. P., and B. N. McLellan. 2000. Population characteristics of the Lake Revelstoke caribou. Pages 639–642 in L. M. Darling, editor. *Proceedings of a Conference on the Biology and Management of Species at Risk, Kamloops, B.C. Volume 2*. B.C. Ministry of Environment, Land, and Parks, Victoria, British Columbia.
- Gustine, D. D., K. L. Parker, R. J. Lay, M. P. Gillingham, and D. C. Heard. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs* 165:1–32.
- Haber, G. C. 1977. *Socio-ecological dynamics of wolves and prey in a subarctic ecosystem*. University of British Columbia.
- Hatter, I. 2006. Mountain Caribou 2006 Survey Results, Subpopulation Trends and Extinction Risk. Pages 4–22 in *Multidisciplinary Approaches to Recovering Mountain Caribou in Mountain Ecosystems*. Columbia Mountains Institute of Applied Ecology, Revelstoke, British Columbia.
- Hatter, J. 1950. Past and present aspects of the moose problem in central British Columbia. Pages 150–154 in *Proc. 13th A. Conf. west. Ass. St. Game Fish Commrs. Volume 30*.
- Hayes, R. D., and A. S. Harestad. 2000. Wolf functional response and regulation of moose in the Yukon. *Canadian Journal of Zoology* 78:60–66.
- Hobson, K. a., B. N. McLellan, and J. G. Woods. 2000. Using stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes to infer trophic relationships among black and grizzly bears in the upper Columbia River basin, British Columbia. *Canadian Journal of Zoology* 78:1332–1339.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12:197–229.

- Hundertmark, K. J., G. F. Shields, I. G. Udina, R. T. Bowyer, A. A. Danilkin, and C. C. Schwartz. 2002. Mitochondrial Phylogeography of Moose (*Alces alces*): Late Pleistocene Divergence and Population Expansion. *Molecular Phylogenetics and Evolution* 22:375–387.
- James, A. R. C., S. Boutin, D. M. Hebert, A. B. Rippin, and J. White. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. *Journal of Wildlife Management* 68:799–809.
- James, A. R. C., and A. K. Stuart-Smith. 2000. Distribution of caribou and wolves in relation to linear corridors. *Journal of Wildlife Management* 64:154–159.
- James, A. R. C. 1999. Effects of industrial development on the predator-prey relationship between wolves and caribou in northeastern Alberta. University of Alberta.
- Johnson, H. E., M. Hebblewhite, T. R. Stephenson, D. W. German, B. M. Pierce, and V. C. Bleich. 2013. Evaluating apparent competition in limiting the recovery of an endangered ungulate. *Oecologia* 171:295–307.
- Karns, P. D. 1998. Population distribution, density and trends. Ecology and management of the North American moose 125–140. Smithsonian Institution Press Washington, DC, USA.
- Kay, C. E. 1997. Aboriginal overkill and the biogeography of moose in western North America. *Alces* 33:141–164.
- Kelsall, J. P., and E. S. Telfer. 1974. Biogeography of moose with particular reference to western North America. *Naturaliste Canadien* 101:117-130.
- Kinley, T. A., and C. D. Apps. 2001. Mortality patterns in a subpopulation of endangered mountain caribou. *Wildlife Society Bulletin* 158–164.

- Kunkel, K. E., and D. H. Pletscher. 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. *Canadian Journal of Zoology* 78:150–157.
- Kuzyk, G. 2002. Wolf Distribution and Movements on Caribou Ranges in West Central Alberta. University of Alberta.
- Latham, A. D. M., M. C. Latham, M. S. Boyce, and S. Boutin. 2011a. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecological Applications* 21:2854–2865.
- Latham, A. D. M., M. C. Latham, N. A. McCutchen, and S. Boutin. 2011b. Invading white-tailed deer change wolf-caribou dynamics in northeastern Alberta. *The Journal of Wildlife Management* 75:204–212.
- Lessard, R. B., S. J. D. Martell, C. J. Walters, T. E. Essington, and J. F. Kitchell. 2005. Should ecosystem management involve active control of species abundances. *Ecology and Society*. Volume 10. <<http://www.ecologyandsociety.org/vol10/iss2/art1/>>.
- Mech, L. D. 1988. *The Arctic wolf: Living with the pack*. Voyageur Press, Stillwater, MN.
- Messier, F. 1991. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. *The Journal of Animal Ecology* 377–393.
- Murie, A. 1944. *The Wolves of Mount McKinley*. Page 238 *in*. U.S. National Park Service Fauna Series. Fifth edition. U.S. Government Printing Office, Washington, D.C.
- Neufeld, L. M. 2006. Spatial dynamics of wolves and woodland caribou in an industrial forest landscape in west-central Alberta. University of Alberta.
- Oakleaf, John, K., D. L. Murray, J. R. Oaklead, E. E. Bangs, C. M. Mack, D. W. Smith, J. A. Fontaine, M. D. Jimenez, T. J. Meier, and C. C. Niemeyer. 2006. Habitat Selection by Recolonizing Wolves in the Northern Rocky Mountains of the United States. *Journal of Wildlife Management* 70:554–563.

- Peek, J. M., D. L. Urich, and R. J. Mackie. 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. *Wildlife Monographs* 32:3–65.
- Peek, J. M. 1998. Habitat relationships. Pages 351–401 *in* A. Franzmann and C. Schwartz, editors. *Ecology and management of the North American moose*. Smithsonian Institution Press, Washington.
- Peters, W., M. Hebblewhite, N. DeCesare, F. Cagnacci, and M. Musiani. 2012. Resource separation analysis with moose indicates threats to caribou in human altered landscapes. *Ecography* 35:001–012.
- Poole, K. G., and R. Serrouya. 2003. Moose population monitoring in the Lake Revelstoke Lake valley, 2002-2003. Revelstoke.
- 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.
- Rominger, E. M., C. T. Robbins, M. A. Evans, and D. J. Pierce. 2000. Autumn foraging dynamics of woodland caribou in experimentally manipulated habitats, northeastern Washington, USA. *Journal of Wildlife Management* 160–167.
- Schaefer, J. A., A. M. Veitch, F. H. Harrington, W. K. Brown, J. B. Theberge, and S. N. Luttich. 1999. Demography of decline of the Red Wine Mountains caribou herd. *Journal of Wildlife Management* 63:580–587.
- 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.
- Serrouya, R., and D. D'Eon. 2003. Winter habitat use and food habits of deer and elk in the northern Selkirk Mountains. Salmon Arm, British Columbia.

- Serrouya, R., B. N. McLellan, S. Boutin, D. R. Seip, and S. E. Neilsen. 2011. Developing a population target for an overabundant ungulate for ecosystem restoration. *Journal of Applied Ecology* 48:935–942.
- Serrouya, R., and H. U. Wittmer. 2010. Imminent extinctions of woodland caribou from national parks. *Conservation Biology* 24:363–364.
- Serrouya, R. 2013. An adaptive approach to endangered species recovery based on a management experiment: reducing moose to reduce apparent competition with woodland caribou. University of Alberta.
- Shackleton, D. M. 1999. Hoofed mammals of British Columbia. Volume 3. University of British Columbia Press, Vancouver, B.C.
- Sih, A., B. G. Jonsson, and G. Luikart. 2000. Habitat loss: ecological, evolutionary and genetic consequences. *Trends in Ecology & Evolution* 15:132–134. Elsevier Current Trends.
- Simpson, K., K. Herbert, and G. P. Woods. 1987. Critical habitats of caribou (*Rangifer tarandus caribou*) in the mountains of southern British Columbia. Ministry of Environment and Parks, Wildlife Branch, Victoria, British Columbia.
- Spalding, D. J. 1990. The early history of moose (*Alces alces*): distribution and relative abundance in British Columbia. Royal British Columbia Museum.
- Stotyn, S. A., B. N. McLellan, and R. Serrouya. 2007. Mortality sources and spatial partitioning among mountain caribou, moose, and wolves in the north Columbia Mountains, British Columbia. Report prepared for the Columbia Basin Fish and Wildlife Compensation Program, Nelson. British Columbia.
- Stotyn, S. A. 2008. Ecological Interactions of Mountain Caribou, Wolves and Moose in the North Columbia Mountains, British Columbia. University of Alberta.

- 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. *The Journal of wildlife management* 61:622–633.
- Telfer, E. S. 1984. Circumpolar Distribution and Habitat Requirements of Moose (*Alces alces*). Pages 145–151 *in* R. Olsen, R. Hastings, and F. Geddes, editors. *Northern Ecology and Management*. Edmonton, Alberta, Canada.
- The Mountain Caribou Technical Advisory Committee. 2002. *A Strategy for the Recovery of Mountain Caribou in British Columbia*. Victoria, British Columbia.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *BioScience* 48:607–615.
- Wittmer, H. U., R. N. M. Ahrens, and B. N. McLellan. 2010. Viability of mountain caribou in British Columbia, Canada: Effects of habitat change and population density. *Biological Conservation* 143:86–93.
- Wittmer, H. U., B. N. McLellan, D. R. Seip, J. A. Young, T. A. Kinley, S. Watts, D. Hamilton, and G. Watts. 2005a. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. *Canadian Journal of Zoology* 83:407–418.
- Wittmer, H. U., A. Sinclair, and B. McLellan. 2005b. The role of predation in the decline and extirpation of woodland caribou. *Oecologia* 144:257–267.
- Wittmer, H. U. 2004. *Mechanisms underlying the decline of mountain caribou (Rangifer Tarandus caribou) in British Columbia*. The University of British Columbia.
- Wixleman, D. A., R. T. Bowyer, and V. Van Ballenberghe. 1998. Diet selection by Alaskan moose during winter: effects of fire and forest succession. *Alces* 34:213–238.
- Wolff, J. O. 1978. Burning and browsing effects on willow growth in interior Alaska. *The Journal of Wildlife Management* 135–140.

CHAPTER 2 Does High-Elevation Logging Attract Moose and thus Wolves into Endangered Mountain Caribou Habitat?

ABSTRACT

Increases in early-seral vegetation on the landscape are threatening the persistence of woodland caribou (*Rangifer tarandus caribou*) by inter-trophic relationships which result in increased predation rates. Of particular concern is the increase in early-seral vegetation in high elevation caribou summer habitat caused by an expansion of the forestry industry from valley bottoms to high elevation forests. Deep snow restricts moose (*Alces alces*) to valleys during winter but they move up slope in the summer, increasing their spatial overlap with caribou. Wolves (*Canis lupus*) follow moose up slope and occasionally encounter and kill the few remaining caribou. I examined whether human-caused early-seral vegetation available in mountain caribou summer habitat attracted moose into mountain caribou habitat thus increasing the spatial overlap between caribou, moose, and wolves. I tested a number of predictions generated by this hypothesis: i) moose forage will be more abundant in high-elevation cutblocks compared to other habitats at high and low elevations, ii) moose will select for cutblocks at high elevation, iii) when moose are at high elevations they are closer to cutblocks than would be expected, iv) the amount of cutblocks at high elevations in a moose home range will be positively related to the amount of time moose spend at high elevations. To test the first prediction I used fecal samples to determine the plant species moose consume in the summer and vegetation surveys to compare the cover of moose forage species amongst habitat types. For predictions ii-iv, I used moose telemetry and landscape cover data. Selection for high elevation cutblocks (prediction iii) was tested for using a binomial mixed effects model. Only the second prediction was supported: moose selected cutblocks at high elevations. The remaining predictions were not supported: i) the

amount of moose forage in high elevation cutblocks did not differ from other habitats; iii) moose locations at high-elevations were not closer to cutblocks than would be expected at random by random; and iv) moose with an abundance of high-elevation cutblocks did not spend more time in caribou habitat than did moose with little or no logging. The results suggest that high-elevation logging does not influence the seasonal movements of moose into mountain caribou habitat. These results have important implications for the conservation of mountain caribou and the management of forests, moose, and predators in caribou habitat.

INTRODUCTION

Moose (*Alces alces*) have expanded their range into temperate rainforests of western Canada (Spalding 2000, Darimont et al. 2005, Serrouya et al. 2011). In southern British Columbia moose numbers have increased in association with more wildfires, forestry operations, and transmission lines which greatly increased the amount of early-seral conditions in these ecosystems (Seip 1992, Spalding 2000, Serrouya et al. 2011). Since 1966, when clear-cuts first began in BC (Stevenson 1991), the amount of early-seral vegetation present on the landscape has increased. As the logging industry expands from valley bottom forests to high elevation forests, the amount of logging occurring in mountain caribou (*Rangifer tarandus caribou*) summer habitat has also increased. The conversion of forests from old-growth to early-seral vegetation produces more moose browse (Wolff 1978) and increases the carrying capacity of an area for moose (Peek 1998) but does not increase the relative predation of moose by wolves in winter (Kunkel and Pletscher 2000). The expansion of moose into interior rainforests and their population increase has corresponded with a decline in mountain caribou (Seip 1992, Wittmer 2004, Wittmer et al. 2007, Stotyn 2008, Apps et al. 2013).

Moose play a key role in the endangerment of mountain caribou via apparent competition. Apparent competition occurs when a species indirectly causes the decline of

another species with which they share a predator(s) (Holt 1977). In the case of mountain caribou in the Columbia Mountains in British Columbia, Canada, predators, and in particular wolves (*Canis lupus*), are sustained primarily by moose (Wittmer et al. 2005a) but they also kill mountain caribou. As the population of moose increases, the population of wolves increases and subsequently the predation of mountain caribou increases (Bergerud and Ballard 1988, Seip and Cichowski 1996, Wittmer et al. 2007). Predation rates on caribou in western Canada in most subpopulations are unsustainable, causing declines and even extirpations (Wittmer et al. 2005a, Festa-Bianchet et al. 2011, Hervieux et al. 2013).

Most mountain caribou predation occurs during the summer (Wittmer et al. 2005b) when there is the greatest spatial overlap between the few remaining caribou and the abundant moose population (Seip 1992, McLoughlin et al. 2005, Serrouya et al. 2011). In mountainous ecosystems such as the Columbia Mountains, moose are restricted to the valley bottoms in winter by deep snow (Stotyn 2008). During winter, 60% of moose locations are in recent clear-cuts and under transmission lines where early-seral browse is abundant (Serrouya et al. 2011). In summer, moose spread out to higher-elevation forests where they overlap with mountain caribou (Stotyn 2008). Mountain caribou occupy high elevation habitat in summer to distance themselves from predators (Bergerud and Ballard 1988), however, this strategy has become less effective with the increased presence of moose.

Until recently, forest harvesting has been most intensive at lower elevations but is now expanding into higher elevation forests. It is uncertain whether logging at higher elevations attracts moose to higher elevations in summer as suggested elsewhere (Seip 1992, Wittmer et al. 2005b). Understanding how logging at high elevations may alter moose distribution is key to managing the interaction between moose, caribou, and wolves. If logging at high elevations is attracting moose into caribou habitat then much more attention must be given to forestry practices at high elevations. Here, I investigate the relationship

between high elevation logging and its potential role in increasing the spatial overlap between moose and mountain caribou and thus predation rates of mountain caribou.

I used four predictions to examine the hypothesis that early-seral conditions caused by forest harvesting at high elevations attracts moose into caribou habitat. First, I predicted that the percent cover of plant forage used by moose would be greater in high-elevation cutblocks compared to other habitats at high and low elevations. Disturbed habitats produce more forage for moose than late succession forest (Peek et al. 1976, Wolff 1978), however, it is unknown if this is consistent with elevation. For moose to undertake the effort to move to high elevation cutblocks a benefit needs to be provided that outweighs the energy cost involved. If moose are moving upslope to forage in high elevation cutblocks then I expected there to be a greater availability of forage compared to other habitats (e.g. cutblocks, old-growth, natural-seral) at low elevations and high elevations. Second, I predicted that moose would more strongly select for cutblocks at high elevations compared to low elevations. Moose select for cutblocks in the summer (Peek et al. 1976), however, it is unknown if moose selection of cutblocks changes with elevation. If moose selection for cutblocks is lower at high elevations compared to low elevations then moose are not moving upslope for cutblocks. Third, I predicted that when moose were in old growth forests at high elevations they were closer to cutblocks than would be expected. When moose forage in open disturbed areas they require forests to use as cover or shelter to be close (Eastman 1974, Wixleman et al. 1998). Thus, I predicted that when moose were using old growth habitat at high elevations they were using it primarily as cover. Finally, I predicted that moose with a greater amount of cutblocks in their home-range would spend a greater amount of time at high elevations. Cutblocks generally produce moose forage and moose select for these habitats, thus I expect that the limiting factor to moose spending more time at high elevations would be the availability of early-seral vegetation produced in disturbed habitats. To test these predictions I used a combination of telemetry data for moose and caribou, moose fecal analyses, and vegetation surveys. These predictions provide a multi-faceted test

of the hypothesis that high elevation logging causes moose to move up slope into mountain caribou habitat, thus exacerbating wolf predation of mountain caribou.

STUDY AREA

The study area was 4500km² and was located north of the town of Revelstoke in south-eastern British Columbia, Canada in the northern Columbia Mountains (51°N, 118°W). The study area was defined by a combination of geographic barriers (roads, mountains, and water bodies) and where data had been collected. The area is rugged with a valley floor elevation of 650 m and ranging up to peaks of 3519 m (Figure 2.1). The area is part of the interior rainforest and receives 1071 mm/yr of precipitation, 447 cm of which falls as snow. The summer temperature is an average of 12°C with an average maximum of 24°C and an average minimum of 1°C (Canadian Climate Normals 1981-2010 Station Data n.d.). Valley bottoms of the study site are characterized by the Interior Cedar-Hemlock (ICH) biogeoclimatic ecosystem classification (BEC) zone with western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and the occasional Douglas fir (*Pseudotsuga menziesii*) (Braumandl and Curran 1992). The Engelmann Spruce-Subalpine Fir (ESSF) zone occurs at elevations of approximately 1,208 m to 1,400 m (Braumandl and Curran 1992 and is dominated by Englemann spruce (*Picea englemannii*) and subalpine fir (*Abies lasiocarpa*) (Braumandl and Curran 1992). The Alpine Tundra (AT) zone is found above 1,800 m and is treeless or trees are krummholtz, instead the vegetation is dominated by dwarf shrubs.

Overall, the dominant landcover type is old-growth forest (42%) and 10% of the study area has been logged. Of the area below 1200 m elevation, 35% of this area was at one point harvested and while the amount of timber harvesting at high elevations has been increasing, the overall amount of area harvested above 1200 m elevation is 3%. The majority of forests that have been harvested are in a state of regeneration, with a small proportion of forests that are mid-seral (30-80 years old) or mature forests (140-250) years of (Serrouya et al. 2011). Almost a third of the study area is unforested, occupied by land

cover such as avalanche chutes and marshes, dominated by thick shrub vegetation (Serrouya et al. 2011), which I have termed natural-seral. The natural-seral habitats tend to be populated primarily by plants such as *Abies* spp., *Alnus* spp., ferns, *Carex* spp., *Oplopanax horridus*, *Pachistima myrsinites*, *Tiarella* spp., and *Tsuga* spp., which are not typical moose forage species. Less than one percent of the habitat is riparian habitat (streams, rivers, lakes) and the remaining habitat is unforested alpine tundra habitat. Beyond forest harvesting, the area is host to a suite of recreational activities such as hunting, trapping, snowmobiling, and heliskiing.

Ungulates in the study area include moose, which are the most abundant. Mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), mountain goats (*Oreamnos americanus*), and elk (*Cervus canadensis*) also occur at low densities (Poole and Serrouya 2003, Serrouya et al. 2011). Mountain caribou are found at low densities in four subpopulations within the study area: Columbia North, Columbia South, Frisby-Boulder, and Central Rockies (Wittmer et al. 2005a, Serrouya et al. 2011, van Oort et al. 2011). These populations declined from 1994 to 2005: the Columbia South population declined from 117 (10-300; 90% CI) to 10, the Columbia North from 232 (203-272) to 142, the Frisby-Boulder from 34 (27-47) to 12, and the Central Rockies from 17 to 3 (Wittmer et al. 2005a, McLellan et al. 2008). Overall, mountain caribou have declined by about 10% each year since 1997 after a relatively stable period between 1994 and 1997 (McLellan et al. 2008). Conversely, moose densities doubled from 0.7/km² to 1.54/km² between 1993 and 2003. In 2003, the Government of British Columbia decided to manage the moose population to reduce the impact of apparent competition with caribou. Hunting permits were increased by a factor of 5 from pre-2003 levels (Serrouya and Pavan 2005). From 2003 to 2009, the moose population declined from 1650 to 447 (Serrouya et al. 2011). Grizzly bears (*Ursus arctos*), black bears (*U. americanus*), wolverine (*Gulo gulo*), wolves, and cougars (*Puma concolor*) are carnivores known to kill caribou and moose in the area (Stotyn 2008). There was no

direct management of the wolf population in my study area, wolves were instead managed indirectly via their primary prey- moose.

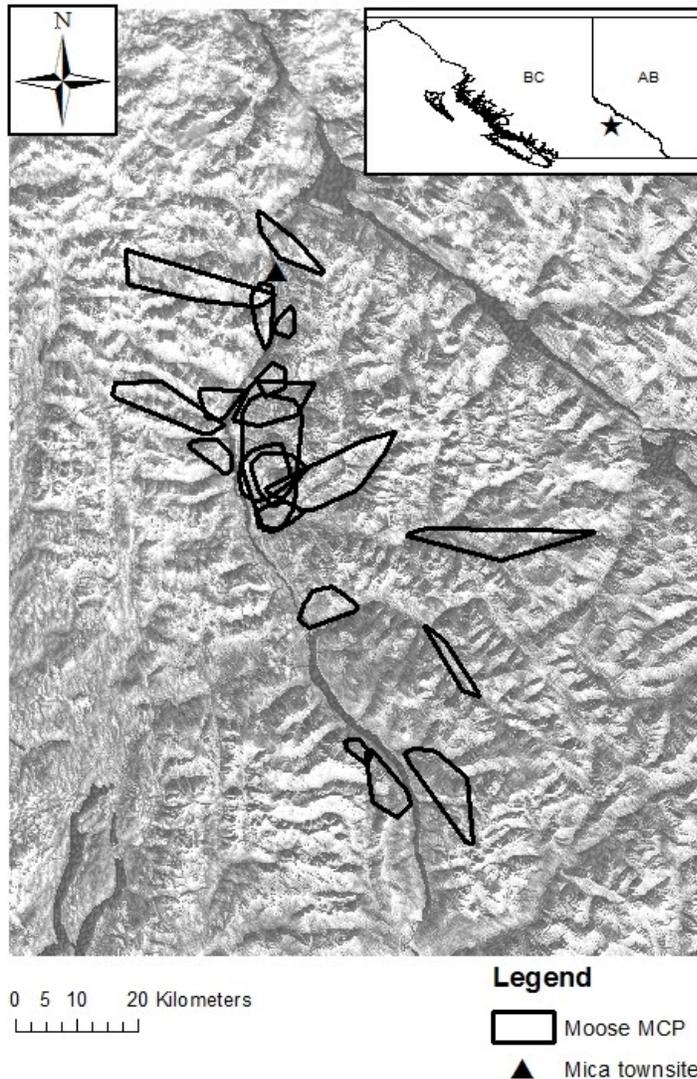


Figure 2.1 Study site in the Columbia Mountains of British Columbia, Canada and moose summer minimum convex polygon home ranges (n=20) from 2004 to 2010.

METHODS

Animal Collaring and Telemetry data

Moose and caribou telemetry data from the Columbia Mountains were collected from 1992 to 2010 (for details see Apps et al. 2001a, Wittmer 2004, Serrouya et al. 2007, Stotyn

et al. 2007, Wittmer et al. 2007b, Stotyn 2008, van Oort et al. 2011). All individuals were captured with a net gun in March when snow pack was deep and animals and their tracks were easily seen. Caribou and moose captures followed animal care protocols for the Province of BC and the University of Alberta (permit # VI08-49757, and 690905, 2004-09D, 2005-19D). From 1992-2010, 92 individual caribou were collared in the Columbia Mountains. As for moose collaring, between 2003 and 2010, 32 moose were collared with GPS collars programmed to download a relocation every 5 hours.

An elevational cutoff was used to study when moose were in mountain caribou habitat because the spatial overlap between moose and caribou occurs when moose move up from the valley bottoms into mountain caribou habitat (Stotyn 2008) and caribou escape predators and alternate prey in the summer by residing at high elevations (Bergerud and Elliot 1986, Wittmer 2004). I used caribou global positioning system (GPS) and very high frequency (VHF) telemetry data to establish the elevational cut-off above which was considered caribou habitat and examine overlap in habitat use between caribou, moose, and thus wolves. Data from 50 caribou with more than 20 relocations in the summer (16 June-22 October) were used. The elevation above which each individual caribou was located > 90% of the time was calculated and the average was used for the elevational cut-off. On average, mountain caribou were located above 1230m 90% of the time. For simplicity 1230 m was then rounded to 1200 m and this elevation defined caribou habitat. This elevation was considered mountain caribou summer habitat and where moose had the potential to overlap spatially with mountain caribou (Figure 2.2).

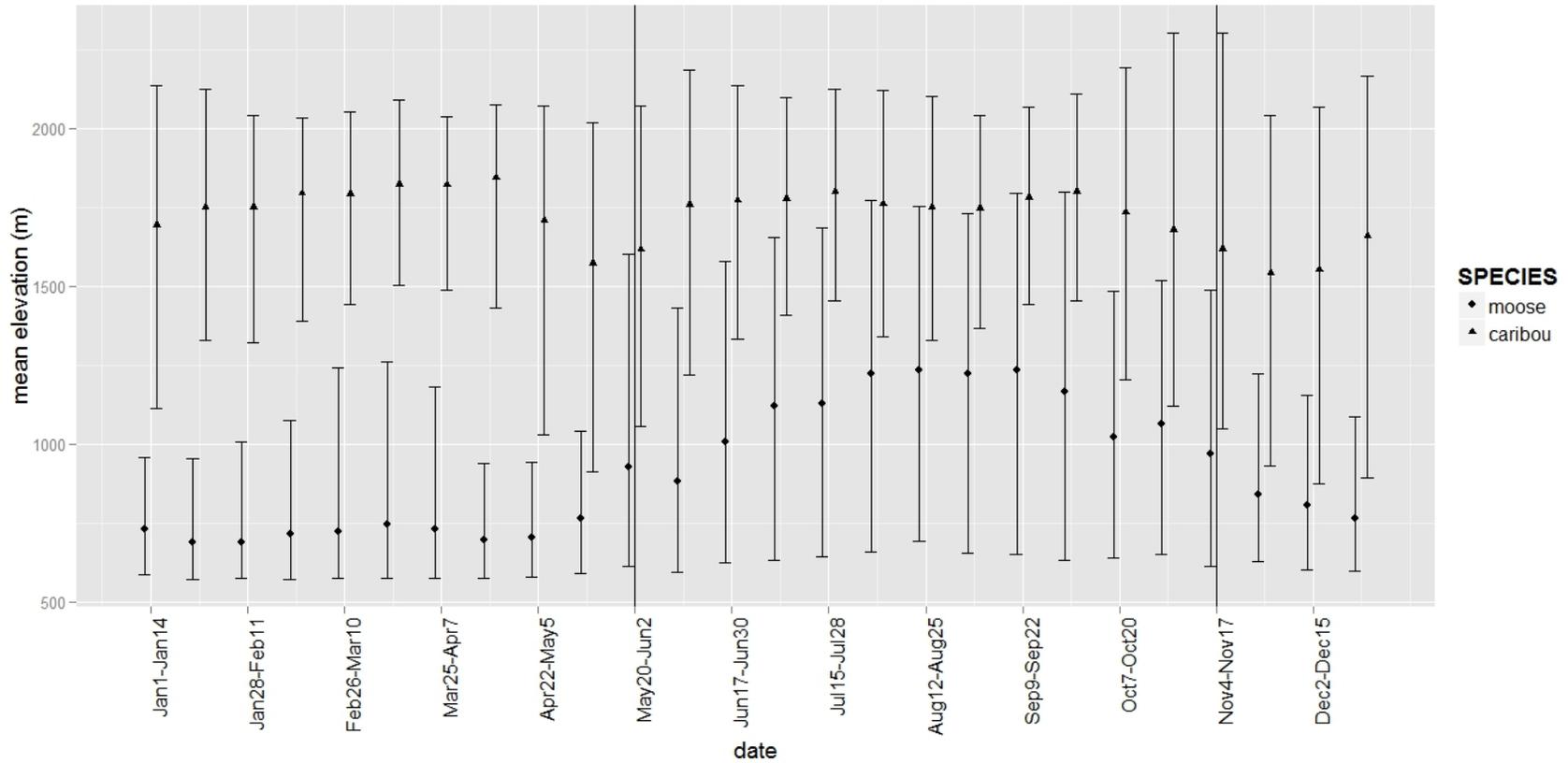


Figure 2.2 Mean and range of elevation for moose (circles) and caribou (triangles) every 14 days. The upper bars are the upper 95th percentiles of the data and the lower bars are the 5th percentiles of the data. The first and last bars that run the entire vertical length of the graph mark the beginning and end of the period defined as summer. Data used consisted of telemetry data for caribou (years 1992-2010), moose (years 2003-2010), and wolves (years 2003-2011) in the Columbia Mountains, British Columbia.

I focused on moose habitat selection and forage during summer because this is when the highest level of mountain caribou predation occurs (Wittmer et al. 2005b) and when there is the highest level of spatial overlap between moose and mountain caribou (Seip 1992, Stotyn 2008). I defined the summer period as 20 May to 17 November. May 20 is the earliest date when at least one moose had > 50% of locations above 1200 m. I considered this to be when moose were no longer restricted by snow levels to valley bottoms and had access to mountain caribou habitat. November 17 is when none of the moose in the sample had >50% of their telemetry locations above 1200 m.

Diet and Vegetation

I expected moose movements to high elevation human-seral habitats would be motivated by the availability of forage. I tested my prediction that human-seral habitat would have a higher cover of moose forage compared to other habitats by first determining which plants moose were foraging on in summer and then comparing the percent cover of these plants among habitat types.

To determine moose forage species in summer the plant content of moose feces was analyzed. Moose fecal samples were collected in summer 2011 from June to September along 20 transects from valleys (600-800m elevation) to 2000m elevation as well as opportunistically. Transects were visited every two to four weeks to collect moose pellets. Given the relatively low moose density in the Columbia Mountains ($0.96/\text{km}^2$) (Serrouya and Poole 2007), I focused the transects in areas of medium to high moose density (see Serrouya and Pavan 2005) to find enough fecal samples. To ensure samples reflected food recently consumed only fresh moose pellets were collected. Fecal samples were frozen the same day after they were collected until they could be dried. Moose fecal samples were then thawed and dried in a drying oven (60°C) (Hinnant and Kothmann 1988) before analysis. Fecal samples were sent to the Washington State University Wildlife Habitat Laboratory

(Pullman, Washington) for microhistological analysis to identify plant species. Two composite fecal samples of moose samples collected above and below 1400 m elevation were created for this analysis (Jenks et al. 1989). The two composite samples above and below 1400 m were created by taking equal weights (Jenks et al. 1989) of all samples collected at each respective elevation. An elevation of 1400 m was used as a cut-off because this was below the average lower elevation for caribou in the summer (1500 m, Apps et al. 2001) and it is the upper transition between the ICH and the ESSF (Braunmandl and Curran 1992). For the other parts of this study, the cut-off was later changed from 1400 m to 1200 m to better capture the majority of mountain caribou summer movement but such a change is not expected to have affected the conclusions. Fecal samples used in the diet analysis were not corrected for digestibility as the salient issue was identifying plants consumed in the two areas rather than any proportional difference in plant use.

Microhistological analysis identifies the plant species consumed by identifying characteristic cells and structures in the plants (Litvaitis 2000). While fecal diet analysis is a commonly used technique a serious drawback is the change in the ratio of identifiable plant fragments to non-identifiable plant fragments during digestion and sample preparation (Litvaitis 2000). Compared to analysing diet composition using rumen samples fecal diets tend to underestimate easily digested forbs and less digestible items, such as coniferous twigs and needles, tend to be overestimated (Anthony and Smith 1974, Holechek et al. 1982, Litvaitis 2000). Digestibility correction factors can be applied to fecal diet samples to improve the biomass estimate of each plant, however, this is a more costly and time consuming procedure and there are no correction factors specifically for moose (Wam and Hjeljord 2010). While fecal diet analyses may be inappropriate for determining the proportional composition of diets (Wam and Hjeljord 2010), to simply identify plants animals are consuming fecal samples are better than field observations which may miss forbs that are only occasionally consumed (Wam and Hjeljord 2010).

Results from the microhistological analysis were combined with data collected in vegetation surveys to test if 1) human-seral habitat above 1200 m produced more forage than other habitats both above and below 1200 m elevation, and 2) once moose were above 1200 m, which habitat produced the most moose forage. For the first comparison of human-seral to all other habitats, anything in the fecal microhistological results that represented >5% of the high and low summer moose diet was considered moose forage. For the second comparison between habitats above 1200 m elevation, anything that was >5% of the high elevation moose diet was considered moose forage. I used data from vegetation surveys from the BEC database from the Ministry of Forests, Land, and Natural Resource Operations (FLNRO) in BC to compare the percent cover of the plant species I considered to be moose forage. The database includes plots collected from various studies, some of which used a stratified random sampling scheme while others used a random sampling scheme. Vegetation surveys were conducted in 400 m² plots in a total of 313 plots in the study area during the summer from 1977-2005. The percent cover of vegetative species in the plots was recorded in nine different layers: i) dominant tree layer, ii) main tree canopy, iii) sub-canopy trees iv) tall shrub layer, v) low shrub layer, vi) herb layer, vii) mosses, lichens and liverworts that occur on rock, viii) mosses, lichens and liverworts that occur on wood, and ix) the epiphyte layer. I only used vegetation layers considered accessible to moose (layers iv-ix). I then averaged the percent cover for each species across each layer to get a single value for each species. Next, I calculated the percent cover of moose forage species in different habitats as an average of the percent cover of the plots for each habitat type. The mean percent cover of the moose forage was compared between three different habitat types: old-growth, human-seral, and natural-seral. Riparian habitat was excluded due to a low number of plots in this habitat type and natural-seral was excluded from the comparison between high and low habitats for the same reason. To compare the percent cover of forage species between all habitats above and below 1200 m elevation the data was logit transformed because of a non-normal distribution (Warton and Hui 2010) and a two-way

analysis of variance (ANOVA) with an interaction term between habitat type and elevation was used. To compare the means in the three habitats above 1200 m elevation a Kruskal-Wallis rank sum ANOVA was used.

Resource Selection

For the next prediction I tested if moose showed stronger selection for human-seral habitat at high elevations relative to human-seral habitat at low elevations. Resource selection models analyze the habitat or resource selection of an animal while accounting for the availability of a resource and can be used to detect the factors that influence their habitat use (Manly et al. 2002). The extent of resource selection can be used to measure the relative importance of a habitat type to an animal (Manly et al. 2002). Thus if moose are moving up to high elevations due to logging at high elevations I expect they will highly select for cutblocks at high elevations.

I used a resource selection function (RSF) combined with an interaction term between cutblocks and elevation to test if the coefficient of selection increased or remained the same with elevation. The strength of a multiple regression model is that interaction effects can be studied instead of isolating single variables (Pedhazur and Schmelkin 1991). Furthermore, if interaction effects are present, interpretation of the model coefficients on their own may be incomplete or misleading. By including an interaction term between habitat types and elevation I tested how selection for each habitat type changed with elevation. If selection for cutblocks did not decrease with elevation then moose were either selecting cutblocks to the same or greater extent than at lower elevations.

Habitat selection was modeled with a binomial mixed effects model to examine habitats moose were selecting in the summer (Gillies et al. 2006) and how their selection of habitats changed with elevation. The study design followed type III habitat selection, in which availability and use were defined at the level of the individual (Manly et al. 2002). Three *a-priori* models were fit to the data: 1) a base model which included all vegetative

and topographic predictor variables (see below), 2) the base model + habitat types*elevation, and 3) the base model + sex + habitat type*elevation*sex. For the third model I chose to include sex of the individual as predictor variable and as an interaction term with habitat types and elevation because female moose with calves will segregate themselves to lower predation risk (Miquelle et al. 1992, Kunkel and Pletscher 2000), causing them to select habitats differently than males. All model variables were checked for collinearity using by plotting the data and using variance inflation factors (VIF) (cutoff value 5) before being included in a model. From the 3 *a-priori* models the top Akaike Information Criterion (AIC) model was selected by comparing the log-likelihood, Δ AIC, and model weights of the three models (Burnham et al. 2011).

Home ranges and availability

The models predicted selection (binomial variable 1 for a use and 0 for available) from a number of independent landscape predictor variables. The models compared which habitats moose used to what was available in their home range. Availability was estimated with randomly located points within an individual's home range.

Summer home ranges were calculated as 100% minimum convex polygons (MCPs) based on telemetry locations from 20 May to 17 November. GPS collared moose were used to build summer home ranges and as a result it was not necessary to set a minimum number of points to build the home ranges since the number of relocations ranged from 336-1592. MCP home ranges were estimated using the *adehabitatHR* package (Calenge et al. 2012) in the R program (R Development Core Team 2012).

The number of random locations/individual matched the number of telemetry locations for each individual (range from 336 to 1592). Determining the sample size of random locations to use can be arbitrary and as such, Manly et al. (2002) and Northrup et al. (2013) suggest varying the sample size used to ensure that the available distribution is

adequately described with a given sample size. Considering this I also estimated the model coefficients using 5000 random locations/moose home range.

The base model included vegetative and topographic predictor variables: slope, aspect, elevation, and habitat type. For habitat types, a layer was compiled in Arc GIS (ESRI 2013) by combining data from multiple sources: VRI data (Vegetation Resource Inventory, BC Ministry of Forests, Lands and Natural Resource Operations), data compiled from Forest Licensees, satellite images, and site visits on the ground. Five habitat classes were used: old-growth, human-caused early-seral, naturally occurring early-seral, riparian, and alpine. Old-growth was forested habitat that had no record of human induced or naturally occurring disturbance. If a particular category represented <1% of the use and available points, it was pooled with the reference category. Human-caused early-seral vegetation (hereafter, human-seral) represented cutblocks and a small amount of powerlines and reclaimed mine sites. Naturally occurring early-seral vegetation (hereafter, natural-seral) were areas classified as having burned in forest fires or were avalanche chutes. Riparian areas were water bodies (rivers, lakes, swamps, wetlands). Alpine was classified as the alpine tundra BEC zone. Aspect is not a true continuous variable (it is circular), therefore aspect was divided into 5 categories (north, east, west, south, and flat). For categorical variables, the most common category was used as the reference category: old-growth forests for habitat types and north for aspect. Elevation was calculated from a 10 m Digital Elevation Model (DEM) and the possible values for elevation ranged from 345 to 3658 meters. The slope and aspect were calculated based on the DEM in Arc GIS (ESRI 2013). Slope was calculated in degrees and the possible range of values for slope was from 0° to 86°. Slope and elevation were standardized before they were used in the models (Zuur et al. 2009). A quadratic term was applied to the variable slope because data exploration indicated non-linear data when graphed.

In addition to the fixed effects, individual moose were used as a random intercept in all the models. By using individual moose as a random effect it was possible to account for

the non-independence of relocations for each moose (Breslow and Clayton 1993). All data analysis and model selection was done in the R program (R Development Core Team 2012) using the lme4 package (Bates et al. 2011). In addition to presenting the model coefficients to aid with visualizing moose habitat selection, habitat use versus availability were presented in a boxplot graph using categorical splits of continuous variables.

Old growth forests as cover

For my third prediction I tested if moose were foraging primarily in human-seral habitat and using old-growth forests as cover. Preliminary data analysis had shown moose spent a lot of time in old growth and I predicted moose were using old growth forest as cover. A study of moose habitat use in the boreal region found there were more pellets in forests than signs of browsing and concluded that forests were primarily being used as shelter (Eastman 1974) and I expected moose in my study area were doing the same. I predicted that if this were the case, moose locations in old-growth forests would be closer to human-seral habitat than would be expected by chance. The distance from moose and random locations in old-growth forests (n=2876) to cutblocks was calculated using Arc GIS (ESRI 2013). Using a mixed effects model I compared these distances to the same number of random locations in old-growth forests above 1200 m elevation. I used a mixed effects model with a random effect for individual moose to account for the differences in sample size between moose. If the distance of moose locations in old growth forests were located closer to cutblocks than expected by random this would indicate moose were using forests as cover and not for forage.

Availability of cutblocks

To test the fourth prediction that the proportion of time moose spent above 1200 m elevation increased with the availability of cutblocks at high elevations a Spearman rank correlation test was used to compare the proportion availability of human-seral habitat to the proportion of time moose spent above 1200 m elevation. In addition I also repeated the

same analysis using the proportion of human-seral and natural-seral habitat at high elevations combined to see if the total proportion of early-seral related habitats was related to the proportion of time moose spent above 1200 m elevation.

RESULTS

Telemetry data

Of the 32 moose GPS collars placed on moose 12 collars either malfunctioned or resulted in < 20 relocations/summer. As a result, I used data from 20 GPS collars, 4 males and 16 females. The number of collared individuals per year varied, as collars were placed on animals, the collars died, and new ones were placed on animals (Table 2.1).

Table 2.1 The number of active GPS collars on moose each year in the Columbia Mountains, southeastern British Columbia.

<i>Year</i>	<i>GPS Collars</i>
2004	4
2005	10
2006	9
2007	6
2008	7
2009	5
2010	2

Diet and Vegetation

Moose forage on different species when they are at high and low elevations (Table 2.2). I limit the comparison of the percentage of each plant in the different diets to notable, large differences between the same species. The primary plant found in moose feces at both low and high elevations were willow leaves (*Salix* spp) at 32% and 40% , respectively. The most notable difference between high and low elevation diets were at low elevations where moose diet consisted primarily of cedar (26%) but cedar was absent from diets at high elevations. Moose also consumed more *Cornus* spp at low elevations (9%) when compared to high elevations (1%).

Table 2.2 Results from the microhistological fecal diet analysis for moose in the Columbia Mountains during the summer of 2011 from June to early September. High elevation fecal samples were collected above 1400m and low elevation samples are those collected below 1400m. Low elevation sample was a composite sample of 21 fecal samples and high elevation sample was a composite of 32 fecal samples.

<i>Plants</i>	<i>Low Elevation</i>	<i>High Elevation</i>
<i>Salix</i> leaf	32.2	40.3
<i>Thuja</i>	26.4	0.0
<i>Vaccinium membranaceum</i>	18.9	13.6
<i>Cornus</i> spp.	9.1	1.1
<i>Athyrium filix-femina</i>	2.1	4.4
<i>Veratrum viride</i>	2.0	0.0
<i>Epilobium angustifolium</i>	1.8	4.6
Fern rhizome	1.8	2.7
<i>Pteridium aquilinum</i>	1.8	2.9
<i>Alnus</i>	1.3	0.5
Lichen	0.4	7.0
<i>Sambucus racemosa</i> leaf	0.4	3.2
<i>Rhododendron albiflorum</i> leaf	0.1	0.0
<i>Astragalus</i> sp.	0.0	1.0
<i>Betula</i>	0.0	1.5
<i>Carex</i>	0.0	0.4
Fern capsule	0.0	0.9
<i>Menziesia ferruginea</i> leaf	0.0	2.2
Moss	0.0	1.0
<i>Rubus</i> leaf	0.0	2.6
<i>Smilacina racemosa</i>	0.0	0.7
Thorn	0.0	0.3
<i>Tsuga</i> sp.	0.0	3.1
Unknown Grass	0.7	1.0
Unknown Forb	0.6	1.7
<i>Viburnum edule</i> stem	0.0	0.9
Unknown Shrub stem	0.4	0.7
Unknown Shrub leaf	0.0	1.7

My first prediction that high elevation cutblocks would produce the most forage was not supported. The difference between the mean percent cover of moose forage in habitats at high and low elevations was not significant (Figure 2.3). The two-factor analysis of variance had no significant main effects or interactions ($F_{(3,309)}=0.45$, $p = 0.72$). As well, there were no significant differences in the mean percent cover of moose forage between human-seral, old-growth, and natural-seral habitats at high elevations. The result of the

Kruskal-Wallis test on the percent-cover of moose forage above 1200 m between habitat types was non-significant ($H=1.75$, 2 d.f., $p=0.42$) (Figure 2.4).

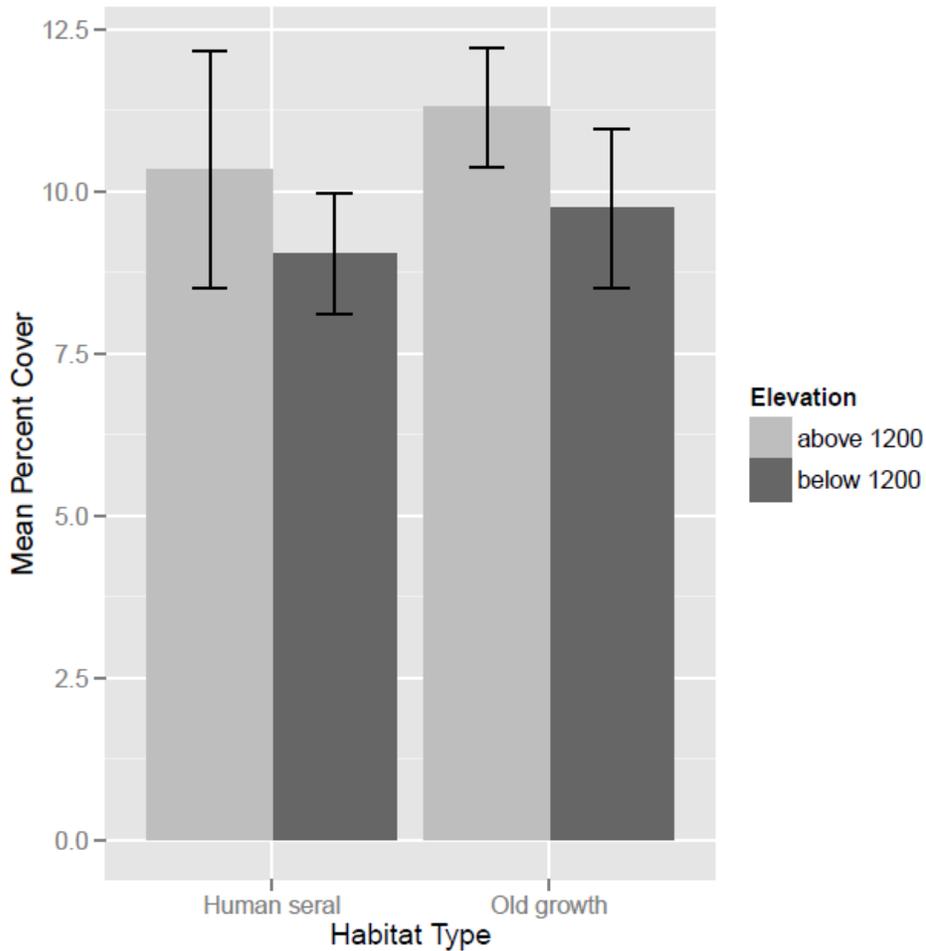


Figure 2.3 Mean percent cover of moose forage in the Columbia Mountains in the human-seral above 1200 m ($n=44$), human-seral below 1200 m ($n=28$), old-growth above 1200 m ($n=115$), and old-growth below 1200 m ($n=126$). Bars represent means and the error bars the standard error of the mean. Moose forage plants represented in this graph are species that had a $>5\%$ occurrence in the moose summer diet (*Salix* sp., *Thuja plicata*, *Vaccinium membranaceum*, *Cornus* sp., and lichen).

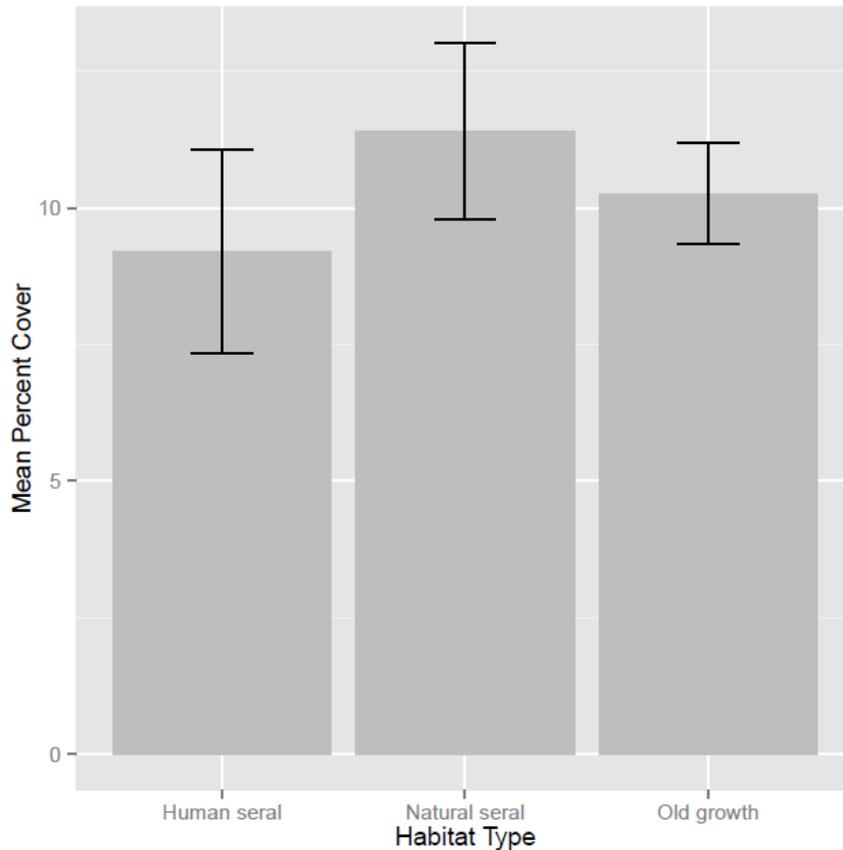


Figure 2.4 Mean percent cover of moose summer forage above 1200 m elevation in the Columbia Mountains in human-seral above 1200 m (n=28), natural-seral above 1200 m (n=92), old-growth above 1200 m (n=126). Bars represent means and the error bars the standard error of the mean. Moose forage plants represented in this graph are species that had a >5% occurrence in the high elevation moose summer diet (*Salix* sp., *Vaccinium membranaceum*, and lichen).

Resource selection

The top AIC model was the third model, indicating that the interaction term improved the model fit over the base model and that habitat selection differed between sexes with habitat type and elevation (Table 2.3). When I compared the coefficients of the top AIC model in which the random locations equaled the number of used locations to the same model with 5000 random point/moose home range (increasing the number of available point 4-5 times/individual) there were no differences in the coefficients, indicating an adequate sampling of the available area.

Table 2.3 Results of model selection from the mixed effect model predicting the relative resource selection of moose. The second model was the top model based on model log-likelihood (LL), AIC, delta AIC, and model weight. Predictor variables were h = habitat type, a = aspect, s =slope, e =elevation, and se =sex. Sample size was 36437 used and random locations from 20 GPS collared moose in the Columbia Mountains.

<i>Model and fixed predictor variables</i>	<i>Log Likelihood</i>	<i>AIC</i>	<i>ΔAIC</i>	<i>W_{AIC}</i>
1. $h + a + s + s^2 + e$	-22560	45147.83	245.76	<0.001
2. $h + a + s + s^2 + e + h*e$	-22467	44968.53	66.46	<0.001
3. $h + a + s + s^2 + e + se + h*e*se$	-22424	44902.07	0.00	1

The results of the RSF model supported my fourth prediction (Table 2.4). The interaction between human-seral habitat and elevation was significant and selection for human-seral habitat increased with elevation for both males and females. As well, moose had a higher relative selection for human-seral habitat compared to old-growth habitat (Table 2.4). Selection was also higher for natural-seral and riparian habitat when compared to old-growth habitat. Alpine habitat was not a significant term in the model compared to the other habitats.

As for the remaining topographic variables in the mixed effects model, selection decreased with slope steepness and selection was greatest for flat aspects, followed by south and east aspects over north aspects. The coefficient for west aspects was not significant compared to the other aspects. The model coefficient for elevation was positive which was due to an interaction between habitat types and elevation. Old-growth habitat was used as the reference category and because moose avoided old-growth less with elevation, the coefficient for elevation was positive. When habitat types were dropped from the model the coefficient for elevation became negative, which was not surprising since moose spent 64% of their time below 1200 m elevation. This fits with what is in Figure 2.4, moose used old-growth habitat more when they were located above 1200 m, compared to when they were below 1200 m.

Of the remaining interactions between elevation, habitat types, and sex that were significant, selection for riparian increased with elevation for females but decreased with elevation for males. The interaction between elevation and sex was not significant indicating that there was no difference in the selection or avoidance of elevation between males (mean elevation= 1091.99, SE=0.12) and females (mean elevation=1092.94, SE=0.02).

Table 2.4 Coefficients from the top mixed effects resource selection model for the summer (May 20-November 17) for moose (n=20) in the Columbia Mountains. The number of used and available locations was 36437. Slope and elevation were standardized before being used in the model. Coefficients in bold were statistically significant.

<i>Variables</i>	<i>β</i>	<i>Std. Error</i>	<i>Lower 95% CI</i>	<i>Upper 95% CI</i>
Intercept	-0.5597	0.0863	-0.7288	-0.3907
Human-seral	1.1324	0.0334	1.0670	1.1977
Natural-seral	0.7674	0.0501	0.6692	0.8656
Riparian	2.6203	0.2577	2.1152	3.1253
Alpine	3.1230	2.6942	-2.1575	8.4035
Slope	-0.4387	0.0153	-0.4687	-0.4087
Slope ²	-0.1659	0.0125	-0.1903	-0.1415
East aspect	0.1226	0.0347	0.0547	0.1906
South aspect	0.2465	0.0370	0.1740	0.3190
West aspect	0.0394	0.0397	-0.0383	0.1171
Flat aspect	0.6567	0.1020	0.4568	0.8567
Elevation	0.1888	0.0222	0.1453	0.2324
Sex	-0.0668	0.1841	-0.4277	0.2941
Human-seral*sex (males)	0.0930	0.0988	-0.1007	0.2868
Natural-seral*sex (males)	0.6010	0.1029	0.3992	0.8027
Riparian*sex (males)	-2.3826	0.7645	-3.8810	-0.8842
Alpine*sex (males)	-10.5024	10.3796	-30.8460	9.8412
Elevation*sex (males)	-0.0592	0.0544	-0.1658	0.0474
Human-seral*elevation	-0.0723	0.0331	-0.1372	-0.0074
Natural-seral*elevation	-0.5079	0.0470	-0.6000	-0.4158
Riparian*elevation	1.0749	0.2796	0.5268	1.6230
Alpine*elevation	-2.7959	1.2114	-5.1702	-0.4215
Human-seral*elevation*sex (males)	0.4388	0.0979	0.2470	0.6306
Natural-seral*elevation*sex (males)	0.1325	0.1136	-0.0902	0.3552
Riparian*elevation*sex (males)	-1.9924	0.5989	-3.1663	-0.8185
Alpine*elevation*sex (males)	4.0475	4.2807	-4.3425	12.4375

Overall, there was considerable variation among moose in their use and availability of habitats above and below 1200m elevation (Figure 2.5). In general the univariate comparison of used to available (Figure 2.5) agrees with the results from mixed effects model. On average, human-seral habitat covered 46% of the low-elevation portions of the moose home ranges and when in low elevations moose were located there an average of 65% of the time. Human-seral habitat covered on average only 15% of the moose summer ranges over 1200 m and they were, on average, located there 27% of the time. The changes in proportion use with elevation show that while moose selected for human-seral habitat within their entire home range their use at high elevations decreased relative to their use at lower elevations because human-seral habitat was less available at high elevation. Old-growth forest covered on average 44% of a moose home range below 1200 m and was used on average 16% of the time when moose were below 1200 m elevation. Old-growth habitat was more available at high elevations: it covered on average 62% of a moose home range above 1200 m elevation and moose were found there on average 48% of the time when they were above 1200 m elevation. Moose increased their use of old-growth habitat 3 fold when they were above 1200 m elevation compared to lower elevations but the availability of old-growth forest increased by just less than half of what was available at lower elevations.

A: Use and available proportions below 1200 m elevation

B: Use and available proportions above 1200 m elevation

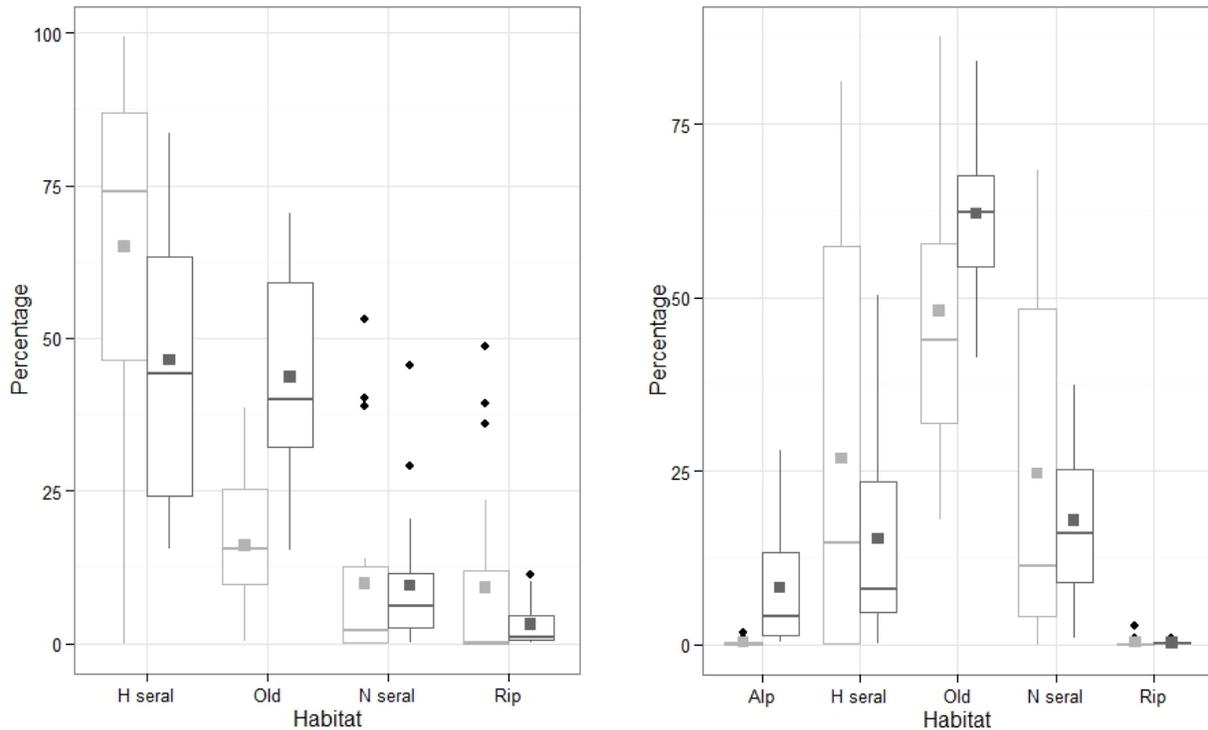


Figure 2.5 Boxplots of percentage of use (light grey boxes) and available (dark grey boxes) for habitat types within home ranges during the summer in home ranges A) below 1200 m elevation and B) above 1200 m elevation. Squares are the mean percentages. Alp= alpine, H seral= human-seral, N seral= natural-seral, Old= old-growth, Rip= riparian. Percentages were calculated on an individual basis using 20 moose with GPS collars in the Columbia Mountains, 2004 to 2010. The horizontal bars are the median proportions, the top of the box shows the 75th percentile of the data, the bottom of the box shows the 25th percentile of the data, and the whiskers show the maximum and minimum values of the data.

Old-growth forests as cover

My third prediction that moose locations at high elevations would be located closer to cutblocks than expected by random was not supported. Moose locations in old-growth forests were located on average 1169 m (SE=22.2) from cutblocks and random locations were located on average 1148 m (SE=19.2) from cutblocks, yet this difference was not statistically significant (linear-mixed effects model Wald $\chi^2= 40$, overall model $P<0.0001$, use/random term $P<0.668$).

Availability of human-seral habitat and time spent in caribou habitat

My fourth prediction was also not supported: there was no relationship between the amount of human-seral available above 1200 m elevation in the home range of a moose

and the amount of time a moose spends above 1200 m elevation (Figure 2.6, $p=0.08$, $\rho=0.40$). Neither is there a relationship between the proportion of human-seral and natural-seral habitat combined with the proportion of time moose spend above 1200 m elevation (Figure 2.7, $p=0.19$, $\rho=0.31$).

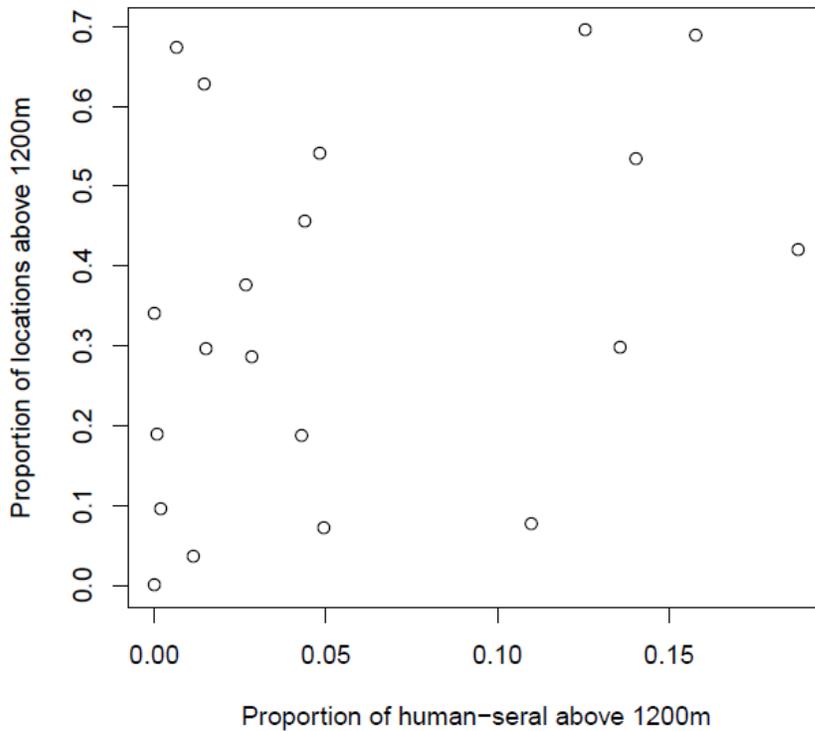
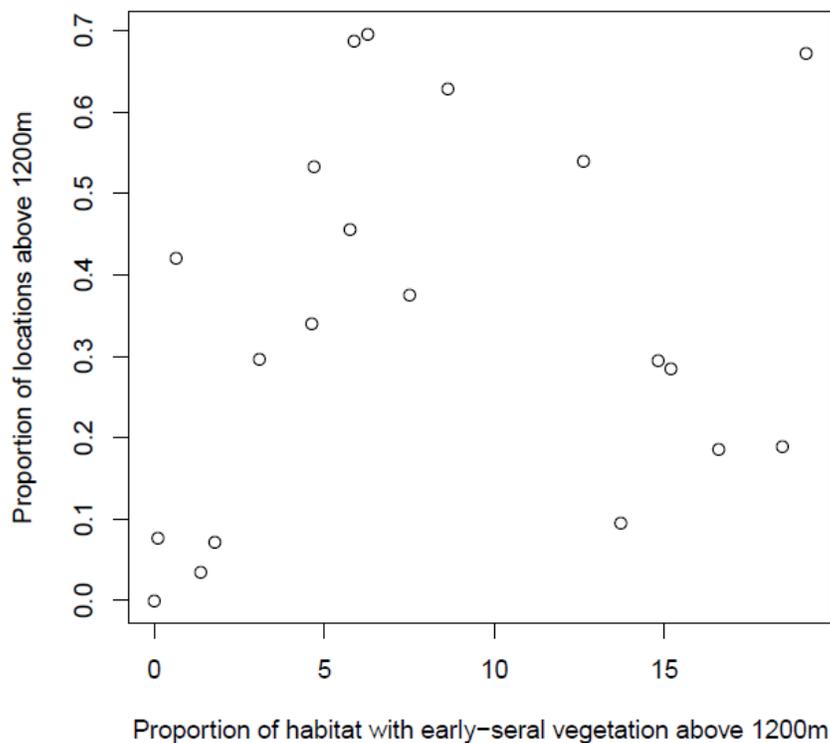


Figure 2.6 Relationship between the proportion of human-seral land cover above 1200 m elevation in summer home range of moose (n=20) and the proportion of telemetry locations above 1200 m elevation of moose monitored during 2004-2010 in the Columbia Mountains, British Columbia, Canada.



2.7 Relationship between the proportion of human-seral and natural-seral land cover above 1200 m elevation in summer home range of moose (n=20) and the proportion of telemetry locations above 1200 m elevation of moose monitored during 2004-2010 in the Columbia Mountains, British Columbia, Canada.

DISCUSSION

Mountain caribou that live in deep-snow ecosystems are an endangered ecotype and are suffering rapid declines; predation has been the dominant, proximate limiting factor (Seip 1992, Wittmer et al. 2005a). Most caribou are killed by predators during summer when more abundant prey such as moose and the predators they support expand from the valleys into the mountains where caribou are found. The more abundant prey species forage primarily on plants that thrive in early-seral conditions. Thus the hypothesis has been developed that increasing the amount of early-seral conditions by logging at high elevations has increased abundant prey and predator's use of caribou habitat resulting in more caribou being killed. Alternatively, these more abundant prey species may be primarily limited by the amount of winter range available in mountainous regions with deep snow and

they may move to higher elevations in summer even in the absence of cutblocks. Testing these hypotheses is critical to identify where to place constraints on logging.

I examined the overall hypothesis that logging at high elevations attracted moose to caribou habitat by focusing on a series of more specific working predictions. Only one of the four predictions were supported. First, if moose are moving up slope into mountain caribou habitat to access high-elevation cutblocks then there should be a greater availability of moose forage in high elevation cutblocks. To test this initial prediction it was necessary to determine which plants moose were consuming in the summer. In both the high and low elevation diets only a few (3-4) plants made up the majority of the summer diet, which is not uncommon for moose (Renecker and Schwartz 1998). The diets between low elevation and high elevations differed primarily in their content of red cedar, which was not available at high elevations and the amount of lichen. Unexpectedly, lichen composed 7% of the moose's high elevation diet and while digestibility was not corrected for, arboreal lichen is reported to be highly digestible (Robbins 1987) and therefore the proportion of lichen found in the feces is unlikely to be overestimated. In a summary of moose forage studies Renecker and Schwartz 1998 report only a few other studies in which moose foraged on lichen. Lichen has a very low protein content (2% crude protein, as a percent of dry matter) (Robbins 1987), given the abundance of high quality forage in the summer, it seems unlikely moose are consuming lichen intentionally. Arboreal lichen is most abundant in old-growth ESSF (Stevenson and Coxson 2006) and moose may be consuming lichen indirectly when it falls onto other forage, dispersing by thallus fragmentation (Goward and Campbell 2005). Alternatively lichen may provide a yet unknown source of macronutrients for moose. The quality of wildlife forage is typically measured in protein and nitrogen content, however, in some cases animals may select foods in order to consume a mixture of macronutrients, which can be important in growth, immune responses, longevity, and fecundity (Simpson et al. 2004, Robbins et al. 2007, Simpson and Raubenheimer 2009, Cotter et al. 2011, Erlenbach et al. 2014).

Using the data on plant species moose consumed in the summer there was no difference in the forage available in human-seral habitat above 1200 m elevation, compared to human-seral below 1200 m elevation and old-growth habitat above and below 1200 m. There was also no difference in the percent cover of moose forage in high elevation cutblocks compared to other high elevation habitats. Therefore, cutblocks in mountain caribou habitat may not offer moose an increase in forage. Lichen was included in the high elevation diet of moose when comparing the percent cover of forage across habitats, but as indicated above moose may not be intentionally consuming lichen. However, the inclusion of lichen in the analysis did not affect the results. Lichen overall comprises such a small portion of the cover of vegetation that including lichen or excluding it does not change the results. The results from the forage analysis are surprising because cutblocks typically support early-seral communities which produce more browse (Wolff 1978). My study likely found no difference in the percent cover of moose forage species because the plants used to represent the diet of moose were a mixture of early-seral associated plants, such as *Salix* spp., and high elevation old-growth associated plants, such as *Vaccinium* spp. Moose are often associated with early-seral forage, however, this is because many moose habitat and forage studies were conducted in winter and moose have different habitat selection and foraging patterns in summer compared to the winter. In summer, studies have shown moose often use and forage in old or mature forests and may even avoid disturbed habitats (Osisko et al. 2004). For example, Pierce and Peek (1984) found mature forest stands and open canopy sites at high elevations were highly used and in these sites the cover of *Menziesia* sp. and alder was highest and were also proportionally the most common food in their diet. Hjeljord et al. (1990) also found that moose in Norway increasingly used the older forests throughout summer and attributed this to plants that were phenologically delayed in the shade of the forest and thus more nutritious. In the Columbia Mountains, moose at higher elevations would have an abundant supply of browse in ESSF forests, in

which the understory is abundant in moose browse (e.g. *Vaccinium sp.*, *Menziesia ferruginea*).

To examine differences in the availability of moose forage between habitat types at different elevations I chose percent cover of a set of moose forage species. Percent cover though does not indicate either biomass or nutrient quality of the forage. In Norway, Hjeljord et al. (1990) found that selection of feeding sites was not related to the density of important moose browse species but instead moose selected feeding sites based on plants present, height of browse, and phenology (Hjeljord et al. 1990). My study did not consider differences in phenology or the height of plants and therefore the interpretation of what was regarded as moose forage may have been too general. While some ungulates make altitudinal migrations to track phenology changes (Hebblewhite et al. 2008, Mysterud 2013), it seems unlikely that this is the case for moose in the Columbia Mountains because the greatest proportion of their points above 1200 m elevation occurs between 29 July and 22 September, at which time high elevation plants are mature or dying back and their nutritional quality would be low.

While cutblocks do not produce more moose forage when compared to other habitat types, moose still highly selected for human-seral habitat and both females and males increasingly selected for human-seral habitat with elevation. As well, moose avoided old-growth habitat less with elevation. The availability of old-growth habitat increased above 1200 m elevation but the proportion of time moose spent in human-seral habitat above 1200 m increased greater than the proportional increase in habitat availability, resulting in a positive interaction between old-growth habitat and elevation. In the summer it is not uncommon for moose to use and/or select for high elevation habitat (Pierce and Peek 1984, Matchett 1985) and similar to the results of this study, moose tend to remain in forested areas and rarely venture above the treeline into alpine (Boonstra and Sinclair 1984). Moose in this study avoided increasingly higher elevations and spent the majority of their time at low elevations during the summer (moose were located below 1200 m 64% of the time).

The measure of selection is as dependent upon availability as it is of how much a habitat is used. A functional response can be observed in animals such that when habitats are rare, they are highly selected for (or used) and when they are abundant the measure of selection (or use) decreases (McLellan 1985, Garshelis 2000, Gillies et al. 2006, Herfindal et al. 2009). The issue of measuring selection when availability of various resources are deemed to be very different (McLellan 1985) has been a long standing issue with habitat studies. Unfortunately, defining availability is problematic (Johnson 1980, Garshelis 2000). There are many approaches to defining availability and if I had chosen a different approach the model results may have differed. When defining availability I chose a scale I believed to be most relevant to the study questions. However, it is unlikely that as a moose moves from habitat unit to habitat unit it is cognizant of all the habitat available in its home range (McLellan 1985). It is also possible that what I defined as an available cutblock or old-growth forest, may in fact be unavailable due to terrain (e.g. steep slopes) or inter and intra-species interactions. The results of any RSF model need to be interpreted with caution as they face the same problems and limitation of other Type III RSF model analysed using a mixed effects model with individuals as a random effect (Gillies et al. 2006, Koper and Manseau 2009). The best fit model successfully distinguished moose habitat use from random location as predicted by a set of variables, as such the model provided a relative measure of habitat quality for moose. I provided no model validation using an independent data set as I did not use the model for predictive purposes. The results from the model provide insight to moose habitat selection with increasing elevation and the relative importance of cutblocks for moose.

Moose spent the majority of their time in old-growth forests in summer but were not using this habitat only for cover, which did not support my third prediction. When moose were in old-growth forests they were not located closer to human-seral habitat than would be expect by random and were likely foraging in both old-growth forests and human-seral habitats. Moose are large ungulates and as such must spend the majority of their time

foraging (Renecker and Schwartz 1998), considering the amount of time they spent in old-growth forests they may be browsing in this habitat.

High elevation human-seral habitat does not produce more forage when compared to other habitats and moose forage in both human-seral and old-growth habitats when they are at high elevations. As a result an increase in the availability human-seral habitat above 1200 m is not related to an increase in the amount of time a moose spends above 1200 m elevation. Even moose with little to no human-seral habitat spend time above 1200 m elevation and thus moose do not require human-seral habitat at high elevations to occupy mountain caribou habitat. Additionally, the proportion of time moose spent above 1200 m elevation was not related to the total proportion of habitat that contained early-seral vegetation (both human and natural). It appears that the amount of time moose spend at high elevations is not related at all to the amount early-seral vegetation at high elevations.

Altogether only 1 of 4 predictions were supported. Taken together the predictions tested improve our understanding of how forest management influences moose summer habitat use in relation to caribou habitat. The results indicate that while moose select human-seral habitat at high elevations, moose are unlikely moving into caribou habitat because of logging at high elevations. Moose appear to be foraging in both old-growth forests and human-seral habitat. Furthermore, an increase in the availability of human-seral habitat above 1200 m was not related to moose spending more time in mountain caribou habitat. It remains uncertain what factors influence the seasonal movements of moose into mountain caribou habitat. Instead, the seasonal movements of moose may be motivated by predator avoidance (Kunkel and Pletscher 2000), the need to cool down in the summer (van Beest et al. 2012), plant phenology (Hjeljord et al. 1990), or a combination of these factors.

MANAGEMENT IMPLICATIONS

While human caused early-seral habitat was selected and highly used by moose in the summer at low and high elevations, moose did not require high-elevation cutblocks in

their home range to use mountain caribou habitat. When moose were in mountain caribou habitat, both human-seral and old-growth habitat were used and provided forage. High elevation logging was not the only reason and may not even be a factor influencing movements of moose into mountain caribou habitat in the summer. While high elevation logging does not produce more moose summer browse and attract them to high elevations, it does however, increase the availability of moose winter browse and is related to an increase in the density of moose (Peek 1998). As such, logging exacerbates apparent competition between moose and caribou via increased moose densities causing increased predator densities and therefore more incidental predation on caribou. A doubling of moose density, from 0.7 moose/km² to 1.54/km² (Poole and Serrouya 2003) was attributed to a higher proportion of young forest on the landscape and milder winters that enhanced overwinter survival (Serrouya and D'Eon 2003). If moose are limited by conditions on their restricted winter ranges, then logging at high elevations, where the snowpack is too deep for moose to winter, may not lead to a population response.

With the evidence from this study that high-elevation logging has little effect on the upward movement of moose in summer then most restrictions on logging should be focused at low elevations if, indeed, moose numbers are to be kept low via habitat management. However, intact, high elevation, old-growth forests are required by caribou as foraging habitat and, even if moose are not attracted by logging at high elevations, the roads associated with logging enables wolves to move efficiently (Thurber et al. 1994, Whittington et al. 2005) and thus kill caribou nearby. I recommend that limiting moose to ecologically historical numbers (Festa-Bianchet et al. 2011, Serrouya et al. 2011) using hunting while allowing early-seral conditions at low elevations to mature to become poor moose habitat will continue to be the basis of caribou recovery. In the long term to keep moose at more historical population numbers land managers should ensure that disturbed habitats are being reforested quickly and efficiently since shrub abundance decreases in proportion to reforestation efforts (Gysel 1957, Roe and Buchman 1963). Logging strategies for high

elevations should focus on maintaining attributes of caribou habitat and ensure that roads do not enhance wolf movement efficiency and thus caribou encounter rates (Apps et al. 2013). Logging strategies to ensure that high-elevation cutblocks are not good summer moose habitat does not appear to be as important.

In summary, strategies for the conservation of mountain caribou should continue to employ short-term strategies such as alternate prey population management and long-term timber harvesting and silvicultural strategies which are aimed at limiting the amount of early-seral vegetation on the landscape to reduce the density of moose.

WORKS CITED

- Andersen, R. 1991. Habitat changes in moose ranges: Effects on migratory behaviour, site fidelity and size of summer home range. *Alces* 27:85–92.
- Anthony, R. G., and N. S. Smith. 1974. Comparison of rumen and fecal analysis to describe deer diets. *Journal of Wildlife Management* 38:535–540.
- Apps, C. D., B. N. McLellan, T. A. Kinley, and J. P. Flaa. 2001. Scale-Dependent Habitat Selection by Mountain Caribou, Columbia Mountains, British Columbia. *Journal of Wildlife Management* 65:65–77.
- Apps, C., B. McLellan, T. Kinley, R. Serrouya, D. Seip, and H. U. Wittmer. 2013. Spatial factors related to mortality and population decline of endangered mountain caribou. *Journal of Wildlife Management* 77:1409–1419.
- Bates, D., M. Maechler, and B. Bolker. 2011. lme4: Linear mixed-effects models using S4 classes.
- Van Beest, F. M., B. Van Moorter, and J. M. Milner. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. *Animal Behaviour* 84:723–735.
- Bergerud, A. T., and W. B. Ballard. 1988. Wolf predation on caribou: the Nelchina herd case history, a different interpretation. *Journal of Wildlife Management* 52:344–357.

- Bergerud, A. T., and J. P. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology* 64:1515–1529.
- Boonstra, R., and A. R. E. Sinclair. 1984. Distribution and Habitat Use of Caribou, *Rangifer tarandus caribou*, and Moose, *Alces alces andersoni*, in the Spatsizi Plateau Wilderness Area, British Columbia. *Canadian Field-Naturalist* 98:12–21.
- Braunmandl, T. F., and M. P. Curran. 1992. A field guide for site identification for the Nelson Forest Region. Ministry of Forests, Victoria, British Columbia.
- Breslow, N. E., and D. G. Clayton. 1993. Approximate Inference in Generalized Linear Mixed Models. *Journal of the American Statistical Association* 88:9–25.
- Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology : some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* 65:23–35.
- Calenge, A. C., S. Dray, and S. Fortmann-roe. 2012. Package " adehabitat ."
- Canadian Climate Normals 1981-2010 Station Data. n.d.
<http://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html?stnID=1365&lang=e&dCode=0&province=BC&provBut=Go&month1=0&month2=12>. Accessed 13 Apr 2014.
- Cotter, S. C., S. J. Simpson, D. Raubenheimer, and K. Wilson. 2011. Macronutrient balance mediates trade-offs between immune function and life history traits. *Functional Ecology* 25:186–198.
- Darimont, C. T., T. E. Reimchen, P. C. Paquet, and V. Crichton. 2005. Range expansion by moose into coastal temperate rainforests of British Columbia, Canada. *Diversity and Distributions* 11:235–239.

- Eastman, D. S. 1974. Habitat use by moose of burns, cutovers and forests in northcentral British Columbia. Pages 238–256 *in*. Proceedings of the North American Moose Conference. Volume 10.
- Erlenbach, J. a., K. D. Rode, D. Raubenheimer, and C. T. Robbins. 2014. Macronutrient optimization and energy maximization determine diets of brown bears. *Journal of Mammalogy* 95:160–168.
- ESRI. 2013. ArcGIS Desktop. Environmental Systems Research Institute, Redlands, CA.
- Festa-Bianchet, M., J. C. Ray, S. Boutin, S. D. Côté, and A. Gunn. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. *Canadian Journal of Zoology* 89:419–434.
- 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 Press, New York.
- Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. a. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology* 75:887–898.
- Goward, T., and J. Campbell. 2005. Arboreal Hair Lichens in a Young , Mid-elevation Conifer Stand, with Implications for the Management of Mountain Caribou Implications for the Management of Mountain Caribou. *The Bryologist* 108:427–434.
- Gysel, L. W. 1957. Effects of silvicultural practices on wildlife food and cover in oak and aspen types in northern Michigan. *Journal of Forestry* 55:803.
- Hebblewhite, M., E. Merrill, and G. McDermid. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecological Monographs* 78:141–166.

- Herfindal, I., J.-P. Tremblay, B. B. Hansen, E. J. Solberg, M. Heim, and B.-E. Sæther. 2009. Scale dependency and functional response in moose habitat selection. *Ecography* 32:849–859.
- Hervieux, D., M. Hebblewhite, N. J. Decesare, M. Russell, K. Smith, S. Robertson, and S. Boutin. 2013. Widespread declines in woodland caribou (*Rangifer tarandus caribou*) continue in Alberta. *Canadian Journal of Zoology* 882:872–882.
- Hinnant, R. T., and M. M. Kothmann. 1988. Collecting, Drying, and Preserving Feces for Chemical and Microhistological Analysis. *Journal of Range Management* 41:168–171.
- Hjeljord, O., N. Hövik, and H. B. Pedersen. 1990. Choice of feeding sites by moose during summer, the influence of forest structure and plant phenology. *Ecography* 13:281–292.
- Holechek, J. L., M. Vavra, and R. D. Pieper. 1982. Botanical Composition Determination of Range Herbivore Diets: A Review. *Journal of Range Management* 35:309–315.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12:197–229.
- Jenks, J. A., J. Leslie David M., R. L. Lochmiller, M. A. Melchiors, and W. D. Warde. 1989. Effect of Compositing Samples on Analysis of Fecal Nitrogen. *Journal of Wildlife Management* 53:213–215.
- Johnson, D. H. 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology* 61:65–71.
- Koper, N., and M. Manseau. 2009. Generalized estimating equations and generalized linear mixed-effects models for modelling resource selection. *Journal of Applied Ecology* 46:590–599.
- Kunkel, K. E., and D. H. Pletscher. 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. *Canadian Journal of Zoology* 78:150–157.

- LeResche, R. E. 1974. Moose migrations in North America. *Naturaliste Canadien* 101:393–415.
- Litvaitis, J. 2000. Investigating Food Habits of Terrestrial Vertebrates. Pages 165–190 in L. Boitani and T. K. Fuller, editors. *Research techniques in animal ecology: controversies and consequences*. Columbia University Press, New York.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, and W. P. Erickson. 2002. *Resource Selection by Animals*. Second edition. Kluwer Academic Publishers, Netherlands.
- Matchett, M. R. 1985. Habitat selection by moose in the Yaak River drainage, northwestern Montana. *Alces* 21:161–189. North American Moose Conference and Workshop.
- McLellan, B. N. 1985. Use and Availability Analysis and Timber Selection by Grizzly Bears. Pages 163–166 in K. Evans, F. Lindzey, C. Servheen, D. Winn, and P. Zager, editors. *Grizzly Bear Habitat Symposium*. United States Department of Agriculture, Missoula, Montana.
- McLellan, B., R. Serrouya, and K. Furk. 2008. Population census of caribou in the north Columbia Mountains. Victoria, British Columbia.
- McLoughlin, P., J. Dunford, and S. Boutin. 2005. Relating predation mortality to broad scale habitat selection. *Journal of Animal Ecology* 74:701–707.
- Miquelle, D. G., J. M. Peek, and V. Van Ballenberghe. 1992. Sexual Segregation in Alaskan Moose. *Wildlife Monographs* 122: 3–57.
- Mysterud, A. 2013. Ungulate migration, plant phenology, and large carnivores: the times they are a-changin'. *Ecology* 94:1257–61.
- Northrup, J. M., M. B. Hooten, C. R. J. Anderson, and G. Wittemyer. 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. *Ecology* 94:1456–1463.

- Van Oort, H., B. N. McLellan, and R. Serrouya. 2011. Fragmentation, dispersal and metapopulation function in remnant populations of endangered mountain caribou. *Animal Conservation* 14:215–224.
- Osko, T. J., M. N. Hiltz, R. J. Hudson, and S. M. Wasel. 2004. Moose Habitat Preferences in Response to Changing Availability. *Journal of Wildlife Management* 68:576–584.
- Peek, J. M., D. L. Urich, and R. J. Mackie. 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. *Wildlife Monographs* 32:3–65.
- Peek, J. M. 1998. Habitat relationships. Pages 351–401 *in* A. Franzmann and C. Schwartz, editors. *Ecology and management of the North American moose*. Smithsonian Institution Press, Washington.
- Pierce, D. J., and J. M. Peek. 1984. Moose habitat use and selection patterns in north-central Idaho. *The Journal of wildlife management* 1335–1343.
- Poole, K. G., and R. Serrouya. 2003. Moose population monitoring in the Lake Revelstoke Lake valley, 2002-2003. Revelstoke.
- R Development Core Team. 2012. *R: A language and environment for statistical computing*. Vienna, Austria.
- Renecker, L. A., and C. C. Schwartz. 1998. *Ecology and Management of the North American Moose*. Wildlife Management Institute, Washington.
- Robbins, C. T., J. K. Fortin, K. D. Rode, S. D. Farley, L. A. Shipley, and L. A. Felicetti. 2007. Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. *Oikos* 116:1675–1682.
- Roe, E. I., and R. G. Buchman. 1963. Effect of herbicide, dosage, and volume on hazel brush at different foliar stages. *Forest Science* 9:477–484.
- Seip, D. R., and D. B. Cichowski. 1996. Population Ecology of Caribou in British Columbia. *Rangifer, Special Issue* 9:73–80.

- 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.
- Serrouya, R., and D. D'Eon. 2003. Winter habitat use and food habits of deer and elk in the northern Selkirk Mountains. Salmon Arm, British Columbia.
- Serrouya, R., B. N. McLellan, S. Boutin, D. R. Seip, and S. E. Neilsen. 2011. Developing a population target for an overabundant ungulate for ecosystem restoration. *Journal of Applied Ecology* 48:935–942.
- Serrouya, R., B. N. McLellan, and J. P. Flaa. 2007. Scale-dependent microhabitat selection by threatened mountain caribou (*Rangifer tarandus caribou*) in cedar–hemlock forests during winter. *Canadian Journal of Forest Research* 37:1082–1092.
- Serrouya, R., and G. Pavan. 2005. Monitoring moose populations in the Lake Revelstoke Valley in the context of Mountain Caribou Conservation 2005 Progress report.
- Serrouya, R., and K. G. Poole. 2007. Moose population monitoring in the Lake Revelstoke (Management Units 4-38 and 4-39) and North Thompson (MUs 3-43 and 3-44) valleys, January 2006 and 2007.
- Simpson, S. J., and D. Raubenheimer. 2009. Macronutrient balance and lifespan. *AGING* 1:875–880.
- Simpson, S. J., R. M. Sibly, K. P. Lee, S. T. Behmer, and D. Raubenheimer. 2004. Optimal foraging when regulating intake of multiple nutrients. *Animal behaviour* 68:1299–1311.
- Spalding, D. J. 2000. The Early history of woodland caribou (*Rangifer tarandus caribou*) in British Columbia. B.C. Ministry of Environment, Land, and Parks, Wildlife Branch, Victoria, British Columbia.

- Stevenson, S. K., and D. S. Coxson. 2006. Arboreal forage lichens in partial cuts – a synthesis of research results from British Columbia , Canada. *Rangifer*, Special Issue 17:1–11.
- Stevenson, S. K. 1991. Forestry and caribou in British Columbia. *Rangifer* Special Issue 7:124–129.
- Stotyn, S. A., B. N. McLellan, and R. Serrouya. 2007. Mortality sources and spatial partitioning among mountain caribou, moose, and wolves in the north Columbia Mountains, British Columbia. Report prepared for the Columbia Basin Fish and Wildlife Compensation Program, Nelson. British Columbia.
- Stotyn, S. A. 2008. Ecological Interactions of Mountain Caribou, Wolves and Moose in the North Columbia Mountains, British Columbia. University of Alberta.
- Thurber, J. M., R. O. Peterson, T. D. Drummer, and S. A. Thomasma. 1994. Gray Wolf Response to Refuge Boundaries and Roads in Alaska. *Wildlife Society Bulletin* 22:61–68.
- Wam, H. K., and O. Hjeljord. 2010. Moose Summer Diet From Feces and Field Surveys: A Comparative Study. *Rangeland Ecology & Management* 63:387–395.
- Warton, D. I., and F. K. C. Hui. 2010. The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92:3–10.
- Whittington, J., C. Cassady St. Clair, and G. Mercer. 2005. Spatial Responses of Wolves to Roads and Trails in Mountain Valleys. *Ecological Applications* 15:543–553.
- Wittmer, H. U., B. N. McLellan, D. R. Seip, J. A. Young, T. A. Kinley, S. Watts, D. Hamilton, and G. Watts. 2005a. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. *Canadian Journal of Zoology* 83:407–418.

- Wittmer, H. U., B. McLellan, R. Serrouya, and C. Apps. 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. *Journal of Animal Ecology* 76:568–579.
- Wittmer, H. U., A. Sinclair, and B. McLellan. 2005b. The role of predation in the decline and extirpation of woodland caribou. *Oecologia* 144:257–267.
- Wittmer, H. U. 2004. Mechanisms underlying the decline of mountain caribou (*Rangifer tarandus caribou*) in British Columbia. The University of British Columbia.
- Wixleman, D. A., R. T. Bowyer, and V. Van Ballenberghe. 1998. Diet selection by Alaskan moose during winter: effects of fire and forest succession. *Alces* 34:213–238.
- Wolff, J. O. 1978. Burning and browsing effects on willow growth in interior Alaska. *The Journal of Wildlife Management* 135–140.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. a. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. M. Gail, K. Krickeberg, J. M. Samet, A. Tsiatis, and W. Wonng, editors. Springer New York, New York, NY.

CHAPTER 3 Do Moose Move into Mountain Caribou Habitat in Response to Summer Wolf Predation Risk?

ABSTRACT

A predator avoidance strategy of ungulates is to spread out, reducing their density and increasing predator search times. The predator avoidance strategy of mountain caribou (*Rangifer tarandus caribou*) to segregate themselves from alternate prey and predators is compromised when moose (*Alces alces*) spread out from their winter habitat in the valley bottoms to high elevation habitat where caribou reside. When moose move into caribou habitat their shared predator, wolves (*Canis lupus*), follow moose, exposing caribou to greater predation risk. The greatest mortality factor for mountain caribou is summer predation and therefore steps to conserve the remaining populations depends on understanding factors behind the high predation. The objective of this study was to test the hypothesis that in the summer moose are exposed to less predation risk in high elevation mountain habitat and that moose move into mountain caribou habitat in response to predation risk. I examined this hypothesis using three predictions: i) the spatial overlap between wolves and moose will decrease during the summer when moose move up slope, ii) moose will be exposed to lower predation risk at high elevations compared to low elevations in their home ranges, iii) moose will select for areas of low predation risk. To test these predictions multi-year global positioning systems (GPS) telemetry data for wolves, moose, and caribou were used. Wolf predation risk was estimated by combining their density of spatial use and pack size. Two of my predictions were supported and one received partial support. Moose were able to distance themselves in the summer by moving upslope (prediction i) and as a result reduced their exposure to predation risk (prediction ii). Exposure to wolf predation was most effectively reduced in the early summer when wolves were constrained by denning activities. Finally, moose selected areas of intermediate predation risk, staying away from areas of high predation risk (prediction iii). The results

demonstrate moose can reduce their predation risk by moving into caribou summer habitat and predation risk may be a motivating factor in moose dispersal from valley bottoms to high elevations.

INTRODUCTION

Predation risk is a dominant factor shaping the behaviour of ungulates (Geist 2002, McLoughlin et al. 2005, Hebblewhite and Merrill 2009) and is often the primary factor that shapes population dynamics and community structure (Schmitz et al. 1997). Ungulates will adapt their behaviour to avoid predators, a response that can occur at multiple scales. Some ungulates undertake large scale migrations to reduce predation (Bergerud et al. 1984, Fryxell et al. 1988), while others avoid predation at much smaller scales. For example, at a small scale, non-migrant elk (*Cervus canadensis*) in the Rocky Mountains select for areas of high human activity where predators are uncommon (Hebblewhite and Merrill 2007).

Ungulates exploit spatial variation in predation risk to avoid predators on a seasonal basis. In areas with heavy snowfall in winter, animals commonly migrate from winter ranges that are characterized by lower snow depths or provide shelter from snow and wind to summer ranges to reduce predation risk (Rautenstrauch and Krausman 1989, Johnson et al. 2002, Ferguson and Elkie 2004, Berger et al. 2006, Robinson et al. 2010, Bauer et al. 2011). In mountainous areas, ungulates reduce predation risk by migrating up mountain slopes once the snow has melted. For example, Hebblewhite and Merrill (2007) found elk that migrated from valleys into mountains in the summer reduced their exposure to predation risk by 70% compared to elk that remained in the valleys. Mountain caribou avoid predation by migrating seasonally and by residing at high elevations in the summer where they segregate themselves spatially from wolves (Bergerud et al. 1984, Bergerud and Page 1987, Seip 1992). However, the ability of caribou to avoid predation by residing at high elevations has been compromised in areas where moose have also adopted a similar

predator avoidance strategy: spacing out into high elevation habitat which places, caribou, moose, and their shared predators in close proximity (Seip 1992, Stotyn 2008). When moose move to high elevations some wolves follow, increasing the spatial overlap between caribou, moose, and wolves. As such moose indirectly increase the predation risk of caribou via apparent competition. Apparent competition occurs when one species indirectly causes the decline in another species via increased predation rates from shared predator(s) (Holt 1977, DeCesare et al. 2009).

The increased predation risk for caribou is concerning because predation is the primary factor causing mountain caribou declines (Wittmer et al. 2005a, Festa-Bianchet et al. 2011, Latham et al. 2011b, Boutin et al. 2012). The high rates of predation are driven by apparent competition between caribou, predators, and alternate prey such as moose (McLoughlin et al. 2005, Wittmer et al. 2005b, Latham et al. 2011b). In the Columbia Mountains caribou experience the highest rates of predation in the summer (Wittmer et al. 2005b) when the spatial overlap between caribou, wolves, and moose home ranges are the highest (Stotyn 2008). Key to conserving mountain caribou populations will be understanding factors facilitating predation rates of mountain caribou.

It is unknown why moose to move to higher elevations in the summer and thereby increase their spatial overlap with mountain caribou. It was suggested that moose move up into caribou habitat in the summer to forage on early-seral vegetation in high elevation cutblocks (Seip 1992). However, the availability of high elevation cutblocks does not appear to influence the elevational movements of moose in the summer and these movements are unlikely to be motivated only by forage (Chapter 2). Alternate hypotheses for why moose may move to high elevation areas in the summer are to thermoregulate (Schwab and Pitt 1991, van Beest et al. 2012) or predator avoidance (Kunkel and Pletscher 2000). Here, the hypothesis is presented that moose are moving into mountain caribou habitat in response to predation risk. Moose may have adopted a strategy similar to caribou to segregate themselves from predators by leaving their winter home ranges in the valley bottoms

(Stotyn 2008) and moving up slope in the summer once the snow has melted. Kunkel and Pletscher (2000) found moose were most vulnerable to predation at low elevations, where wolves focused their hunting and that moose avoid areas of high predation risk (e.g. low elevation areas). Similarly, in the non-mountainous terrain of eastern Canada, moose select habitats with lower predation risk from wolves (Houle et al. 2009). In the Columbia Mountains, Stotyn (2008) found that moose were further from wolves in summer and suggested that moose were moving to higher elevations to avoid predation by wolves, which were more restricted to areas near den sites in valleys.

In this chapter I test whether moose predation risk is reduced at higher elevations and thus may be a factor motivating their movements into caribou summer habitat. This hypothesis was examined using three predictions. First, the spatial overlap between wolves and moose will decrease during the summer when moose move up slope. Similar to what others have reported (Stotyn 2008, Peters 2010), it is expected that because of the shifts up slope by moose the spatial overlap between moose and wolves will decrease in the summer. Second, moose will be exposed to less predation risk at high elevations compared to when they are at low elevation. It is expected that wolf predation risk will be higher for moose at low elevation because wolves will be constrained to valley bottoms by denning activities in the spring and early summer (Murie 1944, Haber 1977, Mech 1988). Third, it is expected that moose will select for areas of low predation risk throughout, given that moose are limited by wolf predation (Messier 1991, Ballenberghe and Ballard 1994) and wolves are a dominant predator.

The primary objective of this study was to examine if moose were responding to wolf predation risk by moving to high elevation habitat to reduce their exposure to predation risk. I tested my above predictions by modeling predation risk based on the spatial intensity of wolf habitat use and wolf pack numbers. Were moose successfully reducing their predation risk exposure by moving into caribou summer habitat at high elevations? Since avoidance of predation risk can occur at multiple spatial scales I tested the ability of moose

to avoid predation risk at both a broad home range level and a finer, moose location scale. At a broad home range scale predation risk above and below 1200 m elevation was compared. At the finer scale how predation risk at moose telemetry points changed with elevation was examined. How moose responded to wolf predation risk was directly tested by seeing if they selected for areas of low predation risk.

STUDY AREA

For a description of the study area please refer to chapter 2 and figure 2.1.

METHODS

For the first more descriptive prediction the biweekly elevation change of moose and wolves for a calendar year was graphed. Predation risk for moose was estimated using wolf telemetry data and wolf yearly pack sizes. Moose exposure to wolf predation was then examined at multiple scales and moose habitat selection in regards to predation risk using wolf, moose, and caribou telemetry data.

Telemetry data

The moose, wolf, and caribou telemetry data from the Columbia Mountains were collected from 1992 to 2011 (see details in Kinley and Apps 2001, Wittmer 2004, Serrouya and Poole 2007, Wittmer et al. 2007, Stotyn 2008, van Oort et al. 2011). All individuals were captured with a net gun in March when snow pack was deep and animals and their track could easily be seen. Wolf, moose, and caribou captures followed animal care protocols for the Province of British Columbia and the University of Alberta (permit # VI08-49757, and 690905, 2004-09D, 2005-19D). From 1992-2010, 92 individual caribou were collared in the Columbia Mountains. Global positioning system (GPS) collars were placed on 47 caribou, very high frequency (VHF) collars were placed on 45 caribou. The caribou GPS collars were programmed to receive relocations every 3-5 hours.

For moose telemetry data was collected between 2003 and 2010 from 20 GPS collars, 4 of these individuals were males and 16 were females. The moose GPS collars were programmed to receive a relocation every 5 hours.

For wolves, telemetry data collected from 2005-2010 in the Columbia Mountains from 7 different wolf packs were used. Only wolves with GPS collars (n=17) were used in order to provide enough relocations (74-2263) to estimate the utilisation distribution function (UD) during the summer period. Five of the collars were programmed to collect a relocation every 4 hours, the remaining 12 collars were programmed to obtain a location every hour in the summer.

Spatial overlap

To test the first prediction the mean and range in elevation of caribou, moose, and wolf locations every 14 days for 365 days were plotted. It was expected that the mean elevation of moose would increase in summer and moose would distance themselves from wolves that would be constrained to valley bottoms by their dens. Caribou were added to the graph to provide a reference to movements of wolves and moose and to further describe the increase in spatial overlap that occurs between caribou, moose, and wolves. The mean and range graphed was the mean of the mean of the telemetry points for each individual animal.

Predation Risk

Moose predation risk was estimated in a spatial context during the three different summer periods: early summer, mid-summer, and late summer. Moose exposure to wolf predation risk during summer was the focus of this study because summer is when the highest level of mountain caribou predation occurs (Wittmer et al. 2005b) and there is the highest level of spatial overlap between moose and mountain caribou (Seip 1992, Serrouya et al. 2011). Summer was defined as 20 May to 17 November. May 20 is the first date in the spring when > 50% of the locations for one individual collared moose were above 1200

m elevation. I considered 20 May to be when moose were no longer restricted by snow to valley bottoms and could use mountain caribou habitat. November 17 is when none of the collared moose had >50% of their telemetry locations above 1200 m elevation. The summer period was further subdivided into 3 other approximately equal length seasons based on the change in mean elevation of wolves: early summer (20 May-28 July) when wolves slowly increased their mean elevation, mid-summer (29 July-29 September) when wolves showed a large increase in their mean elevation and then stabilized around 1200m elevation, and late summer (30 September-17 November) when wolves began to decrease their mean elevation. Studying wolf predation risk during smaller subsets of time is important because wolf predation risk changes throughout the summer (Sand et al. 2008). Beyond estimating predation risk on a yearly and seasonal basis a different predation risk was estimated for diurnal and nocturnal periods since wolf predation risk differs between these times (Theuerkauf et al. 2003, Hebblewhite and Merrill 2007). Wolf locations were classified as being diurnal or nocturnal based on sunrise and sunset data from the National Research Council of Canada (<http://www.nrc-cnrc.gc.ca/eng/services/sunrise/advanced.html>).

Predation risk was estimated as a function of both wolf pack size and habitat use (Kristan and Boarman 2003, Hebblewhite and Merrill 2007, Robinson et al. 2010). Predation risk was calculated in the R program (R Development Core Team 2012) using the Raster Package (Hijmans 2014) on a cell by cell basis (30m x 30m) as product of intensity with which wolves used that cell (Equation 1).

Wolf Habitat use

Wolf intensity of use was estimated using a UD which defines the boundary and relative intensity of use within a home range (Millspaugh et al. 2004). Only individuals with enough data to produce a UD in a season were used (>50 telemetry points; Seaman et al. 1999). Wolf UD were estimated using fixed kernel analysis (Worton 1989) with the "plug-in"

method as the smoothing factor. The plug-in method is suggested when estimating UD for animal locations that tend to have a clumped pattern (Gitzen et al. 2006). UDs were calculated in the R program (R Development Core Team 20012) using the KS package (Duong 2008). One individual per pack was used to estimate the UD for a pack. For two packs (Goldstream and Pettipeace) there was enough telemetry data from 6 individuals in each season to calculate a UD. In this case the UD of each individual wolf was calculated and then merged with individuals of the same pack, taking the average value in cells that overlapped. I merged UD from individuals of the same pack because wolf pack cohesion is low in the summer and members of a pack may not attend every kill (Metz et al. 2011).

Pack size

Wolf pack sizes were estimated annually in winter and occasionally in summer from 2004-2011 for the seven packs. When available, wolf pack size estimates were used from the summer ($n=8$), otherwise winter wolf pack sizes ($n=20$) were used. Wolf pups were included in pack estimates by using a ratio of their biomass equivalent to adults (Metz et al. 2011). Pack sizes were estimated using a combination of aerial telemetry flights and infra-red sensory trail cameras. Cameras assisted with population estimates in the summer when sightability from air was reduced. The cameras were placed near wolf dens and popular wolf travel corridors (see Oort et al. 2009, Serrouya 2012).

Using the UD and pack size, predation risk (PR) was calculated for a 30 m x 30 m cell as follows:

Equation 1

$$PR_i = \sum_{p=1}^n (PS_p \times UD_{pi})$$

where PS is the pack size of pack p in a given year and UD is the intensity of use (0-1) of pack p at cell i and n is the total number of packs that used cell i .

Once predation risk was calculated for each wolf pack, year, and season the predation risk estimated for each pack was combined to create a study site predation risk

layer for each season and year. Where the UD of wolf packs overlapped moose were believed to have an increased exposure to predation risk and therefore predation risk of the two wolf packs were added together in these areas. In some cases prey may find refuge in the area between the borders of wolf packs (Lewis and Murray 1993), however, wolf packs in the study area shared hunting areas (i.e. their UDs overlapped) so prey would not find refuge where packs overlapped but what I assumed would be increased predation risk (Kauffman et al. 2007). The calculated predation risk layer was used to evaluate whether moose reduced their exposure to predation risk at both a broad home range scale and a finer moose location scale, and it was employed in the resource selection function to evaluate if moose were selecting for areas of low predation risk.

Broad scale predation risk

I tested for a difference in wolf predation risk for moose at high and low elevations within moose home ranges. An elevational cutoff was used to study when moose were in mountain caribou habitat because the spatial overlap between moose and caribou occurs when moose move up from the valley bottoms into mountain caribou habitat (Stotyn 2008) and caribou escape predators and alternate prey in the summer by residing at high elevations (Bergerud and Elliot 1986, Wittmer 2004). It was not possible to compare predation risk between summer and winter ranges as has been done elsewhere (Hebblewhite and Merrill 2007) because moose in the Columbia Mountains are not migratory and do not establish distinct summer ranges which are different from the winter ranges, their summer range is merely an expansion of their winter range (unpublished data). Global positioning system (GPS) and very high frequency (VHF) telemetry data were collected from caribou to establish the elevational cut-off above which was considered caribou habitat and compare the predation risk moose were exposed to at high and low elevations. Data from 50 caribou with more than 20 relocations in the summer (16 June-22 October) were used. The elevation above which each individual caribou was located > 90% of the time was

calculated and the average was used for the elevational cut-off. On average, mountain caribou were located above 1230 m 90% of the time, for simplicity this number was then rounded down to 1200 m and this elevation defined caribou habitat for this study. This elevation was considered mountain caribou summer habitat and where moose had the potential to overlap spatially with mountain caribou. The average wolf predation risk for each summer season was compared for above and below 1200 m elevation for moose home ranges using only moose with complete coverage of the predation risk layer. Telemetry points were pooled across years because moose showed high summer range fidelity. Moose home ranges were calculated as 100% minimum convex polygons (MCPs) based on 672-3184 summer telemetry locations per individual for the summer period 20 May to 17 November. Home ranges were estimated using the `adehabitatHR` package (Calenge et al. 2012) in the R program (R Development Core Team 2012). I then calculated the mean value of predation risk in the home ranges and compared the average risk above and below 1200 m using a Wilcoxon paired t-test in the R program because data were non-parametric and paired. In the end a predation risk layer was used that was calculated without distinction between night and day because prior tests indicated that nocturnal and diurnal predation risk were not different at this scale.

Fine scale predation risk

I also examined if moose exposure to predation risk declined with elevation at moose telemetry locations (30 m x 30 m) within home ranges during the three seasons (early summer, mid-summer, and late summer). Only predation risk values for moose telemetry points which had a matching season and year with a predation risk layer were calculated. I tested for a change in predation risk with elevation using a linear mixed effects model (Skrondal and Rabe-Hesketh 2004) with a random effect for each moose that accounted for autocorrelation between sequential relocation (Breslow and Clayton 1993). Wolf habitat use appeared to be variable between years so I added year as a random variable to the model

as well. Predation risk was the response variable and elevation (continuous) and season (categorical) were the predictor variables. Predation risk was standardized to fall between the values of 0-1 so that each value represented the relative risk of predation. Next because predation risk values acted like proportions they were logit transformed (Warton and Hui 2010) before using them in the model. Elevation was standardized or normalized to aid in model convergence (Zuur et al. 2009) by subtracting the mean from each value and dividing the result by the standard deviation. Model selection was done as recommend by Diggle et al. (2002) by selecting random covariates first and then using backwards stepwise selection to select the most parsimonious model. All model selection was done in the R program (R Development Core Team 2012) using the lme4 package (Bates et al. 2011).

Moose habitat use model

To model how moose select habitats in response to predation risk, a mixed effects model was used. A type III habitat use model was followed, in which availability and use were defined at the level of the individual (Manly et al. 2002). The model predicted use (binomial variable, 0 or 1) from predictor variables measured at locations (use and available) within the home range of moose. Use was estimated with location data from 20 GPS collared animals. Availability was estimated with randomly generated points within an individual's 100% MCP home range. The number of random locations/individual matched the number of telemetry points for each individual. Determining the sample size of random locations to use can be arbitrary and as such Manly et al. (2002) and Northrup et al. (2013) suggest varying the sample size of available points to ensure the available distribution is adequately described with a given sample size. Previous tests indicated that the available distribution was adequately sampled using a 1-1 ratio for used-available points (Chapter 2).

Three *a priori* models were established: a predation risk model, landscape cover model, and a predation risk-landscape model (Table 3.1). The best random effects structure was selected to be used in the three *a priori* models as recommended by Diggle et al.

(2002): first a beyond maximal model was defined, where all the fixed effects are included and then selected the random effects. Random effects which were tested for inclusion in the models were: year, sex, season, and moose individual. Random effects were included in the models based on the difference in the AIC scores when the variable was included or dropped from the beyond maximal model (Anderson et al. 1998). Polynomial terms were added to models if preliminary data graphing showed a curve or curves in the data. From the three *a-priori* models the top AIC model was selected by comparing the log-likelihood and model weights of the three models (Burnham et al. 2011). Model selection was done in the R program (R Development Core Team 2012) using the lme4 package (Bates et al. 2011).

Table 3.1 *A priori* defined candidate models with binary response variable (use) that were used to model resource selection by moose during the summer from 2005-2010 in the Columbia Mountains.

Model type	Model formulation
Predation risk and land cover	Predation risk ² + terrain ruggedness ² + distance to forest edge + distance to road + elevation + habitat types + predation risk*elevation + habitat types*elevation
Predation risk	Predation risk ² + terrain ruggedness ² + distance to forest edge + distance to road + elevation + predation risk*elevation
Land cover	Habitat types + slope ² + aspect +elevation + habitat types*elevation

Predictor variables included: habitat types, slope, aspect, elevation, predation risk, terrain ruggedness, distance to roads, and distance to forests. The variables were used because moose habitat and wolf predation risk studies found them to be important variables (Kunkel and Pletscher 2000, Kittle et al. 2008). The habitat type layer was assembled in Arc GIS (ESRI 2013) by combining data from multiple sources: VRI data (Vegetation Resource Inventory, BC Ministry of Forests, Lands and Natural Resource Operations), data compiled from Forest Licences, satellite images, and ground visits. Five habitat classes were used: old growth (undisturbed forested habitat), human-caused early-seral, naturally occurring early-seral, riparian, and alpine. Old-growth was forested habitat that had no record of human induced or naturally occurring disturbance. If a particular category represented <1% of the use and available points, it was pooled with the reference category. Thus human-cause

early-seral vegetation, or for short human-seral represented not only cutblocks but also a small amount of powerlines and reclaimed mine sites. Naturally occurring early-seral vegetation or for short natural-seral were areas that had been classified as having forest fires or were avalanche chutes. Riparian areas were water bodies (rivers, lakes, swamps, wetlands). Alpine was area classified as the alpine tundra BEC zone. Aspect is not a true continuous variable, therefore the aspect was divided into 5 categories (north, east, west, south, and flat). For categorical variables, the most common category was used as the reference category: old-growth forests for habitat types and north for aspect. Elevation was calculated from a 10 m Digital Elevation Model (DEM). The slope and aspect were calculated based on the DEM in Arc GIS. Slope and elevation were standardized before they were used in the models (Zuur et al. 2009). I also applied a quadratic term to the variable slope because prior data exploration indicated a curvature in the data when graphed. Terrain ruggedness was calculated using a vector terrain ruggedness with a neighbourhood of 3 X 3 centered on each 30 m cell, using a moving window routine (Sappington et al. 2007). Vector terrain ruggedness is an index of terrain ruggedness developed for use in wildlife habitat studies and quantifies local variation in terrain at a scale believed to be important to wildlife (3 X 3 neighbourhood). Distance to the nearest road (values ranged from 0-7051 m) and distance to the nearest forest cover (values ranged from 0-2308 m) were calculated in ArcGIS (ESRI 2013). The variable year (range 2005-2010) was treated as a categorical variable with 2005 as the reference category. The variable daylight was a binomial variable in which 0 indicated night time and 1 daytime. Also all continuous variables were standardized or normalized to aid in model convergence (Zuur et al. 2009) by subtracting the mean from each value and dividing the result by the standard deviation. All model variables were checked for collinearity using graphs and variance inflation factors (VIF) (cutoff value of 5) before being included in a model.

RESULTS

The first prediction was supported, the mean elevation of moose began to increase in late May and correspondingly the mean elevation of wolves also began to increase and remained high until October (Figure 3.2). As a result, starting in mid May the overlap in elevation use by caribou, moose, and wolves increased until late October when moose and wolves reduced their mean elevation. However, despite the increase in overlap between the three species, moose were able to distance themselves further in terms of elevation from wolves in the summer compared to the winter, particularly in July and September.

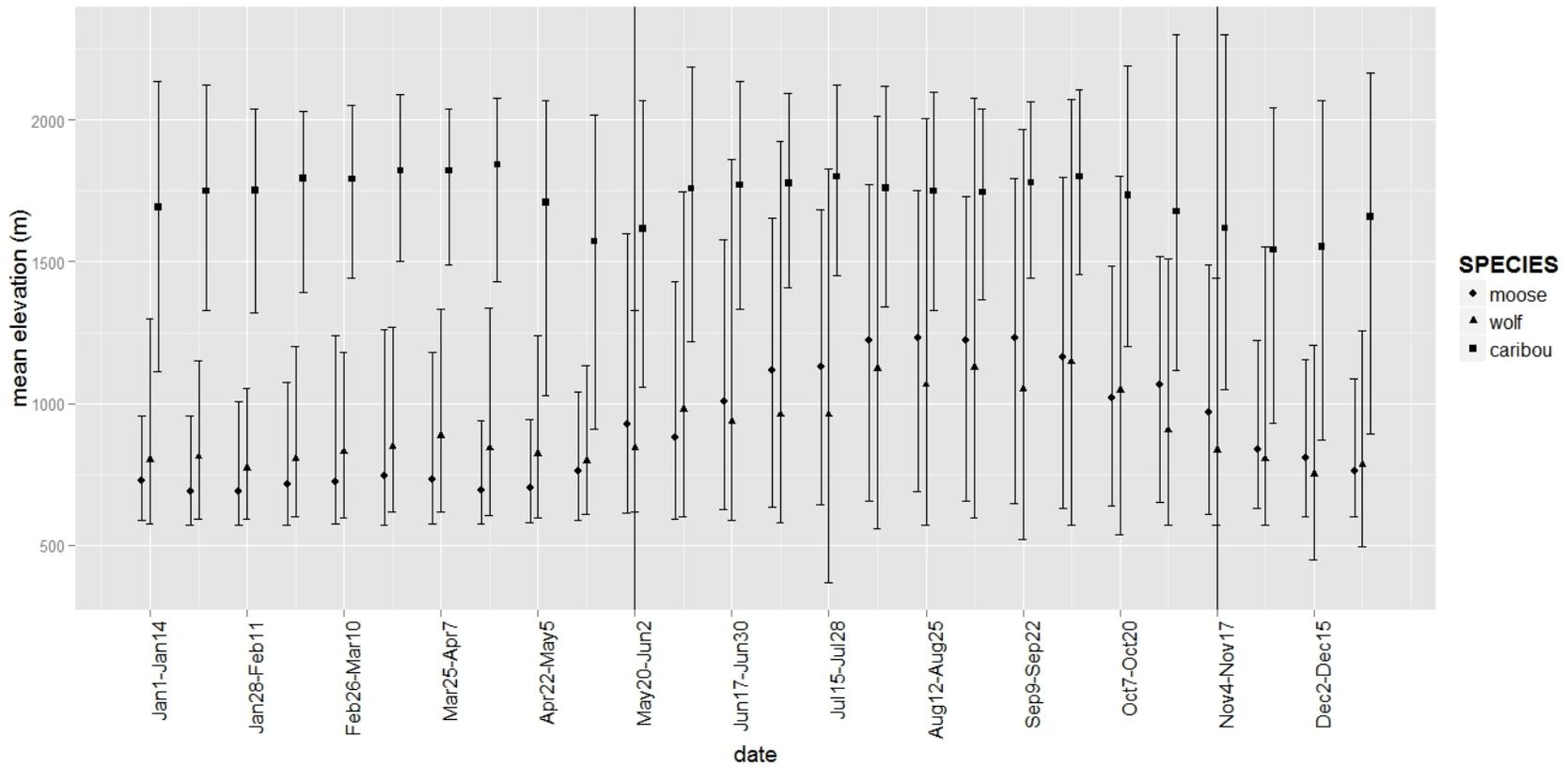


Figure 3.1 Mean and range of elevation for moose (circles), wolves (triangles), and caribou (squares) every 14 days. The upper bars are the upper 95th percentile of the data and the lower bars are the 5th percentile of the data. The first and last bars that run the entire vertical length of the graph mark the beginning and end of the period defined as summer. Data used consisted of telemetry data for caribou (years 1992-2010), moose (years 2003-2010), and wolves (years 2003-2011) in the Columbia Mountains, British Columbia, Canada.

The second prediction was also supported at the two different spatial scales. At the broad home range scale moose were exposed to less predation risk above 1200 m elevation in all three periods: in early summer (Wilcoxon: $P < 0.0001$, $n = 15$), mid-summer (Wilcoxon: $p = 0.0010$, $n = 27$), and late summer (Wilcoxon: $p = 0.0066$, $n = 18$) (Figure 3.3). At the home range scale moose reduced their predation risk by 43% in the early summer, 11% in mid-summer, and 46% in late summer when they were above 1200 m elevation compared to below this elevation.

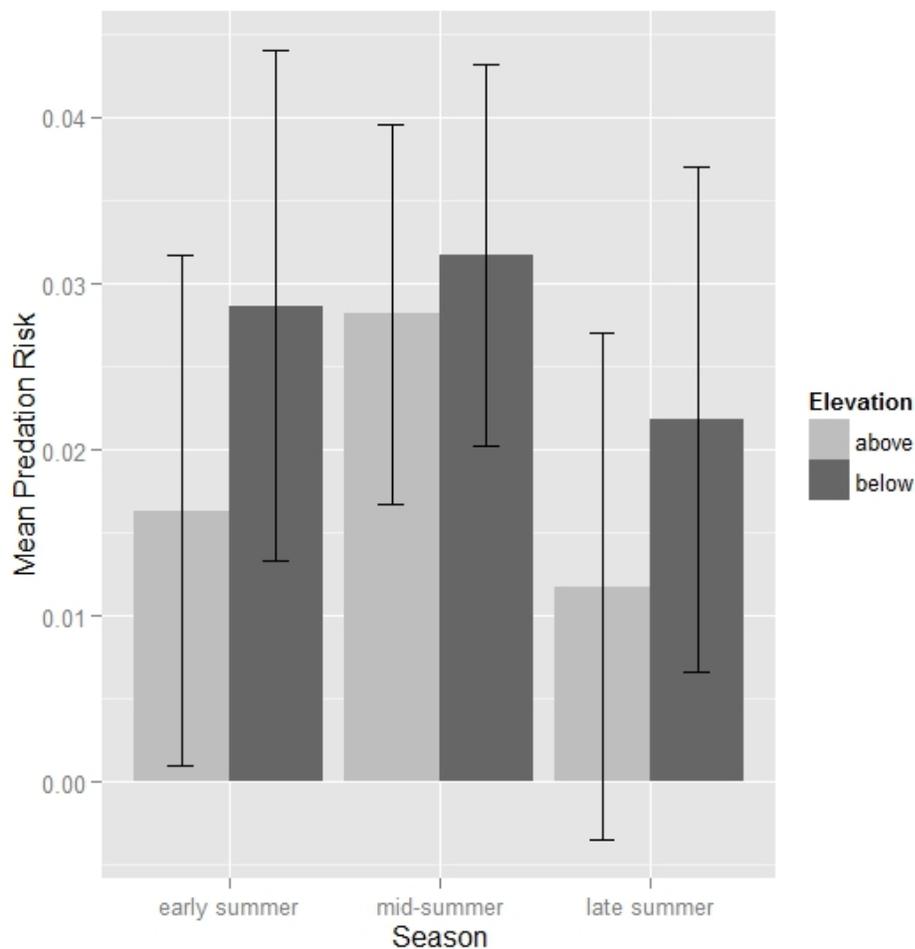


Figure 3.2 Bar graph of the mean predation risk in moose home ranges below 1200 m elevation versus moose home ranges above 1200 m in early summer (20 May-28 July), mid-summer (29 July-29 September), and late summer (30 September-17 November). Error bars are standard errors of the mean. Predation risk calculated for 10 moose in the Columbia Mountains for years 2004-2010. There was a significant difference between predation risk below 1200 m elevation and predation risk above 1200 m elevation in all three seasons (Wilcoxon rank sum paired test, $\alpha = 0.01$).

At the finer scale, predation risk also declined at moose location with elevation (linear-mixed effects model Wald = 15, overall model $P < 0.0001$, elevation term $P < 0.0001$, Figure 3.4). However, this reduction was primarily because of the difference in predation risk in the early summer. In late summer, there was minimal change in predation risk with elevation. Contrary to the other seasons, in mid-summer predation risk increased with elevation. I did not test to see if the difference in the slope between each season was significant, however, in the model there was a significant difference between early summer (reference category) and mid-summer ($P < 0.0001$) but not between early summer and late summer ($P = 0.2233$). Moose were therefore able to reduce their predation risk throughout the entire summer at the home range scale and part of the summer at moose locations.

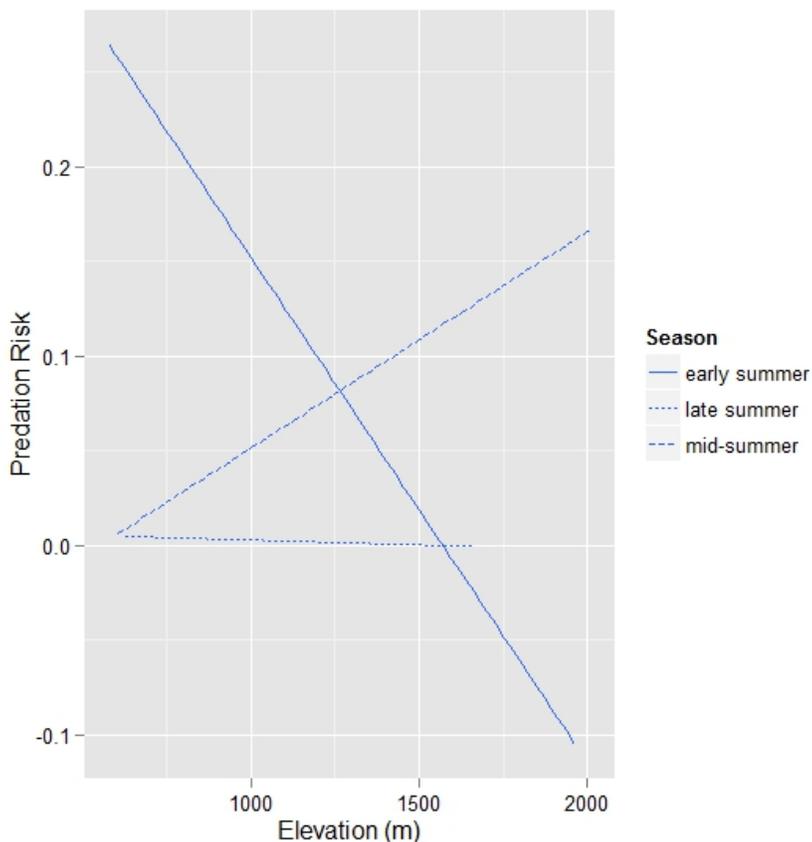


Figure 3.3 Linear model fits of the mean predation risk within moose home ranges at moose telemetry locations in early summer (20 May-28 July), mid-summer (29 July-29 September), and late summer (30 September-17 November). Predation risk calculated for 7 moose in the Columbia Mountains for years 2004-2009.

There was also support for the iv prediction, predation risk was an important variable which influenced the habitat use of moose. When compared to other models, the model that included both predation risk and landscape variables best described moose habitat use (Table 3.3).

Table 3.2 Comparison of the model results for each *a priori* model for moose habitat use in the summer. N moose shows the number of individual moose included in the model, N telemetry points shows the number of telemetry points used in the model, AIC_w is the Akaike's model weight, and $\sigma^2_{(r\text{ eff})}$ is the variance of the random component in the GLMM model (Season | Moose id).

Model	N moose	N telemetry points	Log Likelihood	AIC _w	$\sigma^2_{(r\text{ eff})}$
Predation and land cover	12	5771	-2748	1	27.1276
Predation	12	5771	-2883	8.602898e-56	24.90296
Land cover	12	5771	-2820	7.271065e-33	30.84894

The results of the predation risk-landscape model (Table 3.4) showed that moose selected intermediate levels of predation risk. Important variables influencing moose habitat selection included strong avoidance of rugged terrain, selection of areas far from forest edge, and areas further from roads. Elevation appeared to be selected for in the model because old growth was used as the reference category and the relative selection for old growth habitat increased with elevation.

In terms of the landscape related variables, moose increasingly selected for human-seral, natural-seral, and riparian habitat in comparison to old growth habitat. Of the interaction terms between habitat types and elevation only human-seral and natural-seral were significant, the relative selection for human-seral increased with elevation and the relative selection for natural-seral decreased with elevation.

Table 3.3 Resource use coefficients for moose in the Columbia Mountains (2004-2010) from the predation risk-landscape generalized mixed effects model. Confidence intervals are 95% confidence intervals. The total number of used and available points were 5711 from 20 moose and the AIC score for the model was 6051.

Variables	β	Std. Error	Lower CI	Upper CI
Intercept	-4.8923	0.9389	-6.7325	-3.0522
Human-seral	1.5107	0.1085	1.2981	1.7233
Natural-seral	1.8597	0.2728	1.3251	2.3942
Riparian	1.3593	0.6143	0.1552	2.5633
Ruggedness	-0.6382	0.0677	-0.7708	-0.5056
Ruggedness²	0.0309	0.0089	0.01340	0.0485
Predation Risk	0.9651	0.1118	0.7460	1.1843
Predation Risk²	-0.1520	0.0355	-0.2216	-0.0825
Distance to forest edge	0.0980	0.0467	0.0065	0.1895
Roads	0.2233	0.0721	0.0820	0.3645
Elevation	0.5283	0.0876	0.3566	0.7000
Human-seral*elevation	-0.2322	0.1043	-0.4367	-0.0277
Natural-seral*elevation	-1.2722	0.2573	-1.7764	-0.7680
Riparian*elevation	0.3482	0.4566	-0.5467	1.2431

DISCUSSION

Mountain caribou that live in deep snow ecosystems have declined rapidly across southeastern British Columbia (Wittmer et al. 2010) due to unsustainable rates of predation (Wittmer 2004). Caribou segregate themselves from the predators and alternate prey in the summer by occupying high elevation, subalpine habitat (Bergerud and Page 1987). However, moose may also employ a similar strategy by moving upslope in summer after snow melt to space away from predators. When moose space out into higher elevations they place themselves in mountain caribou habitat, reducing the effectiveness of the anti-predator strategy of caribou since wolves follow moose into caribou habitat. To better conserve mountain caribou it is important to understand the primary factors behind the summer movement of moose into caribou habitat and if predator avoidance is one of these.

I examined the hypothesis that moose, like mountain caribou, space out to distance themselves from predators. I tested a number of predictions to examine if moose were able

to effectively reduce their predation risk by moving into mountain caribou habitat. The first, more descriptive prediction was supported. The spatial overlap between moose and wolves decreased during the summer compared to winter as moose move up slope. Wolves also increase their mean and range in elevation but were more constrained to valley bottoms by den activities and thus the spatial overlap between moose and wolves was still reduced. Wolves tend to place their dens in at low elevations (Norris et al. 2002) or lowlands where they have increased opportunities to hunt beaver, deer, and moose (Mech 1970, Heard and Williams 1992, Packard 2003, Latham 2009).

The second prediction was supported; moose were able to reduce predation risk at both the home range and finer moose location scale by moving into mountain caribou habitat. At the home-range scale moose reduced predation risk if they moved above 1200 m elevations in the early summer and late summer. The seasonal difference related to the habitat use of wolves; wolves used areas above 1200 m elevation more in mid-summer and thus moose predation risk was higher than it was in early and late summer when wolves were more constrained to valley bottoms. Wolves increase the area they use after the denning period (Eriksen et al. 2009), which is why the ability of moose to escape predation risk is reduced in mid-summer. Moose were again more capable of avoiding predation risk at higher elevations in the late summer (30 September - 17 November). It is unclear why moose exposure to predation is reduced in late summer because wolves began to reduce their median elevation, along with moose, and pups are old enough to travel with the pack (Burkholder 1959, Mech 1966, Peterson 1977, Jedrzejewski et al. 1993, Musiani et al. 1998). Potentially wolves, begin to focus more on other prey types, late summer is coincidentally when wolves consume more caribou compared to early spring when they consume primarily moose (Stotyn 2008).

Moose were also capable of avoiding predation at the finer scale within their home ranges. The largest difference in predation risk between high and low elevations at the

within home range scale occurred in early summer when wolves were constrained to lower elevations by denning activities. The results found here are similar to those found in other studies in winter: low elevation areas, where prey tend to be concentrated and snow levels the lowest, is where moose are the most vulnerable to predation (Singleton 1995, Kunkel 2000, Kunkel and Pletscher 2000). Moose located above where wolves are concentrated tend to be the safest from predation (Kunkel and Pletscher 2000). Therefore at both the broad home range and finer location scale moose are able to effectively reduce their exposure to predation risk, particularly in early summer.

Moose were influenced by both habitat type and predation risk as the top model included both. While predation risk related variables are important in moose habitat use, the third prediction was not fully supported since moose selected for intermediate levels of predation risk. This result is likely because moose are not using some habitats with the lowest predation risk, such as alpine, because moose forage would be limited. In terms of the other predation risk associated variables; moose did not use rugged terrain. Interestingly, moose increasingly used areas farther from the forest edge, which indicates they are not staying close to the forest edge to use the forest as cover. This result contradicts previous research which found in the winter moose do not use open habitat which is far from cover (LeResche 1974, Andersen 1991) and in the boreal region the distance to forest cover in general did not exceed 0.5 km (Eastman 1974). Indeed, in the winter, moose are more likely to be killed in open sites, further away from forest cover (Kunkel and Pletscher 2000). Perhaps in the summer moose are able to better hide in tall shrubs when they are in open spaces in the summer and do not need to use the forest as cover. Moose also forage in old growth forests in the summer, increasing their distance away from the forest edge, further into the forest (Chapter 2).

Moose also increasingly used areas further away from roads, which is likely because wolves and hunters use forestry roads to access moose. Results from moose and wolf

interactions with roads have been highly variable in previous studies. Eriksen et al. (2009), similar to this study, found that moose avoided roads as a possible anti-predator strategy since wolves often patrolled the roads. Conversely, in Yellowstone and Isle Royale wolves avoided roads which were associated with human activity and as result moose found refuge on roads (Stephens and Peterson 1984, Berger 2007). Additionally, Kunkel and Pletscher (2000) found that moose were more likely to be killed by wolves in areas with lower road densities which was likely because wolves selected areas with low road densities and as such moose were able to find refuge in areas with higher road densities. While I did not assess the risk of moose to being killed by humans, more moose were killed in the study area by humans than wolf predation during this study (unpublished data). People concentrate their hunting activities near roads, greatly increasing risk for moose near roads for a short period in the autumn. Thus it is possible that moose in the Columbia Mountain avoid roads to avoid both wolves and humans.

Altogether two of the three predictions were supported and one received partial support. The results suggest that moose are able to avoid predation risk by spacing out into mountain caribou habitat and moose are responding to predation risk in their habitat selection. The results lend support to the hypothesis that moose are able to reduce their exposure to predation risk by moving into caribou habitat and as such the reduced predation risk may be a factor in the movement of moose into caribou habitat.

However there are some important shortfalls and assumptions of this study that should be considered. Due to lack of other data only wolf predation risk was modeled, however, there are other predators of moose. Of special concern are bears which maybe greater predators of moose than wolves, particularly in the spring when cows are with young calves (Franzmann et al. 1980, Ballard and Miller 1990, Schwartz and Franzmann 1990, Boutin 1992). The effectiveness of spacing out would be limited against bears. While spacing out still reduces the density of moose in valley bottoms, thus increasing the search time for

predatory bears, it would not be effective at placing moose further away from grizzly bears, which tend to place their home ranges at higher elevations. In contrast, while bears are significant predators of moose calves (Franzmann et al. 1980, Ballard and Miller 1990, Schwartz and Franzmann 1990), wolves have a potentially stronger effect on moose populations dynamics because moose are the preferred prey of wolves year round (Stotyn 2008) and wolves kill all age classes of female and male moose. The adult survival rate of moose has a more pronounced effect on the population growth rate of moose than the calf survival rate (Eberhardt et al. 1982, Nelson and Peek 1982). The significance of wolves as moose predators is potentially why, despite not accounting for other predators, moose still respond to wolf predation risk.

Another important mortality factor I did not consider was hunting risk by humans. Given the increase in hunting permits for moose, humans now harvest more moose than wolves in the Columbia Mountains. While data is available on the potential number of hunters and the timing of the hunt (Government of BC), preliminary data analysis indicated that the timing when moose were primarily above 1200 m elevation and the hunting season did not match (unpublished results) suggesting hunting is not an important factor yet in moose movement to high elevation habitat.

An additional shortfall of the predation risk model, as mentioned in the methods section, is the difficulty in modeling summer predation risk. Wolf habitat use is typically modeled using one individual per pack to represent habitat use of the entire pack when the data is telemetry data (Glenz et al. 2001, Houle et al. 2009, Robinson et al. 2010). However, wolf pack cohesion in the summer is low and not all wolves from a pack will attend a summer kill (Metz et al. 2011). As a result it cannot be assumed that the movements and habitat use of 1 wolf per pack is representative of the entire pack in the summer. While I attempted to correct for low pack cohesion by including the habitat use of more than one

wolf per pack, I was only able to do this for 2 packs and even for those two packs not all individuals in the pack were collared.

Another consideration is that I assumed kill rate increased linearly with wolf habitat use and pack size, however, this assumption may not be correct. Kill rate is believed to increase in a non-linear fashion with pack size (Packard 2003). However, I did not have any summer wolf kill data to estimate the change in kill rates between pack sizes (e.g. Hebblewhite and Merrill 2007, Robinson et al. 2010). Kill rate is a function of moose density (Messier 1994, Hayes and Harestad 2000a), differences in prey available between packs, wolf density, season (Sand et al. 2008, Metz et al. 2012), and pack cohesion (Metz et al. 2012). However, given the numerous variables that influence predation rates I question whether I would be able to accurately estimate a non-constant kill rates as a function of pack size, even with wolf kill data. Furthermore, estimating summer kill rates using telemetry data and kill site investigations can be challenging due to lack of pack cohesion (Metz et al. 2012) and changes in age and size of prey from spring to fall (Sand et al. 2008).

Despite the shortfalls, the results from this study raise questions about how to manage predators and the moose population for the conservation of mountain caribou. Previously it was believed that early-seral vegetation made available by forest harvesting at high elevations attracted moose into caribou summer habitat, however, research has shown this is unlikely (Chapter 2). The predator avoidance strategy of moose to spread out to higher elevation areas in the summer may have important consequences for how caribou and moose are currently managed. In the Columbia Mountains the strategy to date has been to manage the moose population via hunting (Serrouya et al. 2011) but there is a potential for this to result in a greater proportion of moose spreading into mountain caribou habitat or spending more time there. As the ratio of moose to wolves decreases, predation pressure on moose will increase. Moose may respond to the increased predation risk by spending more time in mountain caribou habitat in the summer and thus expose caribou to more predation

risk because wolves follow moose in caribou habitat. Another important question is if moose are reduced too quickly will wolves switch prey and focus more on hunting caribou as moose become less available? To reduce the impact of apparent competition on caribou governments in western Canada are either managing wolf populations (Boutin et al. 2012, Hervieux et al. 2013) or caribou populations (Serrouya et al. 2011). While management of caribou predators and alternate prey is an important management tool for the conservation of caribou (Boutin et al. 2012), there may be important secondary effects we have yet to consider and research.

WORKS CITED

- Andersen, R. 1991. Habitat changes in moose ranges: Effects on migratory behaviour, site fidelity and size of summer home range. *Alces* 27:85–92.
- Anderson, D. R., K. P. Burnham, and G. C. White. 1998. Comparison of Akaike information criterion and consistent Akaike information criterion for model selection and statistical inference from capture-recapture studies. *Journal of Applied Statistics* 25:263–282.
- Ballard, W., and S. Miller. 1990. Effects of reducing brown bear density on moose calf survival in south-central Alaska. *Alces* 26:9–13.
- Ballenberghe, V. Van, and W. B. Ballard. 1994. Limitation and regulation of moose populations: the role of predation. *Canadian Journal of Zoology* 72:2071–2077.
- Bates, D., M. Maechler, and B. Bolker. 2011. *lme4: Linear mixed-effects models using Eigen and syntax classes*.
- Bauer, S., B. A. Nolet, J. Giske, J. W. Chapman, S. Åkesson, A. Hedenström, and J. M. Fryxell. 2011. Cues and decision rules in animal migration. Pages 68–87 in E. J. Milner-Gulland, J. M. Fryxell, and A. R. E. Sinclair, editors. *Animal Migration--A Synthesis*. Oxford, England.

- Van Beest, F. M., B. Van Moorter, and J. M. Milner. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. *Animal Behaviour* 84:723–735.
- Berger, J., S. L. Cain, and K. M. Berger. 2006. Connecting the dots: an invariant migration corridor links the Holocene to the present. *Biology Letters* 2:528–531.
- Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters* 3:620–623.
- Bergerud, A. T., and J. P. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology* 64:1515–1529.
- Bergerud, A. T., R. D. Jakimchuk, and D. R. Carruthers. 1984. The buffalo of the north: caribou (*Rangifer tarandus*) and human developments. *Arctic* 37:7–22.
- 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.
- Boutin, S., M. S. Boyce, M. Hebblewhite, D. Hervieux, K. H. Knopff, M. C. Latham, A. D. M. Latham, J. Nagy, D. Seip, and R. Serrouya. 2012. Why are caribou declining in the oil sands? *Frontiers in Ecology and the Environment* 10:65–67.
- Boutin, S. 1992. Predation and moose population dynamics: a critique. *Journal of Wildlife Management* 56:pp. 116–127.
- Breslow, N. E., and D. G. Clayton. 1993. Approximate inference in generalized linear mixed models. *Journal of the American Statistical Association* 88:9–25.
- Burkholder, B. L. 1959. Movements and behaviour of a wolf pack in Alaska. *Journal of Wildlife Management* 23:1-11.
- Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* 65:23–35.

- Calenge, A. C., S. Dray, and S. Fortmann-roe. 2012. Package "adehabitat."
- DeCesare, N. J., M. Hebblewhite, H. S. Robinson, and M. Musiani. 2010. Endangered, apparently: the role of apparent competition in endangered species conservation. *Animal Conservation* 13:353–362.
- Diggle, P., P. Heagerty, K. Liang, and S. Zeger. 2002. *The Analysis of Longitudinal Data*. Second. Oxford University Press, Oxford, England.
- Duong, T. 2008. KS: Kernel smoothing.
- Eastman, D. S. 1974. Habitat use by moose of burns, cutovers and forests in northcentral British Columbia. Pages 238–256 *in*. *Proceedings of the North American Moose Conference*. Volume 10.
- Eberhardt, L. L., A. K. Majorowicz, and J. A. Wilcox. 1982. Apparent rates of increase for two feral horse herds. *Journal of Wildlife Management* 367–374.
- Eriksen, A., P. Wabakken, B. Zimmermann, H. P. Andreassen, J. M. Arnemo, H. Gundersen, J. M. Milner, O. Liberg, J. Linnell, H. C. Pedersen, H. Sand, E. J. Solberg, and T. Storaas. 2009. Encounter frequencies between GPS-collared wolves (*Canis lupus*) and moose (*Alces alces*) in a Scandinavian wolf territory. *Ecological Research* 24:547–557.
- ESRI. 2013. ArcGIS Desktop. Environmental Systems Research Institute, Redlands, CA.
- Ferguson, S. H., and P. C. Elkie. 2004. Seasonal movement patterns of woodland caribou (*Rangifer tarandus caribou*). *Journal of Zoology* 262:125–134.
- Festa-Bianchet, M., J. C. Ray, S. Boutin, S. D. Côté, and A. Gunn. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. *Canadian Journal of Zoology* 89:419–434.

- Franzmann, A. W., C. C. Schwartz, and R. O. Peterson. 1980. Moose calf mortality in summer on the Kenai Peninsula. *Alces* 44:764–768.
- Fryxell, J. M., J. Greever, and A. R. E. Sinclair. 1988. Why are migratory ungulates so abundant? *American Naturalist* 131:781–798.
- Geist, V. 2002. Adaptive behavioral strategies. Pages 219–277 *in* D. Toweilli and J. Thomas, editors. *Elks of North America- ecology and management*. Stackpole Books, Harrisburg, PA.
- Gitzen, R. A., J. J. Millspaugh, and B. J. Kernohan. 2006. Bandwidth selection for fixed-kernel analysis of animal utilization distributions. *Journal of Wildlife Management* 70:1334–1344. BioOne.
- Glenz, C., A. Massolo, D. Kuonen, and R. Schlaepfer. 2001. A wolf habitat suitability prediction study in Valais (Switzerland). *Landscape and Urban Planning* 55:55–65.
- Haber, G. C. 1977. *Socio-ecological dynamics of wolves and prey in a subarctic ecosystem*. University of British Columbia.
- Hayes, R. D., and S. Harestad. 2000. Wolf functional response and regulation of moose in the Yukon. *Canadian Journal of Zoology* 78:60–66.
- Heard, D. C., and T. M. Williams. 1992. Distribution of wolf dens on migratory caribou ranges in the Northwest Territories, Canada. *Canadian Journal of Forest Research* 70:1504–1510.
- Hebblewhite, M., and E. H. Merrill. 2007. Multiscale wolf predation risk for elk: Does migration reduce risk? *Oecologia* 152:377–387.
- Hebblewhite, M., and E. Merrill. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology* 90:3445–3454.

- Hervieux, D., M. Hebblewhite, N. J. Decesare, M. Russell, K. Smith, S. Robertson, and S. Boutin. 2013. Widespread declines in woodland caribou (*Rangifer tarandus caribou*) continue in Alberta. *Canadian Journal of Zoology* 882:872–882.
- Hijmans, R. J. 2014. Raster Package.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12:197–229.
- Houle, M., D. Fortin, C. Dussault, R. Courtois, and J.-P. Ouellet. 2009. Cumulative effects of forestry on habitat use by gray wolf (*Canis lupus*) in the boreal forest. *Landscape Ecology* 25:419–433.
- Jedrzejewski, W., K. Schmidt, J. Theuerkauf, and B. Jedrzejewski. 1993. Daily movements and territory use by radio collared wolves, *Canis lupus*, in Bialowieza Primeval Forest in Poland. *Canadian Journal of Zoology* 83:1993–2004.
- Johnson, C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002. Movement parameters of ungulates and scale-specific responses to the environment. *Journal of Animal Ecology* 71:225–235.
- Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology letters* 10:690–700.
- Kinley, T. A., and C. D. Apps. 2001. Mortality patterns in a subpopulation of endangered mountain caribou. *Wildlife Society Bulletin* 158–164.
- Kittle, A. M., J. M. Fryxell, G. E. Desy, and J. Hamr. 2008. The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. *Oecologia* 157:163–75.
- Kristan, W. B., and W. I. Boarman. 2003. Spatial pattern of risk of common raven predation on desert tortoises. *Ecology* 84:2432–2443.

- Kunkel, K. E., and D. H. Pletscher. 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. *Canadian Journal of Zoology* 78:150–157.
- Kunkel, K. E. 2000. Predation by wolves and other large carnivores in northwestern Montana and southeastern British Columbia. University Microfilms.
- Latham, A. D. M., M. C. Latham, N. A. McCutchen, and S. Boutin. 2011. Invading white-tailed deer change wolf-caribou dynamics in northeastern Alberta. *Journal of Wildlife Management* 75:204–212.
- Latham, A. 2009. Wolf ecology and caribou-primary prey wolf spatial relationships in low productivity peatland complexes in northeastern Alberta. University of Alberta.
- LeResche, R. E. 1974. Moose migrations in North America. *Naturaliste Canadien* 101:393–415.
- Lewis, M. A., and J. D. Murray. 1993. Modelling territoriality and wolf-deer interactions. *Nature* 366:738–740.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, and W. P. Erickson. 2002. *Resource Selection by Animals*. Second edition. Kluwer Academic Publishers, Netherlands.
- McLoughlin, P. D., J. S. Dunford, and S. Boutin. 2005. Relating predation mortality to broad-scale habitat selection. *Journal of Animal Ecology* 74:701–707.
- Mech, L. D. 1966. The wolves of Isle Royale. Page 210 in. U.S. National Park Service Fauna Series, no. 7. U.S. Government Printing Office.
- Mech, L. D. 1970. *The wolf: the ecology and behaviour of an endangered species*. Natural History Press, Garden City.
- Mech, L. D. 1988. *The Arctic wolf: Living with the pack*. Voyageur Press, Stillwater, MN.

- Messier, F. 1991. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. *Journal of Animal Ecology* 377–393.
- Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. *Ecology* 75:478–488. *Eco Soc America*.
- Metz, M. C., D. W. Smith, J. a Vucetich, D. R. Stahler, and R. O. Peterson. 2012. Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *Journal of Animal Ecology* 81:553–63.
- Metz, M. C., J. a Vucetich, D. W. Smith, D. R. Stahler, and R. O. Peterson. 2011. Effect of sociality and season on gray wolf (*Canis lupus*) foraging behavior: implications for estimating summer kill rate. *PloS one* 6:e17332.
- Millspaugh, J. J., R. a. Gitzen, B. J. Kernohan, M. a. Larson, and C. L. Clay. 2004. Comparability of three analytical techniques to assess joint space use. *Wildlife Society Bulletin* 32:148–157.
- Murie, A. 1944. The Wolves of Mount McKinley. Page 238 in. U.S. National Park Service Fauna Series. Fifth edition. U.S. Government Printing Office, Washington, D.C.
- Musiani, M., H. Okarma, and W. Jedrzejewski. 1998. Speed and actual distance travelled by radiocollared wolves in Bialowieza Primeval Forest (Poland). *Acta Theriol* 43:409–416.
- Nelson, L. J., and J. M. Peek. 1982. Effect of survival and fecundity on rate of increase of elk. *The Journal of Wildlife Management* 535–540.
- Norris, D. R., M. T. Theberge, and J. B. Theberge. 2002. Forest composition around wolf (*Canis lupus*) dens in eastern Algonquin Provincial Park, Ontario. *Canadian Journal of Zoology* 80:866–872.
- Northrup, J. M., M. B. Hooten, C. R. J. Anderson, and G. Wittemyer. 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. *Ecology* 94:1456–1463.

- Van Oort, H., B. N. McLellan, and R. Serrouya. 2011. Fragmentation, dispersal and metapopulation function in remnant populations of endangered mountain caribou. *Animal Conservation* 14:215–224.
- Oort, H. Van, R. Serrouya, and B. Mclellan. 2009. Wolf movement patterns and kill rates in the Columbia Mountains.
- Packard, J. 2003. Wolf behaviour: reproductive, social, and intelligent. Pages 35–65 in L. D. Mech and L. Boitani, editors. *Wolves: behaviour, ecology and conservation*. The University of Chicago Press, Chicago.
- Peters, W. E. B. 2010. Resource Selection and Abundance Estimation of Moose: Implications for Caribou Recovery in a Human Altered Lanscape. The University of Montana.
- Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. National Park Service scientific monograph. Washington, DC: US Government Printing Office.
- R Development Core Team. 2012. R: A language and environment for statistical computing. Vienna, Austria.
- Rautenstrauch, K. R., and P. R. Krausman. 1989. Influence of water availability and rainfall on movements of desert mule deer. *Journal of Mammalogy* 197–201.
- Robinson, B. G., M. Hebblewhite, and E. H. Merrill. 2010. Are migrant and resident elk (*Cervus elaphus*) exposed to similar forage and predation risk on their sympatric winter range? *Oecologia* 164:265–75.
- Sand, H., P. Wabakken, B. Zimmermann, O. Johansson, H. C. Pedersen, and O. Liberg. 2008. Summer kill rates and predation pattern in a wolf-moose system: can we rely on winter estimates? *Oecologia* 156:53–64.
- Sappington, J., K. M. Longshore, and D. B. Thompson. 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. *The Journal of wildlife management* 71:1419–1426.

- Schmitz, O., A. Beckerman, and O. KM. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78.
- Schwab, F. E., and M. D. Pitt. 1991. Moose selection of canopy cover types related to operative temperature, forage, and snow depth. *Canadian Journal of Zoology* 69.
- Schwartz, C. C., and A. W. Franzmann. 1990. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. *Wildlife monographs* 113:58.
- 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.
- Serrouya, R., B. N. McLellan, S. Boutin, D. R. Seip, and S. E. Neilsen. 2011. Developing a population target for an overabundant ungulate for ecosystem restoration. *Journal of Applied Ecology* 48:935–942.
- Serrouya, R., and K. G. Poole. 2007. Moose population monitoring in the Lake Revelstoke (Management Units 4-38 and 4-39) and North Thompson (MUs 3-43 and 3-44) valleys, January 2006 and 2007.
- Serrouya, R. 2012. An adaptive approach to endangered species recovery based on a management experiment: reducing moose to reduce apparent competition. University of Alberta.
- Singleton, P. 1995. Winter habitat selection by wolves in the North Fork of the Flathead River, Montana and British Columbia. University of Montana.
- Skrondal, A., and S. Rabe-Hesketh. 2004. Generalized latent variable modeling: Multilevel, longitudinal, and structural equation models.
- Stephens, P. W., and R. O. Peterson. 1984. Wolf-avoidance strategies of moose. *Ecography* 7:239–244. Wiley Online Library.

- Stotyn, S. A. 2008. Ecological Interactions of Mountain Caribou, Wolves and Moose in the North Columbia Mountains, British Columbia. University of Alberta.
- Theuerkauf, J., W. Jedrzejewski, K. Schmidt, and R. Gula. 2003. Spatiotemporal segregation of wolves from humans in the Bialowieza Forest (Poland). *Journal of Wildlife Management* 67:706–716.
- Warton, D. I., and F. K. C. Hui. 2010. The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92:3–10. Ecological Society of America.
- Wittmer, H. U., R. N. M. Ahrens, and B. N. McLellan. 2010. Viability of mountain caribou in British Columbia, Canada: Effects of habitat change and population density. *Biological Conservation* 143:86–93.
- Wittmer, H. U., B. N. McLellan, D. R. Seip, J. A. Young, T. A. Kinley, S. Watts, D. Hamilton, and G. Watts. 2005a. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. *Canadian Journal of Zoology* 83:407–418.
- Wittmer, H. U., B. McLellan, R. Serrouya, and C. Apps. 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. *Journal of Animal Ecology* 76:568–579.
- Wittmer, H. U., A. Sinclair, and B. McLellan. 2005b. The role of predation in the decline and extirpation of woodland caribou. *Oecologia* 144:257–267.
- Wittmer, H. U. 2004. Mechanisms underlying the decline of mountain caribou (*Rangifer tarandus caribou*) in British Columbia. The University of British Columbia.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168. Eco Soc America.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. a. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. M. Gail, K. Krickeberg, J. M. Samet, A. Tsiatis, and W. Wonng, editors. Springer New York, New York, NY.

CHAPTER 4 Discussion and Conclusion

INTRODUCTION

Mountain caribou, a sub-population of woodland caribou (*Rangifer tarandus caribou*) are predicted to go extinct within the next 200 years (Wittmer 2004, Wittmer et al. 2010), the proximate cause of their decline being increased predation rates subsidized by abundant alternate prey or apparent competition (Seip 1992, Wittmer et al. 2005b). The driver for apparent competition is either human induced habitat change that favours one prey species over the other or introduced prey species. When the cause for apparent competition is human induced landscape changes the effects will either manifest themselves through increased population abundance of the primary species or altered niche overlap between the primary prey and secondary prey species (DeCesare et al. 2010).

Moose (*Alces alces*) are native but historically rare in mountain caribou habitat (Serrouya et al. 2011), however, human induced changes to the landscape have caused the population of moose to increase in caribou habitat (Serrouya et al. 2011). In the Columbia Mountains, moose are the primary prey of wolves (*Canis lupus*) and drive population increases, whereas mountain caribou are the secondary prey species (Serrouya 2013). In summer is when the greatest amount of caribou predation occurs (Wittmer et al. 2005b) and it is also the season during which the spatial overlap between caribou, moose, and wolves increases (Wittmer et al. 2005b, Stotyn 2008). Research has suggested that timber harvesting in high elevation forests in mountain caribou habitat was the reason behind the increased spatial overlap between moose and mountain caribou (Seip 1992, Wittmer et al. 2005b) and thus a driving factor in apparent competition between caribou, moose, and wolves.

The objective of this study was to examine how the niche or spatial overlap between moose, caribou, and wolves was affected by 1) human disturbance to mountain caribou

summer habitat, and 2) a possible predator avoidance behaviour of moose. In chapter 2 I examined the hypothesis that high elevation human-disturbed early-seral habitat, a known food source for moose, was a factor behind the movement of moose into caribou habitat. In chapter 3 I then examined an alternative hypothesis that moose, like mountain caribou, spread out in the summer into high elevation areas in order to avoid predation (Kunkel and Pletscher 2000, Stotyn 2008).

FINDINGS

In winter, moose are often associated with early-seral vegetation (Eastman 1974, Peek 1998). Early-seral habitats produce more moose browse than late succession forests (Wolff 1978). Therefore, it appears plausible that moose would move into caribou habitat in response to logging at high elevation. However, research has found that in the summer moose use and select forested and aquatic habitats (Eastman 1974) and in mountainous areas select upland or subalpine forests (Telfer 1974, Pierce and Peek 1984, Matchett 1985, Peek 1998). My study found that high elevation human-disturbed habitats did not produce more forage than other habitat types (contrary to prediction i of hypothesis 1). Regardless, moose still highly selected for human-seral habitat at high elevations (in agreement with prediction ii of hypothesis 1), but proportional use of human-seral habitat declined at high elevations when compared to low elevations (from 65 to 27%). When at high elevations moose spend the majority of their time in old growth habitat (48%), suggesting that they are foraging in old growth forests. As well, moose were not located closer to cutblocks than would be expected by random (contrary to prediction iii of hypothesis 1), thus they are not foraging in cutblocks and using old-growth as cover. Finally, an increase in the availability of high elevation human-seral habitat did not correspond with an increase in the proportion of time moose spent at high elevations (contrary to prediction iv of hypothesis 1).

These findings lead to the conclusion that the movement of moose into caribou summer habitat was not primarily driven by high elevation human-seral habitat and forage

associated with high elevation human-seral habitat. Instead the mechanism behind moose movement into mountain caribou habitat is likely a natural cause, such as predator avoidance or thermo-regulation.

As discussed in my third chapter, the hypothesis that moose are spreading out into mountain caribou habitat in the summer to avoid predation was at least partially supported. The spatial overlap between moose and wolves decreased during the summer (agreeing with prediction i of hypothesis 2), and as a result, moose were able to reduce their exposure to predation risk at both the broad home-range and the finer moose location scale (agreeing with prediction ii of hypothesis 2). In particular, moose were most effective at reducing their exposure to wolf predation by moving upslope to higher elevations in the early summer when wolves were restricted to the valley bottoms by denning activities. Moose were also influenced by predation risk and related variables in their choice of habitats. Moose selected for areas of intermediate predation risk, potentially as a trade-off between forage and predation risk (as stated in prediction iii for hypothesis 2) because habitats with the lowest predation risk, such as alpine habitat provide little forage for moose.

The predation risk I calculated provided only a limited assessment of predation risk for moose. In addition to wolf predation risk, moose face bear predation and high hunting pressure. It was hunting, not predation that precipitated the drop in moose numbers in the Columbia Mountains (Serrouya 2013) thus one might expect moose to be more sensitive to hunter presence than wolf presence. However, some preliminary data analysis showed that the movement of moose to high elevation areas does not correspond to when hunters are present (unpublished results). Despite the shortfalls in estimating predation risk, I was still able to demonstrate a response to wolf predation risk. Moose may either be slow to adapt to the new hunting pressure or the year round importance of wolves as predators may mean that moose anti-predator behaviour is shaped primarily by wolves.

Results from this study suggest the driver behind the increased spatial overlap between moose and mountain caribou in the summer is not human caused changes to mountain caribou habitat at high elevations. Instead, it appears that a natural anti-predator behavioural response of moose to space out into high elevation habitat in the summer is a factor in the increased spatial overlap between moose and caribou in the summer. Even in high elevation areas devoid of human-caused early-seral vegetation moose will use high elevation habitat in the summer (G. Walker 2010 pers. comm.). While high elevation human-seral vegetation does not influence the movement of moose upslope, the increased availability of human-seral vegetation on the landscape has increased the overall density of moose on the landscape (Serrouya et al. 2011). The high moose population is subsidizing a high wolf population and as a result increasing the number of wolf-caribou encounters.

The key to reducing the effect of apparent competition on the endangerment of mountain caribou will be to reduce the total volume of early-seral vegetation on the landscape, focusing primarily in areas of high moose density. Assuming the density of moose is limited by forage available in their winter range, then reforestation efforts should focus on moose winter habitat. During the summer undisturbed or old growth habitats are selected for (Pierce and Peek 1984, Telfer 1984) and provide a source of forage (Hjeljord et al. 1990), while in the winter moose select for open or disturbed forests (Eastman 1974, Boonstra and Sinclair 1984, Telfer 1984, Peek 1998, Poole and Stuart-Smith 2004). The preference of moose for habitats which produce early-seral vegetation in the winter is why the density of moose increases with an increase in habitat disturbance and thus production of early-seral vegetation (Peek 1998, Serrouya and D'Eon 2003, Serrouya et al. 2011). Moose density is often associated with food abundance (Oldemeyer and Regelin 1987, Thompson and Euler 1987, Renecker and Schwartz 1998), unless other factors are more limiting such as disease or parasites (Renecker and Schwartz 1998). Moose winter forage consists of woody browse such as willow (*Salix spp*), aspen (*Populus tremuloides*), and birch

(*Betula spp*) (Renecker and Schwartz 1998). Therefore, limiting the abundance of moose forage in moose winter habitats is likely to have the greatest impact on their density. In mountainous habitats moose tend to be constrained to valley bottoms in the winter by heavy snow (Stotyn 2008, Kerckhoff et al. 2013) and will select for south and west aspects where solar radiation is the greatest (Poole and Stuart-Smith 2004). Considering these factors, forest restoration efforts should concentrate on fast and effective restoration of valley bottom forests with south and west aspects.

However, restoration of disturbed habitats remains a long term objectives since reforestation of these areas will take time. In the meantime to save mountain caribou land managers will have to resort to short-term solutions such as management of the alternate prey populations and predator populations (Boutin et al. 2012).

FUTURE DIRECTIONS

Human caused early-seral vegetation does not appear to exacerbate apparent competition between mountain caribou, wolves, and moose in terms of increasing the spatial overlap between the three species. Instead moose appear to be spacing out in summer into mountain caribou habitat as an anti-predator strategy. These results hold implications for how predator and alternate prey populations are managed. Depending on the area, land managers are either attempting to conserve caribou by either managing the alternate prey population or the predator population (Serrouya 2013). If moose move to high elevations to avoid predators, reducing the moose population could have potential negative secondary effects of increasing the predation pressure on moose. As a consequence there is the potential for moose to respond by increasing their use of high elevation habitat, therefore increasing the spatial overlap between moose, wolves, and caribou.

More importantly, another potential negative side effect of reducing the alternate prey population would be if wolves switched to caribou as their primary prey to compensate for the loss of moose. If the population of alternate prey are reduced gradually then it is

hoped that wolves will not switch to caribou. Serrouya (2013) monitored the movement and predation rates of wolves as the moose population in the Columbia Mountains was reduced. He found that as the density of moose was reduced, wolves increased their spatial overlap with mountain caribou. Despite the increase in spatial overlap, Serrouya (2013) found no indication that wolves increased their consumption of caribou in response to the reduced availability of moose. However, the amount of caribou in wolf diets can be a poor measure of how many caribou are being consumed because these are rare events and even a small amount of predation could drive a rare prey to extinction (Boutin et al. 2012). In light of the above, Serrouya (2013) concluded that more research was required to determine if a reduction in the moose population had a beneficial effect for caribou or if the increased spatial overlap between caribou and wolves increased the predation rate for caribou. Therefore there are potential negative side effects of reducing the alternate prey population which should be researched further. In the mean time controlling predator populations may be the safer option, although not always politically favourable.

Finally, beyond short term management tools, such as predator and alternate prey control, to conserve caribou in the long term the amount of early-seral vegetation in caribou habitat needs to be reduced (Schneider et al. 2003, Boutin et al. 2012). The most effective method to achieve this is to focus reforestation efforts and restrict habitat disturbance where it will have the maximum effect on alternate prey populations.

Of course it is always possible to do more research but there has already been a wealth of research on various aspects of caribou predation and apparent competition, making it perhaps one of the most researched topics on large mammals in western Canada in the last 3 decades (e.g. Bergerud and Page 1987, Seip 1992, James et al. 2004, Wittmer et al. 2005b, Festa-Bianchet et al. 2011, McLellan et al. 2012, Peters et al. 2012, Apps et al. 2013, Hervieux et al. 2013). The knowledge is available. The next step that remains is for land managers and policy makers to either use this knowledge to change policy around

natural resource extraction in caribou habitat or accept that woodland caribou will be extirpated in south-western Canada.

WORKS CITED

- Apps, C., B. McLellan, T. Kinley, R. Serrouya, D. Seip, and H. U. Wittmer. 2013. Spatial factors related to mortality and population decline of endangered mountain caribou. *Journal of Wildlife Management* 77:1409–1419.
- 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.
- Boonstra, R., and A. R. E. Sinclair. 1984. Distribution and Habitat Use of Caribou, Rangifer tarandus caribou, and Moose, Alces alces andersoni, in the Spatsizi Plateau Wilderness Area, British Columbia. *Canadian Field-Naturalist* 98:12–21.
- Boutin, S., M. S. Boyce, M. Hebblewhite, D. Hervieux, K. H. Knopff, M. C. Latham, A. D. M. Latham, J. Nagy, D. Seip, and R. Serrouya. 2012. Why are caribou declining in the oil sands? *Frontiers in Ecology and the Environment* 10:65–67.
- DeCesare, N. J., M. Hebblewhite, H. S. Robinson, and M. Musiani. 2010. Endangered, apparently: the role of apparent competition in endangered species conservation. *Animal Conservation* 13:353–362.
- Eastman, D. S. 1974. Habitat use by moose of burns, cutovers and forests in northcentral British Columbia. Pages 238–256 *in*. Proceedings of the North American Moose Conference. Volume 10.
- Festa-Bianchet, M., J. C. Ray, S. Boutin, S. D. Côté, and A. Gunn. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. *Canadian Journal of Zoology* 89:419–434.

- Hervieux, D., M. Hebblewhite, N. J. Decesare, M. Russell, K. Smith, S. Robertson, and S. Boutin. 2013. Widespread declines in woodland caribou (*Rangifer tarandus caribou*) continue in Alberta. *Canadian Journal of Zoology* 882:872–882.
- Hjeljord, O., N. Hövik, and H. B. Pedersen. 1990. Choice of feeding sites by moose during summer, the influence of forest structure and plant phenology. *Ecography* 13:281–292.
- James, A. R. C., S. Boutin, D. M. Hebert, A. B. Rippin, and J. White. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. *Journal of Wildlife Management* 68:799–809.
- Kerckhoff, K., B. E. McLaren, S. P. Mahoney, and T. W. Knight. 2013. Moose habitat use throughout Gros Morne National Park. *Alces* 49:113–125.
- Matchett, M. R. 1985. Habitat selection by moose in the Yaak River drainage, northwestern Montana. *Alces* 21:161–189.
- McLellan, M., R. Serrouya, B. McLellan, K. Furk, D. Heard, and H. U. Wittmer. 2012. Implications of body condition on the unsustainable predation rates of endangered mountain caribou. *Oecologia* 169:853–860.
- Oldemeyer, J. L., and W. L. Regelin. 1987. Forest succession, habitat management, and moose on the Kenai National Wildlife Refuge. *Swedish Wildlife Research Supplement* 163–179.
- Peek, J. M. 1998. Habitat relationships. Pages 351–401 in A. Franzmann and C. Schwartz, editors. *Ecology and management of the North American moose*. Smithsonian Institution Press, Washington.
- Peters, W., M. Hebblewhite, N. DeCesare, F. Cagnacci, and M. Musiani. 2012. Resource separation analysis with moose indicates threats to caribou in human altered landscapes. *Ecography* 35:001–012.

- Pierce, D. J., and J. M. Peek. 1984. Moose habitat use and selection patterns in north-central Idaho. *Journal of Wildlife Management* 48:1335–1343.
- Poole, K. G., and K. Stuart-Smith. 2004. Winter habitat selection by moose in the East Kootenay , British Columbia , final report. Nelson, BC.
- Renecker, L. A., and C. C. Schwartz. 1998. Ecology and Management of the North American Moose. Wildlife Management Institute, Washington.
- Schneider, R. R., J. B. Stelfox, S. Boutin, and S. Wasel. 2003. Managing the cumulative impacts of land-uses in the western Canadian sedimentary basin: a modeling approach. *Conservation Ecology* 7:8.
- 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.
- Serrouya, R., and D. D'Eon. 2003. Winter habitat use and food habits of deer and elk in the northern Selkirk Mountains. Salmon Arm, British Columbia.
- Serrouya, R., B. N. McLellan, S. Boutin, D. R. Seip, and S. E. Neilsen. 2011. Developing a population target for an overabundant ungulate for ecosystem restoration. *Journal of Applied Ecology* 48:935–942.
- Serrouya, R. 2013. An adaptive approach to endangered species recovery based on a management experiment: reducing moose to reduce apparent competition with woodland caribou. University of Alberta.
- Stotyn, S. A. 2008. Ecological Interactions of Mountain Caribou, Wolves and Moose in the North Columbia Mountains, British Columbia. University of Alberta.
- Telfer, E. S. 1974. Logging as a factor in wildlife ecology in the boreal forest. *The Forestry Chronicle* 50:186–190.

- Telfer, E. S. 1984. Circumpolar distribution and habitat requirements of moose (*Alces alces*). Pages 145–151 *in* R. Olsen, R. Hastings, and F. Geddes, editors. Northern Ecology and Management. Edmonton, Alberta, Canada.
- Thompson, I. D., and D. L. Euler. 1987. Moose habitat in Ontario: a decade of change in perception. Swedish Wildlife Research Supplement 1:181–193.
- Wittmer, H. U., R. N. M. Ahrens, and B. N. McLellan. 2010. Viability of mountain caribou in British Columbia, Canada: Effects of habitat change and population density. *Biological Conservation* 143:86–93.
- Wittmer, H. U., A. Sinclair, and B. McLellan. 2005. The role of predation in the decline and extirpation of woodland caribou. *Oecologia* 144:257–267.
- Wittmer, H. U. 2004. Mechanisms underlying the decline of mountain caribou (*Rangifer tarandus caribou*) in British Columbia. The University of British Columbia.
- Wolff, J. O. 1978. Burning and browsing effects on willow growth in interior Alaska. *Journal of Wildlife Management* 42:135–140.